Els caròfits del límit Eocè-Oligocè de la Conca de l'Ebre

Josep Sanjuan i Girbau

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FACULTAT DE GEOLOGIA
Departament d'Estratigrafia, Paleontologia
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Programa de Doctorat "Ciències de la Terra"
UNIVERSITAT DE BARCELONA

ELS CARÒFITS DEL LÍMIT EOCÈ-OLIGOCÈ DE LA CONCA DE L'EBRE

TESI DOCTORAL

JOSEP SANJUAN GIRBAU

DIRECTOR: CARLES MARTÍN-CLOSAS

2013

Facultat de Geologia

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Tempus fugit...

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1. AGRAÏMENTS

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2. RESUM

Aquesta tesi doctoral té com a objectiu principal la caracterització taxonòmica, paleoecològica, paleobiogeogràfica i biostratigràfica dels caròfits de l'Eocè superior-Oligocè inferior de la Conca de l'Ebre.

La flora de caròfits de l'Eocè superior-Oligocè inferior del marge est de la Conca de l'Ebre està constituïda per *Sphaerochara labellata, Chara* aff. *antennata, C. artesica* n. sp., *C. rhenana, C.microcera, Psilochara* aff. *acuta, Lamprothamnium* sp., *Gyrogona caelata, Nodosochara jorbae, Lychnothamnus longus, L. stockmansii, L. grambastii, L. vectensis, L. pinguis (=L. major), Nitellopsis (Tectochara) merianii, Harrisichara lineata, H. vasiformis-tuberculata* i *H. tuberculata.* En totes es caracteritza el polimorfisme intraespecífic a parti d'un estudi biomètric dels girogonits. Des d'un punt de vista taxonòmic se sinonimitzen, a partir de les poblacions tipus, dues espècies clau en biostratigrafia del límit Eocè-Oligocè europeu, *Lychnothamnus pinguis* i *L. major*.

L'anàlisi paleoecològica de les associacions de caròfits de l'Eocè superior al sector NE de la conca de l'Ebre ha permés determinar que espècies clau per la biostratigrafia del límit Eocè-Oligocè presenten clares limitacions paleoecològiques. Així, *Harrisichara vasiformis-tuberculata* creixeria només en ambients salabrosos i soms pròxims a la costa, *Harrisichara lineata* es relaciona amb llacs soms d'aigua dolça i *Harrisichara tuberculata* abunda, però no és exclusiva, de llacs perennes i profunds d'aigua dolça. Altres espècies com *Sphaerochara labellata*, *Lychnothamnus stockmansii*, *L. pinguis* (=*L. major*) i *Chara microcera* es troben en llacs permanents. En conclusió, la presència o absència d'aquestes espècies, i per tant, de les biozones homònimes en una determinada conca europea depèn del tipus de fàcies i del paleoambient associat mes que no d'esdeveniments evolutius. Altres espècies com *Lychnothamnus vectensis*, *Nodosochara jorbae*, *Lychnothamnus longus* o *Chara artesica* n. sp., en canvi, no presenten cap limitació ecològica important dins el context dels sistemes aquàtics continentals.

L'anàlisi paleobiogeogràfica de la caroflora de l'Eocè superior-Oligocè inferior d'Europa permet identificar una polaritat latitudinal en la distribució i abundància de les espècies. No obstant, partint de les espècies comunes a totes les conques europees es defineix una bioprovíncia europea per l'Eocè superior-Oligocè inferior la qual es pot caracteritzar a partir dels llinatges *Harrisichara vasiformis-H. tuberculata* i

Lychnothamnus stockmansii-L. major així com de les espècies *Nitellopsis (T.) merianii* i *Chara microcera*. Les variacions regionals d'aquesta flora responen a factors climàtics locals i a factors ecològics lligats a la dinàmica de cada conca. La distribució biogeogràfica de determinades espècies, com *Sphaerochara labellata* o *L. pinguis* ha mostrat que l'us d'aquestes especies en biostratigrafia està condicionada per factors paleogeogràfics. L'anàlisi de la biogeografia històrica del llinatges evolutius *Lychnothamnus stockmansii-L. major* i *Nitellopsis(Tectochara)merianii-N. obtusa* suggereix que les espècies de caràcies fòssils seguien diferents patrons de dispersió en funció de la disposició dels seus gametangis (dioica vs. monoica). És clar que les espècies monoiques com *Lychnothamnus stockmansii-L. major*, amb velocitats d'expansió geològicament instantànies, són idònies alhora de correlacionar biostratigraficament conques allunyades.

Des d'un punt de vista biostratigràfic, les associacions de caròfits han permès precisar l'atribució biostratigràfica de les unitats litostratigràfiques estudiades. S'ha proposat una biozonació de carofits per la conca de l'Ebre a partir d'espècies ecològicament euritípiques. Aquesta biozonació s'ha correlacionat amb la biozonació local de vertebrats i s'ha calibrat amb la magnetostratigrafia definida a l'est de la conca per Barberà et al. (2001) i Costa et al. (2010, 2011). La nova proposta permet caracteritzar el límit Eocè-Oligocè dins la biozona de Lychnothamnus vectensis. A més, s'ha revisat la biozonació europea avui dia en us. La calibració dels límits de les biozones europees amb l'escala del temps absolut mitjançant la magnetostratigrafia ha permès, per primera vegada, precisar la durada temporal de les biozones de caròfits del límit Eocè-Oligocè.

Paraules clau: Caròfits, Conca de l'Ebre, Eocè, Oligocè, paleoecologia, palaeobiogeografia, biostratigrafia, magnetostratigrafia

3. ABRIDGED ENGLISH VERSION

Charophytes from the Eocene-Oligocene boundary in the Ebro Basin

3.1. Introduction

3.1.1. Presentation

This PhD thesis is focused on the study of charophytes from the transitional and non-marine Upper Eocene-Lower Oligocene deposits of the eastern margin of the Ebro Foreland Basin (Catalonia, Spain). Fossil charophytes were studied from the point of view of taxonomy, palaeoecology, palaeobiogeography and biostratigraphy. The results of this study are the object of five interrelated publications in journals indexed in the Journal of Citation Reports (ISI).Three of them already accepted or published, and two more are in revision:

- **Taxonomy**. Sanjuan, J., Martín-Closas, C. Taxonomy and palaeobiogeography of charophytes from the Upper Eocene-Lower Oligocene of the eastern Ebro basin (Catalonia, NE Spain). *Geodiversitas* (in revision-a).

- **Palaeoecology**. Sanjuan, J., Martín-Closas, C., 2012. Charophyte palaeoecology in the Upper Eocene of the Eastern Ebro Basin (Catalonia, Spain). Biostratigraphic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 365-366: 247-262.

- **Palaeobiogeography**. Sanjuan, J., Martín-Closas, C. Biogeographic history of two Eurasiatic Cenozoic charophyte lineages. *Aquatic Botany* (in revision-b).

- **Biostratigraphy** (I). Sanjuan, J., Martín-Closas, C., Serra-Kiel, J., Gallardo, H., 2012. Stratigraphy and biostratigraphy (charophytes) of the marine-terrestrial transition in the Upper Eocene of the NE Ebro Basin (Catalonia, Spain). *Geologica Acta*, 10 (1): 19-31.

- **Biostratigraphy** (II). Sanjuan, J., Martín-Closas, C., Costa, E., Barberà, M., Garcés, M. Calibration of Eocene-Oligocene charophyte biozones in the Eastern Ebro Basin (Catalonia, Spain). *Stratigraphy* (accepted).

3.1.2. Objectives

The aims of this thesis were (1) to describe the charophyte species recorded in the Late Eocene-Early Oligocene of the Ebro Basin and resolve the taxonomic status of some poorly-known species, which are in some cases biozone index-species; (2) to document, through combined taphonomic-sedimentological analyses, the palaeoecological constraints of the charophyte species studied. These constraints may have significant implications in biostratigraphy; (3) to document, through a palaeobiogeographic analysis, the constraints affecting charophyte distribution and the time needed by some species to reach a supracontinental distribution (4) to precise the chronostratigraphic attribution of charophyte biozones by calibration with the new magnetostratigraphic data of Barberà et al. (2001) and Costa et al. (2010, 2011) obtained in the same sections sampled in this study.

3.2. Geological setting

The studied area is located in the eastern margin of the Ebro Foreland Basin. The Ebro Basin is the triangular-shaped southern foreland basin of the Pyrenean Range (Fig. 1). The origin of the Ebro Basin is related to flexural subsidence due to the collision between the Eurasian and Iberian plates from the Late Cretaceous to the Miocene. Maximum compression occurred during the Palaeocene and Eocene and resulted in the superposition of a number of thrust sheets in the south Pyrenean central zone. The main structures display an E-W orientation and the deformation progressed south- and westwards in parallel with the basin depositional centres, the lowermost sedimentary sequences being incorporated into the successive thrust sheets (Puigdefàbregas et al., 1992).

The south Pyrenean foreland basin infill includes marine and continental rocks that range from the Upper Cretaceous to the Upper Eocene. Later, exclusively nonmarine facies were recorded. During most of the Palaeogene the basin formed an Atlantic gulf, a situation that lasted until the Late Eocene, when uplift in the western Pyrenees led to the final isolation from the Atlantic Ocean and the definitive onset of endorheic sedimentation in the Ebro Basin (Puigdefàbregas et al., 1992).

Thrust cyclicity and evaporite events allow differentiation of the basin-fill into three main depositional cycles (Puigdefàbregas et al., 1986). The first cycle coincides with the submarine emplacement of the upper thrust sheets. The second sedimentary cycle coincides with the development of an antiformal stack of thrust sheets in the central Pyrenees which induced deltaic progradation and contemporaneous migration of the basin depocentre southwards. At the same time, the Catalan Coastal Chain was tectonically active and contributed to basin infill with well-developed fan delta progradation systems (e.g. Montserrat, Sant Llorenç del Munt and Montsant fan deltas). This tectonic activity led to the final restriction of the basin and the deposition of an evaporite plug during the Late Eocene. This evaporitic event represents the last marine episode in the southern Pyrenean foreland basin, which became purely endorheic afterwards. The third cycle coincides with the southward thrusting and final emergence of the Vallfogona thrust, which carried the former piggyback thrust sheets. This event supplied clastic sediments to the alluvial fans that were laterally connected with lacustrine areas in the centre of the basin (Puigdefàbregas et al., 1986).

From the stratigraphic point of view, the studied deposits can be divided in two different areas along the Eastern masrgin of the Ebro basin. In the northeastern sector of the basin, the non-marine deposits comprise the marly beds of the transitional Sant Boi Formation (Sanjuan et al., 2012) and the red alluvial and fluvial beds of the Artés Formation (Ferrer, 1971; Sáez, 1987) with interbedded lacustrine limestone beds e.g. Moià Limestone Member (Sáez, 1987) and La Panadella Formation (Colldeforns et al., 1994a) (Figs. 2 and 3). In the southwestern area of the basin the continental deposits comprise proximal alluvial, fluvial, lacustrine and evaporitic beds related to the depositional activity of alluvial fan systems such as Sant Miquel de Montclar, which includes the Sant Miquel de Montclar Formation, and the Montsant depositional system with the Montsant, Margalef, Blancafort, Albi and Cogul Formations described by Colombo (1980, 1986) and Colldeforns et al. (1994a i b) (Figs. 4 and 5).

3.3. Methodology

3.3.1. Methods in field and laboratory work

Many stratigraphic sections showing good exposure of transitional and continental, mainly fluvio-lacustrine, facies were raised and sampled systematically mainly for biostratigraphic purposes in the Upper Eocene-Lower Oligocene deposits on the eastern margin of the Ebro Basin (Fig. 1). Location of the studied sections can be divided into three main areas: (1) In the Vic/Manresa area eleven sections were raised and sampled (La Portelleta, El Perers, Sobremunt, Serrat Rodó, Cal Carreter, Santa Maria d'Oló, Oristà, Torre Casanova, Moià and Santpedor). They include Upper Eocene-Lower Oligocene transitional and continental deposits of the Sant Boi and Artés Formations. (2) In the Igualada area two stratigraphic sections were sampled (Maians and Rubió) which are constituted by Upper Eocene-Lower Oligocene red beds of the mainly fluviatile Artés Formation. Both sections were correlated using stratigraphic correlation beds of cartographic continuity (Costa et al., 2010) (Figs. 2 and 3). In the Conca de Barberà and l'Urgell areas four sections (Rocafort de Queralt, , Sarral and Tarrés) and two outcrops (Solivella and El Talladell) were sampled which comprise a large lithological variety of Upper Eocene-Oligocene non-marine deposits also correlated by layers of cartographic continuity (Barberà, 1999; Barberà et al., 2001) (Figs. 4 and 5).

Fossil remains were obtained from 87 of 145 samples of greyish lacustrine mudstones and marls collected in the aforementioned sections. About 2 kg of sediment per sample were disaggregated in water, oxygen peroxide and Na_2CO_3 solution and later sieved using sieves with mesh apertures of 1.0, 0.5 and 0.2 mm. Gyrogonites were picked out under a light microscope and measured at 40x magnification under a Wild M5A binocular microscope with micrometer incorporated (hundred gyrogonites per species). Selected gyrogonites were studied and photographed using a scanning electron microscope Quanta 200 at the Serveis Científico-Tècnics (Universitat de Barcelona). Thin-sections, about 30 µm in thickness, were prepared from 20 selected charophyte limestone beds of the Moià limestone Member in order to ascertain the microfacies. The material is now housed at the Departament d'Estratigrafia, Paleontologia and Geociències Marines, Universitat de Barcelona.

Three research stages were conducted in different research institutions: (1) Institut des Sciences de l'Évolution of the Université Montpellier II (June and October 2011, funded by FPI grants of the Spanish Ministry of Science), (2) Departement de Biominéralization et Énvironnement Sedimentaires of the Université Pierre et Marie Curie of Paris (September and October 2012, funded by grants of the Spanish Ministry of Science) and (3) Natural History Museum of London (July 2013, funded by a project of the Catalan Automous Government) in order to review the taxonomical determinations, compare charophyte populations between different European basins and formulate palaeobiogeographical and palaeoecological hypothesis of the European charophyte flora during the Late Eocene-Early Oligocene. During these stages I benefitted from the expertise of Dr. Ingeborg Soulié-Märsche, Dr. Monique Feist, Dr. Janine Riveline and Dr. J. Hooker.

3.3.2. Methods in biostratigraphy and calibration

Charophyte assemblages were assigned to biozones defined by Riveline et al. (1996) and Riveline in Hardenbol et al. (1998). Intensive sampling of the sections studied provided abundant and well-preserved charophyte assemblages allowing us to revise Upper Eocene-Lower Oligocene charophyte biozonations. Biozones were correlated with the local mammal biozonation of Barberà et al. (2001) and with European Mammal reference levels (MP) and calibrated with magnetozones that Costa et al. (2010, 2011), and Barberà et al. (2001) identified previously in the same NE sector of the Ebro basin. This calibration could be compared with one calibration of some charophyte zones in Hampshire basin (Isle of Wight, England) by Hooker et al. (2009).

3.3.3. Methods in taphonomy, palaeoecology and palaeobiogeography

The palaeoecology of charophyte assemblages from transitional and terrestrial deposits of the NE margin of the Ebro basin was characterized based on combined sedimentological and taphonomic analyses, taking also into account the information from other palaeobiological remains such as ostracods, molluscs and vertebrates.

The palaeobiogeographic distribution of the fossil charophytes studied was characterized using the bibliography available to the author about the world occurrence of studied species. This information was then plotted in the palaeogeographic maps published by Lorenz et al. (1993) and Blakey (2006).

3.4. Results

3.5. Systematic Palaeobotany

3.5.1. Gyrogonites

Eighteen charophyte species are documented from the Upper Eocene-Lower Oligocene transitional and terrestrial facies on the eastern Ebro Basin (Figs. 6-10). The charophyte assemblage is composed by *Sphaerochara labellata*, *Chara* aff. *antennata* Grambast, 1958, *Chara artesica* Sanjuan and Martín-Closas, (in revision-a), *Chara rhenana* Schwarz and Griessemer, 1994, *Chara microcera* Grambast and Paul, 1965, *Psilochara* aff. *acuta* Grambast and Paul, 1965, *Lamprothamnium* sp., *Gyrogona caelata* (Reid and Groves 1921) Grambast, 1956, *Nodosochara jorbae* Choi, 1989, *Lychnothamnus longus* Choi, 1989, *L. stockmansii* (Grambast 1957) Soulié-Märsche, 1989, *L. grambastii* (Feist-Castel 1971) Soulié-Märsche, 1989, *L. vectensis* (Groves 1926) Soulié-Märsche, 1989, *L. major* (Grambast and Paul 1965) Soulié-Märsche, 1989, *Nitellopsis (Tectochara) merianii* (Al. Braun ex Unger, 1852) Grambast and Soulié-Märsche, 1972, *Harrisichara lineata* Grambast, 1957, *Harrisichara vasiformis-tuberculata*, Feist-Castel 1977a and *H. tuberculata* (Lyell, 1826) Grambast, 1957.

All these species were described and figured with special care in showing the intraspecific polymorphism (Sanjuan and Martín-Closas, in revision-a). After the submission of this study for publication, two additional species were studied, i.e. *Lychnothamnus vectensis* (Groves 1926) Soulié-Märsche, 1989 and *Lychnothamnus pinguis* (Grambast 1958) Soulié-Märsche, 1989, which are index-species of homonymous European biozones of Riveline et al. (1996).The lack of a detailed description and figuration of the polymorphism of these species that are key-species in biostratigraphy, motivated the revision of the A'Court Smith collection in the Natural History Museum in London and the main results, still unpublished, are given below.

(a) *Lychnothamnus vectensis* (Groves 1926) Soulié-Märsche, 1989

Chara vectensis was first determined by Groves (1926) based on ellipsoidal gyrogonites extremely variable in size, 800-1000 µm in high and 500-800 µm in width, with 9-10 concave spiral cells usually swollen at the apex and often forming prominent rosettes. The holotype designated and illustrated by Groves (1926), from the A’Court Smith collection at the Natural History Museum, London, belonged precisely to the few specimens which displayed a prominent apical rosette and this character was further considered as diagnostic of the species, rather than merely an extreme of its total morphological variation. Later, Gambast (1958) redefined *Stephanochara vectensis* using the type population of Groves (1926) without giving supplementary figuration.

The gyrogonite is medium sized, 784-1017µm in high (mean 880 µm), and 600-813 µm in width (mean 695 µm), ellipsoidal in shape with an isopolarity index of 114-140 (mean 126). Spiral cells are about 94-119 µm wide, normally flat to convex. Seven to nine (65% of the population display eight) convolutions are visible laterally. Apex is flat or slightly convex. Spiral cells do not show constrictions in the apical periphery but display a marked thinning in the apical zone, resulting in an apical to periapical depression. Most of the gyrogonites (90% of the population) display an ornamented apex with more or less well-developed tubercles that vary notably in size (varying between 16 and 104 µm in height, in lateral view) depending on the calcification degree of the specimens. The base is mainly rounded with a large and superficial basal pore about 80 µm across. Some well-calcified specimens show an irregularly star-shaped funnel around the basal pore that is about ~62 µm across (Figs. 11-13). This morphometric study allows us to conclude that *L. vectensis* displays a wide range of polymorphism varying from low calcified gyrogonites (reduced sized, flat to concave spiral cells, without apical nodules) to well calcified gyrogonites (large sized, convex spiral cells, with prominent apical nodules) (Figs. 11-13). This large intraspecific polymorphism encompasses the morphotypes that previous authors determined as only affine to *L. vectensis*.

In order to compare charophyte populations between different basins we measured 100 girogonites from the type population in Hampshire (sample V. 18335 of the Natural History Museum, from Gurnard Bay, Isle of Wight), 48 gyrogonites (all the gyrogonites available) from the Paris basin (samples Loges-814 and Loges-816 from Marnes bleues d'Argenteuill, Montereau in the collection of J. Riveline) and 100 gyrogonites from the Ebro basin (samples SP-4, SP-14 and SP-17 from Artés Formation in Santpedor). This comparison showed that the gyrogonite size represented the main difference between the gyrogonite populations of the three basins, with gyrogonites being larger in the northern basins (Paris-Hampshire). In contrast the gyrogonite height/width ratio (ISI) and the convolution number of spiral cells in lateral view remains invariable between populations of the basins studied (Figs. 12-13). These differences were not exclusive of *Lychnothamnus vectensis* since they have also been observed in *Harrisichara tuberculata*. Soulié Märsche (1989) showed that gyrogonite size and morphology in extant charophytes display a wide variation in relation to ecological conditions. Moreover, she showed that gyrogonites of the extant species *Lychnothamnus barbatus* show a high variability in size, while the gyrogonite morphology remained more or less stable.

(b) *Lychnothamnus pinguis* (Grambast 1958) Soulié-Märsche, 1989

This species was first described as *Stephanochara pinguis* by Grambast (1958) based on ellipsoidal to ovoidal gyrogonites variable in size, 800-1150 µm in high and 750-950 µm in width, with 8 to 10 convex spiral cells swollen at the apex and often forming more or less prominent joined apical nodules. The base is usually rounded displaying a superficial basal pore.

A revision of the type population (tube V. 26299 of the Natural History Museum, London) coming from the White band of the Hamstead Member in Hamstead (Isle of Wight, England) showed a wide range of morphotypes that have been biometrically characterised and photographed. The analysis was based on 100 gyrogonites of the type population (tube V. 26299) and 50 specimens from tube V. 26292, labelled as "*St. pinguis* concave" The aim of this analysis is to describe the interspecific polymorphism of this European species significant from the biostratigraphic point of view during Early Oligocene (Rupelian).

The gyrogonites of the type population (V26299) are large, variable in size, 830-1108 µm in high (mean 1003 µm), and 663-966 µm in width (mean 851 µm), ellipsoidal or ovoid in shape with an isopolarity index of 106-145 (mean 118). Spiral cells about 121-183 µm wide (mean 144 µm), normally flat to convex. Seven to nine (75% of the population display eight) convolutions are visible laterally. Some of the gyrogonites (~10% of the population) show a low degree of calcification displaying concave spiral cells with bicarinated sutures. Apex flat or convex depending on the calcification degree. Spiral cells do not show constrictions in the apical periphery but display marked thinning in the apical zone, resulting in an apical to periapical depression. Most of gyrogonites display a marked thickening at the end of spiral cells. However, only ~55% of the population display isolate or joint apical nodules, 20 to 89 µm high in lateral view, depending on the calcification degree of the specimens. The base is rounded with extremely variable basal pore morphology depending on the calcification degree. Well-calcified specimens show a pentagonal basal pore, about 70 µm across, with basal funnel. Medium-calcified gyrogonites show a larger and superficial basal pore, about 95 µm across. Less-calcified gyrogonites display a star-shaped basal funnel. ~60 µm across (Figs. 14 and 15).

In contrast to the type population, the population in tube V. 26292 shows up to a 63% of gyrogonites with concave spiral cells and bicarinated sutures, lacking apical thickening or apical nodules. The base of these concave morphotypes is slightly pointed showing a star-shaped funnel and a basal pore of ~60 µm across. Calcified gyrogonites are similar to those of tube V. 26299 (Fig. 16).

The revision of these two populations allowed us to characterise the high degree of polymorphism of *L pinguis* in its type locality. This variation is related to the gyrogonite calcification. Concave morphotypes (dominant in the tube V 26292) display strong resemblance with the contemporaneous species *Lychnothamnus major* (Grambast and Paul 1965) Soulié-Märsche, 1989. As a matter of fact *Lychnothamnus major* from the Ebro basin (sample SA-19) show biometric parameters (gyrogonite high and width, convolution number of spiral cells in lateral view and isopolarity index) completely coincident with the concave part of the populations from Hampshire (Fig. 17). As a result of this comparison, we propose to synonymise the two species. This synonymy has direct consequences in the definition and range of the biozone of L. pinguis, which should be enlarged to younger intervals.

3.5.2. Thalli

Several types of non-articulate charophyte thalli have been identified: (1) Ecorticate thalli were found associated but not attached to *Harrisichara* gyrogonites, (2) *Charaxis* Harris 1939 thalli with non-contiguous cortical cells were found associated but not attached to *Gyrogona* gyrogonites (Fig. 23) whereas (3) diplostic and (4) triplostic *Charaxis* thalli were found associated with *Chara* gyrogonites.

3.6. Palaeoecology

A palaeoecological study has been performed in Upper Eocene non-marine deposits of the NE sector of the basin (Vic/Manresa area), particularly in: (1) the transitional marls of the Sant Boi Formation and (2) the fluvio-lacustrine red beds with associated grey lutite of the Artés Formation (Sanjuan and Martín-Closas, 2012). A number of species significant in the European biostratigraphy, were found to display restricted ecological distributions. Hence, in the Sant Boi Formation, *Harrisichara vasiformis-tuberculata* occurs in beds related to brackish ponds close to the shoreline, in the context of a lower delta plain, In contrast, *H. lineata* appears to have grown in laterally equivalent freshwater lakes in the upper deltaic plain (Figs. 18 and 19). In the Artés Formation *H. tuberculata* occurred in marls and limestones representing well-developed and perennial freshwater lakes and much more rarely in temporary lakes within an alluvial fan context (Figs. 22-24). Other species such as *Nitellopsis (T.) merianii*, *Sphaerochara labellata*, *Lychnothamnus stockmansii* which occur sometimes associated with *H. tuberculata* were also limited to perennial freshwater lakes. Another stenotypic species is *Lychnothamnus grambastii*, which was found to be related to temporary freshwater lakes with a higher content in organic matter (Figs. 20, 21 and 24).

Other species displayed a larger range of distributions. This is the case of *Lychnothamnus longus* and *Chara artesica* n. sp. which occur both within temporary and perennial freshwater lake facies. The so-far Iberian species *Nodosochara jorbae* displays the largest ecological distribution, since it was represented both in brackish environments and in freshwater, temporary and perennial lakes (Figs. 20, 21 and 24). The possibility of a facies and environmental control is of prime importance in biostratgraphy, since it would mean that some biozones are only recognisable provided that particular palaeoenvironmental conditions occurred.

3.7. Palaeobiogeography

A European palaeobiogeographic analysis of Late Eocene-Early Oligocene charophyte species allow to define a charophyte bioprovince which is characterised on the basis of two important charophyte lineages, *Harrisichara vasiformis-H. tuberculata* and *Lychnothamnus stockmansii-L.major* along with two more species *Nitellopsis (Tectochara) merianii* and *Chara microcera* (Fig. 25). However, the latitudinal distribution of species changes mainly as regards the number of charophyte species and the relative abundance of particular species in the assemblages of different basins. The latitudinal distribution was probably related to the southwards decrease in seasonal humidity during the Late Eocene-Early Oligocene. Moreover, a variation in species richness between European basins (~31 species recorded in northern basins vs. ~18 in southern basins) appears to be related to ecological parameters related to basin dynamics. The hydrology of the Ebro Foreland Basin i.e., its closed drainage (endorheism), the absence of connection with the sea, and the high water turbidity produced by continuous and abundant terrigenous input within the lacustrine systems, probably limited the number of species. In contrast, the Paris-Hampshire basins showed an open drainage leading to a permanent marine connection in the period studied. This along with a low input of terrigenous materials in the aquatic systems, could have favoured the development of a wider range of non-marine ecological niches which resulted in a high number of charophyte species.

The limited biogeographic distribution observed in some charophyte species, which are significant from the biostratigraphic point of view, challenges their inclusion in the general biozonation of European charophytes and suggests that these species would be more appropriate for local, basin-wide, biozonations rather than for a European biozonation.

The biogeographic history of two widely distributed species was studied. The Upper Eocene-Oligocene charophyte lineages, *Lychnothamnus stockmansii-L. major* and *Nitellopsis (Tectochara) merianii-N. obtusa* reached an Eurasiatic distribution following opposite biogeographic patterns. The origin of *Lychnothamnus stockmansii-L. major* is coeval in Europe and Asia, during the Late Priabonian-Early Rupelian. Later, during the Rupelian this species was restricted to Europe, and became probably extinct at the end of the same period (Figs. 26 and 27). In contrast, *N. (T.) merianii-N. obtusa* follows the classical dispersal pattern, with origin in south-western Europe during the Latest Eocene (Late Priabonian), expansion through Europe during the Early Oligocene (Rupelian), reaching the extreme East of the Asiatic continent probably during Late Oligocene (Chattian). The expansion of *N. (T.) merianii-obtusa* was intensified in Eurasia during the Miocene and reached Africa in the Late Miocene, with a range slightly wider than in present time (Figs. 28, 29 and 30).

In order to explore the reasons governing these contrasting biogeographic patterns it is useful to compare them with the biogeographic patterns and mechanisms of the most diversified extant charophyte genus, *Chara*. According to Proctor (1980) *Chara* displays a dual biogeographic pattern i.e. dioecieous species are restricted to continental areas while monoecious grow in large, supracontinental areas or are cosmopolitan. According to Proctor (1980) the arrangement of gametangia would determine the dispersion mechanism of *Chara*, which is mostly dependent on migratory birds that feed on its meadows, mainly ducks belonging to the Anatidae. Monoecious *Chara* species are able to form reproductive populations after a single dispersal event and immediately continue their biogeographic expansion, whilst the expansion of dioecious charophyte populations is a rather improbable occurrence since they usually contain very unequal percentages of each sex (Proctor, 1980). The contrasting dispersal patterns observed in fossil *Lychnothamnus stockmansii-L. major* and *Nitellopsis (T.) merianii-N. obtusa* suggest that the same patterns that govern the dispersal of living *Chara* would influence the dispersal of other characeans in the past. Unfortunately, the monoecious or dioecious condition of fossil charophyte species is difficult to ascertain with only the fossil record on hand. In some occasions monoecy or dioecy may be inferred from extant representatives of the lineage. Thus, extant *Nitellopsis obtusa* was surely a dioecious species in the past as it is today (Soulié-Märsche et al., 2002), whilst *L. stockmansii-L. major* is considered by Soulié-Märsche and Martín-Closas (2003) a direct ancestor of extant *L. barbatus* that is a monoecious species, a status which was perhaps alike in the ancestral species.

We conclude that both monoecious and dioecious charophyte species could reach supracontinental distributions although at different velocities. This analysis suggests that dioecious species would require an expansion up to ten times larger to achieve similar distribution ranges than monoecious species.

3.8. Biostratigraphy

The charophyte assemblage of the Upper Eocene-Lower Oligocene deposits of the Eastern margin of the Ebro basin is composed by many significant species from the biostratigraphic point of view (Sanjuan and Martín-Closas, in revision-a; Sanjuan et al., accepted).

The stratigraphic succession of charophyte assemblages shows some differences with previous charophyte zonations proposed by Anadón et al. (1992) and Feist et al. (1994) for the Ebro basin. New biostratigraphic data allow us to revise also the Late Eocene-Early Oligocene European charophyte zonation (Riveline et al., 1996). Moreover, the integration of new charophyte biostratigraphic results with magnetostratigraphic data provides accurate absolute ages of local and European biozones. Six charophyte zones were identified and characterised in the Upper Eocene-Lower Oligocene of the Ebro basin, i.e. (1) Harrisichara lineata (a new name for the former H. vasiformis-tuberculata biozone); (2) Harrisichara tuberculata, (3) Harrisichara tuberculata-Nodosochara jorbae, (4) Lychnothamnus vectensis, (5) Lychnothamnus major and (6) Chara microcera (Fig. 31).

The Harrisichara lineata biozone is represented in the transitional Sant Boi Formation (El Perers-Serrat Rodó section), which encompasses the middle of the Priabonian. The upper limit of this biozone (former H. vasiformis-tuberculata biozone) is recorded at the base of the Torre Casanova subsection and occurs within a normal magnetozone at the top of chron C16n (C16n.1n), providing an age of ~35.5 Ma (Sanjuan et al., accepted) (Fig. 31).

The Harrisichara tuberculata superzone is well represented in the continental Artés Formation (NE sector of the basin) and in Sarral, Blancafort, Gavatxa and Margalef Formations (SE area of the basin). This superzone is correlated with MP18 or MP19-20, MP21, MP22 and MP23 European mammal reference levels and correlated with the Theridomys golpeae, Th. aquatilis, Th. calafensis and Th. major local mammal biozones of Barberà et al. (2001) (Sanjuan et al. accepted). Moreover, the calibration of this superzone suggests that it spans over 5 Ma ranging from the chron C16n.1n to the chron C12r. These results allow enlarging this superzone to the time span covering younger and older chronostratigraphic intervals (Sanjuan et al., accepted) (Fig. 31).

Harrisichara tuberculata-Nodosochara jorbae local assemblage zone is included within H. tuberculata superzone. It is represented at the base of the Artés Formation and was correlated with the pre Grande-Coupure MP18 or MP19-20 European mammal reference levels and the Theridomys golpeae local mammal biozone of Barberà et al. (2001). Moreover, this biozone has been calibrated with chrons C16 (C16n.1n) to C13 (C13r). The interval represented by this biozone corresponds to an interval undefined biostratigraphycally in the European biozonation since *Nodosochara jorbae* is an especies restricted to the Ebro basin (Sanjuan et al. accepted).

Lychnothamnus vectensis biozone is a European and local biozone integrated within H. tuberculata superzone. In the Ebro basin this biozone is redefined as the total distribution range of *Lychnothamnus vectensis*, while in the European biozonation this biozone has been defined as a partial range biozonation. The local biozone has been correlated with the MP18 or MP19-20 and MP21 European mammal reference levels and with the Theridomys golpeae and Th. aff. aquatilis local mammal biozone of Barberà et al. (2001) in the Santpedor, Rubió and Sarral sections . Moreover this biozone encompasses chrons C13r and C13n, including the upper part of the Priabonian and the basal part of the Rupelian (Fig. 31). Therefore it is crucial to characterise the Eocene-Oligocene boundary on the basis of charophytes. From the upper limit of the local L. vectensis biozone to the base of the L. major biozone there is an interval biostratigraphically undefined in the Ebro basin, which includes a low number of species, i.e. *Harrisichara tuberculata, Lychnothamnus longus* and *Psilochara* aff. *acuta.* This undefined local interval is equivalent to the Lychnothamnus pinguis European zone. This interval is impossible to characterise biostratigraphically in the Ebro basin beyond the range of the Harrisichara tuberculata superzone. This interval is represented in most of the Rubió and Sarral subsections and is correlated with the MP22 or MP23 European mammal reference levels and the Theridomys calafensis or Th. major local mammal biozone of Barberà et al. (2001). Moreover it coincides with the reversed magnetozone of chron C12 indicating a Lower Rupelian age (Fig. 31).

The Lychnothamnus major zone appears to be extremely short in the Ebro Basin (Sanjuan et al. accepted). It can be correlated with the MP23 European mammal reference level and with the Theridomys major local mammal biozone of Barberà et al. (2001). Being an interval zone, its range depends on the variation of the range of adjacent zones, and is now included in the upper part of the reversed magnetozone C12 (C12r) (Fig. 31).

The Chara microcera biozone is recorded in the Albi Formation and its lateral equivalent Tàrrega Limestone Formation. In the Ebro Basin the lower limit of this biozone can be correlated with the MP23 European mammal reference level and with the Theridomys major local mammal biozone of Barberà et al. (2001) (Sanjuan et al. accepted). Moreover this biozone limit occurs within the lowermost part of the normal magnetozone attributed to chron C12 (C12n), providing an age of ~31 Ma suggesting that this biozone appeared earlier in the Ebro basin than other European basins (Fig. 31).

3.9. Discussion

3.9.1. Charophyte taxonomy

Specific assignation of the studied gyrogonites is based on studies by Grambast (1956, 1957, 1958), Grambast and Paul (1965), Grambast and Soulié-Märsche (1972), Feist-Castel (1971, 1977a, b), Feist and Ringeade (1977), Choi (1989), Soulié-Märsche (1989) and Schwarz and Griessemer (1994).

From the 18 species documented in the Upper Eocene-Lower Oligocene deposits from the Ebro basin many were previously unknown. These species are *Chara rhenana*, *Lychnothamnus grambastii*, *Psilochara* aff. *acuta*, *Chara* aff. *antennata* and *Lamprothamnium* sp. Moreover, former *Chara* sp. 2 Choi, 1989 has been formally defined and characterised as *Chara artesica* Sanjuan and Martín-Closas n. sp.

A morphometric analysis of the type populations of *Lychnothamnus vectensis* and *L. pinguis*, which are two index-species of the European charophyte biozonation, reveals that these species display a wide range of intraspecific polymorphism. Less-calcified gyrogonites (reduced size, flat to concave spiral cells, no apical nodules) are in contrast to well-calcified gyrogonites (large size, convex spiral cells and prominent apical nodules). Soulié-Märsche (1989) already reported this link (morphology and calcification degree) in extant and fossil *Lychnothamnus* species. In order to compare charophyte populations of *L. vectensis* between different basins we measured and analysed three populations from Hampshire, Paris and Ebro basins. We concluded that the gyrogonite size tends to be larger in northern basins. Moreover, the revision of two populations of *Lychnothamnus pinguis*, in the type locality at Hampstead (Hampshire basin) shows that concave morphotypes display strong resemblance with the contemporaneous species *Lychnothamnus major* suggesting that both species are synonymous. This has far-reaching consequences in charophyte biostratigraphy, since it would mean that the two biozones Lychnothamnus pinguis and L. major would need to be fused in one biozone.

3.9.2. Palaeoecology

Combination of sedimentological and taphonomic analyses allowed us to characterise the palaeoenvironment of each charophyte species. While some species display a stenotypical distribution (ecologically limited distribution), other species are eurytypical, i.e. capable of growing in a wider range of environments (Sanjuan and

Martín-Closas, 2012). For instance, three species that are significant in the European charophyte biozonation showed limited ecological distributions. *Harrisichara vasiformis-tuberculata* was characterised as a brackish water plant growing close to the shoreline in a lower deltaic plain facies. In contrast, laterally equivalent shallow freshwater lakes of the upper deltaic plain facies contained *H. lineata*. Also *H. tuberculata* was abundant, but not exclusive, from freshwater perennial lakes located in a distal alluvial fan contextes. In conclusion a facies and environmental control is superimposed to the time-distribution. This is of prime importance, in biostratigraphy since it would mean that some biozones are only recognisable provided that particular palaeoenvironmental conditions occurred.

In contrast, the eurytypical nature of species such as *Lychnothamnus longus*, *L vectensis*, *Nodosochara jorbae*, *Psilochara* aff. *acuta* and *Chara artesica* n. sp. corresponds much better to what is generally considered the best ecological status for a biostratigraphic marker, however, some of these species have an extremely large time range.

3.9.3. Palaeobiogeography

The palaeobiogeographic analisys of Late Eocene-Early Oligocene European charoflora allows to recognise a latitudinal distribution of charophyte species (Sanjuan and Martín-Closas, in revision-a). A distributional polarity has been also documented in the Late Eocene-Early Oligocene vascular flora and vertebrate fauna. Many studies show that European plant and mammal communities display regionalisms as a response to climatic deterioration (global cooling and aridification) due to the first Antarctic glaciation (Badiola et al., 2009; Cavagnetto and Anadón, 1996; Mai and Walter 1985; Mai 1989; Mihajlović 1993). Isotopic studies based on continental vertebrates and invertebrates concluded that the Eocene-Oligocene global climatic deterioration occurred differently depending on the regional constraints such as the orography (Sheldon, 2009). This thesis shows that the charophyte flora was also sensitive to these climatic and local ecological constraints. Meridional charophyte assemblages were probably adapted to wetlands subjected to seasonal aridity, while northern charophyte comunities grew in wetlands related to permanently humid conditions

In spite of these latitudinal and basinal differences an European charophyte bioprovince for the Upper Eocene Lower Oligocene, has been characterized based on a number of species (Sanjuan and Martín-Closas, in revision-a).

The interest of charophyte palaeobiogeography is high from the viewpoint of biostratigraphy. The presence or absence of biozone index-species could be influenced by biogeographical constraints rather that solely by the time-range of these species. Two fossil characean lineages, *Lychnothamnus stockmansii-L.major* and *Nitellopsis (Tectochara) merianii-N. obtusa* allow to test hypothesis about the use of certain species in supracontinental biostratigraphic correlation. Sanjuan and Martín-Closas (in revision-b) show that the dioecious evolutive lineage *Nitellopsis (Tectochara) merianii-N. obtusa* displays a gradualistic dispersal pattern, which implies a notable diacrony in the first occurrence of this species between distant basins. In contrast, the monoecious lineage *L. stockmansii-L. major*, displays an eurasiatic distribution from its first occurrence. Thus, from the biostratigraphic point of view, monoecious species, would be best suited to perform correlation between distant basins.

3.9.4. Biostratigraphy

The biostratigraphic results from this study challenge the definition and the use of some Upper Eocene-Lower Oligocene charophyte biozones nowadays in use, both at the scale of the Ebro basin and at the European scale (Anadón et al., 1992; Fiest et al., 1994; Riveline et al., 1996).

(1). Difficulties found in the application of previous biozonations

Interval zones. Interval zones are defined on the basis of appearances/disappearances of species from adjacent zones. This produces that their boundary fluctuations are not related to events of the index-species. This thesis shows two examples of interval zones of limited usefulness, i.e. Harrisichara lineata zone (formerly Harrisichara vasiformis-tuberculata zone) and Lychnothamnus major zone. Their chronostratigraphic ranges have been reduced due to the widening of adjacent biozones. This is especially clear for the biozone of L. major which has now an extremely reduced duration after the limits of adjacent biozones are almost overlapping.

Biozones with palaeoecological constraints. Palaeoecological constraints found in charophytes that are significant in biostratigraphy limits their use as index species. This is the case of the index species of local biozones 2 (Sphaerochara labellata), 3 (Stephanochara vectensis) and 4 (Stephanochara pinguis) of Feist et al. (1994), as documented by Sanjuan and Martín-Closas (2012). From the viewpoint of the European biozonation, many significant species are also restricted to particular environments. This is the case of "*Harrisichara vasiformis-tuberculata*" that is limited to brackish water deposits (Sanjuan and Martín-Closas, 2012). Also *Lychnothamnus stockmansii* and *L. pinguis* (=*L. major*) were found to occur only in permanent lacustrine facies.

<u>Biozones with palaeogeographic constraints.</u> Palaeobiogeographic restrictions observed in the distribution of some charophyte species question their use in biostratigraphy. For instance, the biostratigraphic key-species *Lychnothamnus pinguis* (in the sense of Grambast 1958) occurs mainly in northern European basins (Hampshire, Paris and Rhine Graben), which means that its use would be more appropriate for a biozonation restricted to Northern European basins, rather than for a biozonation at the European scale. In addition, the taxonomic results exposed above, i.e. the synonymy of *L. pinguis* and *L. major*, point out to a revision of this biozone.

(2). Towards a new charophyte biozonation for the Upper Eocene-Lower Oligocene of Europe

The aforementioned difficulties will probably result in a future revision of the European charophyte biozonation currently in use for the Palaeogene. This revision was beyond the scope of this study but some clues are given for future work. (1) The new European biozonation should be proposed based exclusively on partial range zones defined by first appearances of species with wide palaeogeographic distributions (i.e. in most of the European basins). In consequence, interval biozones, such as Harrisichara lineata and Lychnothamnus major, should be avoided. (2) The new biozonation should be constructed with ecologically euritypical species when possible. At least, the palaeoecological constraints of index-species should be clearly indicated in the new proposal. (3) Finally, this new charophyte biozonation should be improved by correlation with mammal reference levels (MP) and its calibration with the time scale of Gradstein (2004).

3.10. Conclusions

The charophyte assemblages from the Upper Eocene-Lower Oligocene of the eastern Ebro Basin have been characterised from the point of view of taxonomy, palaeoecology, palaeobiogeography and biostratigraphy. The charophyte flora is composed by eighteen species, i.e. *Sphaerochara labellata, Chara* aff. *antennata, C. artesica* n. sp., *C. rhenana, C. microcera, Psilochara* aff. *acuta, Lamprothamnium* sp., *Gyrogona caelata, Nodosochara jorbae, Lychnothamnus longus, L. stockmansii, L. grambastii, L. vectensis, L. pinguis (=L. major), Nitellopsis (Tectochara) merianii, Harrisichara lineata, H. vasiformis-tuberculata* and *H. tuberculata,* which were described in detail and figured.

From the palaeoecological point of view, the charophyte flora from the Upper Eocene non marine stratigraphic units of the eastern Ebro Basin was divided in five charophyte assemblages on the basis of sedimentological and taphonomic evidence. The assemblage dominated by species *Harrisichara vasiformis-tuberculata* occurs in brackish environments. In contrast, *Harrisichara lineata* in laterally equivalent stable freshwater lakes. *Lychnothamnus grambastii* occurs in facies similar to the previous assemblage but with a higher content in organic matter. Finally, the assemblage dominated by *Harrisichara tuberculata* Grambast, 1957 is formed by higher number of species and occurs in freshwater perennial lakes located in a distal alluvial fan context. Other local and European biostratigraphic-key species such as *Sphaerochara labellata, Chara microcera*, *Lychnothamnus stockmansii*, *L. pinguis* (=*L. major*) and *Nitellopsis (T.) merianii* were found in perennial lake facies.

The palaeoecological restriction of these species is in contrast to the wide distribution of the Iberian Priabonian species *Nodosochara jorbae*. This species is equally found in brackish ponds from the Sant Boi Formation and in freshwater temporary and permanent lakes from the Artés Formation. Other species such as *Lychnothamnus longus*, *L. vectensis*, *Chara artesica* n. sp. and *Psilochara* aff. *acuta* are found also in a wide range of environements This wide ecological distribution corresponds much better to what is generally considered to be the best ecological status for a biostratigraphic marker. However, many of these species have a very large time range, limiting somewhat its use in biostratigraphy.

From the palaeobiogeographic point of view, the Late Eocene-Early Oligocene European charophyte flora may be included within the same bioprovince, which may be defined on the basis of two important lineages, *Harrisichara vasiformis-H. tuberculata* and *Lychnothamnus stockmansii-L.major* and with two more species, *Nitellopsis (Tectochara) merianii* and *Chara microcera*.

However, the number of charophyte species and the relative abundance of particular species in the assemblages of each basin show a latitudinal polarity. This polarity was possibly related to the southwards decrease in seasonal humidity in Europe during the Late Eocene-Early Oligocene period, as reported in other plant groups. The variation in species richness between European basins has been also related to ecological parameters determined by basin dynamics. The limited biogeographic distribution observed in some charophytes which are significant from the biostratigraphic point of view, challenges their inclusion in the European biozonation and suggests that these species would be more appropriate for local, basin-wide, biozonations.

The historical palaeobiogeogrphy of two Eurasiatic Upper Eocene-Oligocene charophyte lineages i.e. *Lychnothamnus stockmansii-L. major* and *Nitellopsis (Tectochara) merianii-N. obtusa* shows that they underwent two opposite biogeographic patterns. The lineage *Lychnothamnus stockmansii-L. major* displays a geologically instantaneous radiation. In contrast, lineage *N. (T.) merianii-N. obtusa* follows the classical gradual dispersal pattern, with origin in south-western Europe during the Latest Eocene (Late Priabonian), expansion through Europe during the Early Oligocene (Rupelian), reaching the extreme East of the Asiatic continent probably during Late Oligocene (Chattian). The expansion of *N. (T.) merianii-obtusa* intensified in Eurasia during the Miocene and reached Africa in the Late Miocene, with a range slightly wider than in present time.

The patterns that govern the dispersal of living *Chara* could only explain in part the dispersal of characeans from the past. The geologically instantaneous supracontinental distribution of *L. stockmansii-L. major* would clearly correspond to the distribution expected from a monoecious species. In contrast, the Eurasiatic range of *N. (T.) merianii-N.obtusa* lineage, would not correspond to what is expected from a dioecious species, which usually show distributions limited to parts of a continent. Introducing the time dimension in biogeographic analysis is essential to understand that both monoecious and dioecious charophyte species could reach supracontinental distributions although at different velocites. From the case studies analysed, dioecious species would require an expansion up to ten times longer than dioecious species to achieve a similar distribution. Moreover, this analysis suggests that only cosmopolitan monoecious species could be considered a good biostratigraphic marker to perform correlation between distant basins.

From the point of view of biostratigraphy, this thesis presents a new local charophyte biozonation correlated with local mammal biozonation of Barberà et al. (2001) and calibrated with the time scale through the magnetostratigraphic studies by Barberà et al. (2001) and Costa et al. (2010, 2011). This local biozonation is constituted by six charophyte zones i.e. Harrisichara lineata (equivalent to former H. vasiformis-tuberculata biozone); Harrisichara tuberculata, Harrisichara tuberculata-Nodosochara jorbae, Lychnothamnus vectensis, Lychnothamnus major and Chara microcera. The biozone L. vectensis appears to be crucial for the characterization of the Eocene-Oligocene boundary in non-marine facies. The European charophyte biozonation has also been revised on the basis of data from the Ebro Basin, which allowed us to provide absolute ages to the biozone limits and quantify biozone cronostratigraphic ranges.

4. INTRODUCCIÓ

4.1. Presentació de la tesi

La present tesi doctoral és un estudi dels caròfits fòssils de l'Eocè superior (Priabonià)-Oligocè inferior (Rupelià) del marge est de la Conca Terciària de l'Ebre des d'un punt de vista taxonòmic, paleoecològic, paleobiogeogràfic i biostratigràfic. La tesi té la vocació de transcendir els límits de l'estudi d'un grup en particular, en aquest cas els caròfits, i d'una conca en particular, la Conca de l'Ebre, per emmarcar-se dins un context de discussió més general. Així, un dels objectius principals ha estat contribuir a que la biozonació de caròfits pel límit Eocè-Oligocè sigui realment aplicable a totes les conques europees. Un altre objectiu fonamental ha estat conèixer com el canvi climàtic de l'Eocè-Oligocè va afectar als caròfits, un tema que en el camp de la paleobotànica només s'ha estudiat àmpliament a partir de les rests fòssils de plantes vasculars. Aquest canvi climàtic es considera un esdeveniment global de refredament progressiu que s'inicià durant l'Eocè mitjà/superior, s'accentuà a l'Eocè terminal (Priabonià) i culminà amb la primera glaciació Antàrtica durant l'Oligocè basal (Zachos et al., 2001).

Seguint el reglament del doctorat de la Universitat de Barcelona referit a les tesis presentades com a compendi d'articles, aquesta memòria s'ha estructurat en els següents apartats: (1) un resum, (2) una introducció on es presenten els articles i es detallen els objectius, (3) un apartat de metodologia, (4) un apartat de resum dels resultats, (5) un apartat de resum de la discussió i finalment (6) unes conclusions.

Aquesta tesi parteix de les dades procedents de cinc articles, que tracten individualment cadascun dels temes de la tesi. Exposar la interrelació entre aquests articles és un objectiu fonamental d'aquesta memòria de tesi. Tres dels articles ja han estat acceptats o publicats i dos d'altres es troben en revisió, tots ells a revistes indexades per l'ISI en el Journal of Citation Reports. A continuació es destaca de forma resumida les aportacions d'aquests articles, ordenats temàticament:

- **Taxonomia**. Sanjuan, J., Martín-Closas, C. Taxonomy and palaeobiogeography of charophytes from the Upper Eocene-Lower Oligocene of the eastern Ebro basin (Catalonia, NE Spain). *Geodiversitas* (en revisió-a).

  IF: 0.9, Llista: Paleontology, Quartil: 3er

Aquest article presenta una revisió taxonòmica de la flora de caròfits del'Eocè superior i Oligocè inferior del sector oriental de la Conca de l'Ebre tenint en compte tots els paràmetres biomètrics i el polimorfisme intraespecífic. Aquests aspectes no s'havien tingut suficientmente en compte en els estudis anteriors (Colom et al., 1970; Choi, 1989). S'ha definit una nova espècie, *Chara artesica* nov. sp., que anteriorment s'havia descrit amb nomenclatura oberta (*Chara* sp. 2 Choi, 1989). L'estudi taxonòmic també ha permès identificat per primera vegada a la conca de l'Ebre vàries espècies de distribució europea, *Psilochara* aff. *acuta* Grambast i Paul 1965, *Chara* aff. *antennata* Grambast 1958, *Chara rhenana* Schwarz i Griessemer 1994.

L'article presenta, a més, un anàlisi de la distribució biogeogràfica dels caròfits de la Conca de l'Ebre al voltant del límit Eocè-Oligocè. Anteriorment Riveline (1986) i Anadón et al. (1992) foren dels pocs autors que estudiaren la paleobiogeografia dels caròfits de l'Eocè superior i l'Oligocè inferior. El present article contrasta les dades d'aquests autors i formula hipòtesis paleoclimàtiques i paleoecològiques sobre els factors que induïren la distribució heterogènia dels caròfits durant aquest període.

- **Paleoecologia**. Sanjuan, J., Martín-Closas, C., 2012. Charophyte palaeoecology in the Upper Eocene of the Eastern Ebro Basin (Catalonia, Spain). Biostratigraphic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 365-366: 247-262. IF: 2.7, Llista: Paleontology, Quartil: 1er

Massieux i Villatte (1977) i Tambareau et al. (1991) foren de les úniques autores que havien estudiat els aspectes paleoecològics dels caròfits del Paleogen. En aquest treball es reprèn aquest tema a partir de les anàlisis sedimentològica i tafonòmica combinades, i tenint en compte els fòssils associats. Com a resultat s'han caracteritzat els paleoambients on es desenvoluparen les diferents associacions de caròfits de la conca de l'Ebre durant l'Eocè superior. Es conclou que la presència o absència de determinades espècies, i per tant la identificació de determinades biozones, està molt condicionada per factors paleoecològics.

- **Paleobiogeografia**. Sanjuan, J., Martín-Closas, C. Biogeographic history of two Eurasiatic Cenozoic charophyte lineages. *Aquatic Botany* (en revisió-b). IF: 1.5, Llista: Plant Sciences, Quartil: 2^{on}

Aquest article te com a objectiu documentar la paleobiogeografia històrica de dos llinatges evolutius de distribució supracontinental presents als dipòsits no-marins del marge est de la Conca de l'Ebre (*Lychnothamnus stockmansii-L.major* i *Nitellopsis (Tectochara) merianii-N. obtusa*). Partint de les estratègies reproductives de les espècies de caròfits actuals i la relació amb la seva dispersió biogeogràfica (Proctor, 1980) es formulen hipòtesis sobre la velocitat d'expansió de les espècies fòssils (ràpida a escala geològica o progressiva) i la seva implicació en biostratigrafia i en la correlació entre conques geogràficament molt distants.

- **Biostratigrafia (I).** Sanjuan, J., Martín-Closas, C., Serra-Kiel, J., Gallardo, H., 2012. Stratigraphy and biostratigraphy (charophytes) of the marine-terrestrial transition in the Upper Eocene of the NE Ebro Basin (Catalonia, Spain). *Geologica Acta*,10 (1): 19-31. IF: 1.2, Llista: Geology, Quartil: 2^{on}

Aquest treball es centra en la datació mitjançant caròfits de la continentalització de l'extrem NE de la conca de l'Ebre. La datació del moment en que la conca de l'Ebre passà de domini marí a continental ha estat recentment objecte d'interès. Nous treballs magnetostratigràfics procedents del marge est-central mostraren que la continentalització es podia considerar un esdeveniment ràpid a escala geològica i que conduí a la formació sobtada d'una conca endorreica durant el cron C16 del Priabonià (Costa et al., 2010). La flora de caròfits fòssils procedent de l'Eocè superior del Lluçanès (Osona) ha permès caracteritzar aquest procés tant biostratigràficament com des del punt de vista sedimentològic en aquest sector de la conca, on els caròfits no havien estat mai estudiats amb detall.

- **Biostratigrafia (II).** Sanjuan, J., Martín-Closas, C., Costa, E., Barberà, M., Garcés, M. Calibration of Eocene-Oligocene charophyte biozones in the Eastern Ebro Basin (Catalonia, Spain). *Stratigraphy* (acceptat). IF: 1.0, Llista: Geology, Quartil: 3^{er}

L'excel·lent exposició i continuïtat dels dipòsits Paleògens de la Conca de l'Ebre han determinat que aquesta sigui una referència internacional en la biostratigrafia marina i continental del Paleogen. El gran nombre d'estudis biostratigràfics basats en vertebrats i caròfits proporcionaren datacions de les principals unitats litostratigràfiques no-marines que configuren el marge est de la Conca de l'Ebre durant les dècades de 1980 i 1990 (Arbiol i Sáez 1988; Anadón et al., 1986; 1992; Choi, 1989; Feist et al., 1994).

Posteriorment aquest estudis s'han completat amb datacions absolutes basades en la magnetostratigrafia (Barberà, 1999; Barberà et al., 2001; Costa et al., 2010; 2011; Costa, 2011). Aquests darrers estudis, juntament amb una presa de mostres més densa de les sèries estratigràfiques, han permès revisar la biozonació de caròfits dels autors anteriors a la conca de l'Ebre i calibrar-la amb l'escala de temps absolut mitjançant la magnetostratigrafia. Els resultats tenen implicacions a escala europea.

A més dels articles publicats o en revisió, es presenten resultats encara inèdits sobre la revisió taxonòmica de dues espècies claus en biostratigrafia del límit Eocè-Oligocè europeu. Les espècies *Lychnothamnus vectensis* i *L. pinguis* definides a la conca de Hampshire (Illa de Wight, Anglaterra) s'han revisat a partir del material tipus conservat al *Natural History Museum* de Londres. Aquestes espècies son índex biostratigràfics molt importants en la biozonació de caròfits del Eocè superior i Oligocè inferior a escala europea. Els resultats indiquen que *L. vectensis* és una espècie polimorfa mentre que *L. pinguis* i *L. major* serien dues espècies sinònimes corresponents a dos estats de calcificació del girogonit d'un mateix taxó.

4.2. Hipòtesi de partida i objectius

La present tesi doctoral té com a hipòtesi principal que els factors paleoecològics, paleoclimàtics i paleogeogràfics influenciaren la distribució dels caròfits i que aquesta distribució afecta alhora l'ús de les associacions de caròfits en biostratigrafia. Seguint aquesta hipòtesi central, la tesi persegueix assolir objectius centrats en taxonomia, paleoecologia, palebiogeografia/paleoclimatologia i biostratigrafia dels caròfits de l'Eocè superior-Oligocè inferior.

- Objectius taxonòmics. L'objectiu taxonòmic principal ha estat completar i ampliar el coneixement existent sobre les espècies de caròfits del límit Eocè-Oligocè tant a escala local (Conca de l'Ebre) com europea. Algunes espècies importants per la biostratigrafia havien estat caracteritzades a partir de poblacions poc nombroses i necessiten ser revisades tenint en compte el polimorfisme intraespecífic i la possible sinonímia amb altres espècies. En molts casos cal estudiar els holotipus i paratipus per a aclarir els límits entre espècies properes. Aquest és el cas de *Lychnothamnus vectensis* i *L. pinguis*. També cal revisar algunes espècies prèviament descrites a la conca de l'Ebre però que taxonòmicament es trobaven en un estatus indefinit, com per exemple vàries espècies del gènere *Chara*, que s'havien deixat en nomenclatura oberta. Un objectiu addicional ha estat caracteritzar preliminarment les faunes d'invertebrats associades als caròfits, especialment els ostràcodes i els gasteròpodes, i que podien aportar importants informacions paleoambientals. Per això s'ha consultat especialistes en aquests grups.

- Objectius tafonòmics i paleoecològics. Dins d'aquest àmbit l'objectiu principal ha estat caracteritzar el paleoambient de les associacions de caròfits a partir d'anàlisis tafonòmiques i sedimentològiques combinades, i tenint en compte la fauna fòssil associada. També ha estat un objectiu important definir els principals paràmetres paleoecològics que influeixen en la distribució de les espècies. Això és especialment important en el cas d'espècies d'interès biostratigràfic, atès que el seu rang temporal pot estar controlat per les fàcies.

- Objectius paleobiogeogràfics. L'objectiu principal ha estat caracteritzar la paleobiogeografia dels caròfits del límit Eocè-Oligocè establint relacions amb els canvis paleoambientals, paleoclimàtics i paleogeogràfics d'aquest període. Els estudis paleobiogeogràfics sobre els caròfits paleogens són escassos. No obstant això alguns autors han realitzat correlacions biostratigràfiques entre conques distants a partir de la presència d'espècies d'àmplia distribució biogeogràfica. L'estudi de la paleobiogeografia dels caròfits permetrà establir la distribució en l'espai i el temps d'aquestes espècies i avaluar fins a quin punt aquestes espècies son útils per ser utilitzades en les correlacions biostratigràfiques entre conques llunyanes, o si pel contrari, presenten diferencies d'edat significatives en la seva dispersió.

- Objectius biostratigràfics. L'objectiu és caracteritzar la distribució temporal dels caròfits del límit Eocè-Oligocè tant a escala de conca de l'Ebre com a escala d'Europa occidental. S'ha partit de les biozonacions anteriorment establertes per Feist et al. (1994) a la Conca de l'Ebre i Riveline et al. (1996) a escala europea que en part estaven correlacionades amb biozacions i nivells de referència de mamífers. Un objectiu innovador d'aquesta tesi és establir calibracions de la biozonació de caròfits amb l'escala cronostratigràfica a partir dels estudis magnetostratigràfics realitzats per autors anteriors en el marge est de la conca (Barberà et al., 2001; Costa et al., 2010, 2011). A part de contribuir a conèixer l'edat relativa dels dipòsits no-marins del marge oriental de la conca de l'Ebre, es pretén elaborar una nova proposta de biozonació tenint en consideració els resultats en sistemàtica, paleoecologia i paleobiogeografia obtinguts en la present tesi.

5. MARC GEOLÒGIC

La Conca de l'Ebre és una conca d'avantpaís, situada al sud de la cadena pirinenca. Presenta una morfologia triangular i es troba limitada al nord per les làmines encavalcants del Pirineu, a l'est per la cadena litoral catalana i al sudoest per la cadena ibèrica (Fig.1). Els seu origen es relaciona amb la subsidència flexural produïda per la convergència entre les plaques ibèrica i eurasiàtica que s'inicià al Cretaci superior (Santonià-Campanià) i es perllongà fins al Miocè. El moment de màxima compressió es produí durant el Paleocè i l'Eocè que resultà en la superposició de varis encavalcaments a la zona central sud-pirinenca. Les principals estructures posseeixen una orientació est-oest i la deformació progressà en direcció sud i oest paral·lelament als centres deposicionals de la conca. D'aquesta manera, les seqüències sedimentàries basals quedaren incorporades en les làmines encavalcats. (Puigdefàbregas et al., 1992).

El rebliment de la Conca de l'Ebre inclou roques marines i continentals que comprenen un rang d'edats entre el Cretaci Superior fins l'Eocè superior. Posteriorment, la conca enregistra exclusivament una sedimentació continental. Durant gran part del Paleogen la conca formà un golf obert cap a l'Atlàntic. Aquesta situació es mantingué fins l'Eocè superior (Priabonià), quan l'aixecament del sector oest del Pirineu aïllà la conca de l'Oceà Atlàntic i la transformà en una conca endorreica (Puigdefàbregas et al., 1992).

La successió sedimentària paleògena de l'àrea d'estudi (marge est de la Conca) es dividí en nou seqüències deposicionals lligades a l'emplaçament de dels mantells d'encavalcament meridionals del Pirineu i lligades als dos moments de màxima pujada del nivell del mar durant l'Ilerdià (Eocè inferior) i el Bartonià (Eocè mitjà-superior) (Puigdefàbregas et al., 1986). Segons aquests autors, la successió dels encavalcaments i els esdeveniments evaporítics permeten diferenciar tres cicles deposicionals principals en el rebliment de la conca. El primer cicle inclou les seqüències sedimentàries de Cadí, Corones, Armàncies i Campdevànol, que coincideixen amb l'emplaçament submarí dels mantells d'encavalcament superiors. El segon cicle sedimentari inclou les seqüències de Bellmunt i Milany (Lutecià i Bartonià) les quals coincideixen amb el desenvolupament de l'apilament antiforme dels mantells d'encavalcament de l'àrea central pirinenca. Aquesta estructura induí la progradació deltaica i una migració simultània dels depocentres en sentit sud de la conca. Alhora, la cadena costanera catalana experimentà

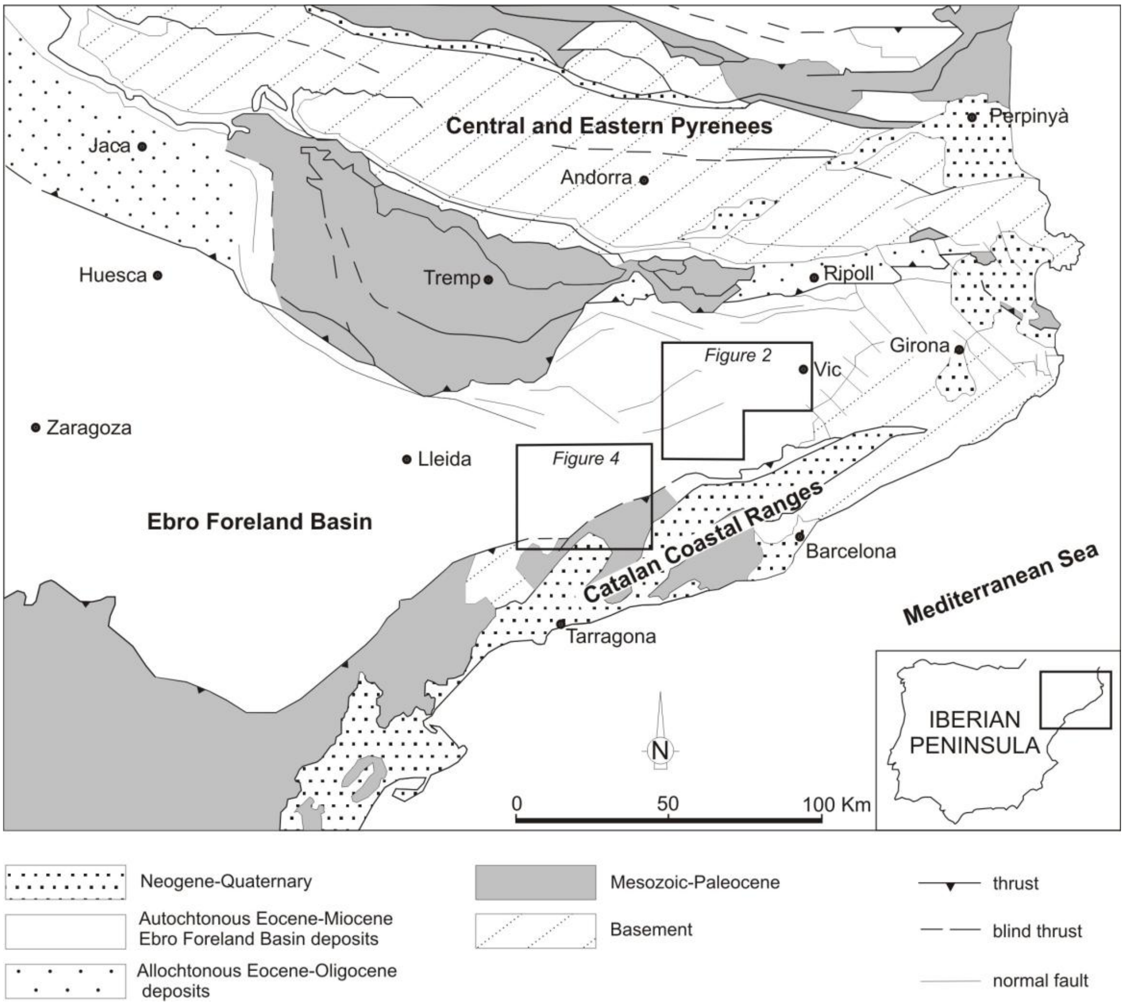


Figura 1. Mapa geològic del NE de la península Ibèrica amb la localització de les àrees estudiades

Figure 1. Geological sketch of NE Iberian Peninsula showing the location of the studied areas

un procés d'activitat tectònica que també contribuí al rebliment de la conca formant sistemes deltaics progradants desenvolupats al llarg del marge est, els deltes de Montserrat, Sant Llorenç del Munt i Montsant. Aquesta activitat tectònica comportà la darrera restricció de la conca i la deposició d'una capa evaporítica durant l'Eocè superior. Aquest esdeveniment evaporític representa el darrer episodi marí de la conca d'avantpaís sud-pirinenca, la qual esdevingué, a partir d'aquest moment, endorreica. El tercer cicle inclou la seqüència de Solsona i les seqüències més modernes. Aquest cicle coincideix amb l'emplaçament dels mantells d'encavalcament mes meridionals i l'emersió de l'encavalcament de Vallfogona,que transportaren a collibé els mantells anteriors. Aquests mantells contribuïren al creixement dels ventalls alluvials que conectaven amb les àrees lacustres del centre de la Conca (Puigdefàbregas et al., 1986).

Dins aquest darrer cicle Anadón et al. (1989) dividiren el rebliment sedimentari del marge est de la conca en cinc seqüències deposicionals que incloïen cinc sistemes lacustres, respectivament La Noguera, l'Anoia, Segarra, l'Urgell i Los Monegros, amb un rang d'edats entre el Priabonià superior i el Catià.

En aquesta tesi doctoral el marge est de la conca de l'Ebre s'ha dividit en tres sectors. en base a criteris geològics i paleogeogràfics. De NE a SW, aquests sectors són: (1) l'àrea de Vic-Manresa (comarques d'Osona i Bages), (2) l'àrea d'Igualada (Comarca de l'Anoia) i (3) l'àrea de la Conca de Barberà i l' Urgell (Fig. 1).

(1). Sector Vic/Manresa: Els darrers dipòsits marins en aquest sector de la conca formen part de Formació deltaica de Sant Martí Xic (Barnolas et al., 1988; Barnolas, 1992) que grada lateralment cap a conca a les margues de prodelta de la Formació Vic (Reguant, 1967), equivalent en direcció sud a la Formació Igualada (Ferrer, 1971). Les roques sobreposades a la Formació Sant Martí Xic inclouen dipòsits marins i transicionals delimitats per disconformitats regionals i agrupats dins el Complex Terminal (Travé, 1992; Travé et al., 1996). Aquesta unitat litològica està composta pels gresos de la Formació Noguera (Reguant, 1967), margues anòxiques, calcàries estromatolítiques i guix, que representen el reompliment progressiu de la conca i el trànsit cap a condicions continentals. Cap al nordest el Complex Terminal perd entitat i potència i passa lateralment a la Formació Sant Boi (Sanjuan et al., 2012), composta per lutites, margues, lignits i gresos d'ambients salabrosos o d'aigua dolça pròxims a la costa i ubicats en un context d'esplanada deltaica. En direcció sudest el Complex Terminal passa lateralment a la Formació Guixos d' Òdena que representa alhora l'equivalent marginal dels dipòsits d'halita i silvinita de la Formació Cardona, situats al centre de la conca (Fig. 3).

Els primers dipòsits estrictament continentals sobreposats als dipòsits de la transició marí-continental del marge nordest de la conca, estan representats per la Formació Artés (Fig. 3), definida per Ferrer (1971) i modificada per Sáez (1987). Aquesta unitat sedimentaria està generalment constituïda per argiles vermelles, llims i cossos de gres canaliformes i es relaciona amb àrees mitjanes i distals de sistemes de ventall al·luvial de procedència catalanídica. Aquests materials s'alternen sovint amb nivells de marga o calcària lacustre més o menys potents amb abundants restes fòssils de caròfits, ostràcodes, gasteròpodes i vertebrats. Inclosa dins la Formació Artés es definí el

Membre Calcàries de Moià, que consta de ~50 m de potència de calcàries i margues lacustres relacionades en direcció est amb el Membre Calcàries de Castelltallat (Anadón et al., 1989) (Fig. 3).

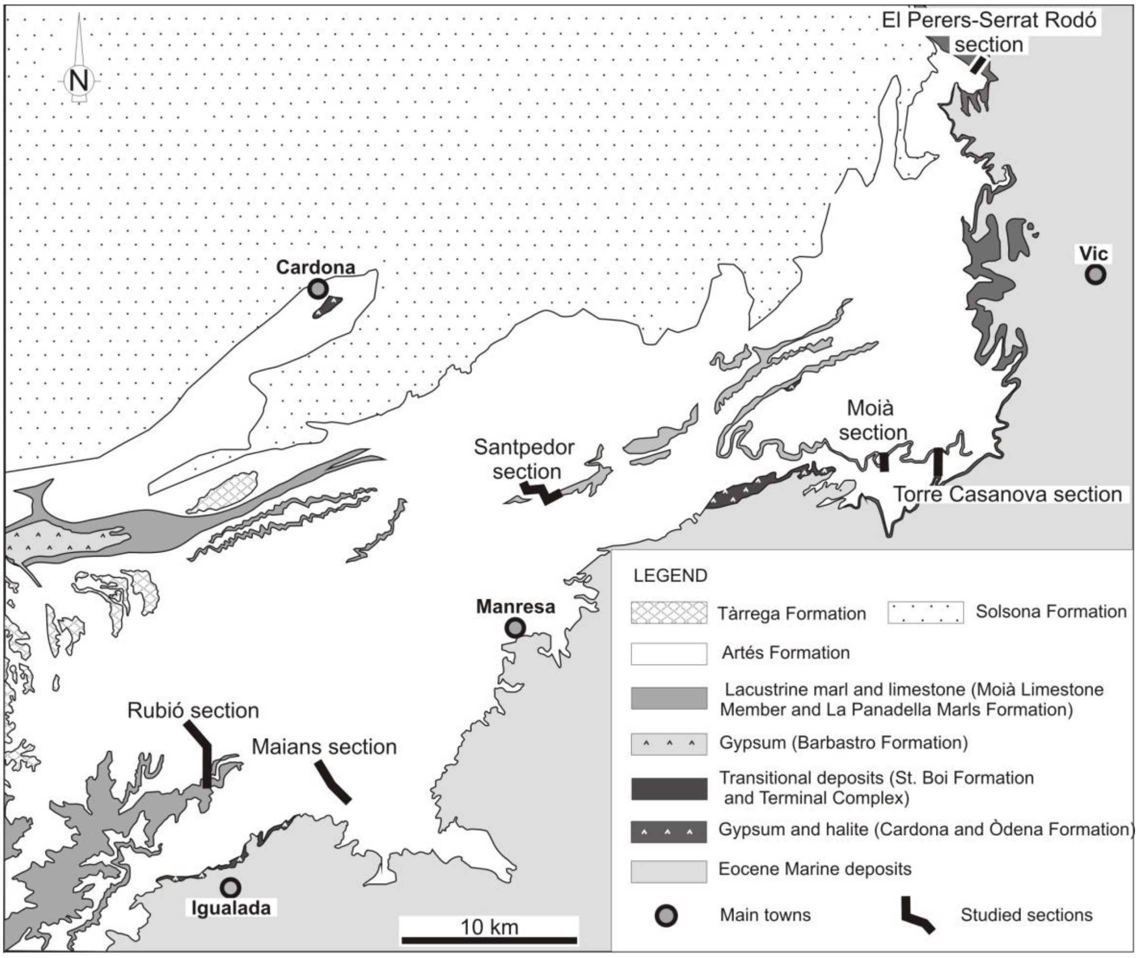


Figura 2. Mapa geològic del sector NE de la conca de l'Ebre amb la localització de les columnes estratigràfiques estudiades (modificat de Sanjuan i Martín-Closas, 2012).

Figure 2. Geological map of the northeastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Sanjuan and Martín-Closas 2012).

(2). Àrea d'Igualada. Dins aquesta àrea s'han estudiat fonamentalment els dipòsits de la Formació Artés que presenta, en aquest sector de la conca, diverses unitats al·luvials terrigenes i evaporítiques d'orígen lacustre (Formacions St. Martí de Tous, St. Genís, Jorba, Clariana, Copons, Sta. Coloma de Queralt, Montmaneu, Talavera, Panadella i Solsona) les quals formen part dels sistemes lacustres de l'Anoia i La Segarra (Anadón et al., 1989; Colldeforns et al., 1994a i b).

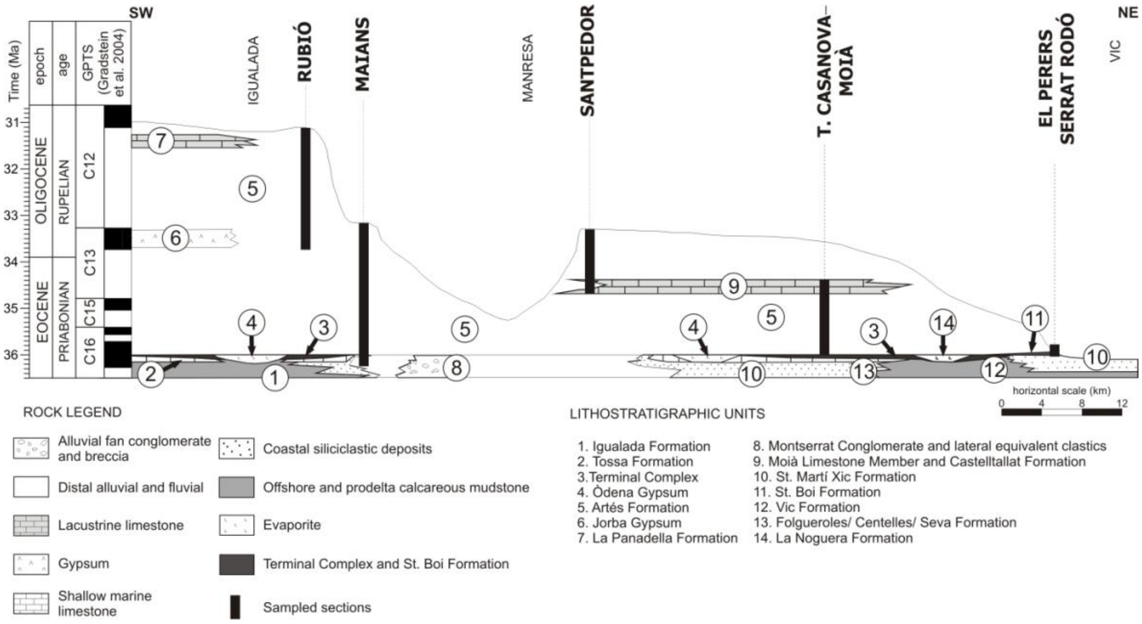


Figura 3. Esquema litostratigràfic del registre sedimentari de l'Eocè superior-Oligocè al sector NE de la conca de l'Ebre (modificat de Costa, 2011).
Figure 3. Lithostratigraphic framework of the Upper Eocene-Oligocene record in the northeastern Ebro Basin (modified from Costa, 2011).

(3). Àrea de la Conca de Barberà i l'Urgell. La divisió litostratigràfica dels dipòsits paleògens d'aquest sector de la conca parteix de varis treballs cartogràfics, estratigràfics i sedimentològics anteriors (Colombo, 1980, 1986; Cabrera,1983; Cabrera et al., 1985; Anadón et al., 1989 i Colldeforns et al., 1994a i b). Els dipòsits no-marins d'aquest sector de la conca consten de diverses unitats terrígenes, carbonatades i evaporítiques d'origen al·luvial i lacustre (Colombo, 1986) (Figs. 4 i 5).

Les unitats al·luvials es dipositaren en un context d'activitat de diversos sistemes deposicionals entre els quals es destaquen el sistema deposicional de Sant Miquel de Montclar, que inclou la Formació Sant Miquel de Montclar, i el sistema deposicional del Montsant, amb les Formacions Montsant, Margalef, Blancafort, Albi i Cogul definides per Colombo (1980, 1986) i Colldeforns et al. (1994b). Juntament amb aquestes formacions existeixen dipòsits d'altres sistemes al·luvials dels que no s'han enregistrat les seves parts proximals (Formació Rauric, Formació Gavatxa). Aquestes unitats litostratigràfiques presenten fàcies relacionades amb zones mitjanes i terminals (marginals i distals) dels sistemes al·luvials on es desenvoluparen extenses zones d'esplanades lutítiques i sistemes lacustres terrígens, carbonatats i evaporítics.

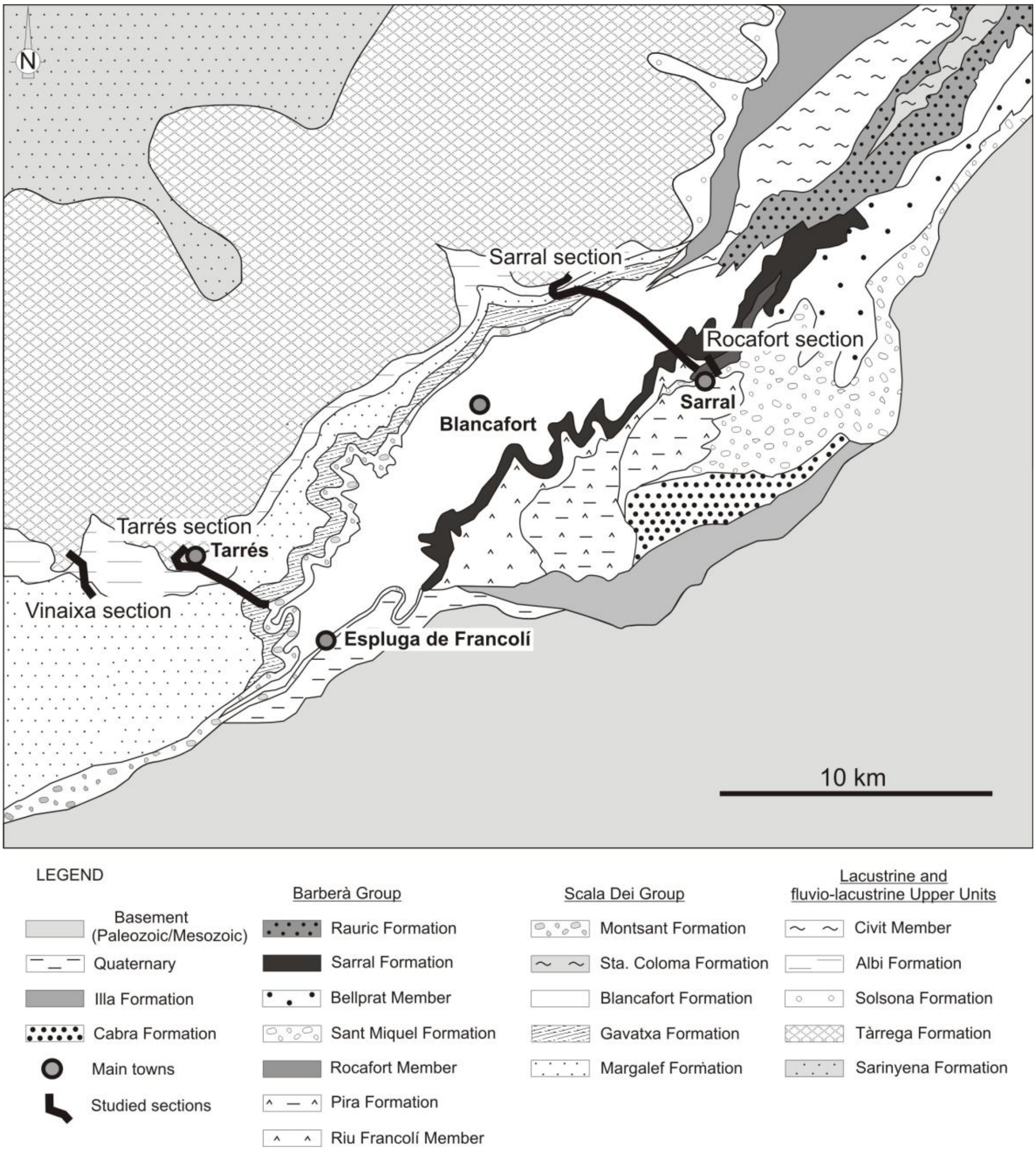


Figura 4. Mapa geològic del sector SE de la Conca de l'Ebre amb la localització de les seccions estudiades (modificat de Barberà, 1999)

Figure 4. Geological map of the southeastern part of the Ebro Foreland Basin showing the location of the studied sections (modified from Barberà, 1999).

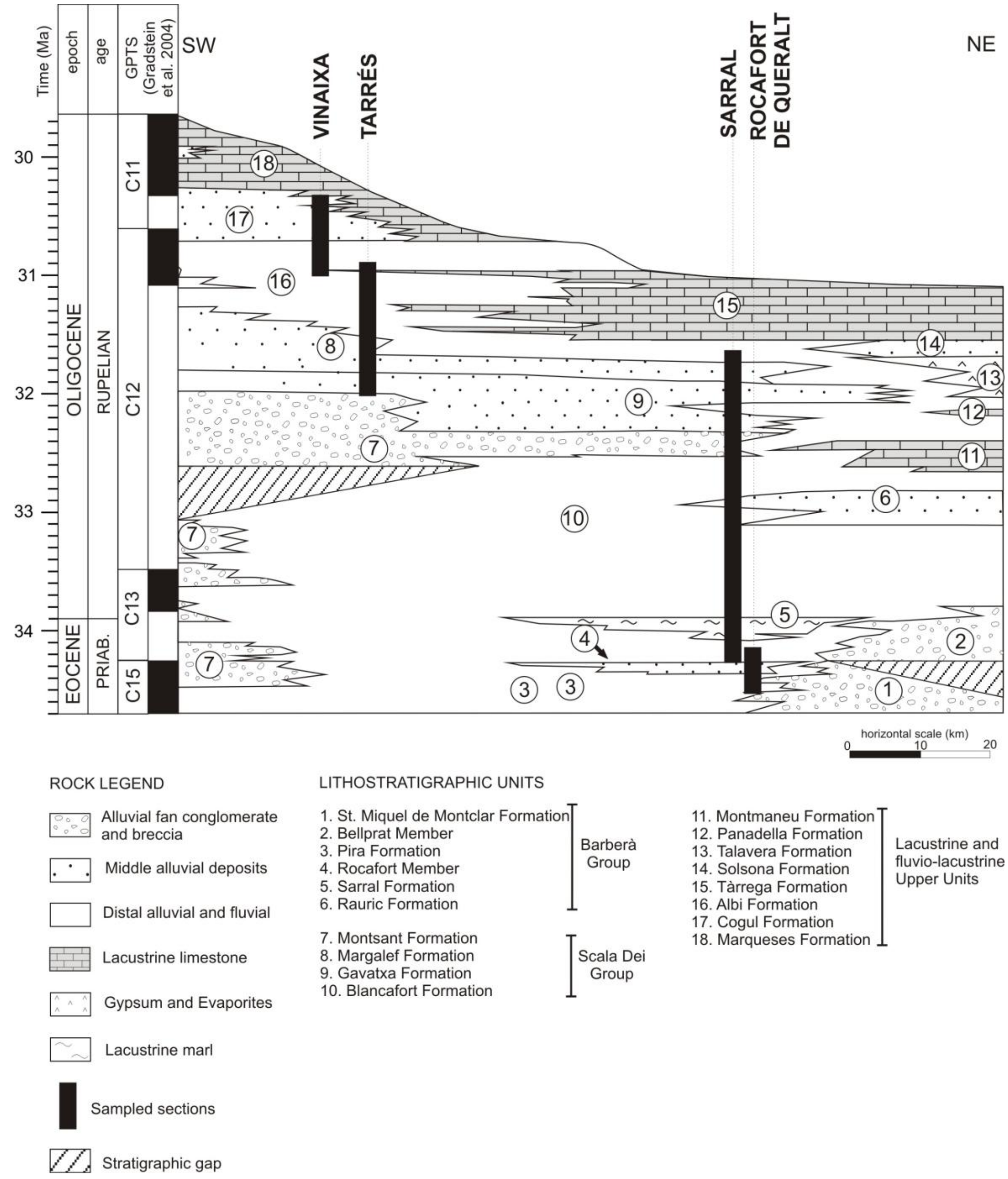


Figura 5. Esquema litostratigràfic del registre sedimentari de l'Eocè superior-Oligocè al sector SE de la conca de l'Ebre (modificat de Barberà, 1999).

Figure 5. Lithostratigraphic framework of the Upper Eocene-Oligocene record in the southeastern Ebro Basin (modified from Barberà, 1999).

6. METODOLOGIA

6.1. Mètodes del treball de camp

L'àrea estudiada se situa en el sector oriental de la conca de l'Ebre, prop del seu límit amb la Cadena Prelitoral Catalana. Aquesta àrea presenta un registre excepcionalment continu de dipòsits no-marins del límit Eocè-Oligocè. En base a critèris geològics l'àrea d'estudi dels caròfits s'ha subdividit en tres sectors de NE a SW, l'àrea de Vic-Manresa (comarques d'Osona i Bages), l'àrea d'Igualada (Comarca de l'Anoia) i l'àrea de la Conca de Barberà i l' Urgell (Fig. 1).

La presa de mostres es va realitzar de manera sistemàtica a tots els nivells de fàcies lacustres o palustres. A l'àrea de Vic-Manresa, s'alçaren i es es van prendre mostres d'un total de nou sèries estratigràfiques a les localitats de La Portelleta, El Perers, Sobremunt, Serrat Rodó, Cal Carreter, Santa Maria d'Oló, Oristà, Torre Casanova, Moià i Santpedor, que comprenen dipòsits transicionals i continentals de la Formació Sant Boi i Artés (Figs. 2 i 3). Aquestes seccions foren correlacionades directament mitjançant nivells de correlació físics amb continuïtat cartogràfica (Sanjuan et al., 2012; Costa et al., 2011). A l'àrea d'Igualada, es varen prendre mostres de dues sèries estratigràfiques, la sèrie de Maians i la sèrie de Rubió (Figs. 2 i 3). Ambdues seccions comprenen materials continentals de la Formació Artés d'edat Priabonià-Rupelià i foren correlacionades directament a partir de nivells de correlació físics amb continuïtat cartogràfica (Costa et al., 2010). Aquestes correlacions permeteren, a més, correlacionar els 50 m inferiors de la secció de Maians amb la part superior dels dipòsits marins més alts del Grup Santa Maria i les unitats litostratigràfiques transicionals del "Complex Terminal", la Formació Sant Boi, i els Guixos d'Òdena i la Formació salina de Cardona (Costa et al., 2010).

A l'àrea de la Conca de Barberà i l'Urgell es varen prendre mostres d'un total de 4 sèries estratigràfiques a Rocafort de Queralt, Sarral, Tarrés i Vinaixa i de 2 afloraments a Solivella i El Talladell que comprenen dipòsits continentals de diverses litologies i ambients deposicionals (Figs. 4 i 5). Aquestes seccions foren correlacionades directament mitjançant nivells de correlació físics amb continuïtat cartogràfica i fotogeològica (Barberà, 1999; Barberà et al., 2001).

6.2. Mètodes del treball de laboratori

S'han rentat un total de 145 mostres de lutites amb garbells sobreposats d'1mm, 0,5 mm i 0,2 mm de llum, desprès de deixar que el material perdés la cohesió i es desfés en una solució d'aigua, peròxid d'hidrogen i carbonat sòdic durant 24-72 hores. La fracció garbellada de cada mostra es trià a ma sota lupa binocular. La quantitat de sediment triat es feu en funció de l'abundància relativa de fòssils en cada mostra. En general es prolongà fins a obtenir una població de 100 girogonits per espècie. Durant el triatge es feu una separació preliminar dels fòssils separant els diferents gèneres de caròfits, així com el altres fòssils associats (tal·lus de caròfits, ostràcodes, microgasteròpodes, restes fòssils de vertebrats). Una vegada el material quedà triat es procedí al rentat dels fòssils coberts de sediment mitjançant la cubeta de vibració amb ultrasons. Per a l'estudi de les microfàcies es varen tallar unes 30 mostres de roca calcària dura per a preparar làmines primes de 2,5 x 5cm i unes 30 μm de gruix. Amb l'objectiu d'obtenir diferents seccions dels fòssils i d'estudiar el canvi en les microfàcies lateralment i de base a sostre es feren talls paral·lels i perpendiculars a l'estratificació de cada mostra. Les mostres de caròfits es troben dipositades la col·lecció de caròfits del Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, i el material tipus (holotipus i paratipus) al Museu Geològic del Seminari Conciliar de Barcelona (MGSCB).

6.3. Mètodes del treball de gabinet

Gran part dels girogonits estudiats es varen mesurar sota un binocular Wild M5A, amb un micròmetre acoblat a l'ocular. Posteriorment l'estudi morfològic prosseguí utilitzant el microscopi electrònic de rastreig Quanta 200 dels Serveis Cientificotècnics de la Universitat de Barcelona i s'obtinguéren fotografies per a cada espècie de girogonit, així com dels fragments de tal·lus, ostràcodes i microgasteròpodes.

Per a cada espècie identificada es mesuraren al miscroscopi òptic 100 girogonits, sempre que fossin disponibles, tenint en compte varis paràmetres biomètrics; l'alçada i l'amplada del girogonit, el nombre de voltes que s'observen en vista lateral, l'amplada de la volta de l'espira a l'equador del girogonit i l' índex d'isopolaritat (ISI). Al mateix temps es feren gràfics dels paràmetres biomètrics estudiats i gràfics de dispersió comparatius entre poblacions i espècies.

6.4. Mètodes en taxonomia

L'estudi taxonòmic es va dur a terme a partir de la bibliografia especialitzada i les col·leccions de referència de caròfits pertanyents al Dept. d'Estratigrafia, Paleontologia i Geociències Marines. També es van realitzar estudis taxonòmics i de comparació amb col·leccions d'altres conques en tres centres de recerca estrangers, que disposen de importants col·leccions de caròfits paleogens. Aquests estudis es van realitzar durant tres estades breus de recerca:

(a) L'estada a l'Institut des Sciences de l'Evolution de l'Université Montpellier II (juny i octubre de 2011) va permetre estudiar gran part dels holotipus i paratipus de les especies determinades a la conca de l'Ebre i comparar-les amb material d'altres conques gràcies a la consulta de les col·leccions creades per L. Grambast i M. Feist. Les determinacions taxonòmiques van ser revisades per la Dra. Monique Feist i la Dra. Ingeborg Soulié-Märsche. A més, l'estada va permetre estudiar comunitats de caròfits actuals del sud de França per tal d'establir anàlegs ecològics actuals amb els caròfits fòssils.

(b) L'estada al Département de Biominéralisation et Énvironnements Sédimentaires de l'Université Pierre et Marie Curie de Paris (octubre i novembre de 2012) ha permès consultar la col·lecció de caròfits de Janine Riveline, procedents de la conca de Paris i es van fer estudis comparatius amb les espècies presents de la conca de l'Ebre. Les determinacions taxonòmiques i les hipòtesis paleoecològiques i paleobiogeografiques varen ser discutides amb la Dra. Janine Riveline. També es van determinar els gèneres d'ostràcodes trobats en les mostres de la conca de l'Ebre amb l'ajuda del Dr. Claude Guernet.

(c) L'estada "Natural History Museum" de Londres (juliol de 2013) va permetre revisar espècies de caròfits de l'Eocè superior i Oligocè de l'Illa de Wight i que són claus per a la biostratigrafia de l'Eocè superior-Oligocè inferior. La col·leccó estudiada va ser realitzada per A'Court-Smith i estudiada per J. Groves a principis del segle XX.

6.5. Mètodes en biostratigrafia

En un primer temps, les associacions de caròfits es van assignar a les biozones definides per Riveline (1986) i Riveline et al. (1996). Posteriorment, a mida que s'anaven tenint mes resultats paleoecològics i biogeogràfics, les biozones han estat redefinides respectant al màxim la biozonació en ús i utilitzant espècies poc limitades des d'un punt de vista facial i d'alt abast biogeogràfic. Les noves biozones es van correlacionar amb els nivells de referència de mamífers (MP) coneguts a partir de la bibliografia i es van calibrar amb les magnetozones definides per Barberà et al. (2001) i Costa et al. (2010, 2011). Aquesta calibració fou possible gràcies a que les mostres de caròfits s'havien obtingut de les mateixes sèries estratigràfiques en les que s'havien realitzat els estudis magnetostratigràfics. Aquesta calibració es va poder comparar amb la única calibració que es coneixia fins al moment i que s'havia establert a la conca de Hampshire (Anglaterra) per Hooker et al. (2009), que no obstant això, resultava d'una presa de mostres molt menys densa que la realitzada a la conca de l'Ebre.

6.6. Mètodes en tafonomia i paleoecologia

Les associacions de caròfits de l'Eocè superior es van caracteritzar paleoambientalment partint de la combinació de l'anàlisi sedimentològica i l'estudi de la tafonomia dels microfòssils de caròfits. També es va tenir en compte la informació aportada per altres fòssils d'interès paleoecològic com foraminífers, ostràcodes, mol·luscs i vertebrats. Per l'estudi tafonòmic dels caròfits es varen tenir en compte la distribució normal/no normal de les mides de les poblacions de girogonits, la presència/absència d'erosions o fracturacions dels girogonits i l'associació de girogonits i tal·lus o presència dels òrgans aïllats, la presència /absència de connexions entre diferents parts dels tal·lus en les mostres de làmina prima.

6.7. Mètodes en paleobiogeografia

Les espècies de caròfits del límit Eocè-Oligocè de la conca de l'Ebre es varen caracteritzar paleobiogeogràficament partint de les dades de distribució pròpies i de la bibliografia existent. En aquest sentit fou de gran utilitat la base de dades del Laboratoire de Paléobotanique de Montpellier creada per Nicole Grambast i que recull totes les entrades de caròfits fòssils descrits fins a l'any 2000. Una còpia d'aquesta base de dades es toba la Departament d'Estratigrafia, Paleontologia i Geociències Marines. Les dades obtingudes per a cada interval cronostratigràfic i corresponents a les biozones de caròfits es representaren sobre els mapes paleogeogràfics de Lorenz et al. (1993 i Blakey (2006).

7. RESULTATS

7.1. Sistemàtica paleobotànica (caròfits)

7.1.1. Girogonits

Les mostres procedents de les diferents seccions estudiades al marge est de la conca de l’Ebre ha proporcionat un total de divuit espècies de girogonits, tres de les quals no havien estat citades anteriorment a la conca i una espècie nova. Totes aquestes espècies han estat descrites amb detall dins l’article de Sanjuan i Martín-Closas (en revisió-a). El conjunt d’espècies s’indica en la següent llista i s’il·lustra a les Figs. 6-10. Les espècies descrites són:

Sphaerochara labellata Feist i Ringeade, 1977

Chara aff. *antennata* Grambast, 1958

Chara artesica Sanjuan i Martín-Closas, (en revisió a)

Chara rhenana Schwarz i Griessemer, 1994

Chara microcera Grambast i Paul, 1965

Psilochara aff. *acuta* Grambast i Paul, 1965

Lamprothamnium sp.

Gyrogona caelata (Reid i Groves 1921) Grambast, 1956

Nodosochara jorbae Choi, 1989

Lychnothamnus longus Choi, 1989

Lychnothamnus stockmansii (Grambast 1957) Soulié-Märsche, 1989

Lychnothamnus grambastii (Feist-Castel 1971) Soulié-Märsche, 1989

Lychnothamnus vectensis (Groves 1926) Soulié-Märsche, 1989

Lychnothamnus major (Grambast i Paul 1965) Soulié-Märsche, 1989

Nitellopsis (Tectochara) merianii (Al. Braun ex Unger, 1852) Grambast i Soulié-Märsche, 1972

Harrisichara lineata Grambast, 1957

“*Harrisichara vasiformis-tuberculata* Feist-Castel, 1977a”

Harrisichara tuberculata (Lyell, 1826) Grambast, 1957

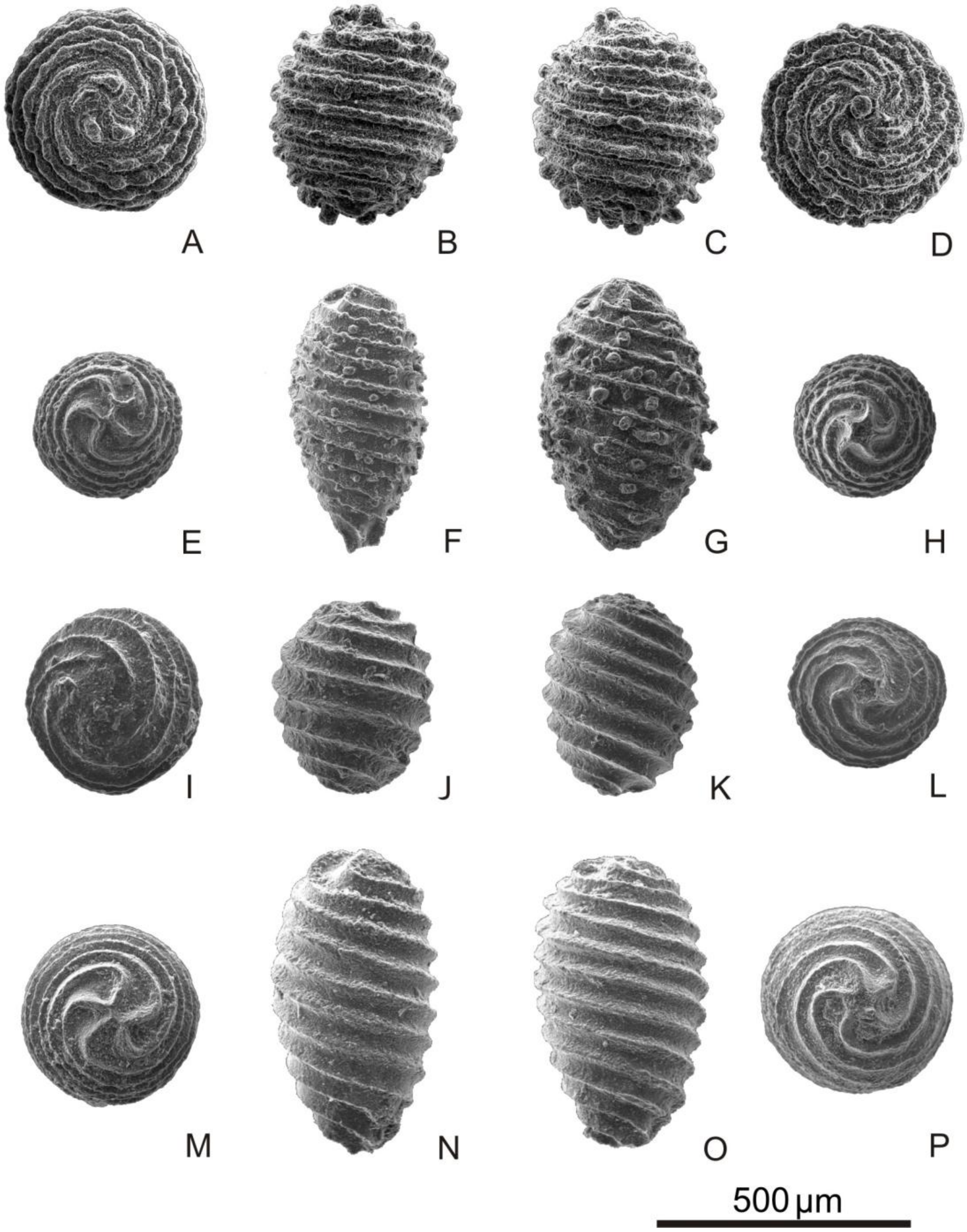


Figura 6. Caròfits de les Fms. Sant Boi i Artés de la Conca de l'Ebre. **A-D**, *Sphaerochara labellata*, sèrie de Torre Casanova (mostra TC-28) ; **A**, àpex; **B i C**, vistes laterals; **D**, base. **E-H**, *Chara* aff. *antennata*, sèrie de La Portelleta (mostra PO-2); **E**, àpex; **F i G**, vistes laterals; **H**, base. **I-L**, *Chara artesica*, sèrie El Perers-Serrat-Rodó, Torre Casanova, Moià, Santpedor, Maians, Rubió (mostra TC-9); **I**, àpex; **J**, vista lateral, holotip nº 79907 MGSCB; **K**, vista lateral; **L**, base. **M-P**, *Chara rhenana*, sèrie El Perers-Serrat Rodó (mostra PE-1); **M**, àpex; **N i O**, vistes laterals; **P**, base.

Figure 6. Charophytes from the Sant Boi and Artés Fm, Ebro Basin. ***A-D***, Sphaerochara labellata, *Torre Casanova section (sample TC-28) ;* ***A***, *apical view;* ***B and C***, *lateral views;* ***D***, *basal view.* ***E-H***, Chara *aff.* antennata, *La Portelleta section (sample PO-2);* ***E***, *apical view;* ***F and G***, *lateral views;* ***H***, *basal view.* ***I-L***, Chara artesica *El Perers-Serrat-Rodó, Torre Casanova, Moià, Santpedor, Maians, Rubió sections (sample TC-9);* ***I***, *apical view;* ***J***, *lateral view, holotype nº 79907 MGSCB;* ***K***, *lateral view;* ***L***, *basal view.* ***M-P***, Chara rhenana, *El Perers-Serrat Rodó section (sample PE-1);* ***M***, *apical view;* ***N and O***, *lateral views;* ***P***, *basal view.*

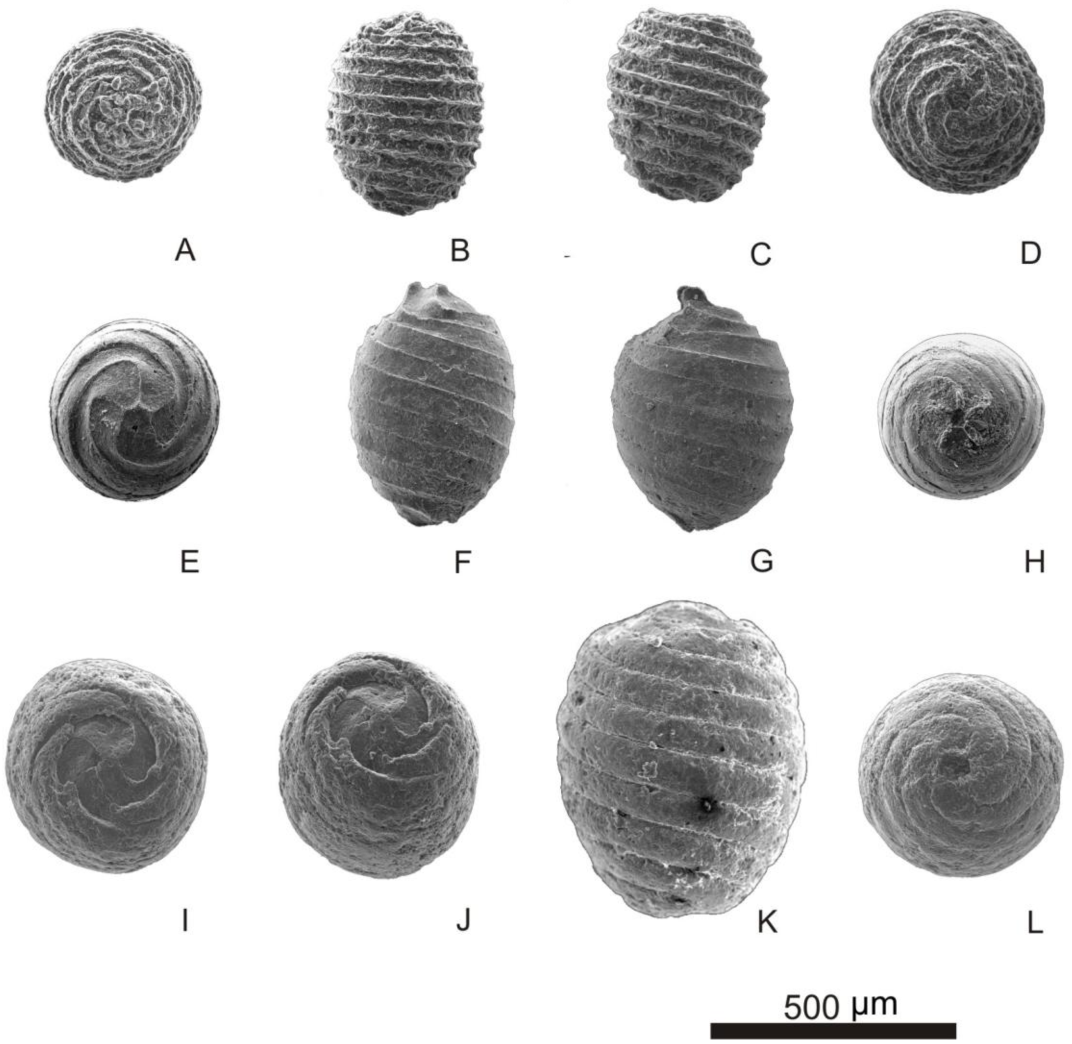


Figura 7. Caròfits de les Fms. Sant Boi, Artés i les Fms. laterals equivalents al sector SE de la Conca de l'Ebre. **A-D**, *Chara microcera*, jaciment d'El Talladell i sèrie de Vinaixa (mostra BO-2); **A**, apex **B i C**, vistes laterals; **D**, base. **E-H**, *Psilochara* aff. *acuta*, sèrie de Sarral (mostra SA-2); **E**, àpex; **F i G**, vistes laterals; **H**, base. **I-L**, *Lamprothamnium* sp. sèrie El Perers-Serrat Rodó (mostra CC-1); **I**, àpex; **J i K**, vistes laterals; **L**, base.

Figure 7. Charophytes from Sant Boi, Artés and laterally equivalent formations in the SE of the Ebro Basin. ***A-D****,* Chara microcera*, El Talladell outcrop and Vinaixa section (sample BO-2);* ***A****, apical view;* ***B and C****, lateral views;* ***D****, basal view.* ***E-H****,* Psilochara *aff.* acuta*, Sarral section (sample SA-2);* ***E****,apical view;* ***F and G****, lateral views;* ***H****, basal view.* ***I-L****,* Lamprothamnium *sp. El Perers-Serrat Rodó section (sample CC-1);* ***I****, apical view;* ***J and K****, lateral views;* ***L****, basal view.*

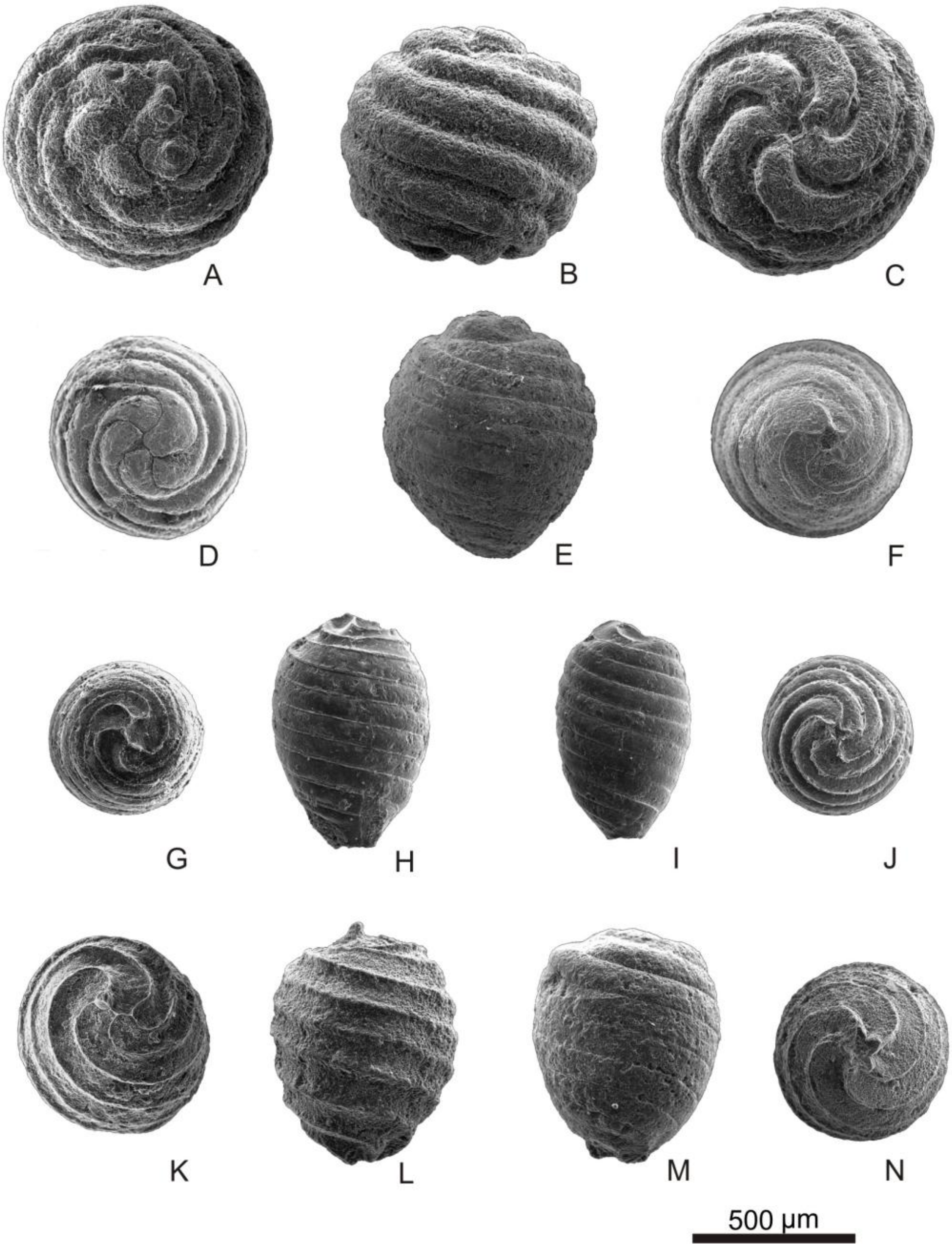


Figura 8. Caròfits de les Fms. Sant Boi, Artés i les formacions lateralment equivalents del sector SE de la Conca de l'Ebre. **A-C**, *Gyrogona caelata*, sèrie Torre Casanova section (mostra TC-25); **A**, àpex; **B**, vista lateral; **C**, base. **D-F**, *Nodosochara jorbae*, sèries El Perers-Serrat Rodó, Santa Maria d'Oló, Oristà i Torre Casanova; **D**, àpex (mostra SBR-2); **E**, vista lateral (mostra O-3); **F**, base (mostra SBR-2). **G-J**, *Lychnothamnus longus*, sèries Oristà, Santa Maria d'Oló, Torre Casanova, Moià, Santpedor i Rubió (mostra RB-24); **G**, àpex; **H i I**, vistes laterals; **J**, base. **K-N**, *Lychnothamnus stockmansii*, sèries Torre Casanova, Moià, Rubió, Rocafort de Queralt i Sarral (mostra TC-31); **K**, àpex; **L i M**, vistes laterals; **N**, base.

Figure 8. Charophytes from Sant Boi and Artés Formations and laterally equivalent formations of the SE Ebro Basin. ***A-C***, Gyrogona caelata, *Torre Casanova section (sample TC-25);* ***A***, *apical view;* ***B***, *lateral view;* ***C***, *basal view.* ***D-F***, Nodosochara jorbae, *El Perers-Serrat Rodó, Santa Maria d'Oló, Oristà and Torre Casanova sections;* ***D***, *apical view (sample SBR-2);* ***E***, *lateral view (sample O-3);* ***F***, *basal view (sample SBR-2).* ***G-J***, Lychnothamnus longus, *Oristà, Santa Maria d'Oló, Torre Casanova, Moià, Santpedor and Rubió sections (sample RB-24);* ***G***, *apical view;* ***H and I***, *lateral views;* ***J***, *basal view.* ***K-N***, Lychnothamnus stockmansii, *Torre Casanova, Moià, Rubió, Rocafort de Queralt and Sarral sections (sample TC-31);* ***K***, *apical view;* ***L and M***, *lateral views;* ***N***, *basal view.*

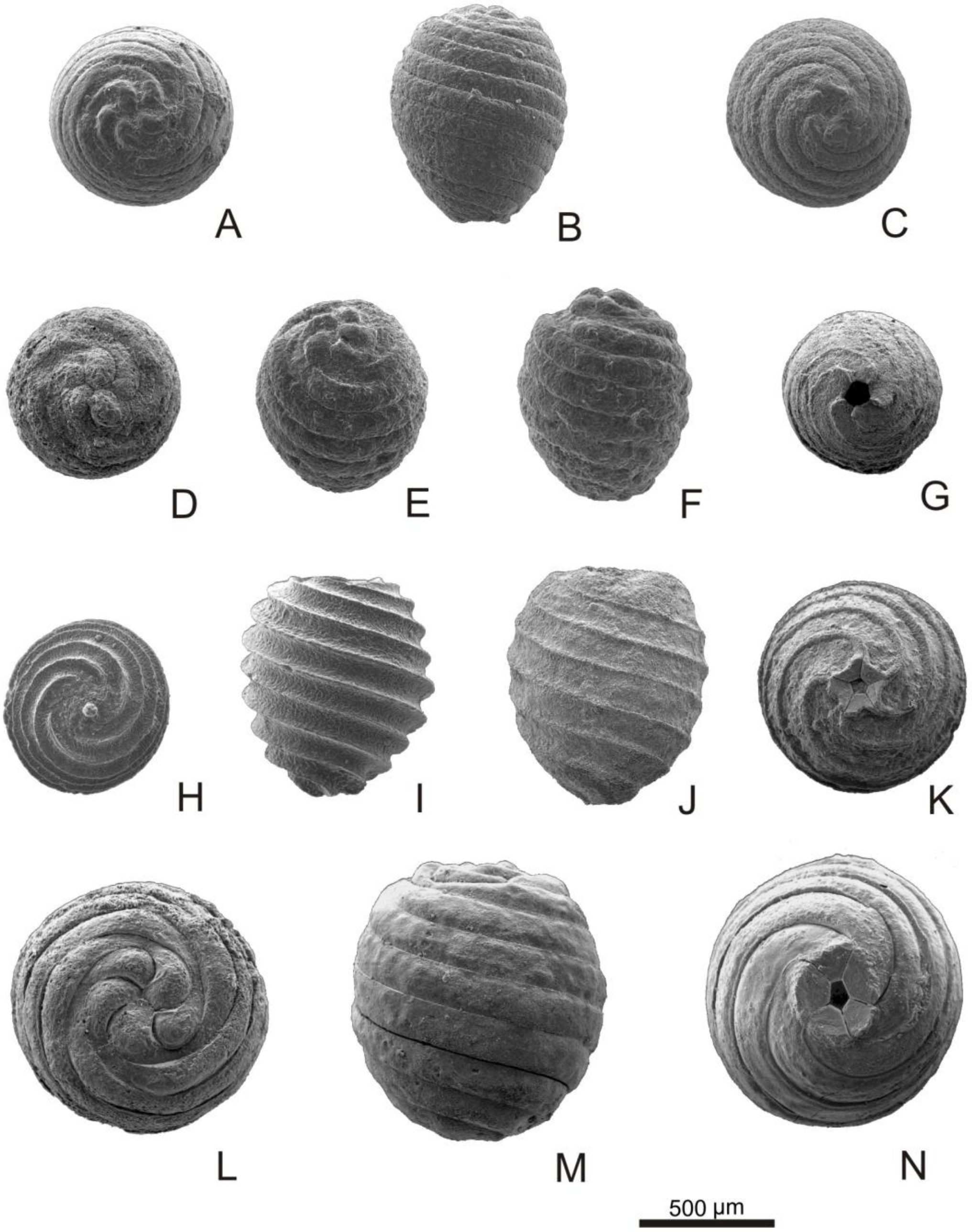


Figura 9. Caròfits de les Fms. Sant Boi, Artés i les formacions lateralment equivalents al sector SE de la Conca de l'Ebre. **A**-**C**, *Lychnothamnus grambastii*, sèrie Torre Casanova (mostra TC-9); **A**, àpex; **B**, vista lateral; **C**, base. **D**-**F**, *Lychnothamnus vectensis*, sèries Santpedor, Rubió i Sarral; **D**, àpex (mostra RB-3); **E**, vista obliqua (mostra SP-18); **F**, vista lateral (mostra SP-18); **G**, base (mostra SP-4). **H**-**K**, *Lychnothamnus major*, sèries Sarral i jaciment de El Talladell; **H**, àpex (mostra BO-1); **I**, vista lateral (mostra BO-1); **J**, vista lateral (mostra SA-19); **K**, base (mostra SA-19). **L**-**N**, *Nitellopsis (Tectochara) merianii*, sèries Torre Casanova i Vinaixa i jaciment de El Talladell (mostra VI-5); **L**, àpex; **M**, vista lateral; **N**, base.

Figure 9. Charophytes from the Artés and laterally equivalent formations in the SE Ebro Basin. ***A**-**C**,* Lychnothamnus grambastii, *Torre Casanova section (sample TC-9);* ***A**, apical view;* ***B**, lateral view;* ***C**, basal view.* ***D**-**F**,* Lychnothamnus vectensis, *Santpedor, Rubió and Sarral sections;* ***D**, apical view (sample RB-3);* ***E**, oblicuous view (sample SP-18);* ***F**, lateral view (sample SP-18);* ***G**, basal view (sample SP-4).* ***H**-**K**,* Lychnothamnus major, *Sarral section and El Talladell outcrop;* ***H**, apex (sample BO-1);* ***I**, lateral view (sample BO-1);* ***J**, lateral view (sample SA-19);* ***K**, basal view (sample SA-19).* ***L**-**N**,* Nitellopsis (Tectochara) merianii, *Torre Casanova and Vinaixa sections and El Talladell outcrop (sample VI-5);* ***L**, apical view;* ***M**, lateral view;* ***N**, basal view.*

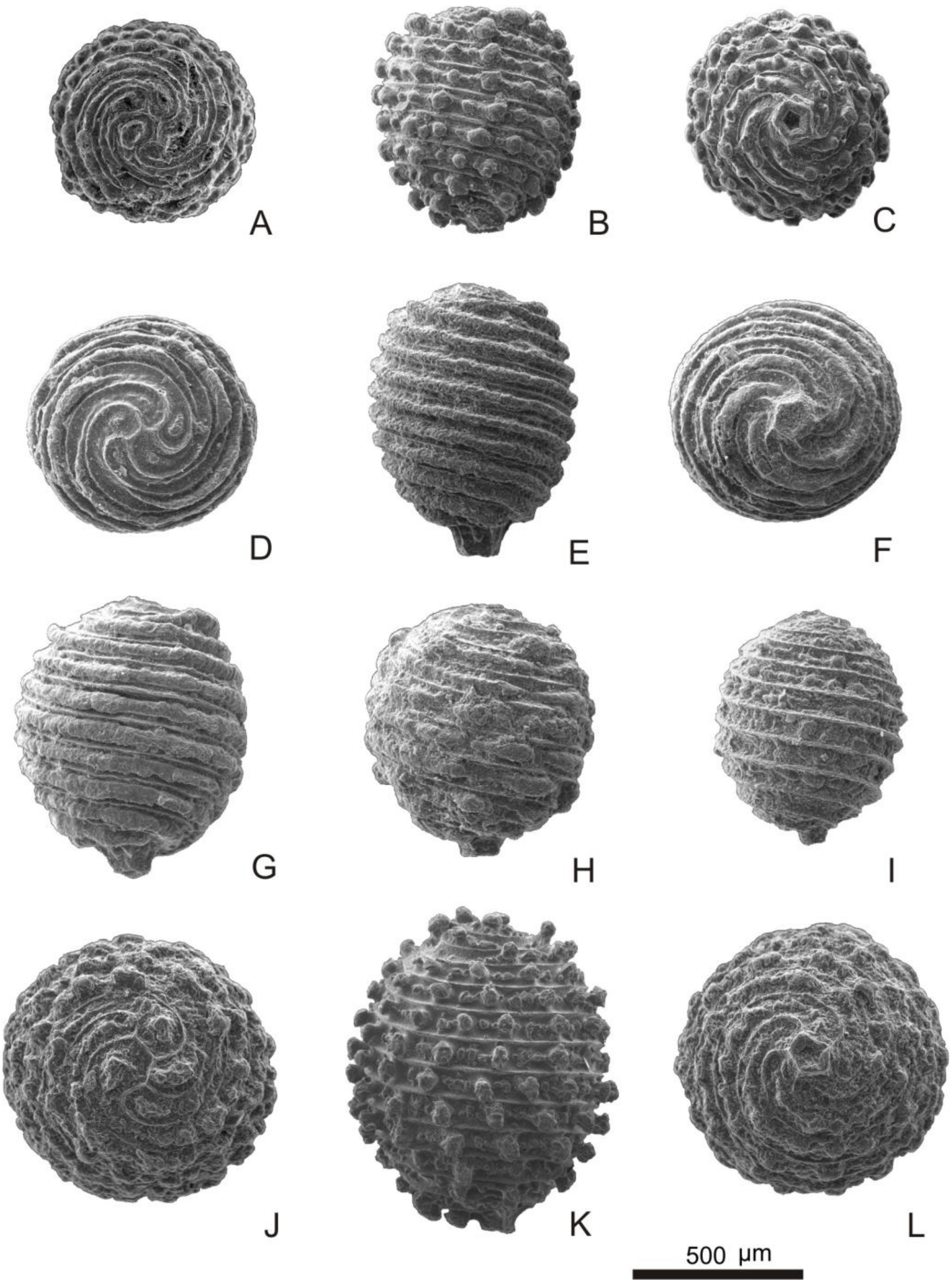


Figura 10. Caròfits de les Fms. Sant Boi, Artés i les formcions lateralment equivalents al sector SE de la Conca de l'Ebre. **A-C**, *Harrisichara vasiformis-tuberculata*, series Serrat Rodó, Carretera de Sobremunt i Cal Carreter (mostra SBR-1); **A**, àpex; **B**, vista lateral; **C**, base. **D-I**, *Harrisichara lineata*, sèrie El Perers (mostra PE-1); **D**, àpex; **E, G, H and I**, vistes laterals; **F**, base. **J-L**, *Harrisichara tuberculata*, sèries Oristà, Santa Maria d'Oló, Torre Casanova, Moià, Santpedor, Rubió i Sarral i jaciment de Solivella; **J**, àpex (mostra MO-1); **K**, vista lateral (mostra SO-2); **L**, base (mostra MO-1).

Figure 10. Charophytes from Sant Boi, Artés and laterally equivalent formations in the SE Ebro Basin. ***A-C***, Harrisichara vasiformis-tuberculata, *Serrat Rodó, Sobremunt road and Cal Carreter sections (sample SBR-1);* ***A***, *apical view;* ***B***, *lateral view;* ***C***, *basal view.* ***D-I***, Harrisichara lineata, *El Perers section (sample PE-1);* ***D***, *apical view;* ***E, G, H and I***, *lateral views;* ***F***, *basal view.* ***J-L***, Harrisichara tuberculata, *Oristà, Santa Maria d'Oló, Torre Casanova, Moià, Santpedor, Rubió and Sarral sections and Solivella outcrop;* ***J***, *apical view (sample MO-1);* ***K***, *lateral view, (sample SO-2);* ***L***, *basal view (sample MO-1).*

A més a més de les espècies descrites en les publicacions adjuntes, en els darrers mesos s'han obtingut resultats sistemàtics importants referents a dues espècies clau en la biostratigrafia del límit Eocè-Oligocè: (a) *Lychnothamnus vectensis* (Groves 1926) nov. comb. Soulié-Märsche 1989 i (b) *Lychnothamnus pinguis* (Grambast 1958) nov. comb. Soulié-Märsche 1989. Es tracta de les espècies índex de les dues biozones de caròfits homònimes del Priabonià superior i el Rupelià inferior (Riveline et al., 1996). L'estudi s'ha dut a terme a partir del material tipus d'aquestes espècies en les col·leccions originals de A'Court Smith del "Natural History Museum" de Londres. Aquests resultats, que encara són inèdits, s'exposen a continuació.

Lychnothamnus vectensis (Groves 1926) nov. comb. Soulié-Märsche, 1989

Antecedents i problemàtica

L'espècie *Chara vectensis* fou descrita per Groves (1926). L'epítet específic deriva del nom en llatí de la localitat tipus, l'Illa de Wight, anomenada "Vectis" pels romans, que significa barrera. Groves (1926) proporcionà la següent descripció per aquesta espècie: "Girogonit de mida extremadament variable, entre 800-1000 µm d'alçada, 500-800 µm d'amplada, de forma el·lipsoïdal amb gran variabilitat de l'alçada i amplada relativa. El porus basal té un diàmetre de ~50 µm. El girogonit presenta 9 o 10 voltes d'espira en vista lateral. Les cèl·lules espirals presenten sovint un aprimament a la zona apical que està normalment proveïda d'una roseta apical prominent."

L'ambigüitat en la descripció d'aquesta espècie fou reconeguda pel mateix autor que assenyalà que l'espècie agrupa un gran nombre de girogonits el·lipsoïdals que no pertanyen a cap altre espècie i que no podia separar satisfactòriament. Aquest autor destacà a més que certs girogonits presenten un inflament molt pronunciat de les cèl·lules espirals a la regió apical i que la majoria dels girogonits presenten les cèl·lules espirals convexes o planes. En conseqüència amb aquests darrers comentaris el tipus figurat per Groves (1926) presenta una forma el·lipsoidal, cèl·lules convexes i roseta apical prominent.

Posteriorment Grambast (1958), en la memòria de la seva tesi doctoral, redefiní l'espècie com a *Stephanochara vectensis* , partint del material conservat al tub V. 18335 estudiat anteriorment per J. Groves. proporcionant una nova descripció. Malgrat que la definició de Grambast (1958) delimitava força mes els caràcters de l'espècie en comparació a la decripció donada per Groves (1926), la manca de figuració de l'holotipus comportà que els únics referents gràfics d'aquesta espècie continuessin essent l'esquema del girogonit tipus i les fotografies de baixa resolució en microscopi òptic proporcionades per Groves (1926). A partir de la tesi de L. Grambast, els autors que han estudiat aquesta espècie han tendit a restringir-ne el concepte a la imatge de la Fig. 19 de Groves (1926) o han anomenat els girogonits com a "sp. aff. *L. vectensis*", o "*L.* cf. *vectensis*".

Atesa la importància d'aquesta espècie per a caracteritzar el límit Eocè-Oligocè a partir dels caròfits i amb l'objectiu d'eliminar l'ambigüitat i la manca de referents figurats s'ha desenvolupat un estudi en detall de la població tipus de l'espècie provinent del material conservat en el tub V. 18335 de la col·lecció A'Court Smith del Natural History Museum procedent de l'Insect Limestone a Gurnard Bay, Illa de Wight, d'acord amb Grambast (1958). A més, dels 100 girogonits mesurats procedents de Hampshire i amb l'objectiu de quantificar les diferències entre poblacions de la mateixa espècie a diferents conques es van mesurar 100 girogonits procedents de 3 poblacions (mostres SP-4, SP-14 i SP-17) de la Formació Artés a Santpedor (conca de l'Ebre) i 48 girogonits (tots els disponibles) procedents de dues poblacions (Loges-814 i Loges-816) provinents de les "Marnes bleues d'Argenteuill" a Montereau (conca de Paris) de la col·lecció creada per J. Riveline.

Descripció de la població tipus

Girogonits de forma el·lipsoidal, àpex arrodonit o prominent i en general base arrodonida. Les dimensions varien de 784-1017 μm d'alçada (mitjana de 880 μm) i 600-813 μm d'amplada (mitjana de 695 μm). La població tipus presenta de 7 a 9 voltes d'espira en vista lateral (el 65% de la població presenta 8 voltes) amb alçades d'entre 94-119 µm, convexes o llises i separades per sutures simples. L'amplada de les cèl·lules a l'àrea periapical no presenta modificació. En canvi, l'engruiximent de les cèl·lules disminueix més o menys fortament en funció del grau de calcificació del girogonit. Les terminacions de les cèl·lules a l'àpex presenten sovint una ornamentació en forma de nòduls aïllats més o menys prominents. Els nòduls apicals presenten una gran variabilitat de mides variant entre 16 a 104 μm d'alçada en vista lateral. No obstant el

~10% de la població no presenta nòduls apicals. En varis espècimens s'observa que els nòduls es formaren a partir de varis punts de nucleació (grànuls que es van unint fins a formar un nòdul). Tal com varen assenyalar Groves (1926) i Grambast (1958) el porus basal consta d'una obertura pentagonal superficial sense embut i de ~70 µm d'amplada (Figs. 11, 12 i 13).

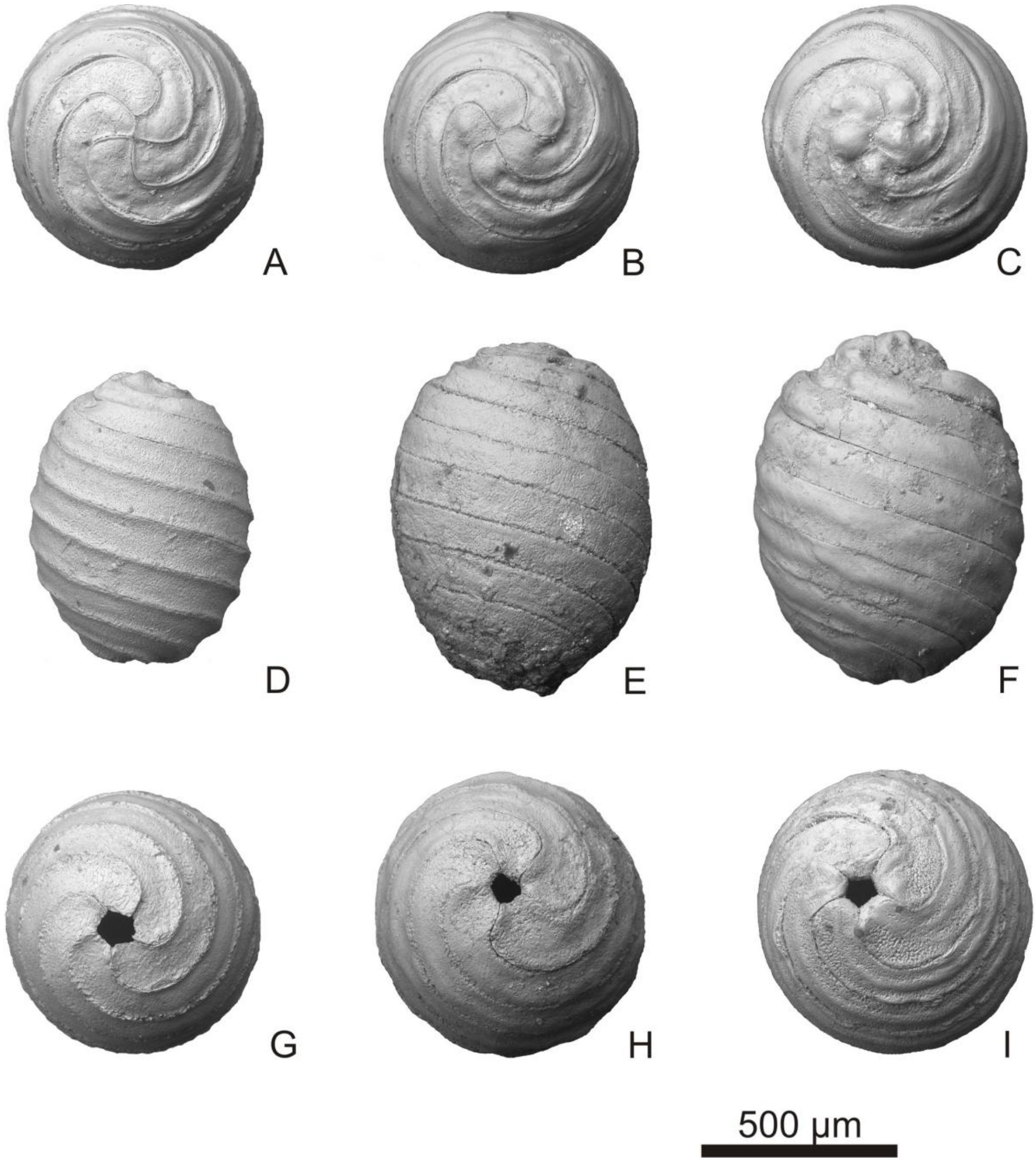


Figura 11. Girogonits de la població tipus (V. 18335) de *Lychnothamnus vectensis* del Priabonià superior a Gurnard Bay (Isle of Wight, Angleterra). **A**-**C**, vistes apicals; **D**-**F**, vistes laterals; **G**-**I**, vistes basals.
Figure 11. Lychnothamnus vectensis *gyrogonites from the type population (V. 18335) Late Priabonian of Gurnard Bay (Isle of Wight, England).* ***A**-**C**, apical views; **D**-**F**, lateral views; **G**-**I**, basal views.*

Comparació de *L. vectensis* de les conques de l'Ebre, Paris i Hampshire.

La comparació de les dades biomètriques de les tres poblacions estudiades, és a dir la conca de l'Ebre, la conca de Paris i la conca de Hampshire, permet observar una tendència general de les poblacions a augmentar de mida dels girogonits del sud al nord. Per contra, la relació alçada/amplada del girogonit (Index d'Isopolaritat) i el nombre de voltes d'espira en vista lateral es manté constant (Figs. 12 i 13).

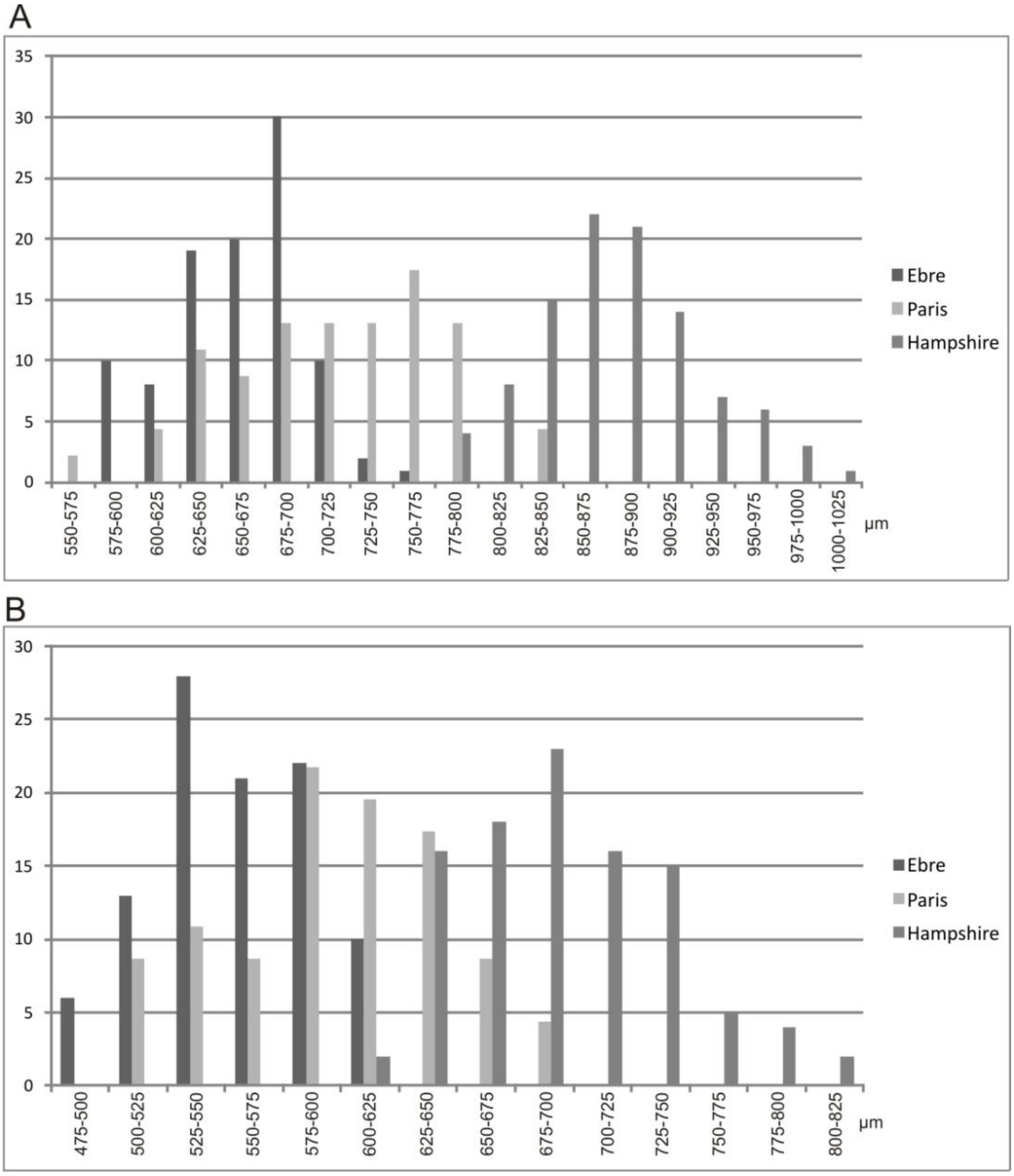


Figura 12. Gràfics de les dades biomètriques per; **A**, alçada i **B**, amplada dels girogonits de *Lychnothamnus vectensis* per a les tres poblacions europees estudiades provinents de les conques de Hampshire, Paris i Ebre.

Figure 12. Biometric graphics of; ***A****, gyrogonite height and* ***B****, gyrogonite width of the studied populations of* Lychnothamnus vectensis *from Hampshire, Paris and Ebro basins.*

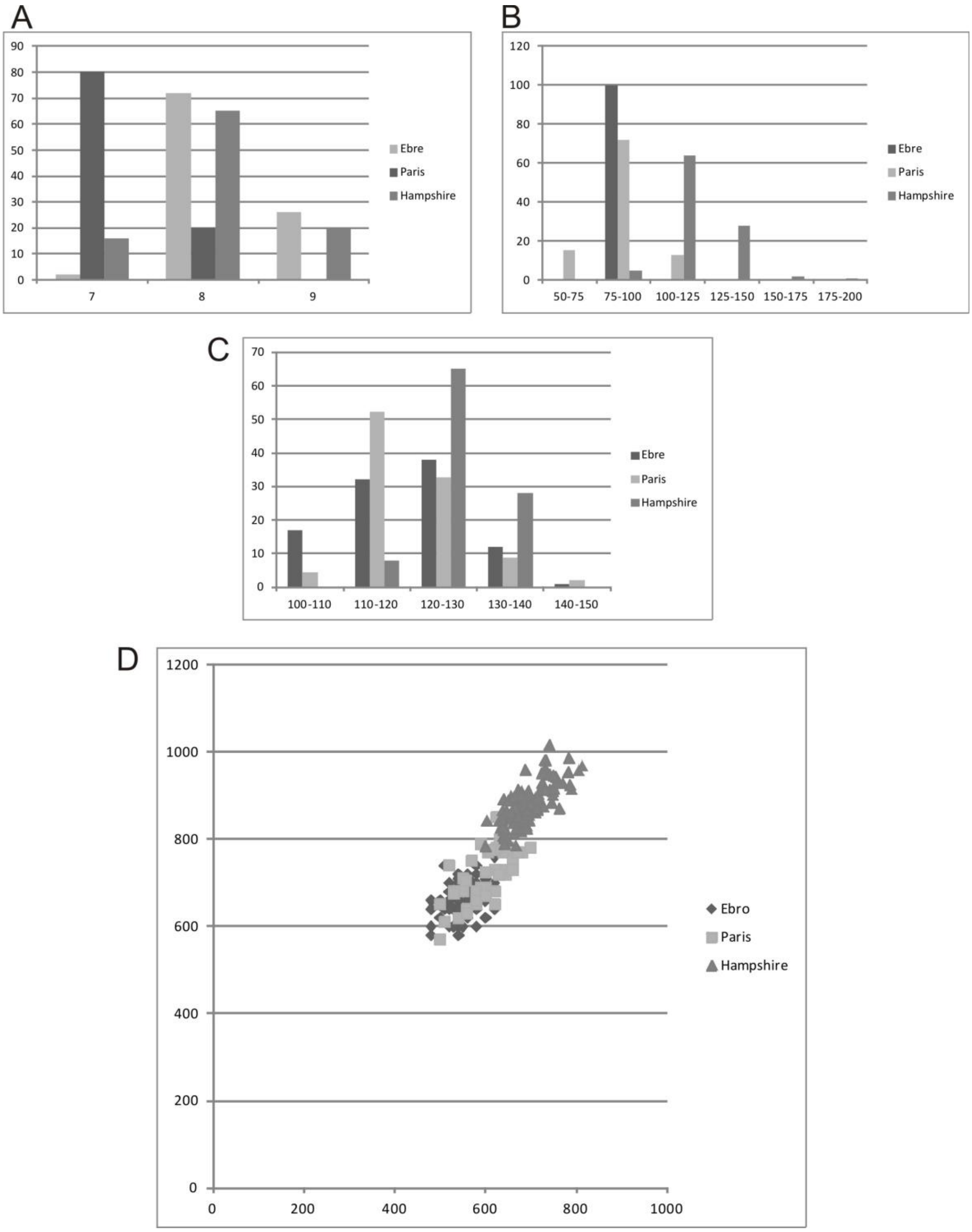


Figura 13. Gràfics de les dades biomètriques dels girogonits de *Lychnothamnus vectensis* per a les tres poblacions europees estudiades provinents de les conques de Hampshire, Paris i Ebre. **A**, nombre de convolucions en vista lateral; **B**, amplada de les voltes d'espira amplada; **C**, Índex d'isopolaritat; **D**, dispersió entre l'alçada i l'amplada.

Figure 13. Biometric graphics of the studied populations of Lychnothamnus vectensis *from Hampshire, Paris and Ebro basins.* ***A****, convolutions number;* ***B****, gyrogonite width;* ***C****, convolution width;* ***D****, Dispersion graphic (height/width).*

Aquest canvi progressiu en la mida del girogonit d'una mateixa espècie no es exclusiu de *Lychnothamnus* ja que altres gèneres fòssils com *Harrisichara* també presenten aquest patró (mides més petites a les conques del sud i mides més grans a les conques nòrdiques).

La morfologia de les parts vegetatives i dels girogonits de certes especies de caròfits actuals poden presentar una gran variabilitat en funció dels factors ecològics (Soulié Märsche, 1989). Algunes espècies com *Nitellopsis obtusa* no presenten cap modificació de la forma ni de la mida del girogonit. En canvi, altres espècies com *Chara globularis* produeixen girogonits de formes i mides molt diferents en funció dels factors ambientals. Finalment, algunes espècies com *Lychnothamnus barbatus* mostren girogonits amb una gran variabilitat en la mida però no en la forma, que es manté més o menys constant.

Com a conclusió es justifica que l'espècie índex de biozona *L.vectensis* presenta un alt grau de polimorfisme intrespecific tant en la població tipus com en poblacions d'altres conques europees, variant desde morfotipus amb un baix grau de calcificació (de dimensions reduides, cèl·lules espirals lleument còncaves o planes i sense noduls apicals) a morfotipus calcificats (de mides més gran, cèl·lules espirals convexes i amb nòduls apicals desenvolupats). L'anàlisi sistemàtica de la població tipus de *L. vectensis*, ha permès redefinir-la com una espècie polimòrfica que, amb la nova definició es confirma que estaria present a moltes conques europees on fins ara s'havia registrat de manera dubtosa (sp aff. *L.vectensis* o *L.* cf *vectensis*). Aquestes precisions taxonòmiques i la seva amplia distribució a Europa permet garantir el seu ús en biostratigrafia del Priabonià superior.

Lychnothamnus pinguis (Grambast 1958) nov. comb. Soulié-Märsche, 1989

Antecedents i problemàtica

L'espècie fou inicialment descrita per Grambast (1958) com a *Stephanochara pinguis*. L'epítet específic deriva del llatí "ample" fent referència al fet que el girogonit és esferoidal, és a dir amb un índex d'isopolaritat relativament baix. A part del seu interès biostratigràfic l'estudi de la població tipus d'aquesta espècie es rellevant ja que

Lychnotamnus (=*Stephanochara*) *pinguis* representa l'espècie tipus del gènere fòssil *Stephanochara* Grambast 1958.

Grambast (1958) va descriure aquesta espècie com a "Girogonit gran de forma el·lipsoidal, a vegades ovoide, àpex obtús i sovint prominent, la base es arrodonida més o menys apuntada. Les dimensions varien entre 800-1150 µm d'alçada, 750-950 µm d'amplada. Les cèl·lules espirals mostren de 8 a 10 voltes en vista lateral amb una alçada aproximada de 190 µm. Les cèl·lules espirals son sovint convexes, a vegades lleument còncaves o llises i separades per sutures simples. A l'àrea periapical les cèl·lules no presenten modificació; les cèl·lules presenten un aprimament marcat a la zona periapical just abans de reinflar-se formant un casquet lleument o fortament prominent; rarament presenten nòduls apicals individualitzats. Les cèl·lules espirals a la base son sovint còncaves formant ocasionalment una base lleugerament en relleu. Presenta un porus basal superficial amb mides d'entre 50 i 75 µm."

Amb l'objectiu de mostrar la variabilitat interespecífica d'aquesta espècie de gran interès biostratigràfic a escala europea s'ha procedit a remesurar i fotografiar dues poblacions de l'espècie procedents de la conca de Hampshire seleccionades pel mateix L. Grambast. Les mostres estudiades provenen de dos tubs diferents; el V. 26299 (població tipus) i el tub V. 26292. Aquesta darrera població fou separada en dues cel·les, probablement per M. Feist durant la seva estada a Londres en la dècada de 1970 i anotats amb la incripció"*St. pinguis*" i "*St. pinguis* concave" respectivament. D'acord amb Grambast (1958) la població tipus prové de la "White band" del Hamstead member (Hamstead, Isle of Wight). S'han mesurat 100 girogonits de cada tub tenint en compte l'alçada i l'amplada del girogonit, el nombre de voltes que s'observen en vista lateral, l'amplada de la volta de l'espira a l'equador del girogonit i l'alçada dels nòduls apicals de cada girogonit.

Descripció de la població tipus (tub V. 26299)

Girogonits de forma el·lipsoidal o ovoide, àpex pla o prominent i de base lleument apuntada. Les dimensions varien de 830-1108 µm d'alçada (mitjana 1003 µm) per 663-966 µm d'amplada (mitjana 851 µm). La població tipus presenta 7-9 voltes d'espira en vista lateral (el ~75% de la població presenta 8 voltes d'espira en vista lateral) amb alçades variables de 121-183 µm (mitjana 144). Les cèl·lules espirals son en general convexes o llises amb sutures simples. Alguns espècimens poc calcificats presenten cèl·lules espirals còncaves i separades per sutures dobles (Fig. 14D).

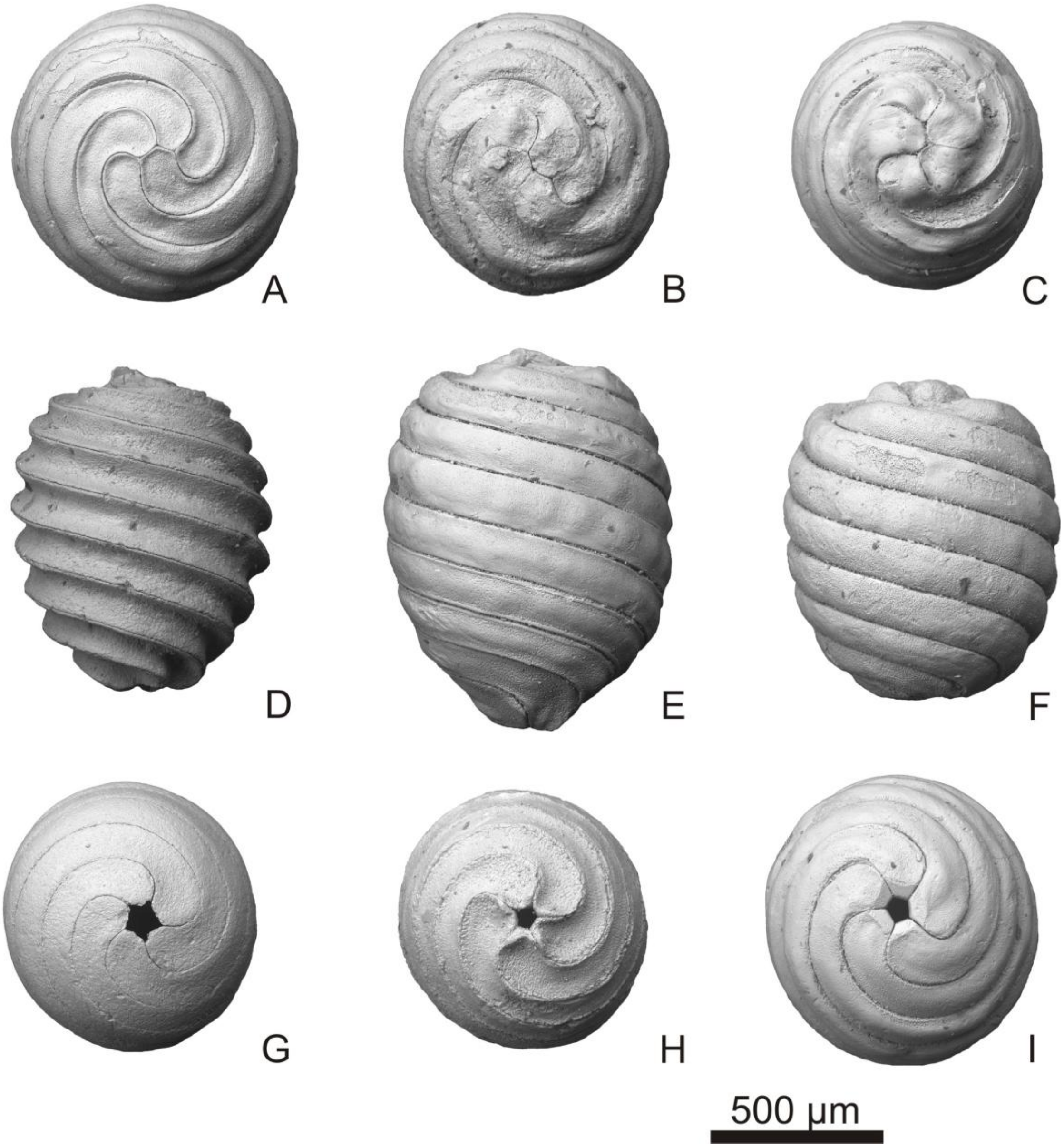


Figura 14. Girogonits de la població tipus (V. 26299) de *Lychnothamnus pinguis* del Rupelià inferior de la “White band” del Hamstead member (Hamstead, Isle of Wight, Angleterra). **A-C**, vistes apicals; **D-F**, vistes laterals; **G-I**, vistes basals.

Figure 14. Lychnothamnus pinguis *gyrogonites from the type population (V. 26299) from the early Rupelian White band of the Hamstead Member (Hamstead, Isle of Wight, England).* ***A-C****, apical views;* ***D-F****, lateral views;* ***G-I****, basal views.*

Les cèl·lules espirals mantenen una amplada constant a l’àrea periapical però s’aprimen més o menys fortament en funció del grau de calcificació del girogonit. Els girogonits ben calcificats (la majoria) presenten un engruiximent (inflament) a les terminacions de les cèl·lules espirals. Sobreposat a aquest engruiximent el 55% de la població presenta nòduls apicals que es poden trobar units formant una casqueta o be aïllats. No obstant, un baix percentatge de la població (~10%) està constituïda per girogonits poc calcificats i de cèl·lules espirals còncaves sense inflament apical ni nòduls apicals (Figs. 14A, D i G). La morfologia del porus basal és molt variable en funció del grau de calcificació del girogonit. Així la base pot presentar una morfologia d'embut pentagonal (girogonit ben calcificats), embut estrellat (girogonits poc calcificats) o pentagonal superficial (girogonits molt poc calcificats). El diàmetre del porus basal varia d'entre 40-80 µm (Figs. 14 i 15).

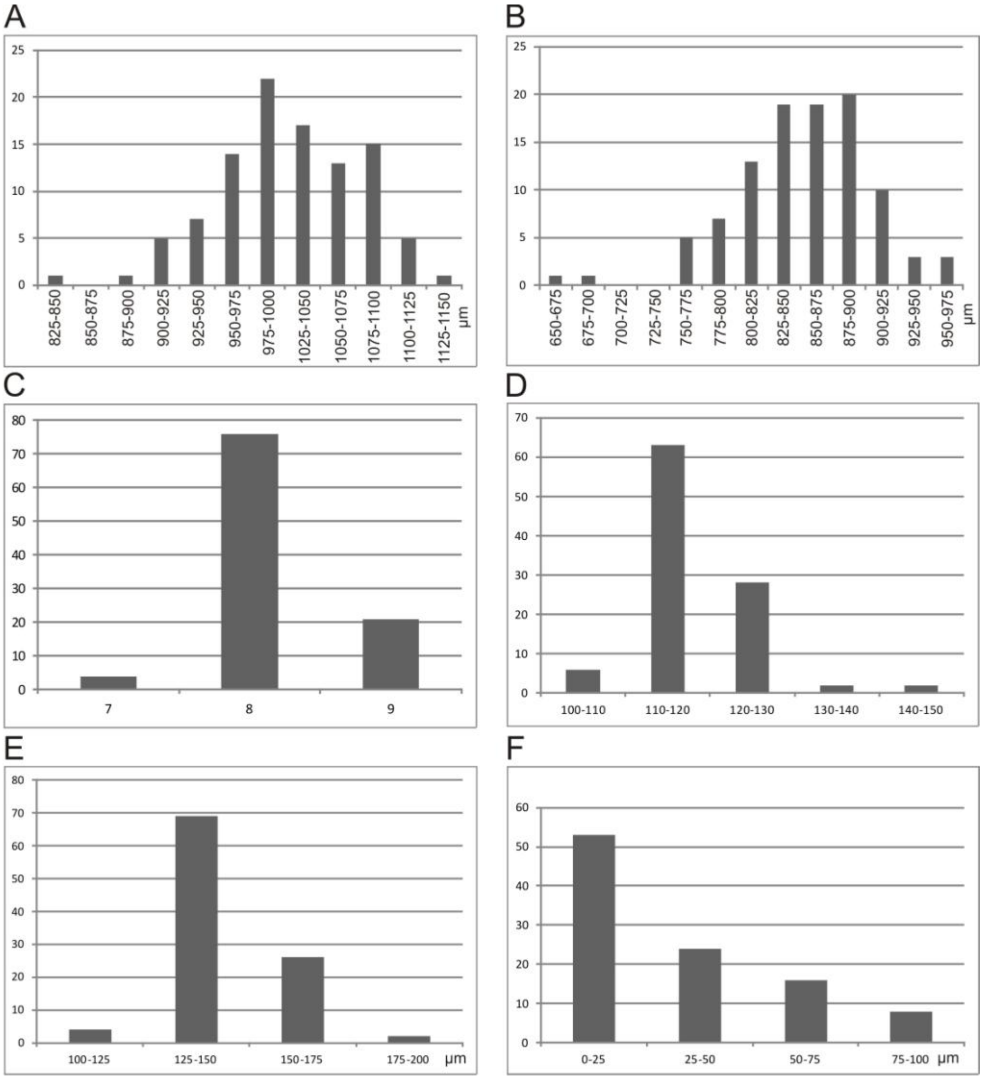


Figura 15. Gràfics de les dades biomètriques dels girogonits de *Lychnothamnus pinguis* de la població tipus (mostra V. 26299) del Rupelià inferior de la "White band" del Hamstead member (Hamstead, Isle of Wight, Anglaterra). **A**. gràfic per a l'alçada; **B**. amplada; **C**. nombre de convolucions en vista lateral; **D**. Índex d'isopolaritat; **E**. amplada de les voltes d'espira; **F**. alçada dels nòduls apicals.

Figure 15. Biometric graphics of the studied populations of Lychnothamnus pinguis *gyrogonites from the type population (V. 26299) from the Early Rupelian White band of the Hamstead Member (Hamstead, Isle of Wight, England).* ***A****. gyrogonite height;* ***B****. gyrogonite width;* ***C****. convolutions number;* ***D****. Isopolarity Index;* ***E****. convolution width;* ***F****. apical nodules height.*

Descripció de la mostra V. 26292

Girogonits de forma el·lipsoidal, àpex pla o prominent, base lleument apuntada. Els girogonits varien de 839-1109 µm d'alçada (mitjana 984 µm) per 713-945 µm d'amplada (mitjana 848 µm). El nombre de voltes d'espira en vista lateral varia entre 7-10 (60% de la població presenta 8 voltes d'espira) amb alçades que varien de105-182 µm (mitjana 142 µm). A diferència de la població tipus, gran part de la població (~63%) presenta cèl·lules espirals còncaves amb sutures sovint bicarenades i desproveïdes de nòduls apicals (àpex pla). La resta de la població presenta les cèl·lules espirals convexes o llises amb sutures simples. Els girogonits ben calcificats presenten un marcat aprimament de les cèl·lules espirals a l'àrea periapical i un reinflament formant un casquet apical sovint proveït de nòduls més o menys prominents, que varien entre 11-97 µm d'alçada en vista lateral. El porus basal és molt variable. Pot presentar tres morfotipus, que són (1) un embut pentagonal en el cas dels girogonits fortament calcificats i amb cèl·lules espirals convexes, (2) un embut estrellat en el cas dels girogonits poc calcificats i amb cèl·lules espirals còncaves o (3) un porus superficial pentagonal en el cas dels girogonits amb cèl·lules espirals planes. L'amplada del porus basal és de ~60 µm d'amplada (Fig. 16).

Sinonímia entre *Lychnothamnus pinguis* i *L. major*

A partir de l'estudi de les poblacions tipus i paratipus de l'espècie *L. pinguis* es mostra que aquesta espècie presenta un elevat polimorfisme intraespecífic. Aquesta variabilitat intrapoblacional ha permès establir comparances amb altres espècies de *Lychnothamnus* amb rangs biostratigràfics similars. Més concretament, s'ha realitzat un estudi comparatiu entre els girogonits de la població procedent del tub V. 26292 amb els girogonits de l'espècie *Lychnothamnus major*. Concretament s'han comparat les dades biomètriques procedents de 50 girogonits de *L. pinguis* (fracció còncava) del tub V. 26292 amb 50 girogonits de *L. major* procedents de la mostra SA-19 de la conca de l'Ebre (Fig 16).

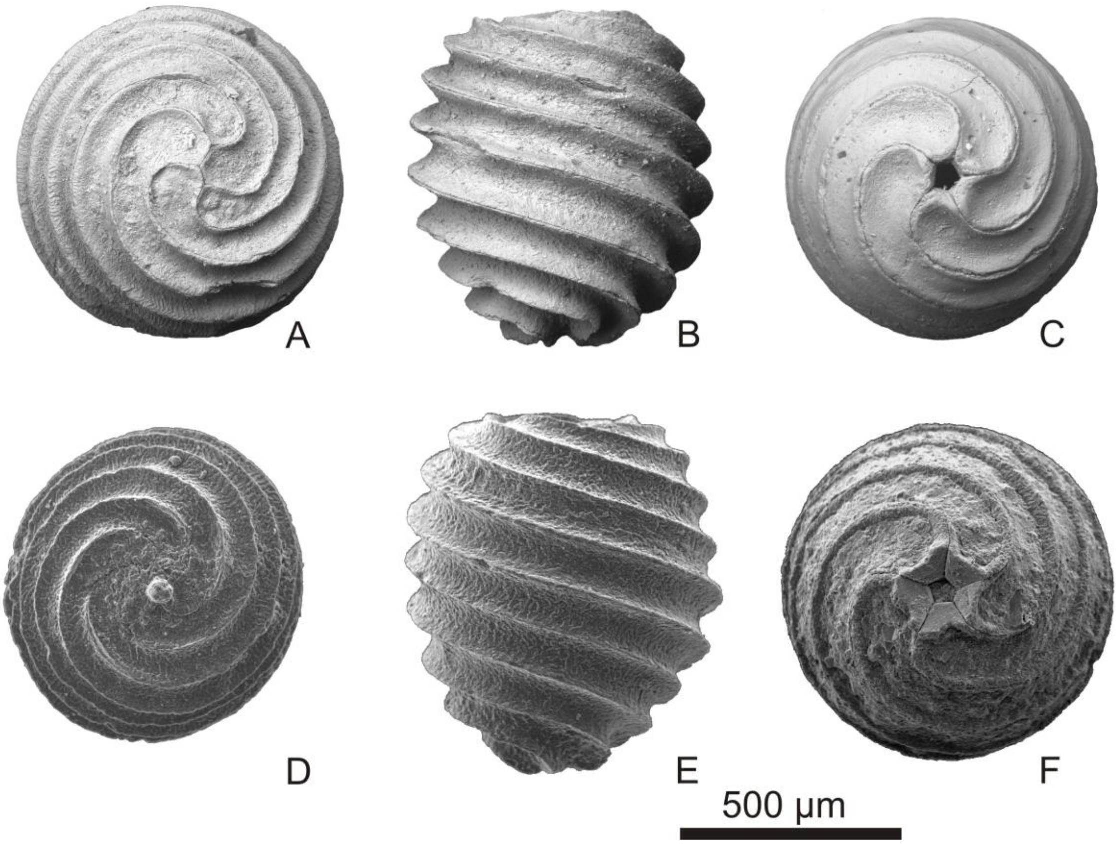


Figura 16. Girogonits de *Lychnothamnus* del Rupelià inferior. **A-C**, *Lychnothamnus pinguis* procedent del tub (V. 26292) de la "White band" del Hamstead member (Hamstead, Isle of Wight, Angleterra); **A**. vista apical, **B**. vista lateral, **C**. vista basal. **D-F**, *Lychnothamnus major* procedent de la mostra SA-19 de la Formació Albi (Conca de Barberà, Catalunya, NE d'Espanya); **D**, vistes apical; **E**, vista lateral; **F**, vista basal.

Figure 16. Lychnothamnus *gyrogonites from the early Rupelian.* ***A-C***, Lychnothamnus pinguis *from the tube (V. 26292) of the White band of the Hamstead member (Hamstead, Isle of Wight, England);* ***A****, apical view;* ***B****, lateral view;* ***C****, basal view.* ***D-F***, Lychnothamnus major *from sample SA-19 from the Albi Formation (Conca de Barberà, Catalonia, NE Spain);* ***D****, apical view;* ***E****, lateral view;* ***F****, basal view.*

Com a resultat s'observa que tots els paràmetres biomètrics, alçada i amplada del girogonit, índex d'isopolaritat (ISI), nombre de voltes d'espira en vista lateral són molt similars. A més, la gràfica de dispersió d'ambdues espècies mostra núvols de punts sobreposats i rectes de regressió amb pendents similars (Fig. 17).

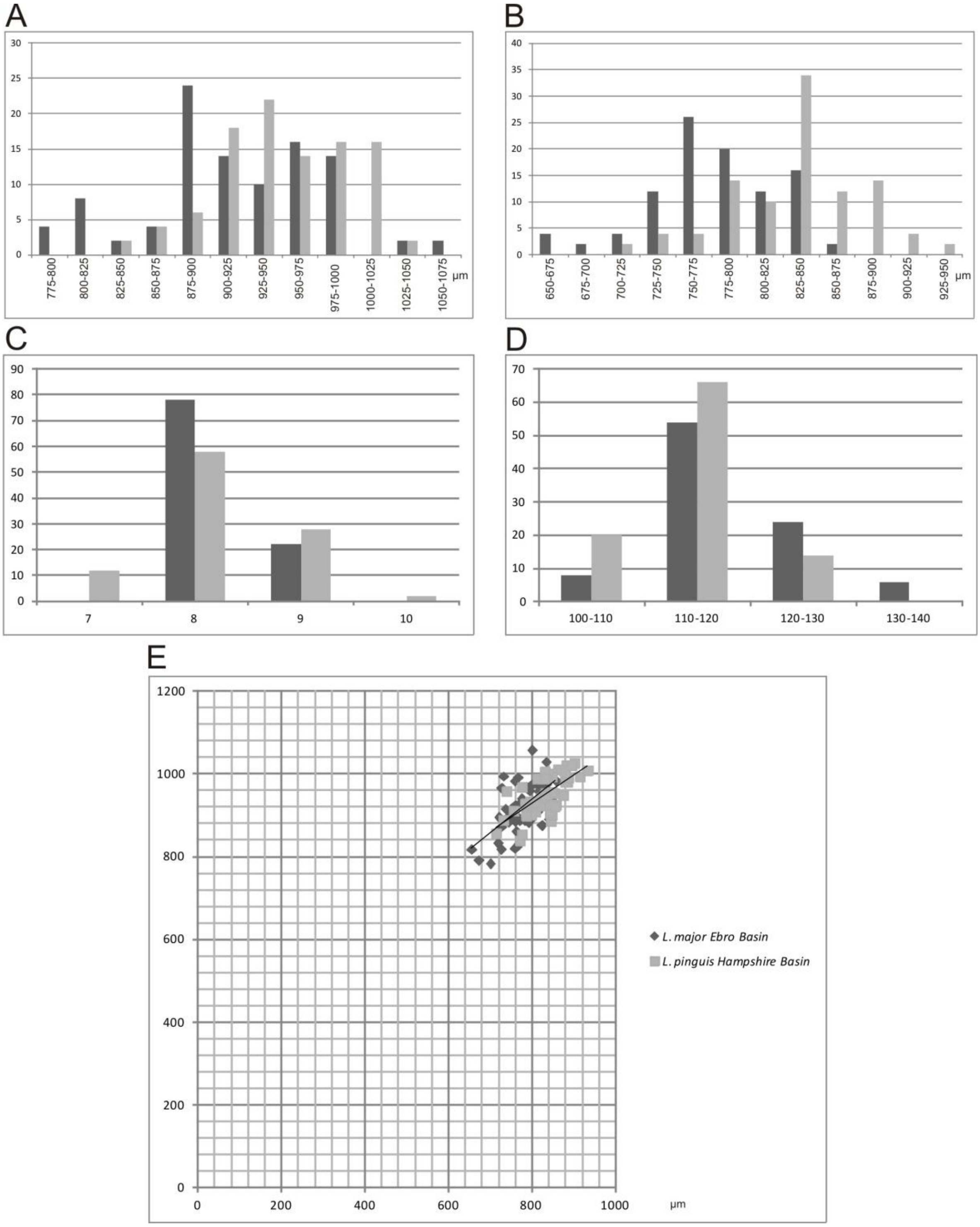


Figura 17. Gràfics de les dades biomètriques dels girogonits de *Lychnothamnus pinguis* procedent de la conca de Hampshire (tub V. 26292) i *Lychnothamnus major* procedent de la conca de l'Ebre (mostra Sa-19). **A**, alçada; **B**, amplada; **C**, nombre de convolucions en vista lateral; **D**, Índex d'isopolaritat; **E**, gràfic de dispersió entre l'alçada i l'amplada.

Figure 17. Biometric graphics of Lychnothamnus pinguis *gyrogonites from Hampshire basin (tube, V. 26292) and* Lychnothamnus major *from Ebro basin (sample SA-19).* ***A****, gyrogonite height;* ***B****, gyrogonite width;* ***C****, convolution number;* ***D****, Isopolarity Index;* ***E****, dispersion graphic (height/width).*

Com a conclusió, tenint en compte que ambdues espècies de *Lychnothamnus* comparteixen paràmetres biomètrics, rangs temporals i paleobiogeogràfics, es pot concloure que l'espècie *Lychnotamnus major* correspon a poblacions poc calcificades de l'espècie *Lychnothamnus pinguis*. D'acord amb el Codi Internacional de Nomenclatura Botànica, aquest darrer taxon té prioritat i és el nom que es conserva. Aquesta sinonimització comporta canvis en el rang de distribució de l'espècie *L. pinguis* i de la biozona que du el seu nom. Així la biozona de L. pinguis s'hauria d'ampliar cap al sostre englobant l'antiga biozona europea de L. major ja molt reduïda en els últims estudis (Sanjuan et al., accteptat). Des d'un punt de vista paleobiogeogràfic, la sinonímia d'aquestes dues espècies de *Lychnothamnus* ha permès atribuir a l'espècie *L. pinguis* una distribució paleogeogràfica més amplia (a totes les conques europees) dins els dipòsits no-marins de l'Oligocè inferior. A més, s'observa una polaritat en els morfotipus de l'espècie. Els morfotipus ben calcificats (amb cèl·lules espirals convexes), corresponents al morfotipus '*pinguis'* són dominants a les conques nòrdiques com Hampshire (Illa de Wight, Anglaterra) i Paris, en canvi, els morfotipus poc calcificats (amb cèl·lules espirals còncaves), corresponents als morfotipus *major* són dominants a les conques del sud d'Europa com Aquitània i Provènça (sud de França) i conca de l'Ebre.

7.1.2. Tal·lus

La tria del material estudiat, permeté identificar 2 tipus de tal·lus de caròfits diferents: (1) Tal·lus acorticats, presents a les mostres a les seccions de El Perers, Torre Casanova, Santpedor. Aquest tipus sempre s'ha trobat associat a girogonits del gènere *Harrisichara*, encra que per ara no s'han trobat en connexió anatòmica.

(2) Tal·lus del morfogènere *Charaxis* Harris 1939 amb varis tipus de corticació. D'un costat s'ha identificat un tal·lus isòstic, amb corticació no contigua, present en algunes mostres de les seccions de Torre Casanova i Moià dins les calcàries del Membre Moià (Fig. 23). Aquests tal·lus es troben associats però sense connexió anatòmica amb girogonits del gènere *Gyrogona*. D'altra banda s'han identificat *Charaxis* diplòstics i d'altres triplòstics, alguns amb acícules, a les seccions de Sarral i El Talladell. Aquests tal·lus es troben associats a girogonits del gènere gènere *Chara*. Malhauradament el grau d'articulació de les restes és molt baix, i s'han trobat molt pocs especímens amb

nusos i verticils conservats, per la qual cosa és difícil d'extreure'n conclusions taxonòmiques més detallades.

7.2. PALEOECOLOGIA

L'anàlisi sedimentològica de les fàcies i microfàcies així com l'estudi tafonòmic de les restes fòssils són una eina clau per entendre els paleoambients del passat on es desenvolpuaren els caròfits de la conca de l'Ebre (Sanjuan et al., 2012; Sanjuan i Martín-Closas, 2012). Aquest estudi s'ha dut a terme en els dipòsits de dues formacions no-marines de l'Eocè superior al sector nord-est de la conca de l'Ebre; la Formació Sant Boi i la Formació Artés.

7.2.1. Formació Sant Boi

La Formació Sant Boi (Sanjuan et al., 2012) esta composta per dos trams diferenciats a nivell sedimentològic que corresponen dos ambients deposicionals diferents. (1) El primer tram comprèn la base de la unitat litostratigràfica i s'ha caracteritzat a les seccions de La Portelleta, El Perers, Serrat Rodó, carretera de Sobremunt, prop de St. Boi de Lluçanès i Cal Carreter prop de Sant Bartomeu del Grau (Fig. 18), (2) el segon tram correspon a la part superior de la formació i aflora a les seccions de La Portelleta i El Perers de St. Boi de Lluçanès (Fig. 18).

(1) El primer tram, de 5-10 m de potència es composa de capes lenticulars de gres, fortament bioturbades o puntualment amb estructures de corrent (ripples), alternant amb llims laminats. Verticalment aquesta alternança passa a un interval d'uns 5 m de margues versicolors, sovint ocres o grises que inclouen horitzons de lignits amb fauna i flora salabroses. Les capes de gres s'atribuïren a canals fluvials de baixa energia en un context d'esplanada deltaica inferior. Els llims laminats s'atribuïren a dipòsits de sobreeximent dels canals. Les margues amb lignits de sostre s'atribuïren a ambients permanentment inundats de tipus paràlic.

(2) El segon tram consta d'una successió de 5 metres de cossos lenticulars de gresos marrons amb estratificació encreuada i llims que passen verticalment a un interval

característic de margues blanques laminades riques en caròfits. Aquesta successió s'atribuí a un ambient fluvio-lacustre en un context d'esplanada deltaica superior.

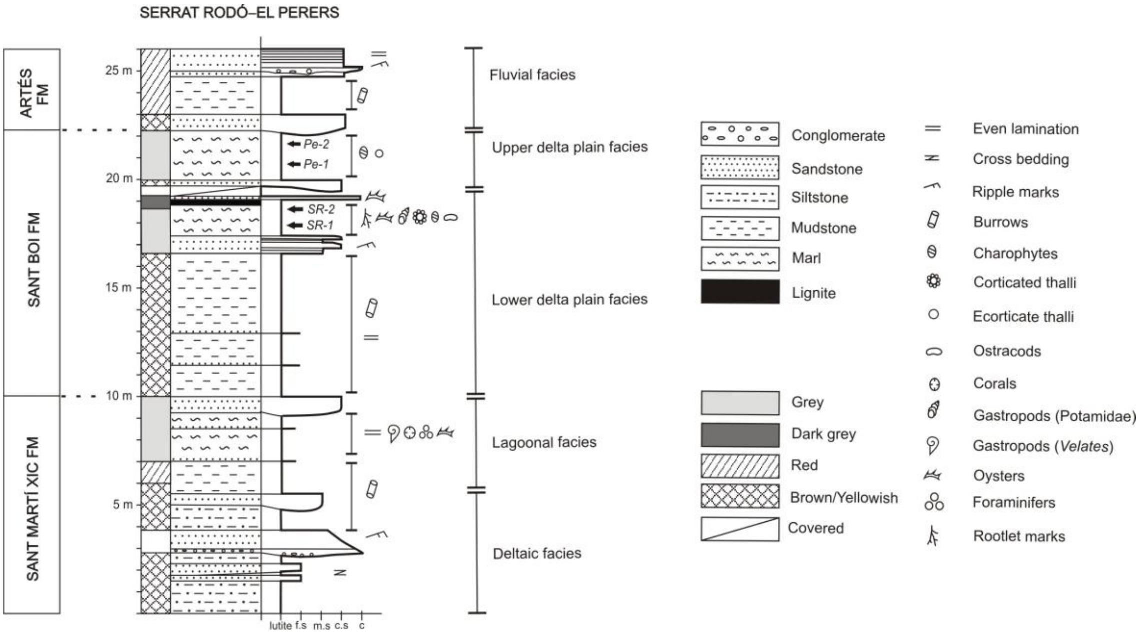


Figura 18. Columnes estratigràfiques del Serrat Rodó-El Perers a l'àrea del Lluçanès on es mostren les diferents associacions de fàcies de la Formació Sant Boi.
Figure 18. Stratigraphic logs for the Serrat Rodó-El Perers section, showing the facies associations of the Sant Boi Formation in the Lluçanès area.

- Tafonomia i paleoecologia de la flora de la Formació Sant Boi

La caroflora de la Formació Sant Boi fou dividida en dues associacions paleoecològicament diferenciades: (1) Associació dominada per *Harrisichara vasiformis-tuberculata* i altres espècies acompanyants com *Nodosochara jorbae*, *Chara artesica* nov. sp., *Lamprothamnium* sp. i *Gyrogona* sp., relacionada amb els ambients deposicionals d'aiguamolls salabrosos d'esplanada deltaica inferior (Fig. 19) i (2) una associació dominada per *Harrisichara lineata* acompanyada de *Chara rhenana*, que es relacionà a ambients lacustres poc profunds situats a l'esplanada deltaica superior (Fig. 19). Aquesta atribució paleoecològica permeté establir que les espècies *Harrisichara vasiformis-tuberculata* i *H. lineata* són espècies subjectes a un important control paleoecològic i facial, concretament, l'us de la primera sembla estar limitada a fàcies salabroses.

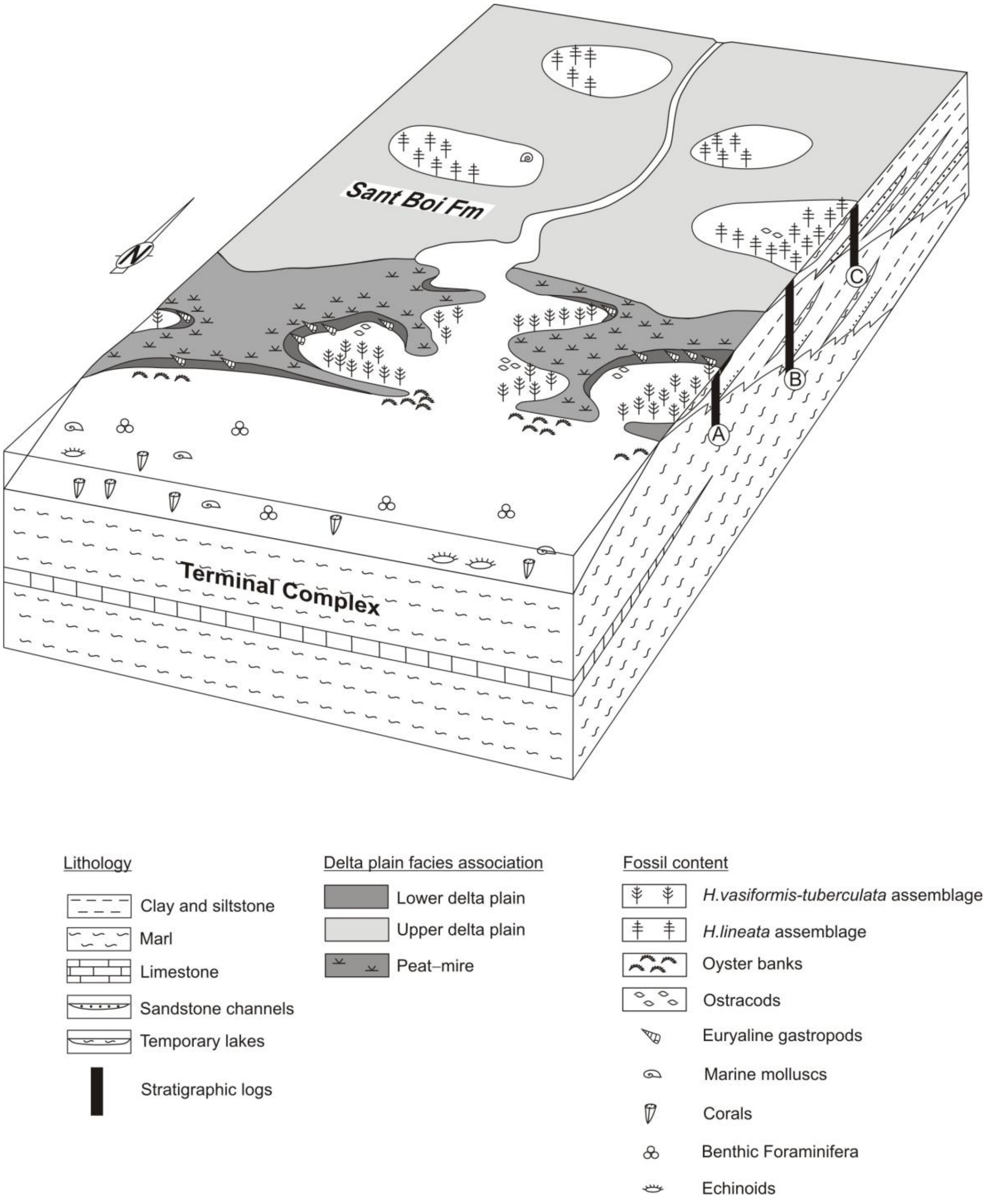


Figura 19. Model paleoambiental resumint la distribució de les associacions dominades per *Harrisichara vasiformis-tuberculata* i *Harrisichara lineata* localitzades a la Formació Sant Boi. Es representen les principals seccions estratigràfiques: **A**, Carretera de Sobremunt; **B**, Serrat Rodó; **C**, El Perers. Sense escala.

Figure 19. *Palaeoenvironmental model summarising the distribution of the assemblages dominated espectively by* Harrisichara vasiformis-tuberculata *and* Harrisichara lineata *in the transitional Sant Boi Formation. The main stratigraphic logs represented are:* ***A****, Sobremunt Road;* ***B****, Serrat Rodó;* ***C****, El Perers. Not to scale.*

7.2.2. Formació Artés

Dins la Formació Artés es caracteritzaren dos grups de fàcies amb caròfits; (a) fàcies de ventall al·luvial i (b) fàcies lacustres (Sáez et al., 2007; Sanjuan i Martín-Closas, 2012).

- Fàcies de ventall al·luvial

Dins les fàcies de ventalls fluvials es diferenciaren tres tipus d'associacions de fàcies i) fàcies de ventall fluvial mitjà (medial fluvial fan), ii) fàcies de lòbul terminal (terminal lobe) i iii) fàcies de planes d'inundació (flood plain). Només les dues darreres contenen restes de caròfits i seran explicades aquí.

(i) *Fàcies de lòbul terminal (terminal lobe facies)*

Les fàcies de lòbul terminal estan principalment constituïdes per nivells de gresos amalgamats tabulars de coloracions grises o marrons, de potència decimètrica i amb una extensió lateral d'entre 100 i 500 m (Fig. 20). Ocasionalment els nivells de gresos s'alternen amb horitzons d'argiles o margues amb caròfits. En general els nivells de gresos tabulars formen successions grano decreixents. La presència de marques de dessecació, *ripples* i traces fòssils (*Cochlichnus anguineus*; *Gruipeda* sp.) al sostre de les capes de gres s'atribueixen a expansions de lòbuls en condicions subaquàtiques (Sáez et al., 2007; Sanjuan i Martín-Closas, 2012). La presència d'horitzons de margues riques en matèria orgànica s'atribuïren a petits llacs temporals que es formaren en moments de màxima inundació. D'acord amb Gibert i Sáez (2009) els dipòsits de lobul terminal quedaren exposats però es mantingueren humits de manera prolongada degut a fluctuacions de la làmina d'aigua.

(ii) *Fàcies d'esplanada d'inundació (Floodplain facies)*

Aquestes fàcies estan constituïdes per trams d'argiles vermelles i gresos alternats amb margues grises (Fig. 20). Els intervals d'argila vermella estan laminats, presenten una potència de varis metres i s'alternen amb petits nivells de gresos o llims amb estructures de paleocorrent. Les argiles vermelles s'interpretaren com a dipòsits de plana d'inundació fluvial formats per la decantació de les partícules fines en suspensió en moments d'avingudes (Sanjuan i Martín-Closas, 2012).

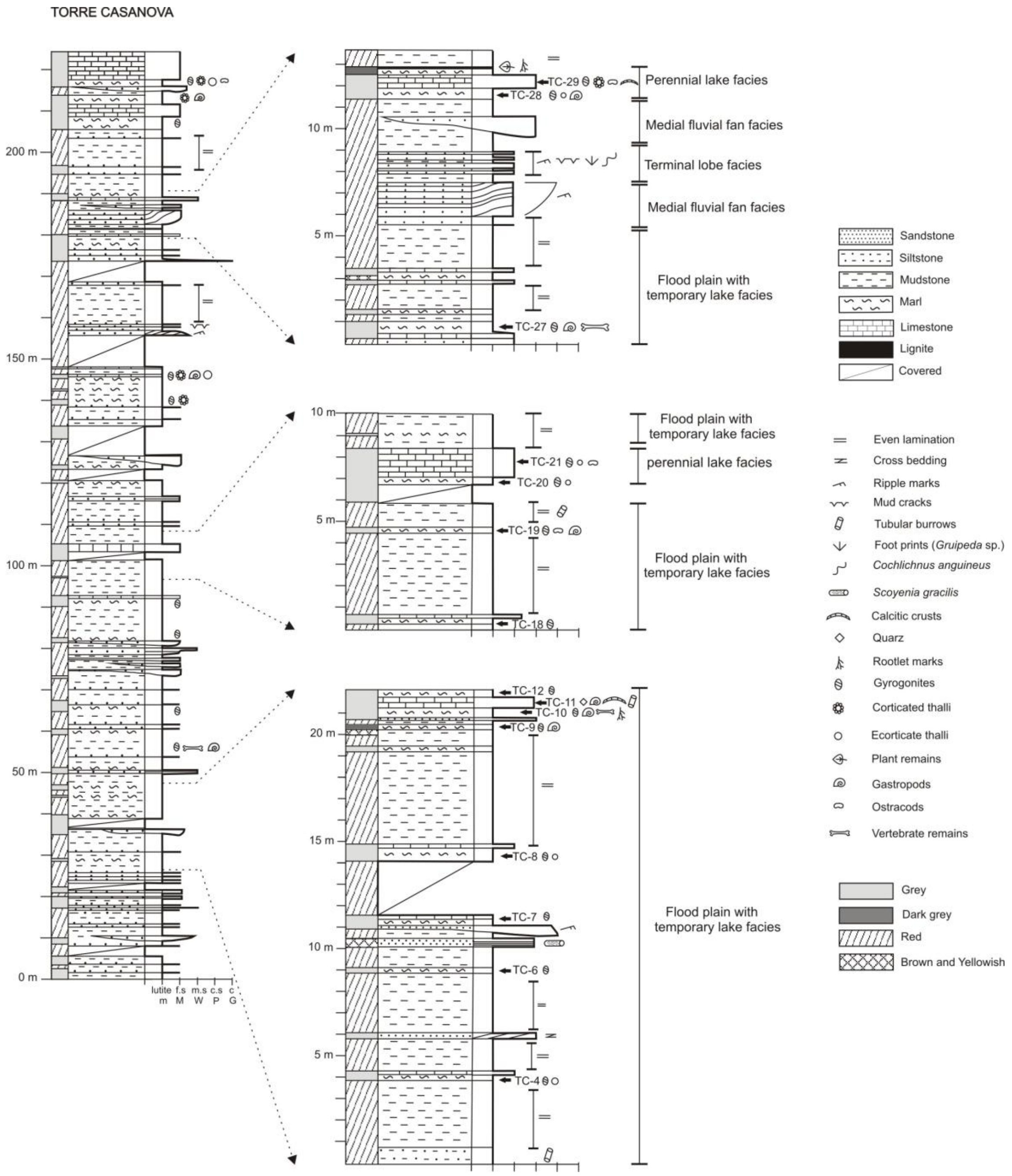


Figura 20. Columnes estratigràfiques de Torre Casanova al sector del Bages on es mostren les diferents associacions de fàcies de la Formació Artés.
Figure 20. Stratigraphic log of Torre Casanova in the Bages area, showing facies associations of the Artés Formation.

Els nivells de margues presenten potències variables entre pocs decímetres a un metre i són molt riques en girogonits i tal·lus de caròfits, gasteròpodes aquàtics, ostràcodes i restes de vertebrats (Fig. 21A). Aquest nivells s'interpretaren com a reompliments de llacs temporals subjectes a un elevat aport terrigènic (Sanjuan i Martín-Closas, 2012). Ocasionalment, sobre els nivells de marga s'hi sobreposen horitzons de calcària de potència centimèrica a decimètrica amb fàbrica tipus *packstone* formades per litoclasts i abundants crostes d'esparita atribuïdes a incrustacions de tiges de macròfits submergits, girogonits i tal·lus de caròfits, ostràcodes, i fragments de gasteròpodes (Figs. 21B i C). Aquests horitzons s'atribuïren a una sedimentació en llacs d'aigües més clares i alcalines (Sanjuan i Martín-Closas, 2012).

Figura 21. Foto de camp de les fàcies d'esplanada d'inundació a Torre Casanova (Moìa). **A**, Vista general de l'aflorament; **B-C**, Detall de dos nivell de marga.

Figure 21. Field photo of floodplain facies in Torre Casanova section (Moià). ***A****, General view of the outcrop;* ***B-C****, Detail of two marlstone layers.*

- Fàcies de llacs permanents

Les fàcies de llacs permanents s'identificaren dins les Calcàries del Membre Moià (Sáez, 1987), integrat dins la Formació Artés, i que aflora a la part superior de la secció de Torre Casanova i a la secció de Moià. El Membre Moià, de ~50 m de potència, està constituït per tres intervals de calcària lacustre separats per trams de marga. Des d'un punt de vista litostratigràfic el Membre Moià correspon lateralment i en direcció SW a la Formació Calcàries de Castelltallat i en conjunt representa el primer sistema lacustre (Sistema lacustre de La Noguera) dels cinc sistemes caracteritzats en el sector oriental de la Conca de l'Ebre (Anadón et al., 1989). Dins el membre Moià es caracteritzaren tres associacions de fàcies (Fig. 22):

(i) *Margues associades a llacs d'aigües tèrboles*

Aquesta associació es composa bàsicament per capes de margues riques en fòssils d'organismes aquàtics, de potència mètrica, versicolors, laminació difusa, riques en matèria orgànica i intraclastos (Fig. 22). L'origen d'aquestes fàcies es relacionà amb processos de decantació de l'argila en suspensió dins la columna d'aigua. La presència continua d'aquestes margues a la base de petits cicles que passen verticalment a margocalcàries i calcàries amb caròfits permeté atribuir-les a les parts relativament mes profundes de llacs que esdevenien mes soms. El pas a sediments mes carbonatats dins els cicles correspondria a un increment progressiu de la productivitat de fang calcari per part d'organismes en aigües poc profundes i ben il·luminades. La laminació difusa observada a les margues podria ser conseqüència de moments d'anòxia a la part més profunda del llac la qual cosa feu impossible la bioturbació (Gierlowski-Kordesch, 2010).

(ii) *Calcàries tipus* wackestone–packstone *amb abundants restes biogèniques*

Aquesta és l'associació de fàcies dominant del Membre Moià. Els cossos de calcària presenten una fàbrica *wackestone* o *packstone* de coloració gris fosc i de potències variables d'entre 0.5–2 m (Fig. 22). A certs trams de calcària s'observà laminació difusa i intraclastos de formes arrodonides situats als sostres d'algunes de les capes. Els components biogènics que composen aquestes calcàries són principalment caròfits (tal·lus i girogonits), valves d'ostràcodes, crostes cilíndriques de textura micrítica atribuïts a incrustacions sobre tiges d'angiospermes aquàtiques, gasteròpodes, fragments

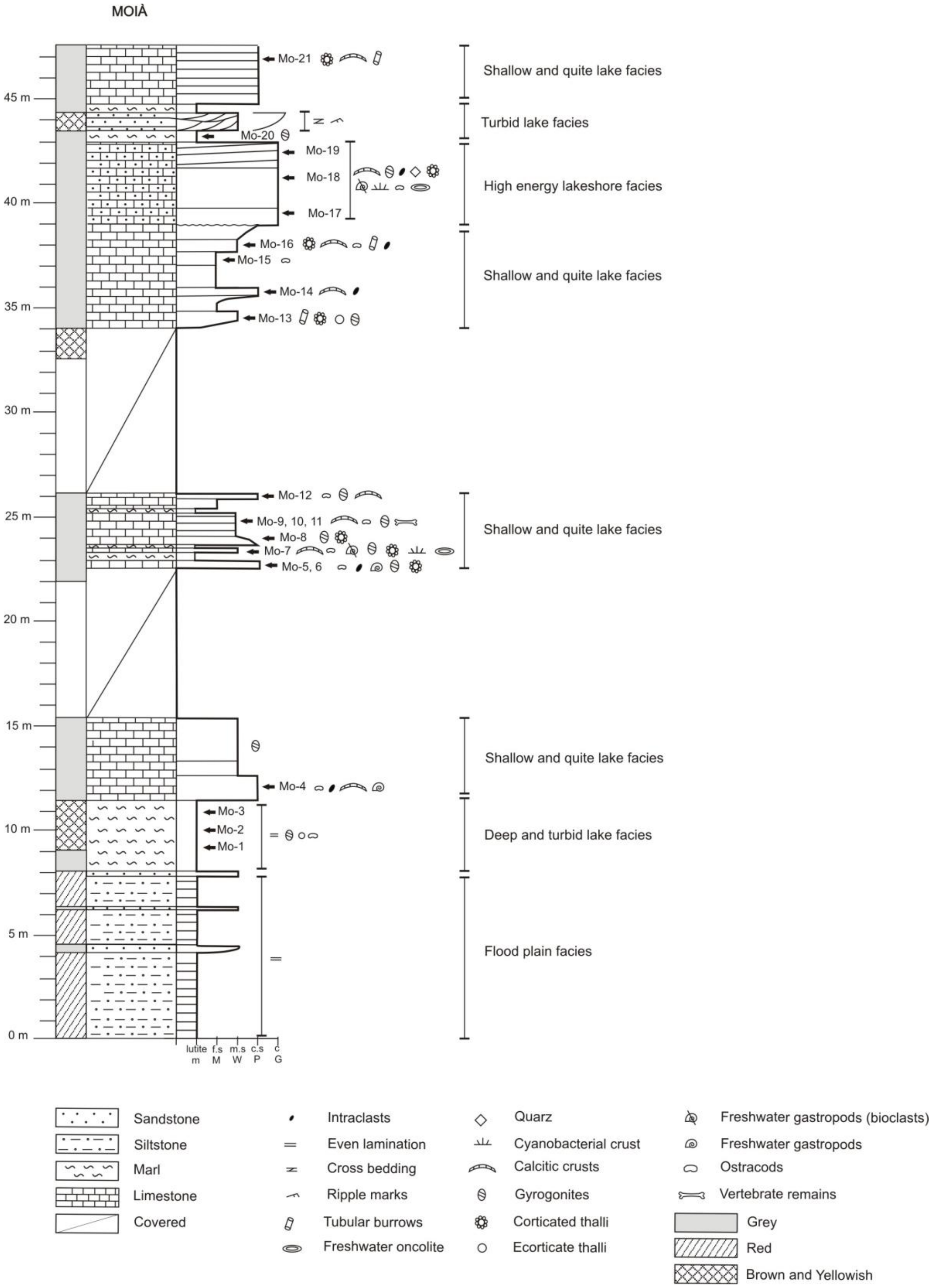


Figura 22. Columna estratigràfica de Moià on s’observen les diferents associacions de facies del Membre Calcàries de Moià.

Figure 22. Stratigraphic log of Moià in the Bages area, showing facies association of the Moià Limestone Member.

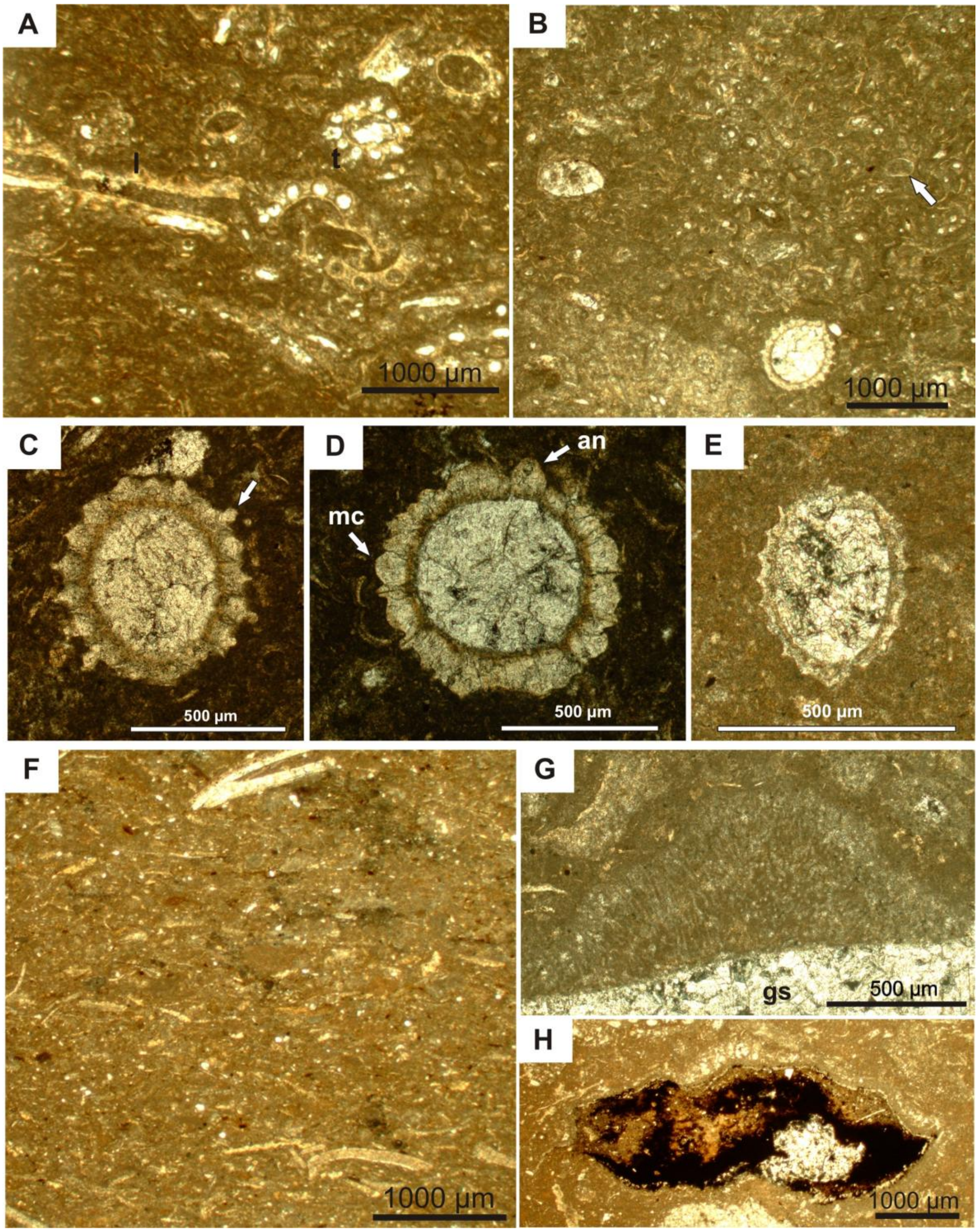
de vertebrats i crostes formades per filaments calcificats de diàmetre micromètric, que s’atribuïren a incrustacions de cianobacteris. La predominança de caròfits formant el component majoritari en calcàries lacustres sub-actuals ha estat motiu d'anàlisi en treballs, que les relacionen amb zones d'herbei de caròfits (Soulié-Märsche et al., 2010; Khanaqa i Karim, 2012). Mitjançant l'ús de lamines primes s'identificaren tres gèneres de girogonits de caròfits; *Harrisichara*, *Gyrogona* i *Chara*. Aquesta fàcies s'atribuí a un paleoambient dominat per llacs permanents, soms, de fons oxigenats i d'aigues alcalines amb condicions subaquàtiques d'energia moderada (Sanjuan i Martín-Closas, 2012).

(iii) *Calcàries amb fàbrica de tipus* grainstone *associades a vores de llac*

Aquesta fàcies caracteritza la part superior del Membre Moià. Les calcàries, són tabulars, massives o amb estratificació lleument encreuada de potències variables (0.5–1.5 m) i presenten una fàbrica tipus *grainstone* (Figs. 22 i 23F-H). Els components principals són grans de quars, intraclastos subangulars i bioclastos incrustats per estructures en forma de dom integrades per filaments cianobacterians, constituint en ocasions oncòlits (Fig. 23). Aquestes fàcies s'atribuïren a cinturons d'alta energia situats a la vora del llac (Sanjuan i Martín-Closas, 2012). Les crostes cianobacterianes presents sobre els bioclastos constitueixen els únics fòssils autòctons de l'associació.

Figura 23 (pàgina següent). Microfacies de les calcàries de la Fm Moià a la localitat tipus. **A.–E**. Microfacies *wackestones–packstones* amb abundant contingut biogenic. **A**, *Charaxis* sp. amb corticació no-contigüa en secció transversal (t) i longitudinal (l); làmina prima Mo-21. **B**, Ostràcodes (fletxa) i girogonits; làmina prima de la mostra Mo-10. **C**, Secció quasi longitudinal de girogonit de *Harrisichara* sp. on s'hi observa la ornamentació consistent en tubercles (fletxa); làmina prima de la mostra Mo-5B. **D**, Secció longitudinal d'un girogonit de *Gyrogona* sp. mostrant els nòduls apicals (ap) i la cresta intracel·lular (mc); làmina prima de la mostra Mo-8B. **E**, Secció longitudinal de *Chara* sp.; làmina prima de la mostra Mo-12. **F–H**, Fàcies d'alta eneregia de vora llac. **F**, Vista general amb abundants bioclastos, làmina prima de la mostra Mo-18. **G**, Secció longitudinal d'una tapís cianobacterià incrustant una conquilla de gasteròpode (gs), làmina prima de la mostra Mo-18. **H**, Oncoid amb un nucli d'ambre; làmina prima de la mostra Mo-7.

Figure 23 (next page). Microfacies of the Moià Limestone Fm at the type locality. ***A–E****, Microfacies of wackestones–packstones with abundant biogenic remains.* ***A****,* Charaxis *sp. showing non-contiguous cortication in transversal (t) and longitudinal (l) sections; thin section from sample Mo-21.* ***B****, Ostracods (arrow) and gyrogonites; thin section from sample Mo-10.* ***C****, Near-longitudinal section of* Harrisichara *sp. gyrogonite showing the ornamentation consisting of tubercles (arrow); thin section from sample Mo-5B.* ***D****, Longitudinal section of* Gyrogona *sp. gyrogonite showing the apical nodules (ap) and mid-cellular crest (mc); thin section from sample Mo-8B.* ***E****, Longitudinal section of* Chara *sp.; thin section from sample Mo-12.* ***F–H****, High energy lakeshore microfacies.* ***F****, General view with abundant bioclasts; thin section from sample Mo-18.* ***G****, Longitudinal section of cyanobacterial incrustation on a gastropod shell (gs), thin section from sample Mo-18.* ***H****, Oncoid with an amber nucleus; thin section from Mo-7.*



- Tafonomia i paleoecologia dels caròfits de la Formació Artés

S'identificaren tres associacions de caròfits dins la Formació Artés (Sanjuan i Martín-Closas, 2012) (Fig. 24). (1) Associació dominada per *Nodosochara jorbae* juntament amb les espècies *Lychnothamnus longus*, *Harrisichara tuberculata*, *Lychnothamnus grambastii* i *Chara artesica*. Aquesta associació es troba a les fàcies de petits estanys temporals subjectes a importants entrades de materials detrítics dins un context d'esplanada d'inundació fluvial a les seccions d'Oristà, Santa Maria d'Oló i gran part de la secció de Torre Casanova (Fig. 24). (2) Associació dominada per una única espècie, *Lychnothamnus grambastii*, la qual es troba també en fàcies d'esplanada d'inundació associada a petits llacs amb gran cobertora vegetal situat a la part basal de la secció de Torre Casanova (Fig. 24). L'excel·lent estat de conservació dels girogonits i la seva associació amb tal·lus, gasteròpodes i ostràcodes d'aigua dolça suggereix que aquestes dues associacions creixien *in situ*. (3) Associació dominada per l'espècie *Harrisichara tuberculata*, juntament amb altres espècies menys abundants com *Nodosochara jorbae*, *Lychnothamnus longus*, *Lychnothamnus stockmansii*, *Lychnothamnus grambastii*, *Gyrogona caelata*, *Sphaerochara labellata*, *Nitellopsis (Tectochara) merianii* i *Chara artesica*, que apareixen a la part alta de la secció de Torre Casanova i al Membre de calcàries lacustres de Moià en la localitat tipus, en fàcies lacustres de llacs ben desenvolupats i permanents (Sanjuan i Martín-Closas, 2012). En general, els girogonits procedents d'aquestes margues presenten un bon estat de conservació i es troben associats a tal·lus, petits gasteròpodes i ostràcodes lacustres del gènere *Ilyocipris* entre altres. La bona preservació dels girogonits i dels tal·lus suggereix autoctonia o para-autoctonia de les restes fòssils (Fig. 24).

Aquests resultats sobre la distribució paleoambiental dels caròfits tenen importants efectes en l'ús de determinades espècies en biostratigrafia. Mentre que les espècies locals com *Nodosochara jorbae, Lychnothamnus longus i Chara artesica* n. sp. semblen ser espècie euritipiques, les espècies *Lychnothamnus grambastii* i *Harrisichara tuberculata*, així com d'altres espècies menys abundants, com *Nitellopsis (T.) merianii*, *Sphaerochara labellata*, *Lychnothamnus stockmansii* i *Gyrogona caelata*, són espècies subjectes a un important control paleoecològic i facial. Cal destacar l'espècie índex de la superzona europea de *Harrisichara tuberculata*, que domina únicament en fàcies relacionades amb ambients lacustres permanents (Sanjuan i Martín-Closas, 2012).

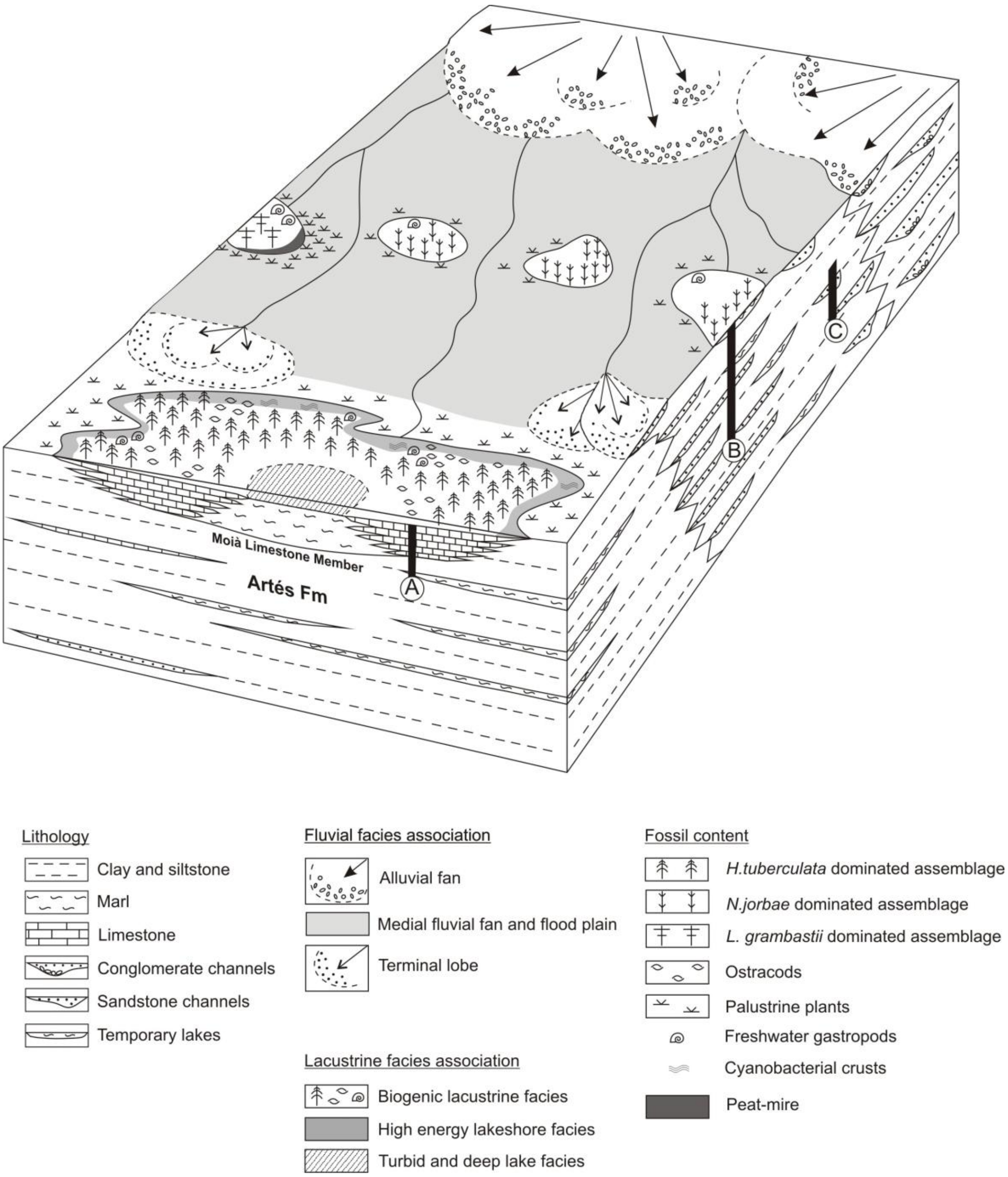


Figura 24. Model paleoambiental sobre la distribució de les associacions dominades per *Nodosochara jorbae*, *Lychnothamnus grambastii* i *Harrisichara tuberculata* localitzades a la Formació Artés. Es representen les principals seccions estratigràfiques: **A**, Moià; **B**, Torre Casanova; **C**, Oristà. Sense escala.
Figure 24. Palaeoenvironmental model summarising the distribution of the Nodosochara jorbae, Lychnothamnus grambastii *and* Harrisichara tuberculata *dominated assemblages in the continental Artés Formation. The main stratigraphic logs represented are:* ***A****, Moià;* ***B****, Torre Casanova;* ***C****, Oristà. Not to scale.*

7.3. PALEOBIOGEOGRAFIA

La paleobiogeografia dels caròfits és un tema d'alt interès ja que la distribució paleogeogràfica de les diferents espècies, lligada a condicions climàtiques i ecològiques, condiciona el seu ús en biostratigrafia i en la correlació biostratigràfica entre conques continentals més o menys llunyanes.

Gran part de les espècies de caròfits estudiades presenten una distribució exclusivament europea (*Harrisichara lineata, H. vasiformis-tuberculata, H. tuberculata, Lychnothamnus vectensis, L. grambastii, L. major, Nitellopsis (Tectochara) merianii, Psilochara* aff. *acuta, Chara* aff. *antennata,* C. *rhenana* ,*C. microcera, Gyrogona caelata* i *Sphaerochara labellata*). Dues de les espècies estudiades presenten una distribució eurasiàtica (*Lychnothamnus stockmansii i Nitellopsis (Tectochara) merianii*). Finalment, tres espècies (*Lychnothamnus longus*, *Nodosochara jorbae* i *Chara artesica sp. Nov*.) presenten una distribució limitada a la conca de l'Ebre a partir del coneixement actual.

Pel que fa a les espècies d'àmbit europeu, s'ha observat l'existència d'una polaritat nord-sud en la riquesa d'espècies i en la seva distribució. Les conques del nord-oest d'Europa (Hampshire, Paris i Rin) presenten un elevat nombre d'espècies (~31 espècies) i comparteixen espècies comunes les quals son alhora absents a les conques del sud-oest d'Europa (Provença, Llenguadoc, Aquitània i Ebre). D'altra banda, seguint el mateix patró, les conques del sud-oest d'Europa presenten un nombre d'espècies relativament inferior (~18 espècies) i també comparteixen espècies comunes diferents de les que es troben a les conques de mes al nord. Altres espècies representades arreu d'Europa mostren una gradació nord-sud en la seva distribució i abundància (Sanjuan i Martín-Closas, en revisió-a).

La presència d'espècies suposadament endèmiques, es a dir, distribuïdes en una única conca o regió concreta, no és una particularitat de la conca de l'Ebre sino que és freqüent a les altres conques europees durant l'Eocè superior i l'Oligocè inferior. Malgrat tot, la distribució més o menys uniforme de detreminades espècies a la majoria de conques del Paleogen d'Europa i la baixa relació amb les espècies asiàtiques ha permès definir una bioprovíncia de caròfits per a les fàcies continentals de l'Eocè superior i l'Oligocè inferior d'Europa (Fig. 25) (Sanjuan i Martín-Closas, en revisió-a).

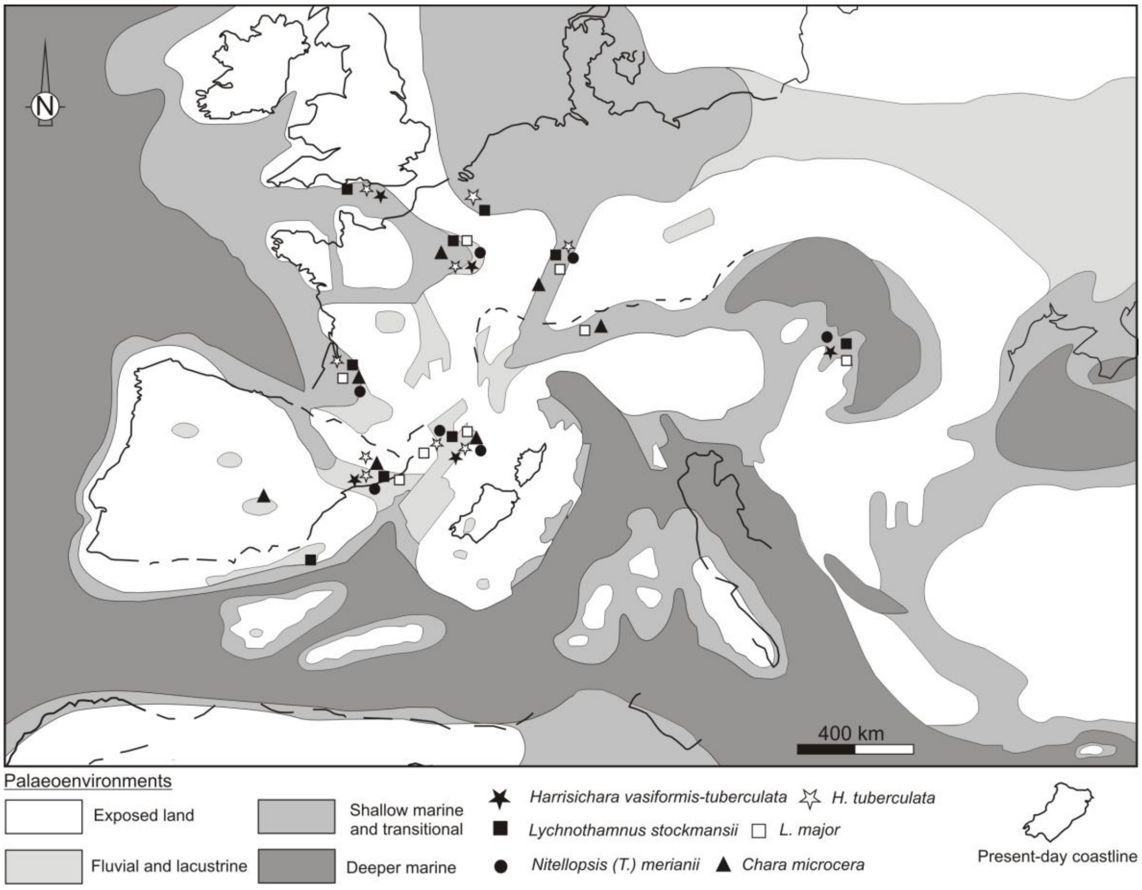


Figura 25. Bioprovincia Europea de caròfits durant l'Eocè terminal (Priabonià) i l'Oligocè basal (Rupelià) sobre un mapa paleogeogràfic del continent Europeu modificat de Lorenz et al. (1993). Distribució dels llinatges *Harrisichara vasiformis-H. tuberculata* i *Lychnothamnus stockmansii-L. major* i de les espècies *N. (T.) merianii* i *Chara microcera*.
Figure 25. European charophyte bioprovince during Uppermost Eocene (Priabonian) and Lower Oligocene (Rupelian) on a palaeogeographic map of Europe modified from Lorenz et al. (1993). Distribution of the Harrisichara vasiformis-H. tuberculata *and* Lychnothamnus stockmansii-L. major *charophyte lineages and the species* N. (T.) merianii *and* Chara microcera.

La distribució latitudinal de les flores de caròfits europeus actuals s'atribueix a un gradient tèrmic (Corillion, 1972) però durant el límit Eocè-Oligocè gran part d'Europa pertanyia a la mateixa àrea climàtica, caracteritzada per un clima sub-tropical sense canvis significatius de temperatura (Scotese, 2003). No obstant això, alguns estudis paleoclimàtics basats en les macro-restes de plantes vasculars de l'interval estudiat conclouen que la situació climàtica a Europa era heterogènia i depenia de la distribució paleogeogràfica de les masses de terra emergida (Mai i Walter 1985; Mai 1989; Mihajlović 1993). La flora del nord-oest i centre d'Europa, influenciada pel Mar del Nord, estava constituïda per una vegetació subtropical humida amb predominança de laurisilves. En contrast, les flores coetànies del sud d'Europa, dependents de l'acció climàtica de la Tetis, estaven constituïdes per lauràcies acompanyades d'abundants espècies xerofítiques, com el ginjoler (gènere *Zizyphus*), indicadores de condicions d'aridesa estacional (Mihajlović, 1993). D'acord amb aquestes dades, els estudis pol·línics, realitzats en dipòsits del Priabonià més superior i Rupelià basal de la Conca de l'Ebre (àrea de Sarral), revelaren la presència de polen relacionat amb taxons de climes àrids i estacionals, com *Ephedra*, Chenopodiaceae, *Combrentum*, *Linum*, Plumbaginaceae, Thymalaeaceae and Boraginaceae (Cavagnetto i Anadón, 1996). A més, d'acord amb aquests autors, l'àmplia diversitat de pol·len de Caesalpinaceae i Leguminoseae indiquen una marcada influència africana (Cavagnetto i Anadón, 1996). Aquest patró podria reflectir-se també en les masses d'aigua continental i suggereix que la polaritat latitudinal identificada en la flora de caròfits durant l'Eocè superior-Oligocè inferior d'Europa podria tenir més relació amb l'increment de l'aridesa cap al sud d'Europa, que amb els canvis tèrmics (Sanjuan i Martín Closas, en revisió-a).

Juntament a les condicions climàtiques, els factors ecològics relacionats amb la dinàmica hidrològica dels llacs i aiguamolls podrien jugar també un paper clau en aquesta diferenciació de la flora de caròfits a Europa durant el límit Eocè-Oligocè. Les característiques hidrològiques de cada conca, l'aport de sediments als sistemes aquàtics o el tipus de drenatge d'una conca contribuïren al control biogeogràfic dels organismes aquàtics (Gierlowski-Kordesch, 2010). Des d'aquest punt de vista, les conques de Paris i Hampshire presenten característiques completament diferents que la conca de l'Ebre. Les primeres formaren part durant el període estudiat d'una gran conca cratònica relacionada a processos de rift intercontinental amb permanent connexió marina, en canvi, la conca de l'Ebre fou una conca d'avantpaís relacionada amb una col·lisió intraplaca que evolucionà en un sistema tancat i endorreic (Einsele, 2000). D'acord amb aquest autor, les conques cratòniques tenen grans dimensions i presenten una subsidència lenta i velocitats relatives de sedimentació baixes. Pel contrari, les conques d'avantpaís són de mides molt variades, de subsidència ràpida i altes velocitats relatives de sedimentació. La contínua connexió amb el mar i la baixa velocitat relativa de sedimentació a les conques de Paris i Hampshire afavoríren el desenvolupament d'un ampli ventall d'ambients inundats, des de llacs d'aigua dolça a aiguamolls salabrosos fet que es va reflectir en una àmplia diversificació de la flora subaquàtica de caròfits. En canvi, l'absència d'influència marina a la conca de l'Ebre a partir del Priabonià mitjà afavorí el desenvolupament d'ambients constituïts per llacs temporals d'aigües tèrboles i de fons inestables que limitaren els nínxols ecològics per a la diversificació dels caròfits (Sanjuan i Martín-Closas, 2012). En conclusió, es pot determinar que les condicions climàtiques i ecològiques lligades a la dinàmica de conca foren decisives en la distribució paleobiogeogràfica dels caròfits durant l'Eocè superior i l'Oligocè inferior.

Mes enllà de la distribució en un determinat interval de temps, també s'ha estudiat la paleobiogeografia històrica dels caròfits al llarg del límit Eocè-Oligocè. La història paleobiogeogràfica dels caròfits es un tema poc estudiat i alhora rellevant per entendre els processos de dispersió geogràfica de les espècies i eventualment els processos que porten a l'expansió de determinades espècies a grans àrees paleogeogràfiques. L'estudi s'ha centrat en dues espècies, que son especialment importants per a la correlació biostratigràfica entre conques distants i presenten una extensió eurasiàtica. Aquestes espècies evolucionaren en dos llinatges evolutius de manera gradualista, es tracta dels llinatges *Lychnothamnus stockmansii-L. major* (Sanjuan i Martín-Closas, en revisió-b) i *Nitellopsis (Tectochara) merianii- N. obtusa* (Soulié-Märsche et al., 2002). La seva paleobiogeografia històrica mostra dos patrons de distribució completament oposats. El llinatge evolutiu extingit *Lychnothamnus stockmansii-L. major* presenta una distribució eurasiàtica a partir de de la seva aparició (Figs. 26 i 27), mentre que el llinatge evolutiu *Nitellopsis (Tectochara)merianii-N. obtusa,* que encara és viu en l'actualitat, presenta una patró de dispersió gradual. El seu origen es trobaria al sud d'Europa durant l'Eocè superior, posteriorment s'expandiria a tot Europa durant l'Oligocè inferior i finalment s'estendria cap a l'est ocupant tot el continent eurasiàtic durant l'Oligocè superior-Miocè. Aquest estatus eurasiàtic es manté fins l'actualitat (Figs. 28, 29 i 30).

Aquests dos mecanismes biogeogràfics semblen tenir relació amb els mecanismes reproductius i de dispersió, coneguts en els caròfits actuals. Els mecanismes de dispersió dels caròfits del génere *Chara* actuals depenen principalment de la disposició conjunta (espècies monoiques) o disjunta (espècies dipoiques) dels gametangis en una mateixa planta i del rol que desenvolupen certs ocells aquàtics que s'en alimenten (ànecs i aus limnícoles) i que dispersen les oòspores i/o girogonits (Proctor, 1962, 1980; Proctor et al., 1967). Aquests autors observaren que en l'actualitat, les espècies monoiques del gènere *Chara* són en general cosmopolites, en canvi les espècies

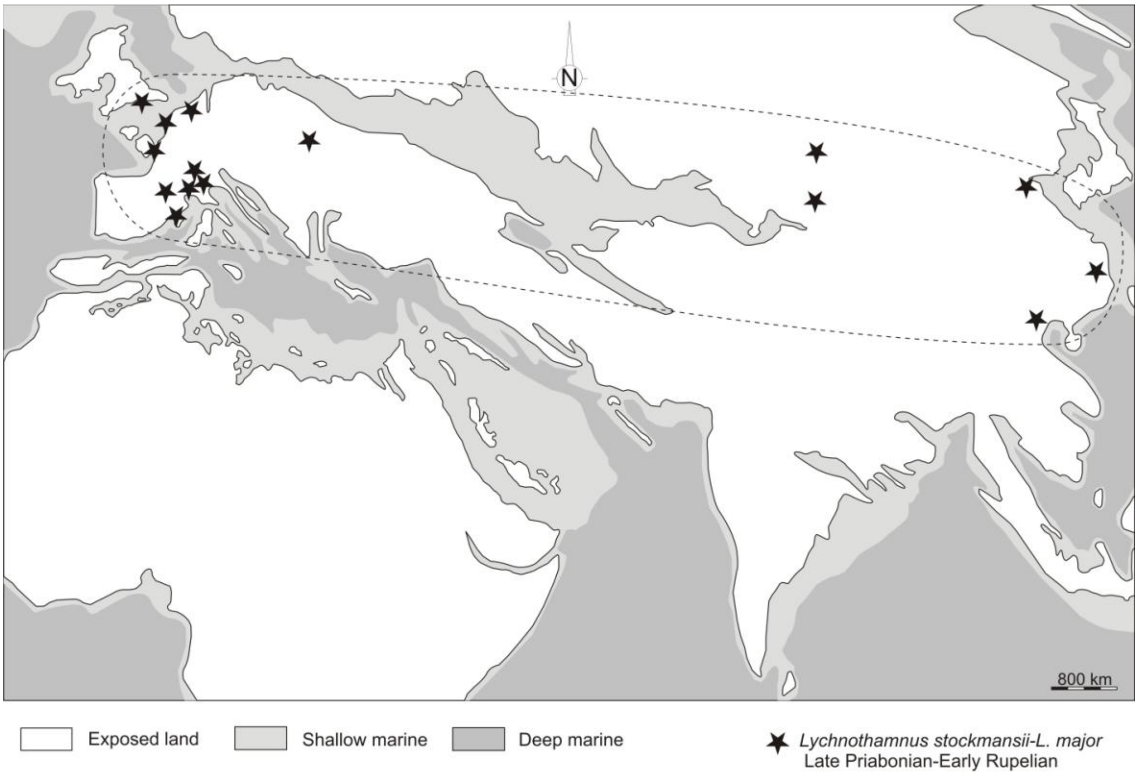


Figura 26. Distribució biogeogràfica de *L. stockmansii-L. major* durant el Priabonia superior-Rupelià inferior (~35-32,5 Ma) traçat sobre un mapa paleogeogràfic de l'Oligocè basal modificat de Blakey (2006). Les estrelles representen el registre per a cada país o àrea.
Figure 26. Biogeographic distribution of L. stockmansii-L. ma*jor lineage showing its earliest Eurasiatic record in Late Priabonian-Early Rupelian (~35-32,5 Ma) and plotted on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent the records for a given country or area.*

dioiques presenten una distribució més localitzada en àreas geogràfiques concretes. Proctor (1980) argumentà que la distribució cosmopolita de les espècies de *Chara* monoiques es deu a la capacitat d'aquestes a produir grans bancs d'oòspores i/o girogonits durant un únic esdeveniment de dispersió, permetent continuar immediatament la seva expansió a altres àrees. La distribució regional que mostren les espècies dioiques, en canvi, es deu a la baixa capacitat d'aquestes en formar abundants bancs de oospores i/o girogonits degut a que sovint presenten un percentatge molt desigual de sexes en una mateixa població i això limitaria de manera significativa la seva expansió biogeogràfica.

Partint d'aquestes hipòtesis, Sanjuan i Martín-Closas (en revisió b) inferiren la naturalesa reproductiva dels llinatges estudiats. Així, el llinatge *L. stockmansii-L. major* probablement fou una espècie monoica des del seu origen, tenint en compte la

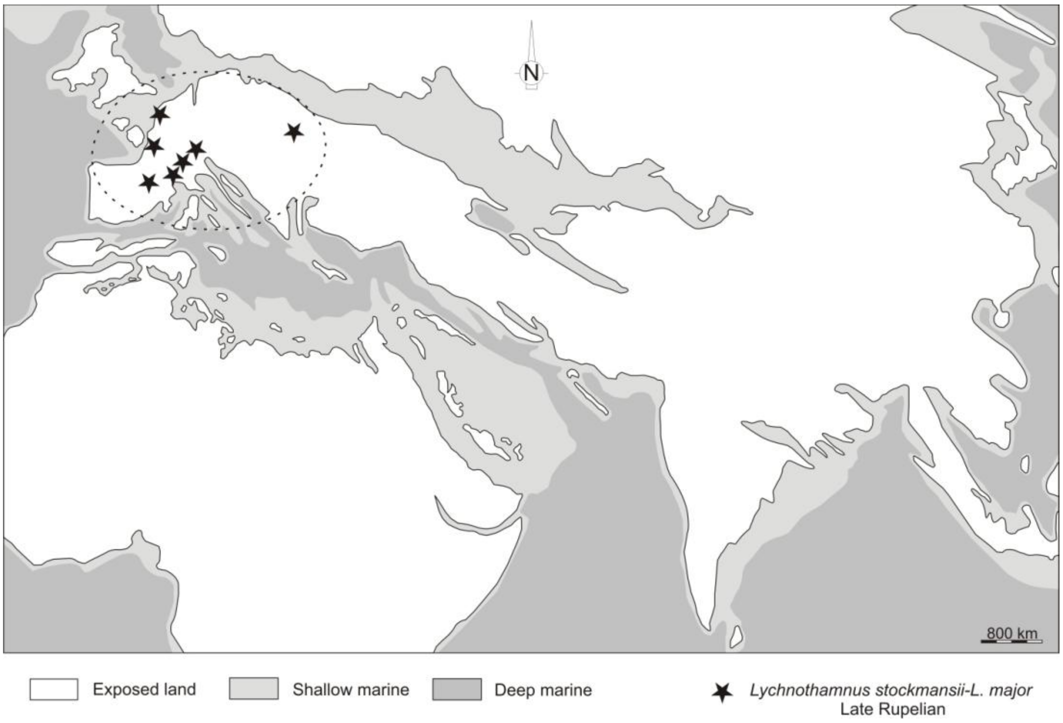


Figura 27. Distribució biogeogràfica de *L. stockmansii-L. major* durant el Rupelià superior (~32,5-30 Ma) traçat sobre un mapa paleogeogràfic de l'Oligocè basal modificat de Blakey (2006). Les estrelles representen el registre per a cada país o àrea.

Figure 27. Biogeographic distribution of L. stockmansii-L. major *lineage showing its restricted western European distribution during Late Rupelian (~32,5-30 Ma) on a palaeogeographic map of the world at Lower Oligocene time modified from Blakey (2006). Stars represent the records for a given country or area.*

disposició conjunta dels gametangis en l'únic representant actual *L. barbatus*, que es considera molt proper a l'spècie estudiada (Soulié-Märsche i Martín-Closas, 2003). Pel contrari, el llinatge *N. (T.) merianii-N.obtusa* es una espècie dioica en l'actualitat. Tenint en consideració els patrons de distribució de *Chara* actual, es conclogué que, malgrat que ambdós llinatges evolutius presenten una distribució eurasiàtica, el llinatge dioic (*N. (T.) merianii-N. obtusa*) necessità més temps per a colonitzar conques allunyades. Aquest retard en l'expansió supracontinental de les espècies dioiques condiciona l'ús d'aquestes en la correlació biostratigràfica entre conques llunyanes (Sanjuan i Martín-Closas, en revisió-b).

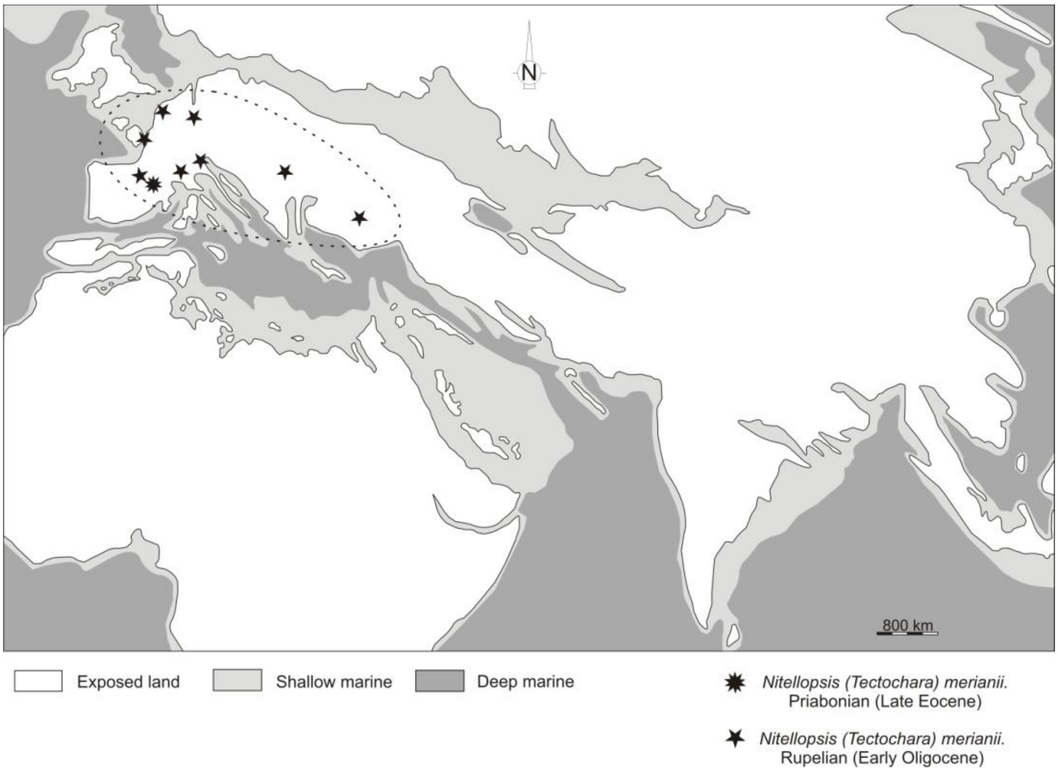


Figura 28. Distribució biogeogràfica del llinatge *Nitellopsis (Tectochara) merianii-N. obtusa* mostrant la seva distribució restringida durant l'Eocé terminal (Priabonià superior, ~34, 2 Ma) i la seva distribució europea a l'Oligocè inferior (Rupelià, ~33,9-28,1 Ma) sobre un mapa paleogeogràfic del mon de l'Oligocè inferior modificat de Blakey (2006). Les estrelles representen el registre per a cada país o àrea.
Figure 28. Biogeographic distribution of Nitellopsis (Tectochara) merianii-N. obtusa *lineage showing its restricted western European distribution during latest Eocene (Late Priabonian, ~34, 2 Ma) and its European distribution in Early Oligocene (Rupelian, ~33,9-28,1 Ma) on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent the records for a given country or area.*

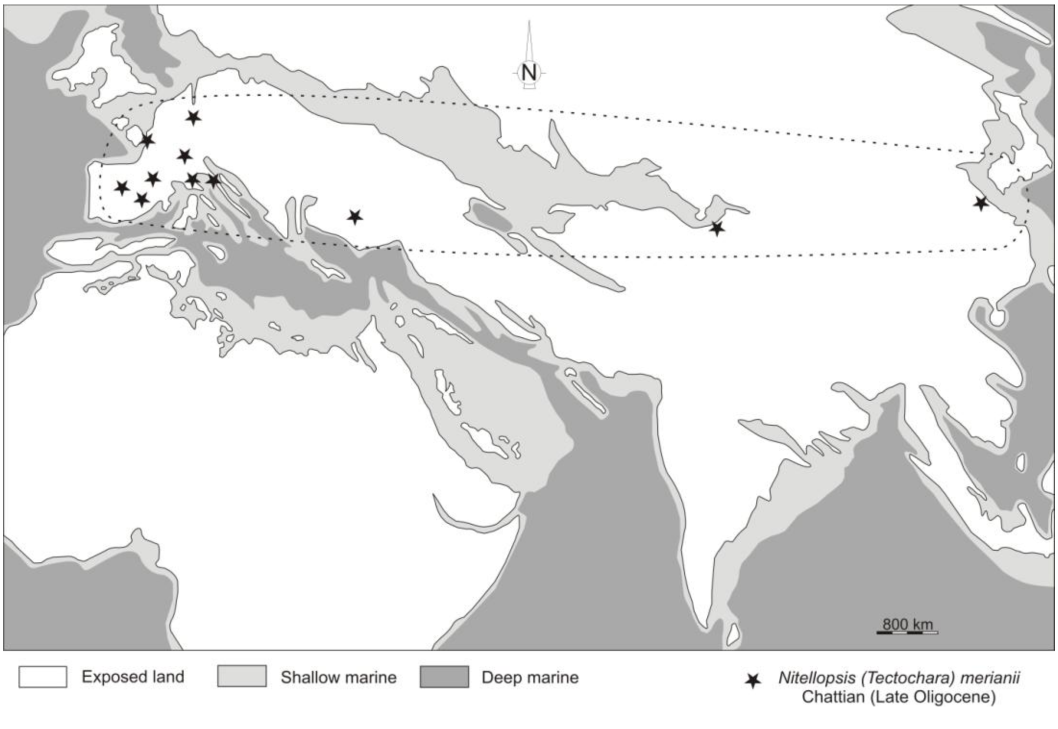


Figura 29 (pàgina anterior). Distribució biogeogràfica del llinatge *Nitellopsis (Tectochara) merianii-N. obtusa* mostrant la seva distribució eurasiática ja durant l’Oligocè superior (Catià, ~28,1-23 Ma) sobre un mapa paleogeogràfic del mon de l’Oligocè inferior modificat de Blakey (2006). Les estrelles representen el registre per a cada país o àrea.
Figure 29 (previous page). Biogeographic distribution of Nitellopsis (Tectochara) merianii-N. obtusa *lineage showing a Eurasiatic distribution already during Late Oligocene (Chattian, ~28,1-23 Ma) on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent the records for a given country or area.*

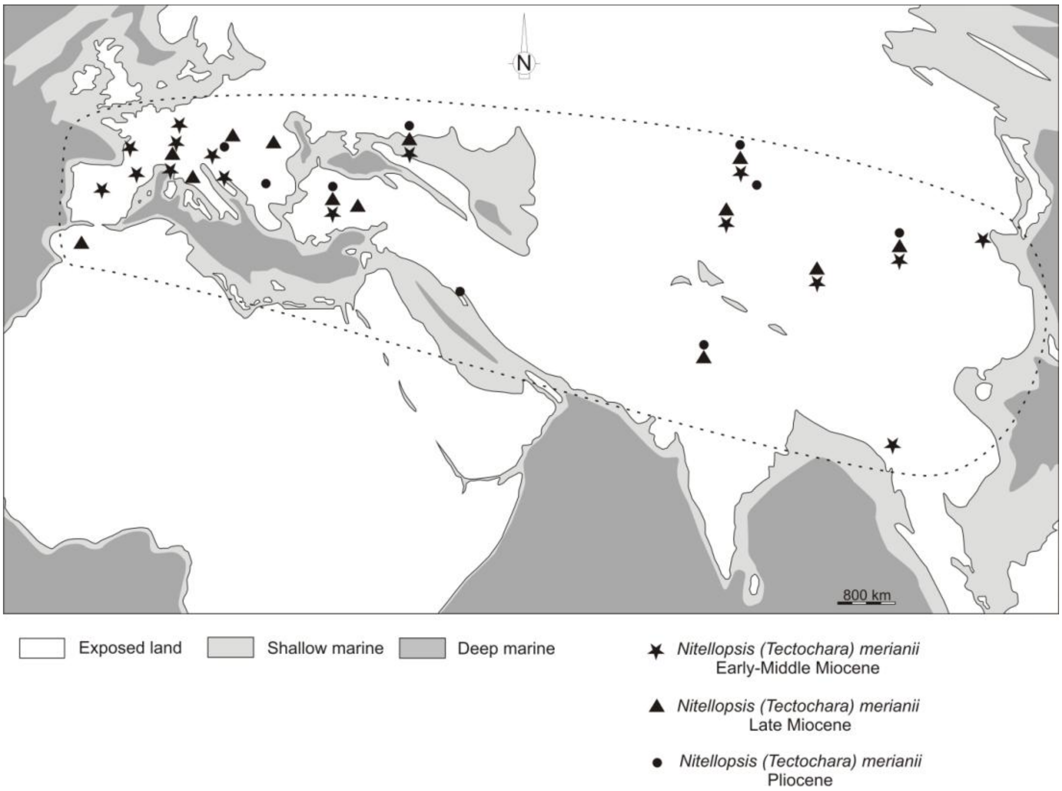


Figura 30. Distribució biogeogràfica del llinatge *Nitellopsis (Tectochara) merianii-N. obtusa* mostrant la seva distribució eurasiática durant el Miocè i Pliocè (*~2,5-23 Ma*) sobre un mapa paleogeogràfic del mon del Miocè inferior modificat de Blakey (2006). Les estrelles representen el registre per a cada país o àrea.
Figure 30. Biogeographic distribution of Nitellopsis (Tectochara) merianii-N. obtusa *lineage showing its Eurasiatic distribution during the Miocene and Pliocene (~2,5-23 Ma) on a palaeogeographic map of the world at Lower Miocene modified from Blakey (2006). Stars represent the records for a given country or area.*

7.4. BIOSTRATIGRAFIA

7.4.1. Antecedents biostratigràfics i problemàtica

L’estudi de la sistemàtica dels girogonits (oospores calcificades de caròfits) fòssils es remunta al segle XVIII,però el seu ús en biostratigrafia és relativament recent. Grambast (1958) assentà les bases de la sistemàtica i biostratigrafia de caròfits fòssils del

Paleogen d'Europa occidental, definint els canvis de flora al llarg dels diferents estatges del Paleogen. Horn af Rantzien (1959) fou el primer autor en descriure, de manera preliminar, la repartició estratigràfica de vàries espècies de caròfits paleogens a Europa. No fou però fins l'any 1972 que, partint de varis treballs anteriors (Grambast, 1962, 1964; Castel, 1968), Grambast (1972) publicà la primera biozonació de caròfits del Paleogen a Europa occidental. Posteriorment, l'atribució biostratigràfica basada en caròfits dels dipòsits continentals d'algunes conques Europees es reflectiren en un gran nombre d'estudis regionals (Riveline, 1973,1976, 1979; Feist-Castel, 1977a, b; Feist i Ringeade, 1977; Anadón i Feist, 1981; Anadón et al., 1992; Feist et al. , 1994), que culminaren en l'elaboració d'una biozonació europea de caròfits per part de Riveline (1984, 1986) i Riveline et al. (1996), avui dia en ús per al Paleogen i la base del Neogen d'Europa occidental. Posteriorment s'han proposat algunes modificacions a aquesta biozonació, com la de Martín-Closas et al. (1999), basada en la correlació entre caròfits i macroforaminífers.

El primer autor que esmenta la presència de girogonits fòssils a la conca de l'Ebre fou Dalloni (1930). No fou però fins la dècada dels seixanta que Rosell et al. (1966) donaren una atribució biostratigràfica a les seqüències no marines del Lutecià Superior al sector d'Igualada a partir de les associacions de girogonits de caròfits. Colom et al. (1970) dataren per primera vegada mitjançant l'ús de girogonits les fàcies transicionals del sector NE de la conca de l'Ebre (Sant Boi de Lluçanès) d'edat Eocè mitjà-superior. Durant la dècada de 1970 els estudis biostratigràfics a partir de caròfits fòssils es centraren al marge oriental de la conca. Així, Ferrer (1971) i Ramírez del Pozo et al. (1975) definiren i cartografiaren vàries unitats continentals molt generalitzades proporcionant alhora datacions preliminars mitjançant l'ús de caròfits. A partir de vàries tesis doctorals sobre l'estratigrafia i la sedimentologia del Paleogen del marge oriental de la conca de l'Ebre (Anadón, 1978; Colombo, 1980; Cabrera, 1983; Sáez, 1987) es publicaren un seguit de treballs centrats en la biostratigrafia dels caròfits d'aquesta conca. Així, Anadón i Feist (1981) dataren i subdividiren per primera vegada les formacions del sector central del marge est de la conca de l'Ebre des del Tanetià al Bartonià mitjançant les flores de caròfits. Anadón et al. (1983) establiren correlacions biostratigràfiques entre nivells marins i continentals de l'Eocè mitjà al marge est de la conca de l'Ebre. Els estudis centrats en biostratigrafia de caròfits prosseguiren amb la tesi doctoral de Choi (1989) que estudià les associacions de caròfits fòssils de l'Eocè superior i Oligocè de la conca de l'Ebre. Aquesta autora identificà un total de 10 gèneres i 18 espècies de caròfits, dues de les quals foren espècies noves i endèmiques de la conca (*Nodosochara jorbae* i *Lychnothamnus longus*).També precisà l'atribució biostratigràfica de vàries unitats sedimentàries localitzades al marge est de la conca, com el Complex Lacustre de Sanaüja, la Formació Artés i la Formació de les Calcàries de Tàrrega. Simultàniament es desenvoluparen treballs biostratigràfics utilitzant mamífers que permeteren donar atribucions cronostratigràfiques a vàries unitats del Paleogen continental de la conca de l'Ebre (Truyols i Crusafont, 1961; Anadón et al., 1987; Agustí et al., 1987, 1988; Arbiol i Sáez, 1988).

Partint dels treballs centrats en biostratigrafia continental (caròfits i vertebrats) Anadón et al. (1992) i Feist et al. (1994) elaboraren una biozonació local de caròfits per al Paleogen i la base del Neogen de la conca de l'Ebre. Entre l'Eocè superior i el Miocè inferior Feist et al., (1994) definiren un total de 9 biozones de caròfits representades en 5 àrees d'estudi situades al llarg del marge oriental de la conca.

7.4.2. Resultats biostratigràfics

L'estudi dels caròfits procedents de les diferents seccions del marge est de la conca ha proporcionat una flora suficientment rica per a permetre l'atribució biostratigràfica de les diferents unitats litostratigràfiques. Les associacions de caròfits trobades a les noves seccions estudiades s'ha comparat i contrastat amb les que configuraren la biozonació local d' Anadón et al. (1992) i Feist et al. (1994). Els resultats mostren que algunes de les biozones definides en aquests treballs presenten problemes en la seva aplicació. Aquest es el cas de la biozona local 2 (biozona de Sphaerochara labellata) definida com l'interval entre les primeres aparicions de *Sphaerochara labellata* i *Lychnothamnus longus*. Les noves dades demostren que *L. longus* apareix abans que *Sphaerochara labellata* fent inviable l'ús d'aquesta biozona. Altres biozones definides per Feist et al. (1994) utilitzaren espècies molt limitades paleoecològicament, com és el cas de les biozones locals 3 i 4 el límit entre les quals es definí a partir de l'espècie *Nitellopsis (T.) merianii*. Aquesta espècie es limita a ambients lacustres permanents i profunds.

D'acord amb Sanjuan et al. (acceptat) s'han definit un total de 6 biozones d'ús local situades al marge est de la conca i distribuïdes entre el Priabonià mitjà i el Rupelià mitjà, que s'han calibrat amb l'escala del temps gràcies a la correlació dels resultats obtinguts amb les dades magnetostratigràfiques d'autors anteriors. Aquests resulats han permès aportar dades significatives a la biozonació europea (Fig. 31).

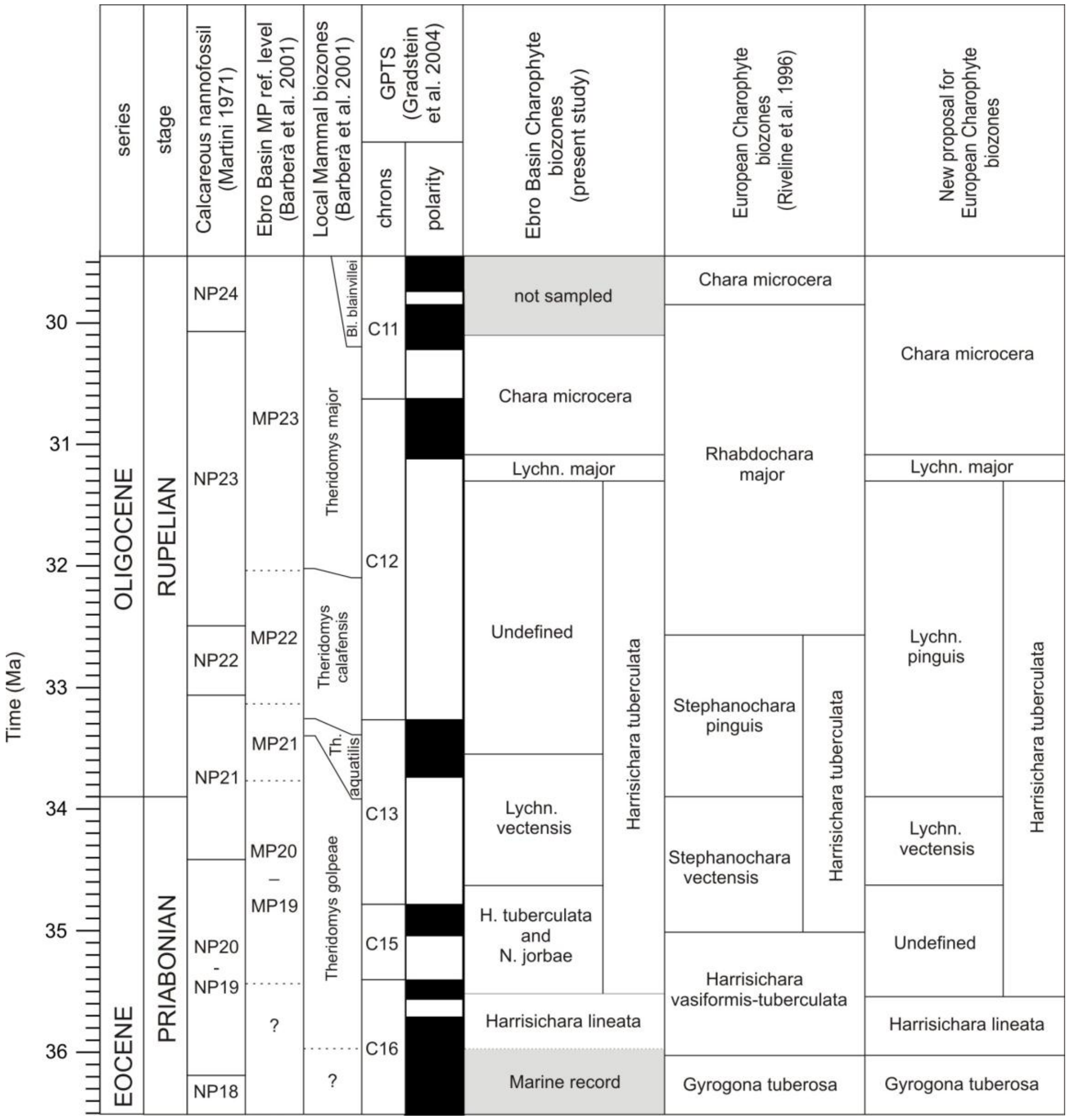


Figura 31. Calibració de la nova proposta de biozonació de l'Eocè terminal-Oligoce basal amb les GPTS (Gradstein et al. 2004). Es mostra la calibració prèvia de les biozones de nannofòssils calcàris (Martini, 1971), la biozonació local de mamífers (Barberà et al., 2001), els nivells de referència de mamífers europeus MP atribuits per Barberà et al. (2001) i Costa et al. (2011) a la Conca de l'Ebre. SCG, Sant Cugat de Gavadons. RO, Rocafort de Queralt. SP, Santpedor. CA l., Calaf inferior. CA u., Calaf superior. PQ, Porquerisses., VI, Vimbodí. FO, Forés. TA, Tàrrega. CI, Ciutadilla. TR, Tarrés. VN, Vinaixa. La biozonació europea de caròfits correspon a Riveline et al. (1996) i Riveline en Hardenbol et al. (1998).

Figure 31. Calibration of the new Late Eocene-Early Oligocene charophyte biozonation to the GPTS (Gradstein et al. 2004). Previous calibrations of calcareous nannofossil biozones (Martini, 1971), the Local Mammal biozonation of Barberà et al (2001) and the Ebro Basin MP reference levels according to Barberà et al. (2001) and Costa et al. (2011) are also shown. SCG, Sant Cugat de Gavadons. RO, Rocafort de Queralt. SP, Santpedor. CA l., Lower Calaf. CA u., Upper Calaf. PQ, Porquerisses., VI, Vimbodí. FO, Forés. TA, Tàrrega. CI, Ciutadilla. TR, Tarrés. VN, Vinaixa. European charophyte biozonation is based in Riveline et al. (1996) and Riveline in Hardenbol et al. (1998).

Biozona de Harrisichara lineata. Equival a la biozona europea de Harrisichara vasiformis-tuberculata definida per Riveline et al. (1996) com a biozona d'interval. D'acord amb aquesta autora, es delimita entre l'ultima aparició de *Gyrogona tuberosa* i la primera aparició de *Harrisichara tuberculata*. A la conca de l'Ebre les associacions d'aquesta biozona es localitzen a la Formació Sant Boi (seccions de El Perers, Serrat Rodó, Sobremunt, Sant Bartomeu del Grau) i base de la Formació Artés a Maians (Sanjuan et al., 2012; Sanjuan et al., acceptat). El canvi de nóm de la biozona es fonamenta en (1) la limitació paleoecològica de *H. vasiformis-tuberculata* , que s'ha associat a fàcies salabroses (Sanjuan i Martín-Closas, 2012) i (2) la inexistència de *H. vasiformis-tuberculata* com a espècie formal. Feist-Castel (1977a) va crear informalment aquest nom per anomenar un morfotipus intermedi en una successió gradual entre *H. vasiformis* i *H. tuberculata*. Posteriorment aquesta successió va ser posada en dubte per Sille et al. (2004) que mostrà, mitjançant el metode d'anàlisi morfostructural Eigenshape, que "*H. vasiformis-tuberculata*" era un morfotipus de l'espècie *H. vasiformis*. Aquesta biozona es correlaciona amb el nivell de referència de mamífers europeus MP18 o MP19-20 i amb la biozona local de vertebrats de Theridomys golpeae (Barberà et al., 2001). Partint de les dades magnetostratigràfiques del sector de Moià i Maians, el límit superior d'aquesta biozona d'interval, es correlaciona amb el cron C16n (C16n.1n) d'edat~35.5 Ma (Fig. 31).

Superzona de Harrisichara tuberculata. Aquesta superzona fou definida per Riveline et al. (1996) com el rang total de distribució de *Harrisichara tuberculata*. El límit inferior d'aquesta biozona es correlaciona amb el nivell de referència de mamífers europeus MP18 o MP19-20, biozona local de vertebrats Theridomys golpeae de Barberà et al. (2001) i es calibra amb la magnetozona C16n (C16n.1n) a ~35.5 Ma. El límit superior de la superzona es correlaciona amb el nivell de referència de mamífers europeus MP23, biozona local de vertebrats Theridomys major de Barberà et al. (2001) i en aquest treball s'ha calibrat amb la magnetozona C12 (C12r) d'edat ~31.5 Ma (Fig. 31). Les noves dades procedents de la conca de l'Ebre han permès precisar l'extensió total (de ~4,2 Ma) d'aquesta superzona clau en la biostratigrafia europea del límit Eocè-Oligocè. El seu rang cronostratigràfic s'amplia cap a la seva base i cap al sostre (Fig. 31). La calibració d'aquesta superzona a la conca de l'Ebre només es pot comparar amb les dades procedents de la conca de Hampshire (Illa de Wight, Angleterra) on fou estudiada per Hooker et al. (2009). El límit basal d'aquesta biozona i per tant la primera aparició de l'espècie homònima és lleugerament diacròn a ambdues conques car *H. tuberculata* aparegué ~ 0,4 Ma abans a la conca del'Ebre.

Biozona de Nodosochara jorbae-Harrisichara tuberculata. És una nova biozona local, per la conca de l'Ebre, que s'inclou dins la superzona de H. tuberculata. Es defineix com a biozona d'associació de les espècies *Harrisichara tuberculata* i *Nodosochara jorbae* entre la primera aparició de *H. tuberculata* i la primera aparició de *Lychnothamnus vectensis*. El límit superior de la biozona es correlaciona amb el nivell de referència europeu de vertebrats MP18 o MP19-20 i amb la biozona local de vertebrats Theridomys golpeae de Barberà et al. (2001). Segons que s'ha determinat a la secció de Torre Casanova, aquesta biozona s'estén des del cron C16n (C16n.1n) al cron C13 (C13r), d'edat ~35,5 a ~34,6 Ma (Priabonià superior) (Fig. 31).

L'interval representat per aquesta biozona d'us local (conca de l'Ebre) correspon, a escala europea, a un interval sense biozona definida atès que *Nodosochara jorbae* és una espècie limitada a la conca de l'Ebre durant l'Eocè superior, segons el coneixement actual.

Biozona de Lychnothamnus vectensis. És una biozona europea i local integrada dins la superzona de H. tuberculata. Aquesta biozona és especialment important en la biozonació dels caròfits atès que comprèn el límit Eocè-Oligocè i serveix per a caracteritzar-lo. En el seu estat actual, la biozona presenta una definició diferent a escala de la conca de l'Ebre o a escala europea. A escala local es defineix com a biozona de rang total mentre que a escala europea és una biozona de rang parcial.

El límit inferior d'aquesta biozona es correlaciona amb el nivell de referència de mamífers Europeus MP18 o MP19-20 i es calibra amb el cron C13 (C13r), d'edat ~34.5 Ma. Aquesta dada suposa una modificació del límit inferior actualment conegut de la biozona, que es pensava que coincidia amb l'aparició de *H. tuberculata* mentre que els resultats obtinguts mostren que és clarament posterior.

El límit superior de la biozona local (extinció de *L. vectensis*) es correlaciona amb el nivell de referència de mamífers Europeus MP21, biozona local de vertebrats Theridomys aff. aquatilis de Barberà et al. (2001) i s'ha calibrat amb el cron C13 (C13n), d'edat ~33.5 Ma (Fig. 31). Per sobre del límit superior de la biozona local de L. vectensis fins a la base de la següent biozona (L. major) a la conca de l'Ebre hi ha un interval sense biozona definida, mes enllà del marc de la superzona de H. tuberculata. Aquest interval indefinit vé produit per la poca riquesa de caròfits a la conca de l'Ebre, on únicament s'hi troben registrades *Harrisichara tuberculata, Lychnothamnus longus* i *Psilochara* aff. *acuta* i s'estén des del cron C13 (C13n) d'edat ~33.5 Ma al cron C12 (C12r) d'edat 31,3 Ma (Fig. 31). A escala europea el límit ve definit per l'aparició de *L. pinguis*.

Biozona de Lychnothamnus pinguis. És una biozona no representada a la conca del'Ebre per manca de l'espècie índex, *L. pinguis*. Riveline et al. (1996) la definiren com a biozona de rang parcial, que comprèn l'interval entre la primera aparició de *Lychnothamnus pinguis* i la darrera aparició de *Harrisichara tuberculata*. D'acord amb Riveline et al. (1996) aquesta biozona es correlaciona amb el nivell de referència europeu de mamífers MP21 i amb la biozona de nanoplàncton calcari NP22. Les noves dades d'aquest estudi mostren que aquesta biozona es correlacionaria amb els nivells de referència europeus de mamífers MP21, MP22 i MP23 i es calibra amb les magnetozones C13 (C13n) i C12 (C12r) d'edat ~33,9 a ~31,3 Ma. Aquesta calibració determina que el límit superior d'aquesta biozona sigui mes modern del que proposaven Riveline et al. (1996) (Fig. 31).

Biozona de Lychnothamnus major. Segons la definició de Riveline et al. (1996) aquesta és una biozona d'interval delimitada entre la darrera aparició de *Harrisichara tuberculata* i la primera aparició de *Chara microcera*. A la conca de l'Ebre la representació d'aquesta biozona d'interval es extremadament reduïda i es correlaciona amb el nivell de referència de mamífers europeus MP23, biozona local de vertebrats Theridomys major de Barberà et al. (2001) i es pot calibrar amb la magnetozona C12r d'edat aproximada de ~31, 2 Ma (Fig. 31). A escala europea aquesta biozona es definí en base un registre fossil pobre, procedent de poques localitats a la conca d'Aquitània (sud de França). Segons Riveline et al. (1996), la biozona d'interval *Lychnothamnus* *major* es correlaciona amb el nivell de referència europeu de mamífers MP22 i amb la biozona de nanoplàncton calcari NP23. Les noves dades procedents de la conca de l’Ebre qüestionen l’ús d’aquesta biozona ja que la seva durada seria extremadament reduïda (Fig. 31). D’altra banda, els resultats taxonòmics exposats mes amunt i obtinguts amb posterioritat a la publicació de Sanjuan et al. (acceptat), indiquen que *Lychnothamnus major* seria un morfotipus poc calcificat, i per tant sinònim de *L. pinguis* i portarien a considerar que les biozones basades en aquestes dues especies s’haurien de fusionar.

Biozona de Chara microcera. Segons la definició de Riveline et al. (1996) aquesta biozona és de rang parcial i abasta l’interval entre la primera aparició de *Chara microcera* i la primera aparició de *Lychnothamnus ungeri*. En aquest treball només s’ha estudiat el límit inferior de la biozona, que es correlaciona amb el nivell referència de mamífers europeus MP23, la biozona local de vertebrats Theridomys major de Barberà et al. (2001) i que s’ha calibrat amb la magnetozona C12r d’edat ~31 Ma (Fig. 31).

Riveline et al. (1996) correlacionaren la biozona de Chara microcera amb els nivells de referència europeus de mamífers MP24 i MP25 i amb la biozona de nanoplàncton calcari NP24. Les noves dades procedents de la Conca de l’Ebre mostren que el límit inferior d’aquesta biozona seria notablement més antic.

8. DISCUSSIONS

8.1. Sistemàtica

L'identificació de les diferents espècies de caròfits d'aquesta tesi parteix dels treballs clàsics en sistemàtica dels caròfits del Paleogen europeu. En aquest sentit cal destacar els treballs de Grambast (1956, 1957, 1958), Grambast i Paul (1965), Grambast i Soulié-Märsche (1972), Feist-Castel (1971, 1977a, b), Feist i Ringeade (1977), Choi (1989), Soulié-Märsche (1989) i Schwarz i Griessemer (1994). Mes enllà de l'estudi taxonòmic detallat de les espècies fòssils de l'Eocè superior i Oligocè inferior de la conca de l'Ebre, incloent la identificació d'espècies no trobades anteriorment a la conca i la resolució de la taxonomia d'espècies que autors anteriors havien deixat en nomenclatura oberta, la present tesi s'endinsa en temes que tradicionalment han estat poc estudiats en sistemàtica dels caròfits fòssils paleogens, com el polimorfisme interespecífic.

Nombroses espècies de caròfits actuals presenten un grau de polimorfisme més o menys variable dels seus girogonits, en funció de les condicions ecològiques del medi subaquàtic (Soulié-Märsche, 1989). A més, la posició que ocupa la oòspora i/o girogonit en els verticils de diferents edats del caròfit també pot afectar la seva forma i mida (Pedrola i Acuña, 1986). Segons Soulié-Märsche (1989) el grau de polimorfisme dels girogonits és una variable específica, essent gairebé nul en certes espècies actuals com *Nitellopsis obtusa* o molt variable en altres com *Chara globularis*. Altres espècies actuals com *Lychnothamnus barbatus* produeixen girogonits de forma invariable, però amb una gran variabilitat de mida (Soulié-Märsche, 1989). Estudis recents centrats en girogonits sub-fòssils del gènere *Chara* procedents de l'Albufera de València relacionen la ornamentació tuberculada de varis espècimens amb la salinitat del medi subaquàtic (Alonso-Guillén, 2011).

El polimorfisme interespecific també s'observa en girogonits d'espècies fòssils (Soulié-Märsche, 1989). Al Paleogen de la Conca de l'Ebre, l'espècie *Harrischara lineata* és un clar exemple de la variabilitat en la mida i en l'ornamentació del girogonit, com s'ha descrit i es pot observar a la Fig. 10E, G, H i I. La importància en la descripció i quantificació d'aquest polimorfisme és especialment important en les espècies d'interès biostratigràfic. Aquest es el cas de les espècies índex de biozones europees *Lychnothamnus vectensis*, *L.major* i *Lychnothamnus pinguis* que mostren una gran variabilitat morfològica en funció del grau de calcificació del girogonit (Figs. 11 i 13). La relació morfologia-grau de calcificació en *Lychnothamnus* fou estudiada per Soulié-Märsche (1989) qui conclogué que els antics gèneres *Stephanochara* i *Rhabdochara* equivaldrien a girogonits amb diferents graus de calcificació del gènere *Lychnothamnus*. Així, per una banda, el girogonits antigament atribuïts al gènere *Stephanochara* serien en realitat girogonits de *Lychnothamnus* amb un grau de calcificació superior (cèl·lules espirals convexes i nòduls apicals), en canvi els girogonits atribuïts a l'antic gènere *Rhabdochara* pertanyen a girogonits de *Lychnothamnus* amb un baix grau de calcificació (cèl·lules espirals còncaves i apex plans i no ornamentats).

L'anàlisi biomètrica dels girogonits de les poblacions tipus de *Lychnothamnus vectensis* i *Lychnothamnus pinguis* ha permès definir i quantificar aquest polimorfisme lligat al grau de calcificació. La població tipus de *Lychnothamnus pinguis* mostra un ventall de morfotipus amb estadis de calcificació diferents que no havien estat caracteritzats fins ara. Un nombre significatiu de girogonits presenten un baix grau de calcificació, amb cèl·lules espirals còncaves, àpex plans i porus basals en forma d'embut estrellat. La similitud d'aquests girogonits amb els girogonits d'una espècie contemporània, *Lychnothamnus major*, condueix a establir una sinonómia entre *L. pinguis* i *L. major* (Figs. 14 i 15). Aquesta sinonímia té repercussions en la biostratigrafia de l'Oligocè inferior i en la biogeografia d'aquesta espècie.

8.2. Paleoecologia

A partir de les anàlisis tafonòmica, sedimentològica i dels fòssils associats, els resultats obtinguts mostren que la distribució de determinades espècies de caròfits de l'Eocè superior estava sotmesa a controls facials i paleoecològics significatius. La limitació ecològica que presenten algunes espècies de caràcies actuals és ben coneguda (Corillion, 1972), però a la pràctica no s'ha tingut mai en compte alhora de dur a terme estudis biostratigràfics. Conèixer els limitants ecològics de les espècies fòssils de caròfits és clau per determinar el seu ús en biostratigrafia, atès que la presència/absència d'una espècie no es pot atribuir només, com s'ha fet sovint, a variables evolutives o temporals.

En l'Eocè superior de la Conca de l'Ebre, *Harrisichara vasiformis-tuberculata* estaria relacionada amb ambients salabrosos pròxims a la costa, *H. lineata* viuria en ambients lacustres poc profunds i *H. tuberculata* dominaria, però no és exclusiva, en ambients lacustres permanents i profunds (Sanjuan i Martín-Closas, 2012). Això també és cert per altres espècies sense tant interès biostratigràfic com *Lychnothamnus grambastii* que es relacionà amb fàcies de llacs efímers rics en matèria orgànica. En canvi l'espècie endèmica *Nodosochara jorbae*, no presenta cap limitació paleoecològica destacable, encara que el seu ampli rang cronostratigràfic determina que el seu us en biostratigrafia s'hagi de fer per associació amb una altra espècie (Sanjuan i Martín-Closas, 2012).

A més de *N. jorbae*, altres espècies presents a la conca de l'Ebre no mostren cap limitació ecològica aparent. Cal destacar *Lychnothamnus longus*, *Lychnothamnus vectensis*, *Psilochara* aff. *acuta* i *Chara artesica* n. sp. Aquestes espècies aparentment euritípiques podrien ser útils en la caracteritzacó biostratigràfica de la conca ja que la seva presència o absència està probablement lligada a causes d'extinció real, però en molts casos tenen amplíssims rangs cronostratigràfics, igual que *N. jorbae*.

8.3. Paleobiogeografia

L'anàlisi paleobiogeogràfica de les diferents espècies de l'Eocè superior-Oligocè inferior d'Europa ha permès reconèixer una certa polaritat latitudinal en la distribució i abundància de les espècies (Sanjuan i Martín-Closas, en revisió-a). Aquesta polaritat no és un patró biogeogràfic exclusiu dels caròfits. La flora vascular i la fauna del continent europeu també presenta cert grau de regionalisme en el límit Eocè-Oligocè com a conseqüència de la resposta climàtica continental al descens global de les temperatures i la baixada del nivell del mar que comportà la primera glaciació antàrtica (Badiola et al., 2009; Cavagnetto i Anadón, 1996; Mai i Walter 1985; Mai 1989; Mihajlović 1993). Els estudis isotòpics en vertebrats i invertebrats continentals del límit Eocè-Oligocè conclouen que el canvi climàtic actuà heterogèniament en funció dels factors locals com l'orografia (Sheldon, 2009). Aquests factors més locals resultarien en la presència de regionalismes que contribuïren a formar sistemes ecològics més o menys aïllats.

Seguint aquesta idea, la present tesi mostra la resposta de les flores de caròfits als condicionants climàtics i de l'ecologia local. Mentre que la definició d'una bioprovincia europea de caròfits ja fou proposada per Riveline (1986) a l'Eoce mitjà, ha estat possible caracteritzar-la a l'Eocè superior-Oligocè a partir d'un nombre concret d'espècies (Sanjuan i Martín-Closas, en revisió a). També s'ha posat de manifest que aquesta bioprovincia presentava una estructura latitudinal interna deguda a la distribució de determinats regionalismes o en les mides dels girogonits i abundàncies relatives de les espècies característiques. Per analogia amb les flores de plantes vasculars es pot concloure que aquesta estructura interna estaria bàsicament produïda per l'aridesa dels paleoambients en que es desenvolupaven les comunitats de caròfits meridionals respecte als medis relativament mes permanents de les conques nòrdiques.

L'anàlisi paleobiogeogràfica de les espècies de caròfits d'interès biostratigràfic es significativa ja que l'absència o presència d'espècies índex de biozona dependrà de la seva distribució geogràfica, lligada més al control climàtic i ecològic de cada conca, que a l'evolució. A més, aquest tipus d'anàlisis representa una eina clau en la correlació biostratigràfica entre conques més o menys allunyades. L'anàlisi paleobiogeogràfica de dos llinatges evolutius eurasiàtics (*Lychnothamnus stockmansii-L .major* i *Nitellopsis(Tectochara) merianii-N. obtusa*) ha permès desenvolupar hipòtesis contrastables sobre l'ús de determinades espècies en la correlació biostratigràfica a escala supracontinental. Sanjuan i Martín-Closas (en revisió b) mostren que el llinatge evolutiu dioic *Nitellopsis (Tectochara) merianii-N. obtusa* presenta un patró de dispersió gradual. Aquest patró comporta una diacronia notable en l'aparició d'aquesta espècie a conques geogràficament allunyades. Pel contrari, el llinatge evolutiu monoic *L. stockmansii-L. major*, presenta una distribució eurasiàtica ja des de la seva primera aparició. Des d'un punt de vista biostratigràfic, sembla clar que les espècies monoiques, amb velocitats d'expansió geològicament instantànies, són més útils alhora d'establir correlacionar conques continentals allunyades.

8.4. Biostratigrafia

Les noves dades biostratigràfiques de la present tesi doctoral han permès qüestionar l'ús i la definició d'algunes de les biozones de l'Eocè superior-Oligocè inferior definides en treballs anteriors (Anadón et al., 1992; Feist et al., 1994; Riveline et al., 1996). Així es plantegen un seguit de dificultats que afecten a la biozonació de caròfits i es formulen possibles solucións per a la elaboració d'una biozonació més coherent.

(1). Dificultats en les biozones definides per autors anteriors

Biozones d'interval. Les biozones d'interval es defineixen en funció de primeres i/o darreres aparicions de les espècies índex de les biozones adjacents i en conseqüència presenten límits que fluctuen independentment dels esdeveniments que afecten l'espècie índex de la biozona. Dues de les biozones estudiades són d'interval, la biozona de Harrisichara lineata (anteriorment zona de Harrisichara vasiformis-tuberculata) i la biozona de Lychnothamnus major. Els resultats obtinguts a la conca de l'Ebre comporten una reducció del seu rang cronostratigràfic per ampliació dels rangs de les espècies índex de les biozones adjacents. Això és especialment clar en el cas de la biozona de L. major, que actualment té una duració extremadament reduïda atès que els límits de les biozones adjacents s'han ampliat fins a gairebé sobreposar-se.

Biozones amb espècies amb limitacions ecològiques. Les limitacions palaeoecològiques de vàries espècies qüestiona el seu ús en biostratigrafia de l'Eocè superior-Oligocè inferior. Aquest es el cas de les biozones locals 2 (Sphaerochara labellata), 3 (Stephanochara vectensis) i 4 (Stephanochara pinguis) de Feist et al. (1994). Aquestes biozones es definiren a partir de les espècies *Sphaerochara labellata* i *Nitellopsis (T.) merianii*, molt limitades a ambients lacustres permanents i relativament profunds (Sanjuan i Martín-Closas, 2012). A nivell europeu, la presència de "*Harrisichara vasiformis-tuberculata*", està condicionada per l'existència d'ambients salabrosos. Altres espècies d'ús biostratigràfic europeu com *Lychnothamnus stockmansii* o *L. pinguis* (=*L. major*) semblen mostrar també un control paleoecològic clar ja que es troben associades a facies relacionades a ambients lacustres permanents.

Biozones amb especies limitades paleogeogràficament. Les limitacions paleobiogeogràfiques de vàries espècies significatives en la biostratigrafia de l'Eocè superior-Oligoce inferior qüestionen la seva aplicabilitat en la correlació entre conques. A nivell europeu, l'espècie índex *Lychnothamnus pinguis* (en el sentit de Grambast, 1958) presenta una clara limitació biogeogràfica (Sanjuan i Martín-Closas, en revisió-a). L'absència d'aquesta espècie dins les conques del sud d'Europa (Aquitània, Llenguadoc, Provènça i Ebre) permet concloure que l'ús d'aquesta espècie en biostratigrafia hauria de quedar restringit a un àmbit regional.

(2). Vers una nova biozonació per l'Eocè superior-Oligocè inferior

Vistos els problemes anteriors és clara la necessitat de replantejar l'actual biozonació europea de tot el Paleogen. Encara que aquest objectiu va mes enllà del propòsit d'aquesta tesi, es proposen una sèrie de claus per dur-la a terme en futurs treballs. (1) La nova biozonació, s'hauria de construir mitjançant biozones de rang parcial i d'àmbit realment europeu. Aquestes biozones es basarien únicament en primeres aparicions d'espècies de caròfits d'àmplia distribució paleogeogràfica (distribuïdes a la majoria de conques europees). Com a resultat, les actuals biozones d'interval, com Harrisichara lineata i Lychnothamnus major haurien de desapareixer. (2) La nova biozonació, a més, hauria d'emprar espècies ecològicament euritípiques (generalistes) sempre que fos possible, o be assenyalar clarament la limitació paleoecològica de les espècies índex, si n'hi hagués. (3) Finalment, la correlació de la nova proposta amb altres biozonacions continentals com els nivells de referència de mamífers (MP) i la calibració amb l'escala temporal de Gradstein (2004) permetria crear una biozonació útil per a la correlació entre conques.

9. CONCLUSIONS

Les associacions de caròfits de l'Eocè superior-Oligocè inferior de la conca de l'Ebre s'han estudiat des d'un punt de vista taxonòmic, paleoecològic, paleobiogeogràfic i biostratigràfic tot establint comparances amb la caroflora europea contemporània. A la conca de l'Ebre s'han descrit un total de divuit espècies. Entre les espècies ja citades en treballs anteriors s'han identificat: *Harrisichara vasiformis-tuberculata* Feist-Castel, 1977a; *H. lineata* Grambast, 1957; *H. tuberculata* (Lyell, 1826) Grambast, 1957; *Nitellopsis (Tectochara) merianii* (Al. Braun ex Unger, 1852) Grambast i Soulié-Märsche, 1972; *Lychnothamnus stockmansii* (Grambast 1957) Soulié-Märsche, 1989; *L. longus* Choi, 1989; *L. vectensis* (Groves 1926) Soulié-Märsche, 1989; *L. major* (Grambast i Paul 1965) Soulié-Märsche, 1989; *Gyrogona caelata* (Reid i Groves 1921) Grambast, 1956; *Chara microcera* Grambast i Paul, 1965; *Sphaerochara labellata* Feist i Ringeade, 1977 i *Nodosochara jorbae* Choi 1989. També s'han descrit espècies de caròfits, fins ara desconegudes a la conca de l'Ebre com *Lychnothamnus grambastii* (Feist-Castel 1971) Soulié-Märsche, 1989, *Chara rhenana* Schwarz i Griessemer, 1994, *Chara* aff. *antennata* Grambast, 1958, *Psilochara* aff. *acuta* Grambast i Paul, 1965 i *Lamprothamnium* sp. S'ha definit formalment una nova espècie corresponent a *Chara* sp. 2 Choi, 1989 amb el nom de *Chara artesica* sp. nov. Sanjuan i Martín-Closas (en revisió a). A més, des d'un punt de vista taxonòmic, s'ha quantificat el polimorfisme interespecífic de les espècies índex de biozones (*Lychnotahmnus vectensis* i *L. pinguis*) a partir de l'anàlisi morfomètrica de les poblacions tipus procedents de la conca de Hampshire (Illa de Wight, Angleterra). Aquesta anàlisi implica sinonimitzar les espècies *Lychnothamnus pinguis* i *L. major*.

La paleoecologia de les associacions de caròfits de l'Eocè superior al sector NE del marge est de la conca de l'Ebre s'ha estudiat a partir d'anàlisis tafonòmiques i sedimentològiques combinades. Els resultats mostren que espècies clau en biostratigrafia presenten limitacions paleoecològiques clares. La caracterització dels limitants ecològics d'aquestes espècies suposa alhora un avenç significatiu en la biostratigrafia de caròfits durant l'Eocè superior-Oligocè inferior ja que la seva presència o absència dependrà, més del tipus de fàcies i del paleoambient que d'esdeveniments evolutius. D'entre les espècies d'interès biostratigràfic amb limitacions ecològiques cal destacar *Harrisichara vasiformis-tuberculata* i *Harrisichara tuberculata*. Altres espècies d'interès biostratigràfic com *Sphaerochara labellata*, *Lychnothamnus stockmansii*, *L. pinguis* (=*L. major*) i *Chara microcera* creixien en llacs permanents. De manera oposada, hi ha espècies sense limitacions ecològiques importants dins el context de les aigües continentals, com *Lychnothamnus vectensis*, *Nodosochara jorbae*, *Lychnothamnus longus* o *Chara artesica* n. sp.

Des d'un punt de vista biogeogràfic els caròfits de l' Eocè superior-Oligocè inferior europeu mostren una cert control latitudinal en la seva distribució i abundància. Aquesta distribució coincideix amb la distribució de la flora vascular i fauna terrestre durant aquest mateix interval, determinada per diferències climàtiques (sobre tot l'aridesa). A més, els factors ecològics lligats a la dinàmica de cada conca influenciaren directament en la distribució i abundància de caròfits. Malgrat aquestes diferències, l'existència d'espècies comunes a tot Europa permeten definir una bioprovíncia europea en l'interval estudiat.

L'anàlisi paleobiogeogràfica-històrica del llinatges evolutius *Lychnothamnus stockmansii-L. major* i *Nitellopsis (Tectochara) merianii-N. obtusa* mostra que les espècies fòssils seguien comportaments biogeogràfics diferents en funció de la disposició disjunta o conjunta dels gametangis (dioica vs. monoica). Així, des d'un punt de vista biostratigràfic, les espècies monoiques com *Lychnothamnus stockmansii-L. major*, amb velocitats d'expansió geològicament instantànies, permeten correlacionar conques allunyades sense que calgui tenir en compte el decalatge temporal produït per una migració lenta a escala geològica.

Des del punt de vista biostratigràfic s'ha proposat una biozonació de caròfits per la conca de l'Ebre, a partir d'espècies ecològicament euritípiques tot establint correlacions directes amb la biozonació local de vertebrats i calibrant les biozones amb les magnetozones caracteritzades al Paleogen de la Conca de l'Ebre per Barberà et al. (2001) i Costa et al. (2010, 2011). També s'ha revisat la biozonació europea. S'ha proposat un canvi en el nom de la biozona de Harrisichara vasiformis-tuberculata, un taxon que no s'ha descrit mai formalment, i es redefineix la biozona Lychnothamnus vectensis, que passa a ser de rang parcial. Els límits d'aquestes biozones han estat, a més, correlacionats amb els diferents nivells de referència de mamífers europeus (MP) i calibrats, per primera vegada, mitjançant la magnetostratigrafia amb l'escala del temps absolut proposada per Gradstein et al. (2004). Aquesta calibració ha permès precisar l'edat absoluta dels límits de les biozones.

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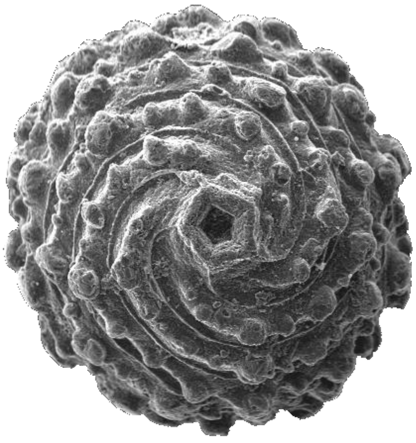
11. ANNEXOS

PUBLICACIONS DE LA TESI



SANJUAN, J., MARTÍN-CLOSAS, C. Taxonomy and palaeobiogeography of charophytes from the Upper Eocene-Lower Oligocene of the eastern Ebro basin (Catalonia, NE Spain). *Geodiversitas* (en revisió-a).

Taxonomie et paléobiogéographie des charophytes de l'Éocène supérieur-Oligocène inférieur de l'est du bassin de l'Ebre (Catalogne, NE de l'Espagne).

Taxonomy and palaeobiogeography of charophytes from the Upper Eocene-Lower Oligocene of the eastern Ebro basin (Catalonia, NE Spain).

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RÉSUMÉ

Dix-huit espèces de charophyte sont documentées dans les faciès transitionnels et terrestres de l'Éocène supérieur-Oligocène inférieur du bassin de l'Ebre oriental. L'assemblage de charophytes est composé par une espèce eurasiatique, *Lychnothamnus stockmansii*, onze espèces avec répartition dans l'Europe (*Harrisichara vasiformis-tuberculata*, *Harrisichara lineata*, *Harrisichara tuberculata*, *Nitellopsis (Tectochara) merianii*, *Lychnothamnus vectensis*, *L. grambastii*, *L. major*, *Gyrogona caelata* , *Psilochara* aff. *acuta*, *Chara* aff. *antennata*, *Ch. rhenana*, *Ch. microcera*, *Sphaerochara labellata*) et deux espèces limitées au bassin de l'Ebre (*Nodosochara jorbae* et *Lychnothamnus longus*). Une nouvelle espèce, *Chara artesica* n. sp. montre des gyrogonites très petits avec un nombre de tours de spire reduit. L'analyse biogéographique des espèces étudiées suggère que au cours de l'Éocène supérieur-Oligocène inferieur l'europe comprenait une bioprovince qui était caractérisée par la présence, régulière et abondante dans tous les bassins, des espèces appartenant aux lignées de *Harrisichara vasiformis-H. tuberculata* et *Lychnothamnus stockmansi-L. major* en plus de *Nitellopsis (Tectochara) merianii* et *Chara microcera*. Dans cette bioprovince, la distribution des charophytes présente une polarité nord -sud de l'abondance relative de plusieurs espèces. Les caractéristiques écologiques liées au dynamisme du bassin de l'Ebre, notamment l'important apport de matériels terrigèniques dans les milieux d'eau douce pendant l'Eocène supérieur-Oligocène, sont opposées aux systèmes carbonatées et avec connexion marine des bassins de Paris, Hampshire et Rhin. Ceci determine que la richesse d'espèces dans le bassin de l'Ebre soit relativement faible. Ces tendances biogéographiques ont des implications dans la biozonation européenne des charophytes, car certaines des biozones ne seraient pas d'utilisation générale.

MOTS CLÉS
Charophyta,
Biogéographie,
Paléogène,
Bassin d'avant-pays de l'Ebre,
bassin de Paris.

ABSTRACT

Eighteen charophyte species are documented from the Upper Eocene-Lower Oligocene transitional and terrestrial facies on the eastern Ebro Basin. The charophyte assemblage is composed of one Eurasian species, *Lychnothamnus stockmansii*, eleven species distributed throughout Europe (*Harrisichara vasiformis-tuberculata, Harrisichara lineata, Harrisichara tuberculata, Nitellopsis (Tectochara) merianii, Lychnothamnus vectensis, L. grambastii, L. major, Gyrogona caelata, Psilochara* aff. *acuta*, Chara aff. *antennata, Ch. rhenana, Ch. microcera, Sphaerochara labellata*) and two species restricted to the Ebro Basin during the interval considered (*Nodosochara jorbae* and *Lychnothamnus longus*). A new species, *Chara artesica* n. sp, with very small gyrogonites ans showing a reduced number of convolutions, is described. A biogeographic analysis of the assemblage studied suggests that during the Upper Eocene and Lower Oligocene, Europe represented a bioprovince characterised by the regular and abundant occurrence of species belonging to the lineages of *Harrisichara vasiformis-tuberculata* and *Lychnothamnus stockmansi-major*, along with *Nitellopsis (Tectochara) merianii* and *Chara microcera* in all European basins. Charophyte distribution in this bioprovince displays a north to south polarity in the relative abundance of a number of species. Ecological features related to the dynamics of the Ebro basin, such as the high terrigenous input in freshwater wetlands during the Upper Eocene-Oligocene, are in contrast to the sea-connected and carbonatic systems of the Paris, Hampshire and Rhine basins. This resulted in low species richness in the Ebro Basin. These biogeographic patterns have implications in the use of some European biozones, which would not be of general use.

KEY WORDS
Charophyta,
Biogeography,
Paleogene,
Ebro foreland basin,
Paris basin.

INTRODUCTION

As aquatic plants that live in brackish and freshwater environments, charophytes are sensitive to environmental distribution factors and are therefore suitable for biogeographical analyses. In contrast to the substantial body of knowledge obtained on the time distribution of Eocene-Oligocene charophyte species from biostratigraphic studies, fossil charophyte assemblages have been poorly studied from the palaeobiogeographic point of view. Riveline (1986) and Anadón et al. (1992) are among the few authors to have addressed the biogeography of the Tertiary charophytes of Europe. Riveline (1986) reported that there were significant differences between charophyte assemblages from different European basins, and she was able to characterise a European charophyte province during the Middle Eocene. Later, in a study of Tertiary charophytes from the Ebro Basin, Anadón et al. (1992) emphasised that this basin displayed a relatively high number of endemic species that could be the result of dispersal barriers related to endorheism. Most subsequent palaeobiogeographic stu-dies on European charophytes have focused on Neogene species, such as *Nitellopsis (Tectochara) merianii* and *Lychnothamnus barbatus* (Soulié-Märsche et al. 1997, 2002 ; Bathia 1999) or on Jurassic and Cretaceous charophytes (Schudack et al. 1998 ; Martín-Closas & Wang 2008).

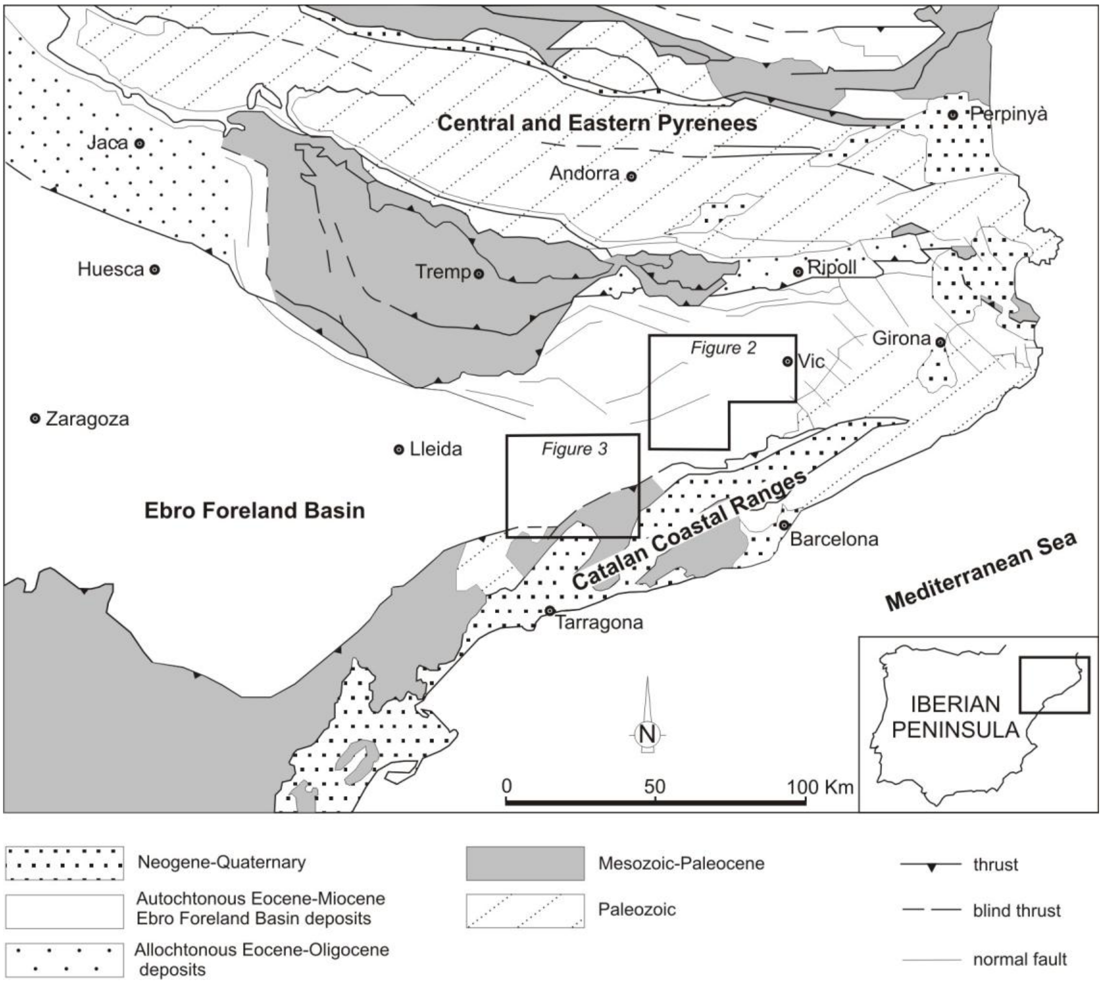


Fig. 1. – Geological sketch of the eastern part of the Ebro Foreland Basin showing location of studied area (modified from Vergés et al., 1998).

The aim of this paper is to describe the charophyte species recorded in the Late Eocene-Early Oligocene of the Ebro Basin, and to document their distribution in order to understand the reasons for their biogeographic range. The implications of their distribution for other fields related to basin analysis, such as palaeoecology and biostratigraphy, are also considered.

MATERIAL AND METHODS

Charophyte species described in this study were obtained from 13 stratigraphic sections showing good exposure of transitional and continental, mainly fluvio-lacustrine, facies that were sampled in the Upper Eocene-Lower Oligocene deposits on the eastern margin of the Ebro Basin (Table 1). In the north-eastern sector of the basin, the studied sections are located near the villages of Sant Boi de Lluçanès, Sobremunt, Sant Bartomeu del Grau, Oristà, Santa Maria d’Oló, Moià, Santpedor, Maians and Rubió (Figs. 1, 2 and Table 1). In the south-eastern sector, the sections and outcrops are located near the villages of Rocafort de Queralt, Sarral, Solivella, Tarrés, Vinaixa and El Talladell (Figs. 1, 3, Table 1).

Fossil remains were obtained from greyish lacustrine mudstones and marls. About 2 kg of sediment per sample was disaggregated in water, oxygen peroxide and Na_2CO_3 solution and later sieved using sieves with mesh

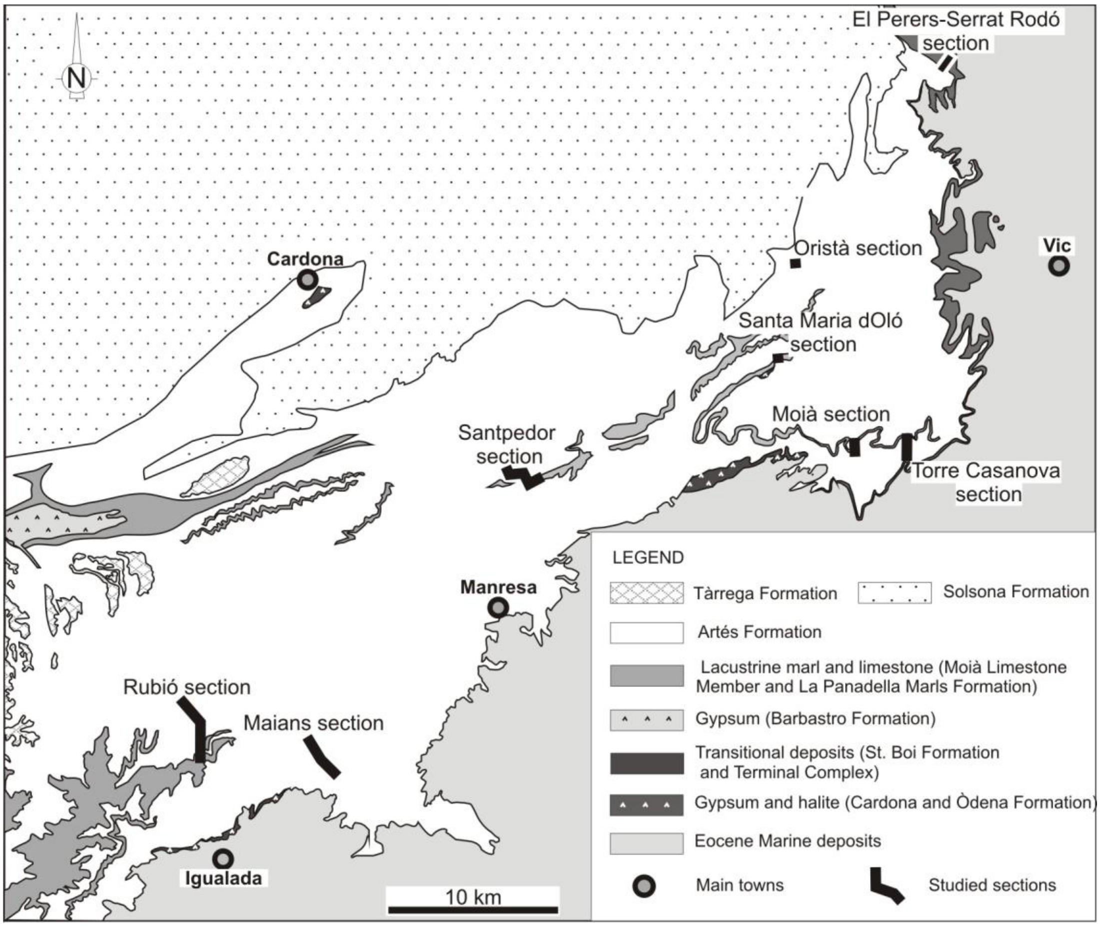


Fig. 2.– Geological setting of the north-eastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Sanjuan and Martín-Closas, 2012).

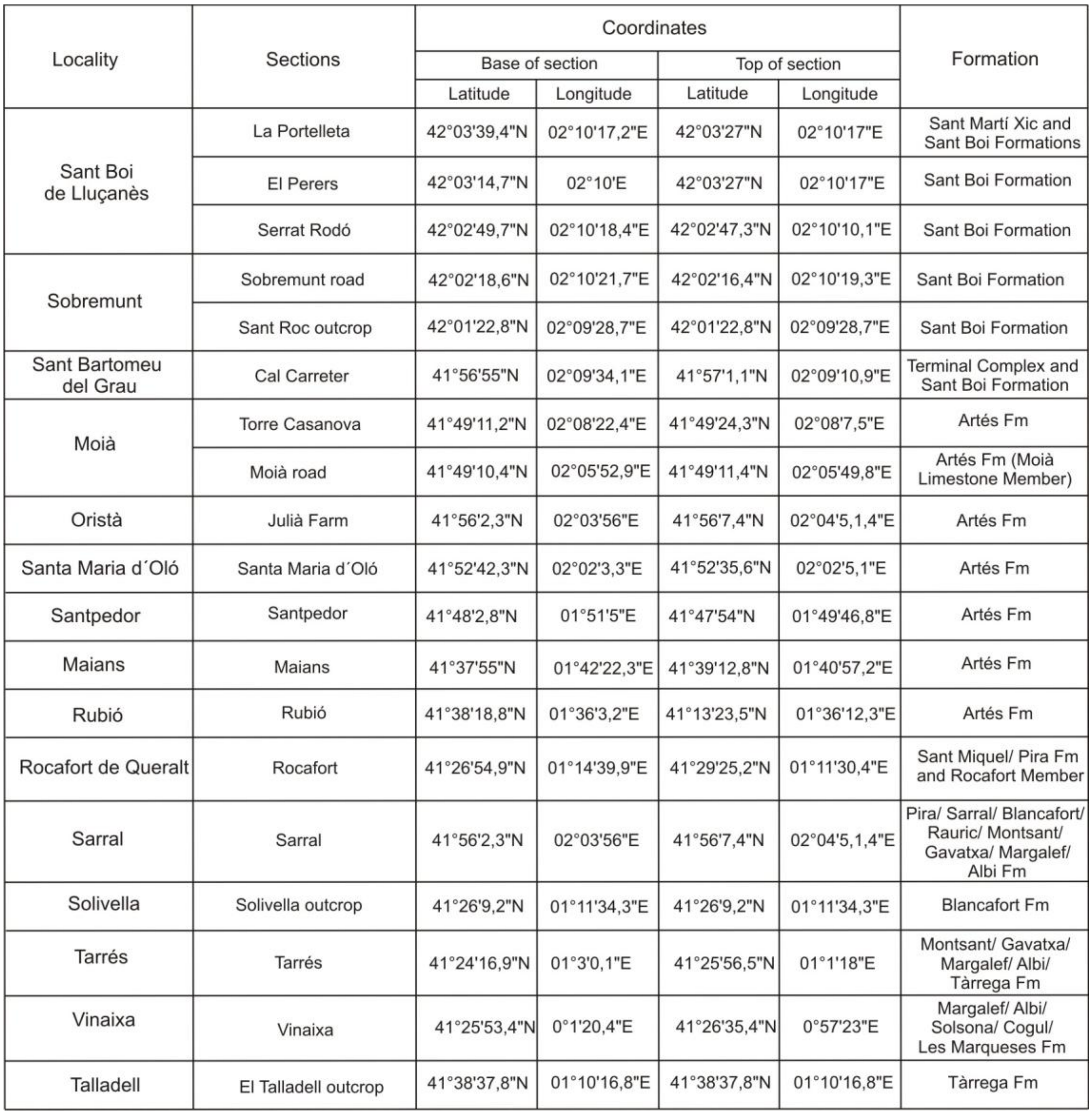
apertures of 1.0 cm, 0.5 and 0.2 mm. Gyrogonites were picked out under a light microscope and measured at 40x magnification (hundred gyrogonites per species). Selected gyrogonites were studied and photographed with a scanning electronic microscope Quanta 200 at the Serveis Científico-Tècnics (Universitat de Barcelona). The material is housed in the Departament d'Estratigrafia, Paleontologia i Geociències marines, Universitat de Barcelona and the Museu Geològic del Seminari Conciliar, Barcelona. Localities and relative abundance of the studied species in each locality are shown in Tables 2, 3 and 4.

ABBREVIATIONS

MSSCB Museu Geològic del Seminari Conciliar de Barcelona

GEOLOGICAL SETTING AND STRATIGRAPHY

The Ebro Basin is the triangular-shaped, southern foreland basin of the Pyrenean Range (Fig. 1). The geological structure of the basin was influenced by flexural subsidence due to the collision between the Iberian and the European plates from the Upper Cretaceous to the Miocene. The



Locality	Sections	Coordinates				Formation
		Base of section		Top of section		
		Latitude	Longitude	Latitude	Longitude	
Sant Boi de Lluçanès	La Portelleta	42°03'39,4"N	02°10'17,2"E	42°03'27"N	02°10'17"E	Sant Martí Xic and Sant Boi Formations
	El Perers	42°03'14,7"N	02°10'E	42°03'27"N	02°10'17"E	Sant Boi Formation
	Serrat Rodó	42°02'49,7"N	02°10'18,4"E	42°02'47,3"N	02°10'10,1"E	Sant Boi Formation
Sobremunt	Sobremunt road	42°02'18,6"N	02°10'21,7"E	42°02'16,4"N	02°10'19,3"E	Sant Boi Formation
	Sant Roc outcrop	42°01'22,8"N	02°09'28,7"E	42°01'22,8"N	02°09'28,7"E	Sant Boi Formation
Sant Bartomeu del Grau	Cal Carreter	41°56'55"N	02°09'34,1"E	41°57'1,1"N	02°09'10,9"E	Terminal Complex and Sant Boi Formation
Moià	Torre Casanova	41°49'11,2"N	02°08'22,4"E	41°49'24,3"N	02°08'7,5"E	Artés Fm
	Moià road	41°49'10,4"N	02°05'52,9"E	41°49'11,4"N	02°05'49,8"E	Artés Fm (Moià Limestone Member)
Oristà	Julià Farm	41°56'2,3"N	02°03'56"E	41°56'7,4"N	02°04'5,1,4"E	Artés Fm
Santa Maria d´Oló	Santa Maria d´Oló	41°52'42,3"N	02°02'3,3"E	41°52'35,6"N	02°02'5,1"E	Artés Fm
Santpedor	Santpedor	41°48'2,8"N	01°51'5"E	41°47'54"N	01°49'46,8"E	Artés Fm
Maians	Maians	41°37'55"N	01°42'22,3"E	41°39'12,8"N	01°40'57,2"E	Artés Fm
Rubió	Rubió	41°38'18,8"N	01°36'3,2"E	41°13'23,5"N	01°36'12,3"E	Artés Fm
Rocafort de Queralt	Rocafort	41°26'54,9"N	01°14'39,9"E	41°29'25,2"N	01°11'30,4"E	Sant Miquel/ Pira Fm and Rocafort Member
Sarral	Sarral	41°56'2,3"N	02°03'56"E	41°56'7,4"N	02°04'5,1,4"E	Pira/ Sarral/ Blancafort/ Rauric/ Montsant/ Gavatxa/ Margalef/ Albi Fm
Solivella	Solivella outcrop	41°26'9,2"N	01°11'34,3"E	41°26'9,2"N	01°11'34,3"E	Blancafort Fm
Tarrés	Tarrés	41°24'16,9"N	01°3'0,1"E	41°25'56,5"N	01°1'18"E	Montsant/ Gavatxa/ Margalef/ Albi/ Tàrrega Fm
Vinaixa	Vinaixa	41°25'53,4"N	0°1'20,4"E	41°26'35,4"N	0°57'23"E	Margalef/ Albi/ Solsona/ Cogul/ Les Marqueses Fm
Talladell	El Talladell outcrop	41°38'37,8"N	01°10'16,8"E	41°38'37,8"N	01°10'16,8"E	Tàrrega Fm

Table 1. –Geographic (coordinates) and lithostratigraphic occurrence of the studied sections on the eastern margin of the Ebro Basin.

Palaeogene sedimentary record is divided into nine depositional sequences related to the emplacement of the south Pyrenean thrust sheets and linked to two widespread marine units of Ypresian and Lutetian-Bartonian ages (Puigdefàbregas et al. 1986). During the Late Eocene, the Pyrenean uplift led to the closing of the basin drainage, restricting marine influence on the basin and causing the deposition of an evaporite plug representing the last marine episode in the southern Pyrenean foreland basin. Since then, uninterrupted Late Eocene to Middle Miocene continental sedimentation has progressively filled the Ebro Basin in (Puigdefàbregas et al. 1992).

Sections located at the north-eastern sector of the Ebro Basin record the last marine-influenced deposits, i.e. marls of the Sant Boi Formation (Sanjuan et al. 2012), sandstones, marls and limestones of the Terminal

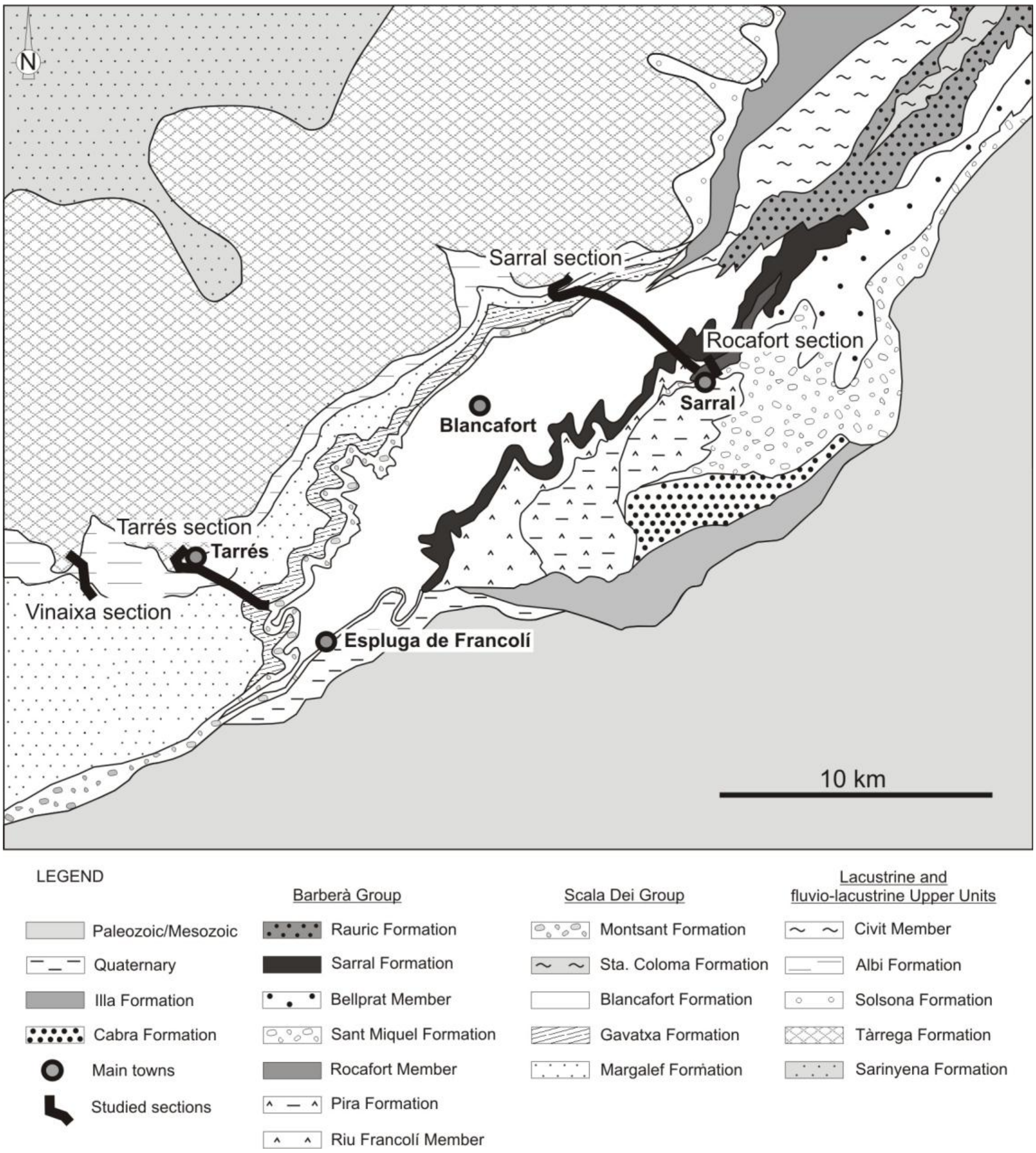
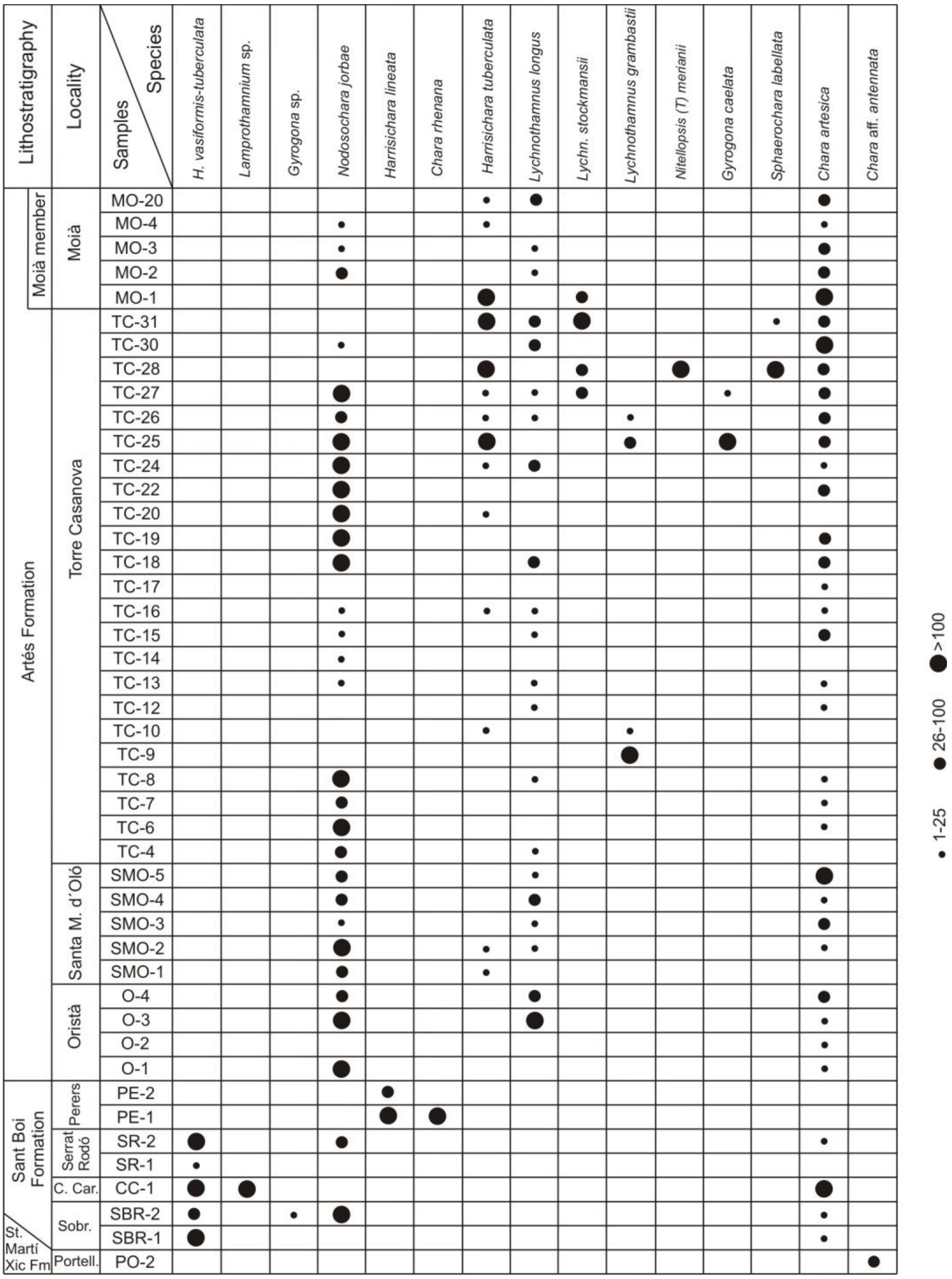


Fig. 3. –Geological setting of the south-eastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Barberà, 1999).

Complex (Travé et al., 1996) and evaporites of the La Noguera, and Òdena Formation (Reguant 1967). Overlying exclusively terrestrial materials are represented by the red beds of the Artés Formation (Sáez 1987) with an isochronous base along the entire north-eastern margin of the Basin (Costa et al. 2010). Sections located in the south-eastern sector of the basin record variable continental deposits laterally equivalent to



Lithostratigraphy	Locality	Samples \ Species	*H. vasiformis-tuberculata*	*Lamprothamnium* sp.	*Gyrogona* sp.	*Nodosochara jorbae*	*Harrisichara lineata*	*Chara rhenana*	*Harrisichara tuberculata*	*Lychnothamnus longus*	*Lychn. stockmansii*	*Lychnothamnus grambastii*	*Nitellopsis (T) merianii*	*Gyrogona caelata*	*Sphaerochara labellata*	*Chara artesica*	*Chara aff. antennata*
Artés Formation Moià member	Moià	MO-20							•	●						●	
		MO-4				•			•							•	
		MO-3				•				•						●	
		MO-2				●				•						●	
		MO-1							⬤		●					⬤	
	Torre Casanova	TC-31							⬤	●	⬤				•	●	
		TC-30				•				●						⬤	
		TC-28							⬤		●		⬤		⬤	●	
		TC-27				⬤			•	•	●			•		●	
		TC-26				●			•	•		•				●	
		TC-25				⬤			⬤			●		⬤		●	
		TC-24				⬤			•	●						•	
		TC-22				⬤										●	
		TC-20				⬤			•								
		TC-19				⬤										●	
		TC-18				⬤				●						●	
		TC-17														•	
		TC-16				•			•	•						•	
		TC-15				•				•						●	
		TC-14				•											
		TC-13				•				•						•	
		TC-12								•						•	
		TC-10							•			•					
		TC-9										⬤					
		TC-8				⬤				•						•	
		TC-7				●										•	
		TC-6				⬤										•	
		TC-4				●				•							
	Santa M. d´Oló	SMO-5				●				•						⬤	
		SMO-4				●				●						•	
		SMO-3				•				•						●	
		SMO-2				⬤			•	•						•	
		SMO-1				●			•								
	Oristà	O-4				●				●						●	
		O-3				⬤				⬤						•	
		O-2														•	
		O-1				⬤										•	
Sant Boi Formation	Perers	PE-2					●										
		PE-1					⬤	⬤									
	Serrat Rodó	SR-2	⬤			●										•	
		SR-1	•														
	C. Car.	CC-1	⬤	⬤												⬤	
	Sobr.	SBR-2	●		•	⬤										•	
		SBR-1	⬤													•	
St. Martí Xic Fm	Portell.	PO-2															●

• 1-25 ● 26-100 ⬤ >100

Table 2. –Charophyte species and gyrogonite abundances of samples studied from the eastern margin of the Ebro Basin (sections of La Portelleta, El Perers-Serrat Rodó, Oristà, Santa Maria d'Oló, Torre Casanova and Moià). Vertical position of samples does not represent their relative stratigraphic position.

the aforementioned Artés Fm, i.e. proximal alluvial fans, fluvial systems, lacustrine and evaporitic beds of the Barberà and Scala Dei Groups which grade upwards to the so-called 'Upper Lacustrine Units' (Colombo 1986).

SYSTEMATIC PALAEOBOTANY

Division CHAROPHYTA Migula, 1897
Class CHAROPHYCEAE Smith, 1938
Order CHARALES Lindley, 1836
Family CHARACEAE Richard ex C. Agardh, 1824
Subfamily Nitelloideae Al. Braun in Migula, 1897
Genus *Sphaerochara* Mädler, 1952, emend. Horn af Rantzien and Grambast, 1962

Sphaerochara labellata Feist and Ringeade, 1977
Fig. 4A-4D.

1977 *Sphaerochara labellata* sp. nov. – Feist & Ringeade, p. 348, pl. 6, figs 1-6.

Description. Gyrogonites small, 329-466 µm high (mean 406 µm) and 310-443µm wide (mean 387µm), oblate or suboblate in shape with an isopolarity index of 90-126 (mean 105). Spiral cells flat or concave. Seven to nine (frequently eight) convolutions are visible laterally, 39-68 µm high. The ornamentation is formed by a midcellular crest, irregularly thickened. The ornamentation disappears in the apical perimeter and reappears at the end of the apical cells, forming a characteristic and well-developed tubercle. Apex flat or slightly convex without modification. Basal plate visible from outside and frequently ornamented with a small rounded tubercle, about 40 µm across.

Distribution. *Sphaerochara labellata* has been found in Upper Priabonian beds of the Aquitaine Basin (Feist and Ringeade 1977). This species has already been reported in the eastern part of the Ebro Basin (Choi 1989 ; Anadón et al. 1992 ; Feist et al. 1994). In this study, *Sphaerochara labellata* is reported from the Torre Casanova (Moià), Santpedor, Rocafort de Queralt and Sarral localities (Tables 2, 3 and 4). The absence of this species in the northern European basins suggests that *Sphaerochara labellata* grew exclusively in southern Europe.

Subfamily Charoideae Al. Braun in Migula, 1897

Genus *Chara* Vaillant, 1719
Chara aff. *antennata* Grambast 1958
Fig. 4E-4H.

1958 *Chara antennata* Grambast, pp. 188, fig. 79.

Description. Gyrogonites small to medium, 350-620 µm high (mean 506 µm) and 235-335 µm wide (mean 304 µm), very elongate in shape, with a high isopolarity index ranging from 117 to 202 (mean 154). Spiral cells concave (about 48 µm wide). Ornamentation consists of irregularly shaped and spaced tubercles (very variable in size, ranging from 15-40 µm in diameter) arranged along the spiral cells. Eight to twelve (frequently nine to ten) convolutions are visible in lateral view. Apex psilocharoid and slightly convex. Base pointed with small pentagonal pore (about 35 µm across).

Discussion. Width of gyrogonites from La Portelleta section (Sant Boi de Lluçanès) was about 75 µm smaller than the type population of Verzenay (France), resulting in a dominance of prolate to perprolate gyrogonite morphologies. Moreover, the specimens studied usually display smaller tubercles than the type population.

Distribution. *Chara antennata* has previously been reported in Upper Eocene deposits from many European basins, i.e. Paris (Grambast 1958; Riveline 1986), Languedoc (Feist-Castel 1971), Provence (Feist-Castel 1977a) and Hampshire basins (Feist-Castel 1977b ; Riveline 1986). In the Ebro Basin, *Chara antennata* has been found at Sant Boi de Lluçanès, associated with benthic foraminifera and marine ostracoda (Table 2). This, along with taphonomic and sedimentological evidence, suggests that it was growing in brackish water.

Chara artesica sp. nov.

Fig. 4I-4L.

Diagnosis. Very small gyrogonites of genus *Chara*, 329-455 µm high and 232-368 µm, ellipsoidal elongate in shape, with a reduced number of convolutions (generally seven) and concave spiral cells.

Holotype. Number 79907 of the Museu Geològic del Seminari Conciliar, Barcelona

Paratypes. Numbers 79908-79911 of the Museu Geològic del Seminari Conciliar, Barcelona.

Type locality. Torre Casanova (Moià, Catalonia, NE Spain). Coordinates: 41º49'13, 6"N, 02º08'13, 2"E.

Type stratum. Marls of the Artés Formation, in a bed at 45 m from the base of the Torre Casanova stratigraphic section (sample TC-9 of Fig. 7 in Sanjuan & Martín-Closas 2012).

Age. Middle Priabonian to Lower Rupelian according to its association with *H. vasiformis-tuberculata* and *Harrisichara tuberculata*.

Derivation of name. From the Artés Formation.

Repository. Museu Geològic del Seminari Conciliar, Barcelona (MGSCB).

Description. Gyrogonites small, 329-455 µm high (mean 397 µm) and 232-368 µm wide (mean 304 µm), prolate and elongate in shape, with an isopolarity index ranging from 109-157 (mean 129). Spiral cells concave to almost flat (about 48 µm wide) and without ornamentation. Six to nine (frequently seven) convolutions are visible in lateral view (Fig. 5). Apex flat or slightly convex. Apical ends of cells unmodified or slightly widening in the centre. Base frequently pointed with a small pentagonal pore (about 45 µm in diameter). Well-calcified gyrogonites show a rounded base.

Affinity. This new species belongs to genus *Chara* as shown by its ellipsoidal gyrogonite, the shape of the apical region, with slightly widening cell endings, and by the shape of the base, pointed to rounded with the spiral cell ends forming a superficial pentagonal pore. The combination of the very small size of gyrogonites, a low number of convolutions and the concavity of the spiral cells allows distinction of the new species from similar species. *Chara artesica* shows strong similarities with *Chara* sp. 2 from the Ebro Basin described by Choi (1989), especially as regards their biometrical characters. However, *Chara artesica* shows concave spiral cells and a flat apex, whereas *Chara* sp.2 shows a convex apex and spiral cells.

Chara rhenana Schwarz and Griessemer, 1994

Fig. 4M-4P.

1994 *Chara rhenana* sp. nov. – Schwarz & Griessemer, p.148, pl. 1, fig. 1-4.

Description. Medium-sized gyrogonites, 550-750 µm high (mean 640 µm) and 283-575 µm wide (mean 392 µm), very elongate, prolate to perprolate in shape, with a high isopolarity index ranging from 111-195 (mean 164). Concave to flat and non-ornamented spiral cells (61 µm wide). Eight

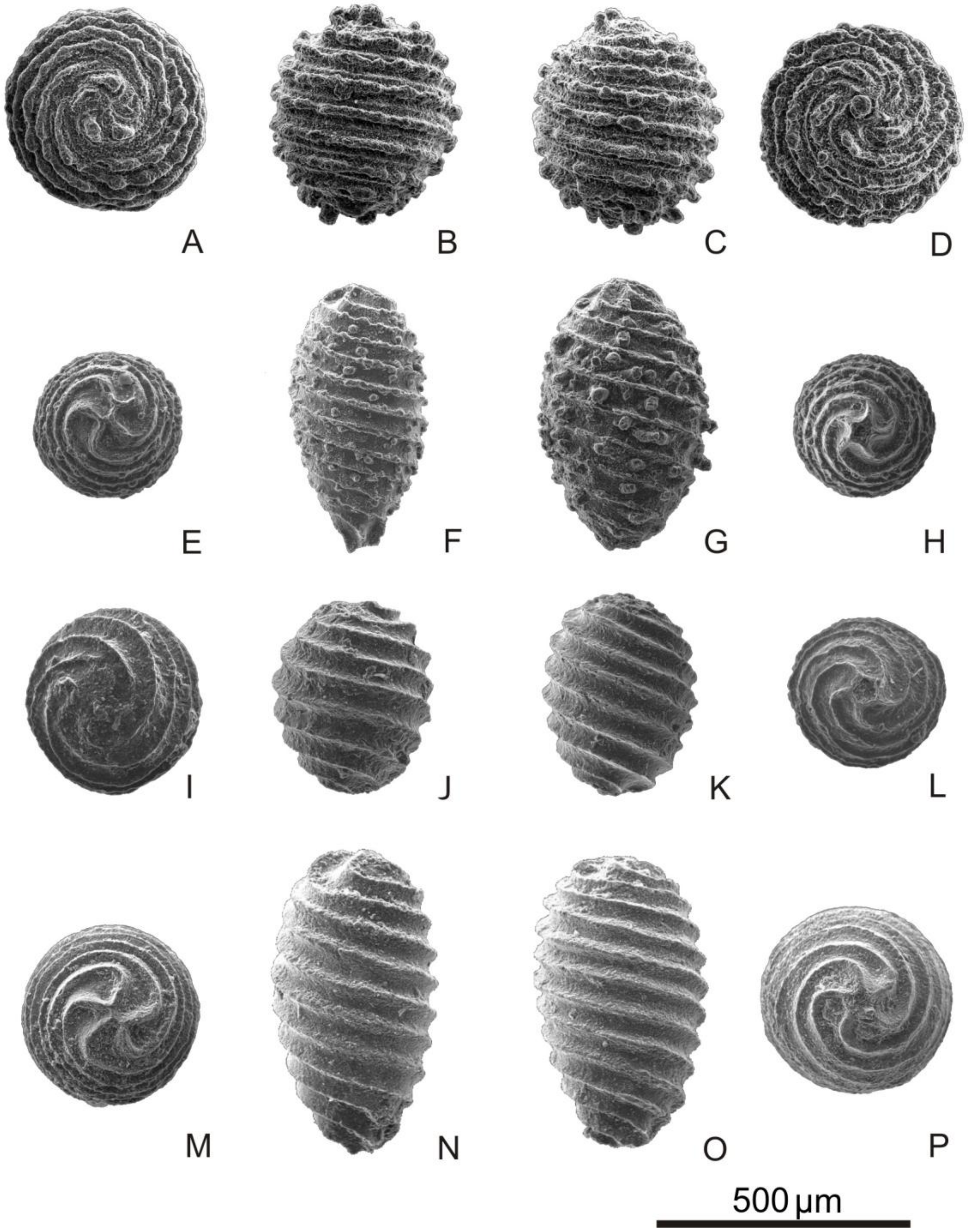


Fig. 4. –Charophytes from the Sant Boi and Artés Fm, Ebro Basin. **A-D**, *Sphaerochara labellata*, Torre Casanova section; **A**, apical view, nº 80063 MGSCB, sample TC-28; **B**, lateral view, nº 0.064 MGSCB, sample TC-28; **C**, lateral view, nº 80065 MGSCB, sample TC-28; **D**, basal view, nº 80066 MGSCB, sample TC-28. **E-H**, *Chara* aff. *antennata*, La Portelleta section; **E**, apical view, nº 80067 MGSCB, sample PO-2; **F**, lateral view, nº 80068 MGSCB, sample PO-2; **G**, lateral view, nº 80069 MGSCB, sample PO-2; **H**, basal view, nº 80070 MGSCB, sample PO-2. **I-L**, *Chara artesica* El Perers-Serrat-Rodó, Torre Casanova, Moià, Santpedor, Maians, Rubió sections; **I**, apical view, paratype nº 79908 MGSCB, sample TC-9; **J**, lateral view, holotype nº 79907 MGSCB sample TC-9; **K**, lateral view, paratype nº 79909 MGSCB, sample TC-9; **L**, basal view, paratype nº 79910 MGSCB, sample TC-9. M-P, *Chara rhenana*, El Perers-Serrat Rodó section; **M**, apical view, nº 80071 MGSCB, sample PE-1; **N**, lateral view, nº 80072 MGSCB, sample PE-1; **O**, lateral view, nº 80073 MGSCB, sample PE-1; **P**, basal view, nº 8007 MGSCB, sample PE-1.

to eleven (frequently nine to ten) convolutions visible in lateral view. Apex flat. Apical ends of spiral cells distinctly widened. Base progressively tapering to pointed. Many specimens show a somewhat conical appearance. Basal pore mainly within a shallow pentagonal depression.

Remarks. Most specimens of *Chara rhenana* from El Perers (Sant Boi de Lluçanès, NE Ebro Basin) are about 100 µm longer than the type population from the Rhine Graben (Schwarz and Griessemer, 1994). The specimens studied are also similar to *Chara vespiformis* Groves, 1926 from the Bembridge flora (Isle of Wight, England). However, *Chara vespiformis* shows more convolutions in lateral view (twelve to thirteen) and the spiral cells are flat or convex.

Distribution. Previously, this species had only been reported in the Upper Eocene/Lower Oligocene from the Rhine Graben in Germany (Schwarz and Griessemer 1994 ; Schwarz 1997). The occurrence of this species in Sant Boi de Lluçanès provides the first occurrence of this species in southern Europe (Table 2).

Chara microcera Grambast & Paul, 1965
Fig. 6A-6D.
1965 *Chara microcera* sp. nov. – Grambast & Paul, p.244, pl. 2, fig. 10-14.

Description. Small-sized gyrogonites, 366-500 µm high (mean 440 µm) and 280-360 µm wide (mean 320 µm), elongate, prolate to perprolate in shape, with an isopolarity index ranging from 120-160 (mean 129). Concave spiral cells (42 µm wide) ornamented with characteristic isolated tubercles arranged along the spiral cells. Nine to eleven (frequently nine) convolutions visible in lateral view. Apex psilocharoid, flat and slightly prominent, ornamented with isolated small tubercles. Base rounded to slightly pointed showing a shallow pentagonal basal pore.

Distribution. *Chara microcera* has been recorded from numerous localities in Europe ranging in age from the Lower Oligocene (Middle Rupelian) to Lower Miocene (Upper Aquitanian). In France, this species occurs in the Paris Basin (Riveline 1986), the Aquitaine Basin (Feist and Ringeade 1977) and the Provence Basin (Feist-Castel 1977a). In Switzerland, this species has been recorded in the western sector of the Swiss Molasse Basin (Kissling 1974). Moreover, this species occurs in many Oligocene localities from the Rhine Graben in Germany (Schwarz 1997). In Spain, this species has already been reported in Lower Oligocene beds of the Ebro Basin (Feist et al. 1994) and in the Loranca Basin (Julia de Agar 1991). In this study, *Chara microcera* is reported from lacustrine marls in the El Talladell and Vinaixa localities (NE Ebro Basin) (Table 4).

Genus *Psilochara* Grambast, 1959
Psilochara aff. *acuta* Grambast & Paul 1965
Fig. 6E-6H.
1965 *Psilochara acuta* sp. nov. – Grambast & Paul, p.243, pl. 2, fig. 5-9.

Description. Gyrogonites small to medium, 360-549 µm high (mean 478 µm) and 280-450 µm wide (mean 327 µm), prolate and elongate in shape, with an isopolarity index ranging from 103-184 (mean 147). Spiral cells flat to concave, about 53 µm wide and without ornamentation. Eight to ten (frequently nine) convolutions are visible in lateral view. Apex psilocharoid and prominent, frequently pointed. This apical cap is very variable in size, ranging between

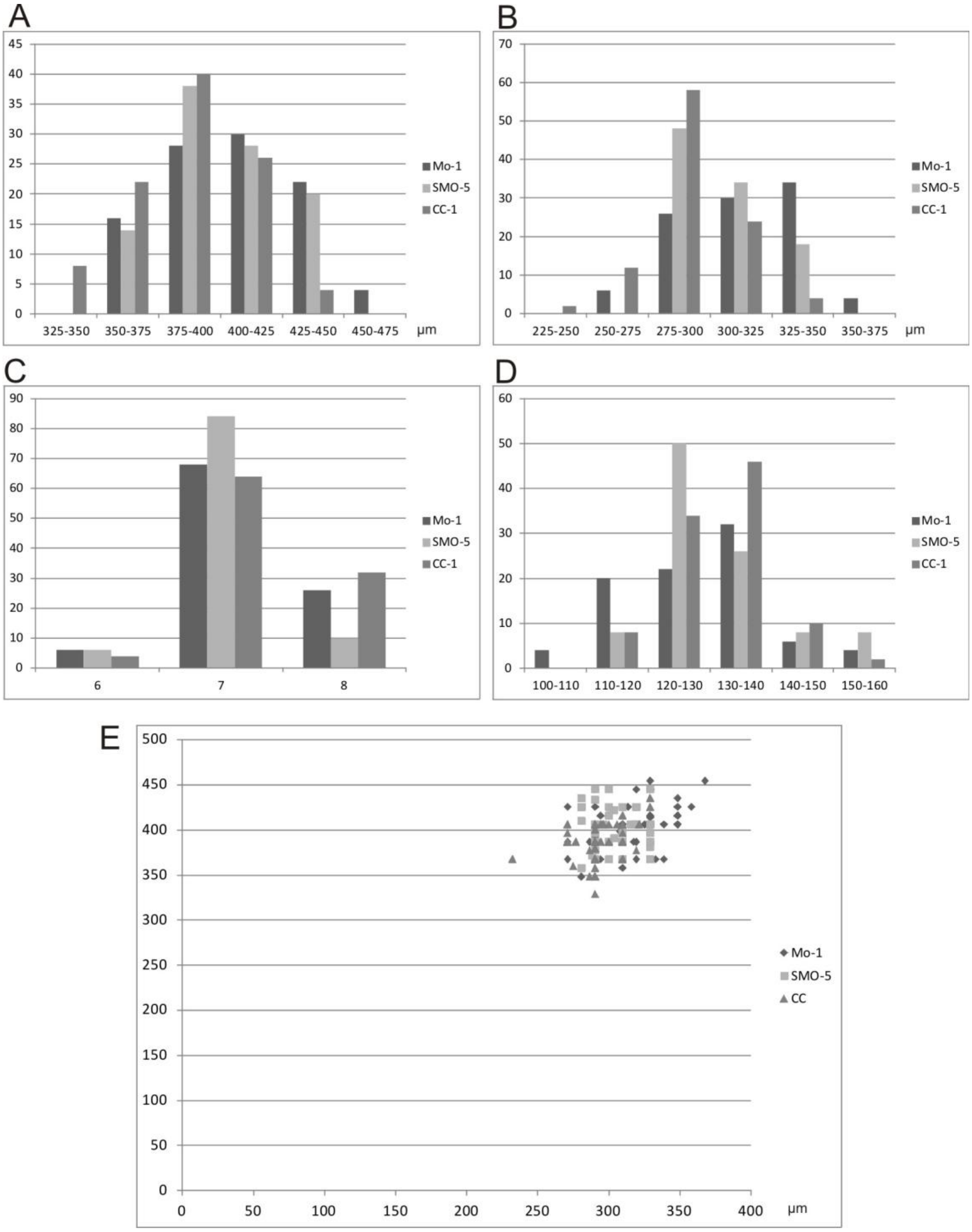


Fig. 5. –Frequency distribution of the length, width, number of convolutions, length/width ratio (ISI) and dispersion graphic of three populations (50 gyrogonites per population) of *Chara artesica.* Populations from samples CC-1 (El Perers-Serrat Rodó section) SMO-5 (Santa Maria d'Oló section) and Mo-1 (Moià section).

15 and 77 µm in high. Base rounded in well-calcified gyrogonites and slightly pointed in poorly calcified gyrogonites, showing a small pentagonal pore (about 40 µm in diameter).

Remarks. The main difference between the population from Sarral (NE Ebro Basin) and the type material from Soisy-sur-École (Paris Basin) is the size of the gyrogonites, which is about 250 µm smaller in the Ebro Basin.

Moreover, gyrogonites from the type population display a larger range of convolutions (eight to twelve).

Distribution. *Psilochara acuta* has been recorded from many localities in Europe. In France, this species has been reported in the Lower Oligocene (Rupelian) of the Paris Basin (Riveline 1986). Schwarz (1997) recorded this species in the Oligocene from the Rhine Graben (Germany). This species was later reported from Upper Eocene (Priabonian) beds in the Transylvanian Basin, Rumania by Baciu & Hartenberger (2001). The occurrence of this species in the Ebro Basin (Sarral locality) represents the

Lithostratigraphy	Locality	Species / Samples	*H. vasiformis-tuberculata*	*Harrisichara tuberculata*	*Lychnothamnus longus*	*Lychnothamnus stockmansii*	*Lychnothamnus vectensis*	*Sphaerochara* sp.	*Sphaerochara labellata*	*Gyrogona caelata*	*Chara artesica*
Artés Formation	Rubió	RB-24			⬤						●
		RB-23			⬤						⬤
		RB-19		•	●						⬤
		RB-18		•							⬤
		RB-17		•							●
		RB-16			•	•					•
		RB-13		•							●
		RB-12		•	•						•
		RB-7									•
		RB-3					●				
	Santpedor	SP-18		•			•				⬤
		SP-17					●				
		SP-15					•				•
		SP-14		•			•				●
		SP-13					•				•
		SP-12		•	•		•		•		⬤
		SP-11					•				•
		SP-10									•
		SP-9					•				⬤
		SP-8		•							
		SP-7					•			•	
		SP-6					•				•
		SP-5			●						●
		SP-4		•			●				⬤
		SP-3					•				•
		SP-2		•		•	●				●
		SP-1		•			•				●
		SPB-5		•			•				●
		SPB-4									⬤
		SPB-3		•	•		•	•			⬤
Sta. Maria Group		SPB-1		●	●	●	●		•		●
	Maians	MA-1	•								

• 1-25 ● 26-100 ⬤ >100

Table 3. –Charophyte species and gyrogonite abundances of samples studied from the eastern margin of the Ebro Basin (sections of Santpedor, Maians and Rubió). Vertical position of samples does not represent their relative stratigraphic position.

southernmost record of this species (Table 4). Riveline (1986) showed that the biostratigraphic range of this species encompasses three charophyte biozones i.e. Lychnothamnus pinguis, Lychnothamnus major and Chara microcera. However, the occurrence of this species within the European Harrisichara vasiformis-tuberculata biozone in the Transylvanian Basin and within the Lychnothamnus vectensis biozone in the Ebro Basin suggests that the occurrence of *Psilochara acuta* starts in the middle part of the Priabonian.

Genus *Lamprothamnium* Groves, 1916

Lamprothamnium sp.
Fig. 6I-6L.

Description. Medium-sized gyrogonites, 432-648 µm high (mean 547 µm) and 297-513 µm wide (mean 434 µm), elongate, prolate to sub-cylindrical in shape, with an isopolarity index ranging from 111-163 (mean 127). Apex lamprothamnoid, truncated, showing a marked periapical depression due to decreasing cell thickness. The base is rounded with a small basal pore (45 µm). Spiral cells flat to convex, without ornamentation. Eight to ten (frequently nine) convolutions are visible in lateral view.

Remarks. A population from Sant Bartomeu del Grau (NE Ebro Basin) belongs to the genus *Lamprothamnium* according to the general sub-cylindrical shape and the apical structure (Table 2). Gyrogonites of *Lamprothamnium* sp. from sample CC-1 is similar in gyrogonite width and convolution number to the Lower Eocene *Lamprothamnium priscum* Castel & Grambast, 1969. However, gyrogonites from the Ebro Basin are about 115 µm shorter, resulting in a more rounded morphology. Poor preservation hinders their specific attribution.

Gyrogona caelata (Reid & Groves, 1921) Grambast, 1956
Fig. 7A-7C.
1921 *Chara caelata* sp. nov. – Reid & Groves, p.184, pl. 4, fig. 4-6.
1956 *Gyrogona caelata* (Reid and Groves) nov. comb. – Grambast, p. 280.
1981 *Gyrogona caelata* forme *fasciata* – Grambast & Grambast-Fessard, p. 21, fig. 11f.

Description. Gyrogonites large, 581-909 µm high (mean 755 µm) and 697-911 µm wide (mean 832 µm), oblate spheroidal in shape with an isopolarity index of 79-112 (mean 92). Five to seven (frequently six), convolutions are visible laterally. Spiral cells large and convex, 161 µm wide, ornamented with a wide midcellular crest. A few gyrogonites from one population are ornamented with large rounded and prominent tubercles which are about 160 µm in diameter. The apical area is flat or rounded with a well-marked periapical depression. The apex is ornamented with prominent apical nodules slightly elongated following the apical cells. These nodules are about 106 µm high and 200 µm wide and they are clustered to form an apical rosette. The base is rounded with a small pentagonal basal pore, about 60 µm across.

Distribution. This species was first described in the Headon beds and in the Bembridge marlstones from the Isle of Wight, England (Reid & Groves 1921). *G. caelata* was later recorded from Upper Lutetian to Upper Priabonian beds from the Paris Basin (Grambast & Grambast-Fessard 1981), the north-eastern part of the Languedoc Basin (Feist-Castel 1971), the

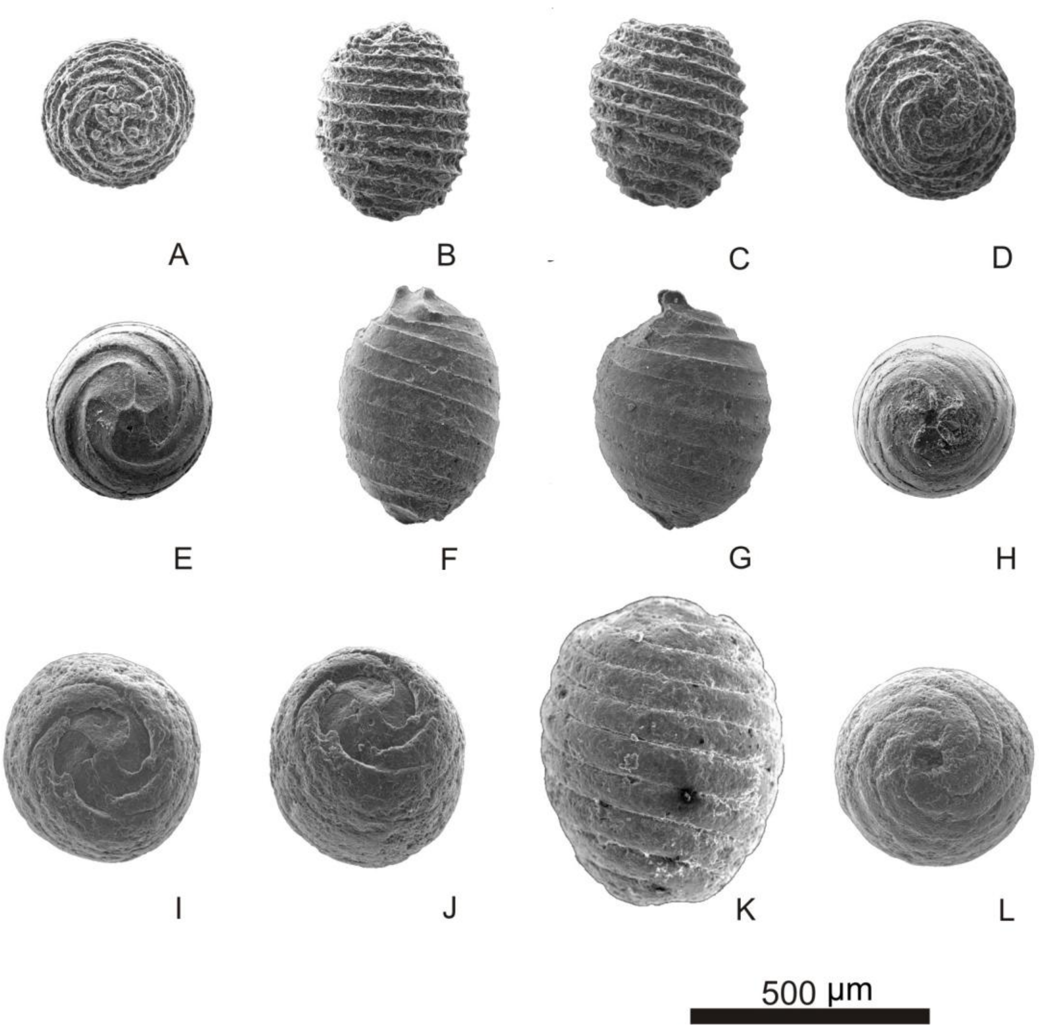


Fig. 6. –Charophytes from Sant Boi, Artés and lateral south-western Formations, Ebro Basin. **A-D**, *Chara microcera*, El Talladell outcrop and Vinaixa section; **A**, apical view, nº 80075 MGSCB, sample BO-2; **B**, lateral view, nº 80076 MGSCB, sample BO-2; **C**, lateral view, nº 80077 MGSCB, sample BO-2; **D**, basal view, nº 80078 MGSCB, sample BO-2. **E-H**, *Psilochara* aff. *acuta*, Sarral section; **E**,apical view, nº 80079 MGSCB, sample SA-2; **F**, lateral view, nº 80080 MGSCB, sample SA-2; **G**, lateral view, nº 80081 MGSCB, sample SA-2; **H**, basal view, nº 80082 MGSCB, sample SA-2. **I-L**, *Lamprothamnium* sp. El Perers-Serrat Rodó section; **I**, apical view, nº 80083 MGSCB, sample CC-1; **J**, lateral view, nº 80083 MGSCB, sample CC-1; **K**, lateral view, nº 80084 MGSCB, sample CC-1; **L**, basal view, nº 80085 MGSCB, sample CC-1.

Aquitaine (Feist & Ringeade 1977) and Provence (Feist–Castel 1977a) basins. In Spain, this species occurs in Upper Lutetian to Upper Priabonian beds from the Ebro Basin (Anadón & Feist 1981 ; Choi 1989). Two more records are added here to the previous localities from the Ebro Basin, Torre Casanova (Moià) and Santpedor (Table 2). Moreover, *G. caelata* has been reported by Iva (1987) in Middle Eocene beds from the north-western part of the Transylvanian Basin (Rumania). This species has also been found in the central part of the Sahara, Algeria (Mebrouk et al. 1997).

Genus *Nodosochara* Mädler, 1955
Nodosochara jorbae Choi, 1989
Fig. 7D-7F.

1989 *Nodosochara jorbae* n. sp. – Choi, p. 33-36, pl. 6, fig. 1-9, pl. 15, fig. 3.

Description. Gyrogonites large, 660-912 µm high (mean 758 µm), and 540-860 µm wide (mean 680 µm), inversely pear-shaped but

Lithostratigraphy	Locality	Species Samples	*Harrisichara tuberculata*	*Lychnothamnus stockmansii*	*Lychnothamnus vectensis*	*Lychnothamnus major*	*Sphaerochara* sp.	*Sphaerochara labellata*	*Nitellopsis (T.) merianii*	*Chara microcera*	*Psilochara* aff. *acuta*
Marqueses Fm	Vinaixa	VI-5							●		
Albi Fm		VI-2								•	
Tàrrega Fm	El Talladell	FA-2				•					
		BO-2								•	
		BO-1				●			•		
	Tarrés	TA-4					•				
Albi Fm	Sarral	SA-19				⬤					●
Margalef Fm		SA-18	•								•
		SA-17									●
Gavatxa Fm		SA-16	•								•
		SA-14	•								●
		SA-13	•								•
Blancafort Fm		SA-10									●
		SA-9									●
		SA-8									●
		SA-7b									⬤
		SA-7a		•	•			•			⬤
		SA-6			•						
Sarral Fm		SA-5	•	●							●
		SA-3	•								●
		SA-2	⬤	●							⬤
	Solivella	SO-2	•								•
Rocafort member	Rocafort de Queralt	RQ-6									•
		RQ-5		•				•			
		RQ-3		⬤				●			●
		RQ-2		•				•			
		RQ-1		•				•			

• 1-25 ● 26-100 ⬤ >100

Table 4. –Charophyte species and gyrogonite abundances of the samples studied from the eastern margin of the Ebro Basin (sections of Rocafort de Queralt, Sarral, Tarrés and Vinaixa sections and Solivella and El Talladell outcrop are represented). Vertical position of samples does not represent their relative stratigraphic position.

sometimes sub-spherical or ellipsoidal, with an isopolarity index ranging from 90-140 (mean 112). Spiral cells 86 µm wide, convex and smooth. Eight to ten convolutions, more often nine, are visible laterally. Apex nitellopsidoid, slightly convex or sub-rounded, with a well-marked thinning and narrowing of the spiral cells in the periapical zone. Periapical depression frequently well-defined. Apical nodules are distinct, more or less prominent, and clustered in an apical rosette. Base rounded or conical. Basal pore superficial and small, without a basal funnel.

Remarks. *Nodosochara thevallensis* Riveline, 1986 from the Upper Eocene of the French Brittany, shows similarities with *N. jorbae*. However, gyrogonites from the single known population of *N. thevallensis* are about 300 µm higher and 230 µm wider than *N. jorbae*, show a higher number of convolutions and the apex is in general less prominent than the type of *N. jorbae*. Other *Nodosochara* species are ornamented.

Distribution. Formerly, *N. jorbae* was thought to be exclusive to the Upper Priabonian to Lower Rupelian of the Ebro Basin (Stephanochara vectensis local biozone of Feist et al. 1994). However, Sanjuan et al. (2012) recently showed that this species already occurred in the middle part of the Priabonian (Harrisichara vasiformis-tuberculata biozone). In the present study, *N. jorbae* is reported abundantly in Sant Boi de Lluçanès, Sobremunt, Sant Bartomeu del Grau, Oristà, Santa Maria d'Oló and Torre Casanova near Moià (Table 2). Moreover, *Nodosochara* aff. *jorbae* has been reported by Mebrouk et al. (1997) in the Middle Eocene from the north-eastern Sahara (Algeria).

Genus *Lychnothamnus* (Ruprecht, 1845)
Leonhardi, 1863 emend. A. Braun in Braun
& Nordstedt, 1882

Lychnothamnus longus Choi, 1989
Fig. 7G-7J.

1989 *Lychnothamnus longus* n. sp. – Choi, p. 7-10, pl. 5, figs 1-12.

Description. Gyrogonites are medium in size, 450-724 µm high (mean 618 µm), and 380-580 µm in width (mean 464 µm). They are ellipsoidal to ovoidal in shape with an isopolarity index of 104-180 (mean 130). The apex is rounded to truncate, in some cases pointed in the centre, and displays a marked apical thinning. The base shows variable morphology, in some cases elongated to form a broad column, and the basal pore shows a small star-shaped funnel. The spiral cells, flat to concave, are devoid of ornamentation and separated by prominent sutures, which in some specimens are bicarinate. Seven to ten (frequently eight) convolutions are visible laterally.

Remarks. *Lychnothamnus longus* is very variable in size, shape and calcification. Many populations show a continuous change from small, cylindrical gyrogonites with concave spiral cells to large broadly rounded specimens with flat spiral cells.

Distribution. Up to now, *L. longus* has only been found in the Late Priabonian-Earliest Rupelian of the eastern part of the Ebro Basin (Choi 1989 ; Sanjuan and Martín-Closas 2012 ; Sanjuan et al. 2012). In the present study, this species was found in the Oristà, Santa Maria d'Oló, Torre Casanova (Moià), Moià, Santpedor and Rubió localities (Tables 2 and 3).

Lychnothamnus stockmansii (Grambast,
1957) nov. comb. Soulié-Märsche, 1989
Fig. 7K-7N.

1957 *Rhabdochara stockmansi* n. sp. – Grambast, p. 355, pl. 8, figs 10-14.
1989 *Lychnothamnus stockmansi* (Grambast, 1957) n. comb. – Soulié-Märsche, p.160.

Description. Gyrogonite large, 581-776 µm high (mean 659 µm), and 387-619 µm wide (mean 561 µm), variable in shape, generally ellipsoidal, with an isopolarity index ranging from102-150(mean 120). The apical zone shows a remarkably constant width of spiral

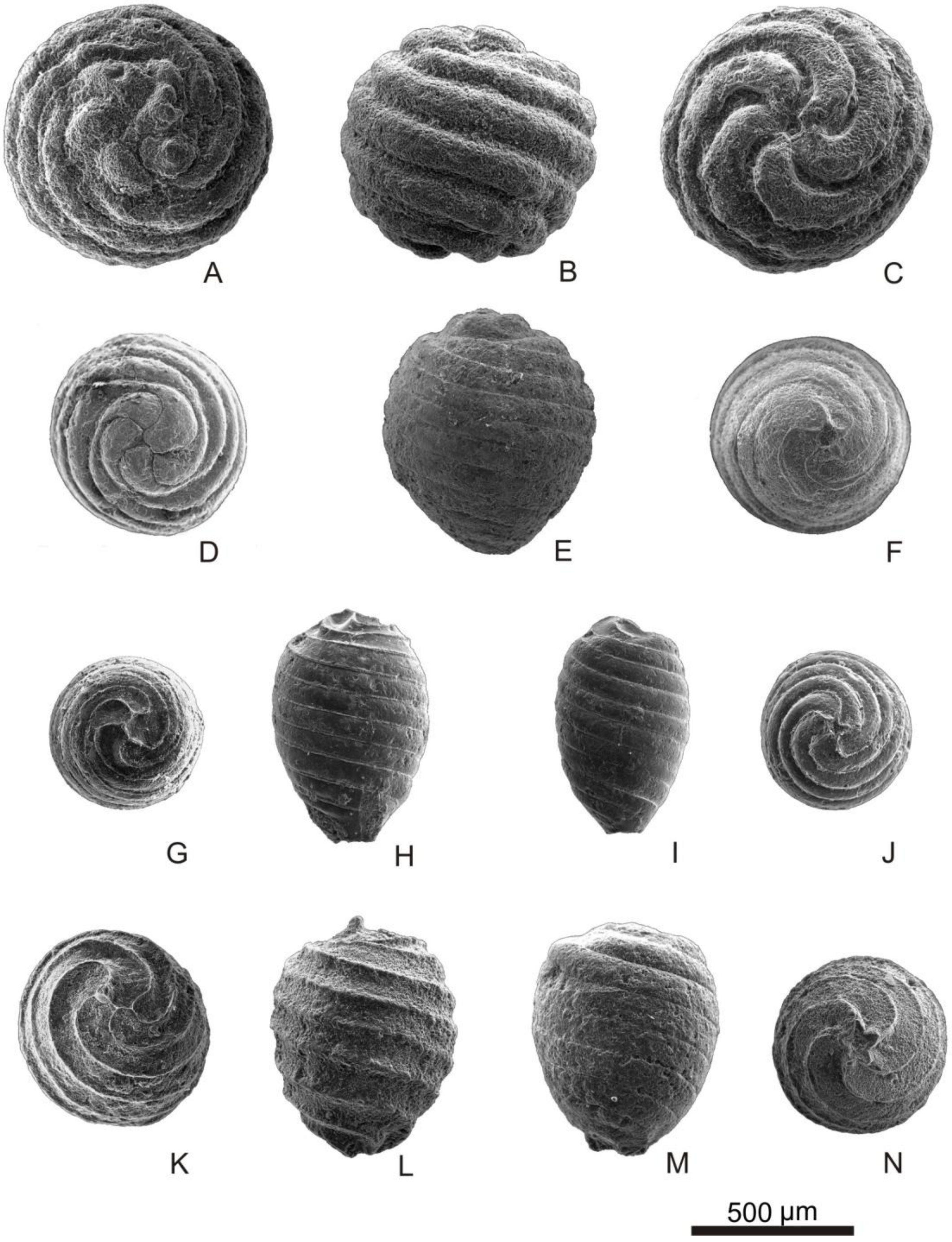


Fig. 7. –Charophytes from Sant Boi and Artés Formations and lateral south-western Formation, Ebro Basin. **A-C**, *Gyrogona caelata*, Torre Casanova section; **A**, apical view, nº 80086 MGSCB, sample TC-25; **B**, lateral view, nº 80087 MGSCB, sample TC-25; **C**, basal view, nº 80088 MGSCB, sample TC-25. **D-F**, *Nodosochara jorbae*, El Perers-Serrat Rodó, Santa Maria d'Oló, Oristà and Torre Casanova sections; **D**, apical view, nº 80089 MGSCB, sample SBR-2; **E**, lateral view, nº 80090 MGSCB, sample O-3; **F**, basal view, nº 80091 MGSCB, sample SBR-2. **G-J**, *Lychnothamnus longus*, Oristà, Santa Maria d'Oló, Torre Casanova, Moià, Santpedor and Rubió sections; **G**, apical view, nº 80092 MGSCB, sample RB-24; **H**, lateral view, nº 80093 MGSCB, sample RB-24; **I**, lateral view, nº 80094 MGSCB, sample RB-24; **J**, basal view, nº 80095 MGSCB, sample RB-24. **K-N**, *Lychnothamnus stockmansii*, Torre Casanova, Moià, Rubió, Rocafort de Queralt and Sarral sections; **K**, apical view, nº 80096 MGSCB, sample TC-31; **L**, lateral view, nº 80097 MGSCB, sample TC-31; **M**, lateral view, nº 80098 MGSCB, sample TC-31; **N**, basal view, nº 80099 MGSCB, sample TC-31.

cells, which results in a flat apex. Some specimens show a small triangular-shaped tubercle, about 45 µm across, located at the junction of the apical cells, which is reminiscent of the sylvula described by Soulié-Märsche (1989) in recent *Lychnothamnus barbatus*. The base is tapered with a star-shaped basal funnel, which is poorly developed in specimens with flat spiral cells. Basal pore about 95 µm in diameter. Six to nine, frequently eight, cells visible laterally. These are normally concave, non-ornamented and separated by prominent sutures which in some specimens are bicarinate.

Distribution. *Lychnothamnus stockmansii* has been recorded from numerous localities ranging in age from the Upper Eocene (Middle Priabonian) to the Lower Oligocene (Lower Rupelian). In France, this species occurs in the Paris (Grambast 1957), Aquitaine (Feist and Ringeade 1977) and Provence (Montenat 1968 ; Touraine,1971) basins. In England, this species has been reported in the Isle of Wight (Feist-Castel 1977b ; Riveline 1986). Stockmans (1960) found this species at a number of Oligocene localities from Belgium. *L. stockmansii* also occurs in Oligocene beds in Germany (Schwarz 1985). In Spain, this species has already been reported from the island of Mallorca (Martín-Closas & Ramos 2005) and in Upper Eocene beds of the Ebro Basin (Choi 1989). In the present study, *L. stockmansii* was found to occur in the Upper Priabonian-Lower Rupelian from the Torre Casanova (Moià), Moià, Santpedor, Rubió, Rocafort de Queralt and Sarral localities (Table 2, 3 and 4). Baciu & Feist (1999) reported it from the Lowermost Oligocene of the Transylvanian Basin (Rumania). The species is well-represented in many Chinese localities. Xinlun (1978) found it in Upper Eocene-Lower Oligocene beds in the Bohai coastal region (NE China). Liu & Wu (1990) and Lu & Luo (1990) reported *L. stockmansii* from the Tarim Basin in the provinces of Qinghai and Xinjiang (NW China). In southern China, this species was reported by Huang et al. (1988) in Guangdong province and by Liu (1989) in Yunnan province. This database suggests that *Lychnothamnus stockmansii* was a Eurasiatic species widely distributed from Western Europe to China.

Lychnothamnus grambastii (Feist-Castel, 1971) nov. comb. Soulié-Märsche, 1989

Fig. 8A-8C.

1971 *Stephanochara grambastii* n. sp. – Feist-Castel, p. 166-168, pl. 11, figs. 1-5.

1989 *Lychnothamnus grambastii* (Grambast, 1957) n. comb. – Soulié-Märsche, p.160.

Description. Medium to large gyrogonite, variable in size, 667-1000 µm high (mean 850 µm), and 560-859 µm in width (mean 703 µm), normally inversed pear-shaped to ellipsoidal with an isopolarity index of 100-144 (mean 120). Spiral cells 100 µm wide, convex and smooth. Eight to ten (frequently nine), convolutions are visible laterally. Apex flat or slightly convex. Spiral cells display marked thinning resulting in a periapical depression. Apex ornamented by tubercles, frequently comma shaped and about 80 µm high and 100 µm wide. Base slightly conical with large basal pore, about 80 µm across, and located within a well-marked funnel.

Remarks. *Lychnothamnus grambastii* shows similar dimensions and morphology to *Lychnothamnus edwarsii* (Grambast 1958) Soulié-Märsche 1989. Moreover, both species have apical nodules and a basal funnel. However, whereas *Lychnothamnus grambastii* shows a slightly pointed base which finishes in a well-marked and wide funnel, *Lychnothamnus edwarsii* shows a rounded base with a superficial basal funnel. Moreover, *Lychnothamnus grambastii* does not show a periapical constriction which occurs in *Lychnothamnus edwarsii*.

Distribution. *Lychnothamnus grambastii* was previously reported from its type locality in the Lower to Middle Priabonian of the Alés Basin, southern France (Feist-Castel 1971). In the Ebro Basin, this species has been reported in many samples from the Torre Casanova (Moià) locality (Table 2). The new data not only widen its distribution to the south but also its biostratigraphic range, which should be enlarged to reach the Upper Priabonian, since it occurs in association with *Harrisichara tuberculata*.

Lychnothamnus vectensis (Groves 1926) nov. comb. Soulié-Märsche, 1989
Fig. 8D-8G.

1926 *Chara vectensis* – Groves, p. 172, pl. 2, figs 2-8.
1958 *Stephanochara vectensis* – Grambast, p. 158.
1989 *Lychnothamnus vectensis* (Grambast, 1957) n. comb. – Soulié-Märsche, p.160.

Description. Medium sized gyrogonite, variable in size, 580-760 µm in high (mean 660 µm), and 480-620 µm in width (mean 560 µm), normally ellipsoidal but sometimes ovoidal in shape with an isopolarity index of 103-145 (mean 121). Spiral cells about 90 µm wide, normally flat to convex. Seven to nine (frequently eight), convolutions are visible laterally. Apex flat or slightly convex. Spiral cells do not show constrictions in the apical periphery but display marked thinning in the apical zone, resulting in an apical to periapical depression. In some gyrogonites, the apex is ornamented by tubercles that vary notably in size depending on the specimen. The base is rounded with a large and superficial basal pore about 70 µm across.

Remarks: *Chara vectensis* was first determined by Groves (1926) based on ellipsoidal gyrogonites extremely variable in size, 800-1000 µm in high and 500-800 µm in width, with 9-10 concave spiral cells usually swollen at the apex and often forming prominent rosettes. The holotype designated and illustrated by Groves (1926), from the A'Court Smith collection at the Natural History Museum, London, belonged precisely to the few specimens which displayed a prominent apical rosette and this character was further considered as diagnostic of the species, rather than as merely an extreme version of its total morphological variation. Taking into account this range of variation, the main difference between the material from the Ebro Basin and the type material is the size of the gyrogonites, which are about 200 µm smaller in the Ebro Basin. Gyrogonites of this species from the Paris Basin gathered in the collection created by J. Riveline (Laboratoire de Biominéralization et énvironnement sedimentaires, Université Pierre et Marie Curie, Paris) show similar biometric parameters (mean values of 715 µm high, 595 µm wide, isopolarity index of 115 and 8 convolutions). Furthermore, most of the gyrogonites from the Paris Basin show a swollen apex and concave spiral cells whilst the presence of prominent apical nodules is not common.

Distribution: *Lychnothamnus vectensis* has been recorded in the Hampshire (Reid & Groves 1921) and Paris (Riveline 1986) basins. In the Ebro Basin, this species occurs within Uppermost Priabonian-Lower Rupelian deposits in Santpedor, Rubió and Sarral (Tables 3 and 4).

Lychnothamnus major (Grambast & Paul 1965) nov. comb. Soulié-Märsche, 1989

Fig 8H-8K.

1965 *Rhabdochara major* n. sp. – Grambast & Paul, p. 241-242, pl. 2, figs 1-4.

1989 *Lychnothamnus major* (Grambast and Paul 1965) nov. comb. – Soulié-Märsche, p. 159.

Description. Gyrogonites very large, 780-1000 µm high (mean 900 µm) and 680-840 µm wide (mean 780 µm), ellipsoidal in shape with an isopolarity index ranging from 105-128, (average 117). Spiral cells in the apical zone show a remarkably constant width, which results in a flat apex. The base is tapered with a star-shaped basal pore, about 180 µm in diameter. Eight to nine (frequently eight) cells visible laterally. These are normally concave, about 118 µm in width, non-ornamented and separated by prominent sutures which in some specimens are bicarinate.

Remark. Many authors have reported that transitional morphotypes occur between *L. stockmansi* and *L. major* (Feist-Castel 1977a; Baciu and Feist 1999).

Distribution. *Lychnothamnus major* has hitherto been recorded from numerous European sites of various ages within the Rupelian. In France, this species occurs in the Paris (Grambast & Paul 1965 ; Riveline 1986), Aquitaine (Feist and Ringeade 1977), Provence (Feist-Castel 1977a) and Languedoc (Grambast 1962) basins. In Germany, this species has been documented by Feist-Castel (1977a) and Schwarz (1985). Moreover, Kissling (1974) reported this species in the western sector of the Swiss Molasse. *L. major* was reported in north-western Rumania by Baciu & Feist (1999). In Spain, it has already been described from some localities of the Ebro Basin by Choi (1989) and we found it in Sarral and El Talladell (Table 4).

Genus *Nitellopsis* Hy, 1889

Subgenus *Tectochara* Grambast & Grambast-Fessard, 1954

Nitellopsis (Tectochara) merianii (Al. Braun ex Unger, 1852) Grambast & Soulié-Märsche, 1972.

Fig. 8L-8N.

1852 *Chara meriani* Unger, p.82, Pl. 25, fig. 10-12.

1954 *Tectochara meriani* n. sp. – Grambast & Grambast-Fessard, p. 668.

1972 *Nitellopsis (Tectochara) meriani*– Grambast & Soulié-Märsche, p. 11.

Description. Large gyrogonites, variable in size, 818-1262 µm high (mean 1084 µm), and 716-1045 µm wide (mean 909 µm), normally ovoid but sometimes ellipsoidal in shape with an isopolarity index of 96-146 (mean 121). Spiral cells 126 µm wide, generally convex. Eight to eleven (often nine) convolutions visible in lateral view. Apex nitellopsidoid, slightly convex or sub-rounded, with well-marked thinning and narrowing of the spiral cells in the periapical zone. Apical nodules present, more or less prominent. Base rounded or slightly conical with large basal pore, 100 µm across, and located within a pentagonal funnel.

Remarks. This species shows a notably reduced size in comparison with coeval *Nitellopsis* species such as *N. (T) wannacotti*, *N. (T) aemula* and *N. (T) latispira*, which are about 300 µm larger and are in general more rounded in shape.

Distribution. *Nitellopsis (Tectochara) merianii* appears to be exclusive to Europe during the Upper Eocene (Upper Priabonian)

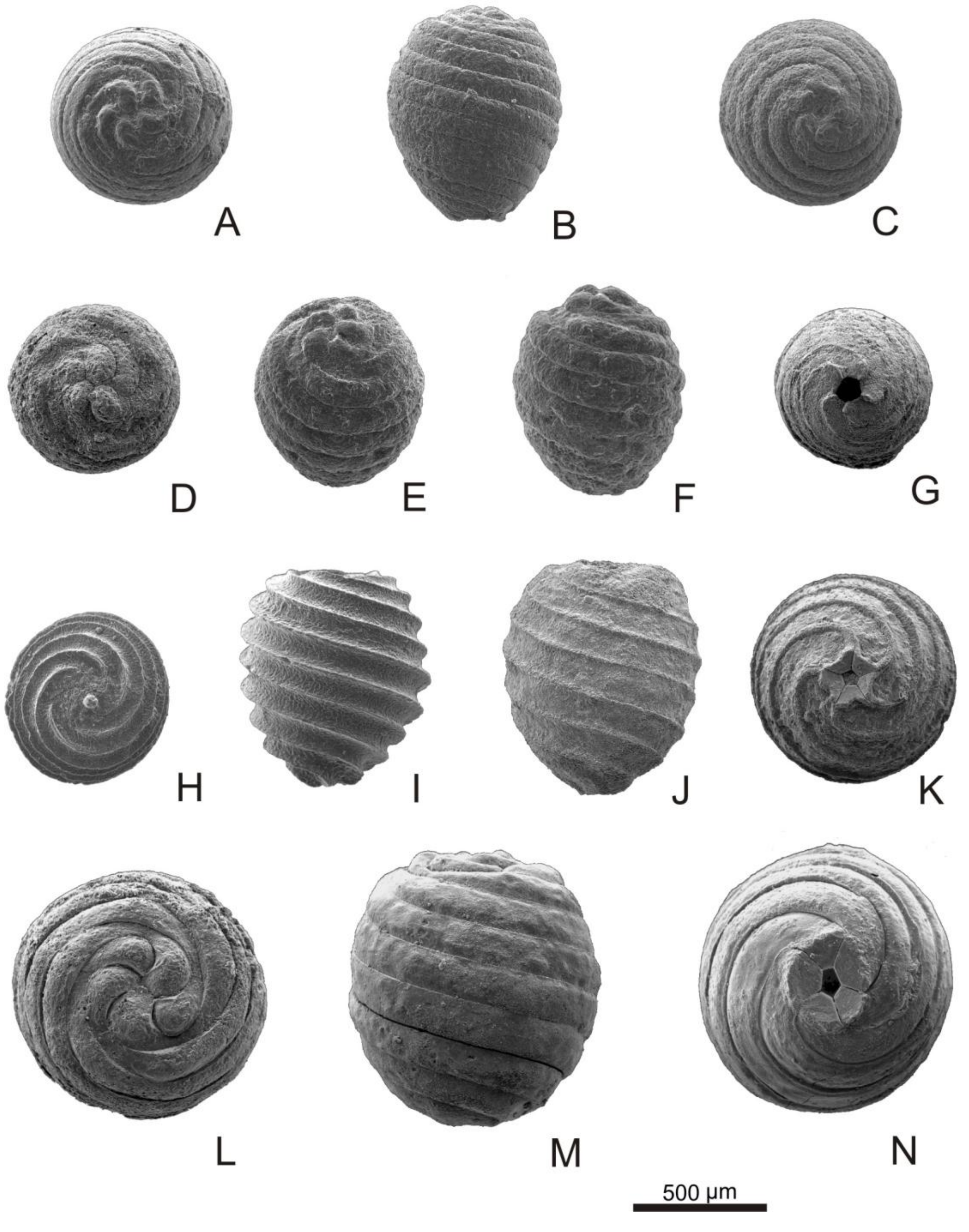


Fig. 8. –Charophytes from the Artés and lateral south-western Formations, Ebro Basin. **A-C**, *Lychnothamnus grambastii*, Torre Casanova section; **A**, apical view, nº 80100 MGSCB, sample TC-9; **B**, lateral view, nº 80101 MGSCB, sample TC-9; **C**, basal view, nº 80102 MGSCB, sample TC-9. **D-F**, *Lychnothamnus vectensis*, Santpedor, Rubió and Sarral sections; **D**, apical view, nº 80103 MGSCB, sample RB-3; **E**, oblicuous view, nº 80104 MGSCB, sample SP-18; **F**, lateral view, nº 80104 MGSCB, sample SP-18; **G**, basal view, nº 80105 MGSCB, sample SP-4. **H-K**, *Lychnothamnus major*, Sarral section and El Talladell outcrop; **H**, apex, nº 80106 MGSCB, sample BO-1; **I**, lateral view, nº 80107 MGSCB, sample BO-1; **J**, lateral view, nº 80108 MGSCB, sample SA-19; **K**, basal view, nº 801 MGSCB 09, sample SA-19. **L-N**, *Nitellopsis (Tectochara) merianii*, Torre Casanova and Vinaixa sections and El Talladell outcrop; **L**, apical view, nº 80110 MGSCB, sample VI-5; **M**, lateral view, nº 80111 MGSCB, sample VI-5; **N**, basal view, nº 80112 MGSCB, sample VI-5.

and Lower Oligocene (Rupelian). It has been reported in Rupelian lacustrine deposits from many French localities, i.e. Paris (Grambast and Paul, 1965; Riveline; 1986), Aquitaine (Feist and Ringeade, 1977), the western sector of Languedoc (Grambast 1962 ; Feist-Castel 1971) and Provence (Touraine 1971). This species was reported in Lower Oligocene beds from the Rhine Graben in Germany (Schwarz 1997). Moreover, this species has been recorded in Lower Rupelian deposits from the Transylvanian Basin in Rumania (Baciu and Feist 1999). In Spain, this species has been documented in Upper Eocene-Lower Oligocene deposits from the Ebro Basin (Choi 1989) and from Upper Oligocene rocks in the central Iberian Peninsula (Loranca Basin) by Julia de Agar (1991). Recently, Sanjuan & Martín- Closas (2012) reported the oldest record of this species in the Upper Priabonian of the eastern Ebro Basin, namely at Torre Casanova (Moià), El Talladell and Vinaixa (Tables 2 and 4). During the Uppermost Oligocene-Lower Miocene, this species expanded from western Europe across the Paratethys realm to NE China and SE Asia, ranging from latitude 18º N to 50º N and covering the entire Eurasian landmass (Soulié-Märsche et al. 1997 and references therein). Recently, Soulié-Marsche et al. (2002) also reported *N (T) merianii* in Miocene beds from Morocco (Africa).

Genus *Harrisichara* Grambast, 1957
Harrisichara lineata Grambast, 1957
Figs 9D-9I.

1957 *Harrisichara lineata* n. sp. – Grambast, p. 27, pl. 4, figs 5-7.

Description. Gyrogonite large, 642-960 μm high (mean 753 μm), and 520-853 μm wide (mean 659 μm), sub-spherical, ellipsoidal or oval in shape with an isopolarity index of 83-133(mean 115). Spiral cells flat or concave. Eight to eleven (frequently nine), convolutions are visible laterally. While most of the gyrogonites show a characteristic regular midcellular crest, some specimens are smaller and show an ornamentation consisting of small nodules arranged along the central line of the spiral cells (Figs. 9G-9I). Apex flat to rounded, frequently ornamented with comma-shaped tubercles. Base elongated, terminating in a small column.

Remarks. The specimens found at El Perers (Sant Boi de Lluçanès, NE Ebro Basin) display variable size and ornamentation patterns, the two characters being closely related. Smaller specimens present small and irregular, shortly spaced tubercles (Fig. 9I), and in some cases small nodules are poorly connected showing an incipient midcellular crest (Fig. 9H). In contrast, most of the gyrogonites are larger and show a regular midcellular crest. The largest gyrogonites show a slightly rippled midcellular crest, especially marked in the apical zone (Fig. 9G). This range of variation is possibly controlled by the palaeoenvironment.

Distribution. *H. lineata* is distributed in the Middle Bartonian to Upper Priabonian of Europe. In France, it occurs in the Paris Basin (Riveline 1986), the north-western part of the Languedoc Basin (Feist-Castel 1971) and the Aquitaine (Feist and Ringeade 1977) and Provence (Feist-Castel 1977a) basins. In Germany, *H. lineata* occurs in the Rhine Graben Basin (Schwarz and Griessemer 1994). *H. lineata* has also been reported in the North of Spain. It has recently been reported by Mochales et al. (2012) within Upper Eocene deposits of the Ainsa Basin (south-central Pyrenees). In the eastern Ebro

Basin, this species only occurs in Sant Boi de Lluçanès (Table 2).

Harrisichara vasiformis-tuberculata Feist-Castel, 1977b
Figs 9A-9C.
1977b *Harrisichara vasiformis-tuberculata* – Feist-Castel, p. 152, pl. 21, figs 2-3.

Description. Gyrogonites medium to large, 594-756 µm high (mean 655 µm), and 567-675 µm wide (mean 619 µm), ovoidal or sub-ovoidal in shape with an isopolarity index of 96-116(mean 106). Nine to eleven (frequently ten) convolutions visible laterally. Spiral cells flat or concave, 75-125 µm in width. The ornamentation consists of regularly spaced elongated tubercles, which may be joined by a fine central crest. Apex flat or rounded, generally without any periapical modification in the spiral cells, but with comma-shaped tubercles in a few specimens. Base rounded, conical or elongated in a small column. Basal pore pentagonal, 54 µm across.

Distribution. *H. vasiformis-tuberculata* occurs in the Hampshire Basin, England (Feist-Castel 1977b). In France, it occurs in the Paris (Riveline 1986) and Provence (Feist-Castel 1977a) basins. It has also been reported from Transylvania (Rumania) by Baciu & Feist (1999). In Spain, this species has been reported by Martín-Closas & Ramos (2005) in the Island of Mallorca and by Sanjuan et al. (2012) in the eastern part of the Ebro Basin. In the present study, this species has been recorded in Sant Boi de Lluçanès, Sobremunt, Sant Bartomeu del Grau and Maians (Tables 2 and 3). Sanjuan & Martín-Closas (2012) showed that in the Ebro Basin, this species grew solely in brackish environments.

Harrisichara tuberculata (Lyell, 1826) Grambast, 1957
Fig. 9J-9L.
1826 *Chara tuberculata* – Lyell, p. 94, pl. 13, figs 7-8.
1957 *Harrisichara tuberculata* n. sp. – Grambast, p. 10, pl. 6, figs 1-3,8-10.

Description. Gyrogonite large, 717-1040 µm high (mean 901 µm), and 670-940 µm wide (mean 802 µm), prolate spheroidal in shape with an isopolarity index of 86-125(mean 112). Spiral cells flat or concave. Nine to eleven (frequently nine), convolutions are visible laterally. The ornamentation is typically formed by large, regularly spaced tubercles, which have a variable size ranging from 54-90 µm. In some cases, tubercles may be joined. Apex flat or slightly convex and ornamented with tubercles as well. Base elongated, terminating in a short column.

Distribution. *H. tuberculata* is widely distributed in the Upper Priabonian to Lower Rupelian of Europe. In France, this species occurs in the Paris Basin (Riveline, 1986), the north-eastern part of the Languedoc basin (Feist-Castel 1971) and the Aquitaine (Feist and Ringeade 1977) and Provence (Feist-Castel 1977a) basins. *H. tuberculata* was reported in the Isle of Wight, England by Feist-Castel (1977b) and Riveline (1986), and in Belgium (Stockmans 1960), Germany (Schwarz 1997) and Rumania (Baciu & Feist 1999). In Spain, Adrover et al. (1982) found this species in the Barranco de la Calera (Teruel Province) locality in the Iberian Chain and it is especially common in the eastern Ebro Basin (Feist et al. 1994; Sanjuan & Martín-Closas 2012). In the area studied, this species occurs within Upper Priabonian-Lower Rupelian deposits from Oristà, Santa Maria d'Oló, Torre Casanova (Moià), Moià, Santpedor, Rubió, Sarral and Solivella (Tables 2, 3 and 4).

CHAROPHYTE PALAEOBIOGEOGRAPHY

Palaeogeographic distribution of charophytes from the Ebro Basin during the Upper Eocene-Lower Oligocene.

Present knowledge indicates that most of the charophyte species reported from the Ebro Basin near the Eocene –Oligocene boundary were characteristic of and exclusive to the European basins. These thirteen European species were *Harrisichara lineata, H. vasiformis-tuberculata, H. tuberculata, Lychnothamnus vectensis, L. grambastii, L. major, Nitellopsis (Tectochara) merianii, Psilochara* aff. *acuta, Chara* aff. *antennata,* C. *rhenana ,C. microcera, Gyrogona caelata* and *Sphaerochara labellata*.

Species with supra-continental ranges, such as *Lychnothamnus stockmansii*, appear to be rare in the Ebro basin during the interval studied. In contrast, three of the species recorded in the Ebro Basin appear to be unique to this basin during the interval studied, *Lychnothamnus longus, Nodosochara jorbae* and *Chara artesica sp. nov.* The two former species were considered as endemic to this basin by Anadón et al. (1992), but later *N. jorbae* was documented in the Middle Eocene from the north-eastern Sahara (Algeria) by Mebrouk et al. (1997). Despite their apparently restricted distribution, the above-mentioned three species are extremely abundant in the Upper Priabonian-Lower Rupelian record of the Ebro Basin and display wide ecological tolerances (Sanjuan & Martín-Closas 2012).

The occurrence of species limited to one basin is a general pattern in Upper Eocene-Lower Oligocene European basins rather than a particularity of the Ebro Basin. Thus, present knowledge indicates that six species are restricted to the Rhine Graben, *Chara nannocarpa* Schwarz, 1985; *Chara praemicrocera* Schwarz & Griessemer, 1992; *Lychnothamnus semisculpta* (Schwarz, 1988) nov. comb. Soulié-Märsche, 1989; *Lychnothamnus exigua* (Schwarz 1988) nov. comb. Soulié-Märsche 1989, *Sphaerochara pygmaea* Schwarz & Griessemer, 1992 and *Sphaerochara inexpectata* Schwarz, 1997. In addition, the distribution of at least three charophyte species is limited to the Hampshire Basin, namely *Nitellopsis (Tectochara) latispira* Feist-Castel, 1977b; *Lychnothamnus compta* (Grambast, 1958) nov. comb. Soulié-Märsche, 1989 and *Sphaerochara major* Riveline, 1986. The Aquitaine Basin has also yielded two charophyte species unique to this basin, namely *Lychnothamnus lychnothamnoides* (Feist & Ringeade, 1977) Soulié-Märsche, 1989 and *Hornichara blayaci* (Feist & Ringeade, 1977) nov. comb. Feist and Grambast-Fessard in Feist et al., 2005.

Definition of a European charophyte bioprovince during the Priabonian-Rupelian

Seventy-two charophyte species are known from the Upper Eocene (Priabonian) to Lower Oligocene (Rupelian) European record (Riveline 1986). The available dataset reveals that many charophytes were common in all European basins, permitting the definition of a European charophyte bioprovince. This has already been suggested by Riveline (1986) for Middle Eocene charophyte species but has not been explored before for the Upper Eocene and Lower Oligocene. Two well-distributed and

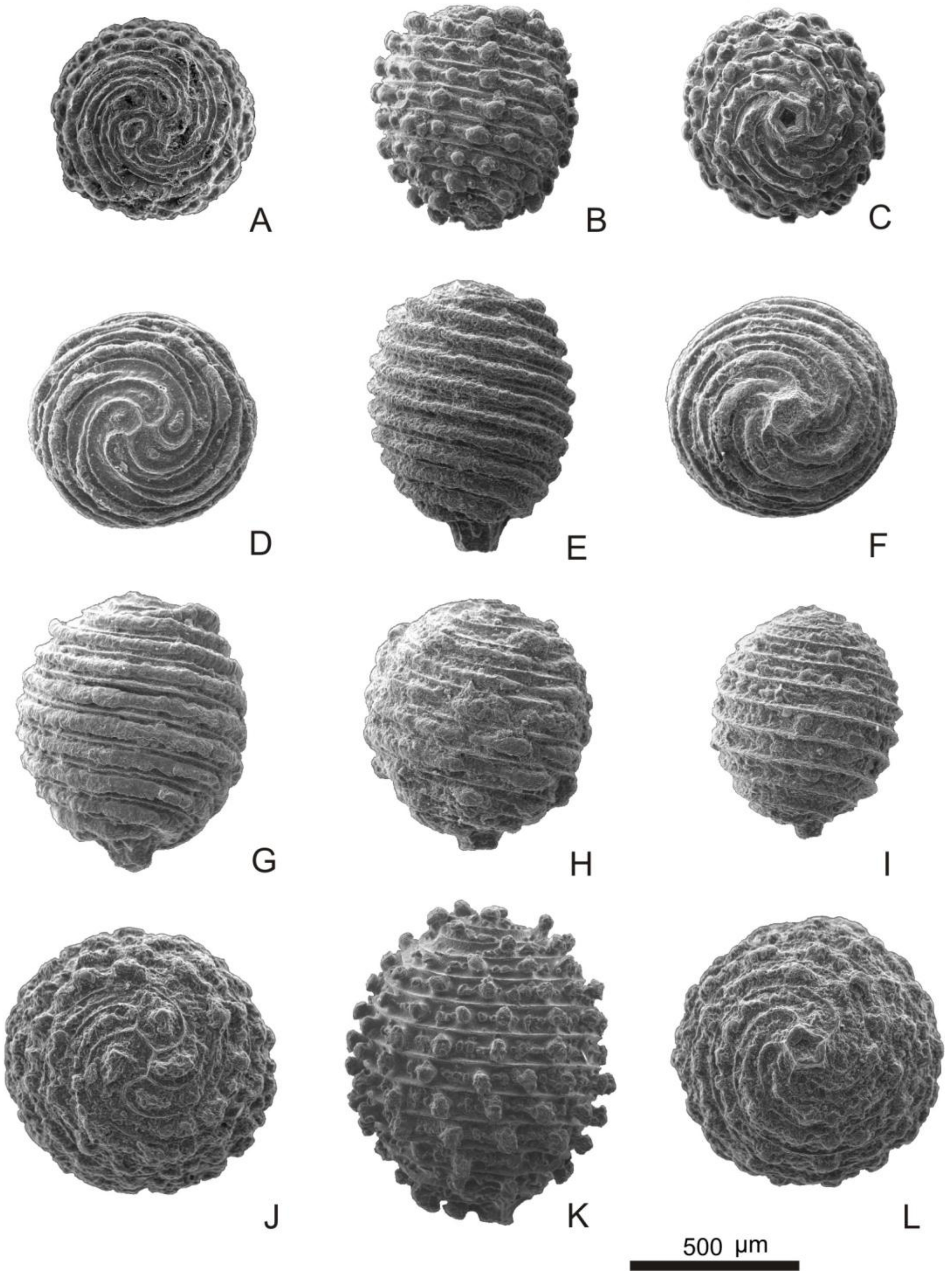


Fig. 9. –Charophytes from Sant Boi, Artés and lateral south-western Formations, Ebro Basin. **A-C**, *Harrisichara vasiformis-tuberculata*, Serrat Rodó, Sobremunt road and Cal Carreter sections; **A**, apical view, nº 80113 MGSCB sample SBR-1; **B**, lateral view, nº 80114 MGSCB, sample SBR-1; **C**, basal view, nº 80115 MGSCB, sample SBR-1. **D-I**, *Harrisichara lineata*, El Perers section; **D**, apical view, nº 80116 MGSCB, sample PE-1; **E**, lateral view, nº 80117 MGSCB, sample PE-1; **F**, basal view, nº 80118 MGSCB, sample PE-1; **G**, lateral view, nº 80119 MGSCB, sample PE-1; **H**, lateral view, nº 80120 MGSCB, sample PE-1; **I**, lateral view, nº 80121 MGSCB, sample PE-1. **J-L**, *Harrisichara tuberculata*, Oristà, Santa Maria d'Oló, Torre Casanova, Moià, Santpedor, Rubió and Sarral sections and Solivella outcrop; **J**, apical view, nº 80122 MGSCB, sample MO-1; **K**, lateral view, nº 80123 MGSCB, sample SO-2; **L**, basal view, nº 80124 MGSCB, sample MO-1.

abundant charophytes lineages, *Harrisichara vasiformis-H. tuberculata* and *Lychnothamnus stockmansii-L. major*, comprise the main species, enabling the characterisation of this bioprovince (Fig. 10). The distribution of these species is homogeneous in the different basins and most of them represent the dominant taxa of the assemblages. In addition to these species, some other species were common to all basins only during particular time spans. For instance, *Nitellopsis (T) merianii* characterises the European basins starting from the Uppermost Priabonian and Rupelian whilst *Chara microcera* was abundant only during the Rupelian.

Europe and Asia are the two regions of the world with the best-documented charophyte record from the Eocene-Oligocene boundary. Data from the Americas and most of Africa are still scarce, and they are missing altogether from Australia. Therefore, the definition of a European charophyte bioprovince in the Upper Eocene-Lower Oligocene interval is only possible by comparison with other Eurasian, mainly Chinese, assemblages. Most of the genera described in European basins during the Late Eocene (Priabonian) and Early Oligocene (Rupelian), i.e. *Harrisichara*, *Lychnothamnus*, *Chara*, *Hornichara*, *Grovesichara*, *Gyrogona*, *Nitellopsis*, *Nodosochara* and *Sphaerochara*, also occur in China. Only the European genus *Psilochara* has not been reported there for the same period. Meanwhile, some Chinese charophyte genera, which are regarded as defined with criteria equivalent to the European by Feist et al. (2005), do not occur in Europe. For example, the genus *Neochara* Wang & Lin in Wang, 1978 occurs in Upper Cretaceous to Upper Eocene deposits from the Yangtze-Han River Basin (eastern China), whilst *Linyechara* Xinlun, 1978 and *Shandangochara* Xinlun, 1978 were described in Upper Eocene-Oligocene deposits from the north-eastern Chinese region of Bohai, Hebei province.

Although Europe and China share many charophyte genera from the time span studied, only a few species are common to both extremes of the Eurasian landmass. For instance, only twelve out of ninety-seven charophyte taxa from NE China have been recorded in Europe (Xinlun 1978). Similarly, only four out of sixteen species from NW China (Xinjiang province) occur in Europe (Liu and Wu 1990). In southern China (Yunnan province), twelve species have been reported by Liu (1989), of which only four have been documented in Europe. Furthermore, in central China (Qinghai Province), seven out of forty-four charophyte species have also been found in Europe (Wang 1961).

Latitudinal distribution of species within the European Priabonian-Rupelian charophyte bioprovince.

Upper Eocene-Lower Oligocene charophyte species appear to display a latitudinal polarity in their distribution, as happens in extant species (Corillion 1972). Thus, during the Late Eocene-Early Oligocene, the north-western European basins (Hampshire, Paris and Rhine Graben basins) shared some charophyte species, mainly belonging to the genera *Psilochara* and *Chara*, which did not occur in the south. These are *Psilochara conspicua* Grambast, 1958; *Psilochara polita* (Reid & Groves, 1921) Grambast, 1959; *Nitellopsis (Tectochara) wonnacotti* Grambast, 1972; *Chara cylindrica* Horn af Rantzien, 1959; *Chara subcylindrica* Reid and Groves, 1921; *Chara tornata* (Horn af Rantzien, 1954) Grambast, 1958 and

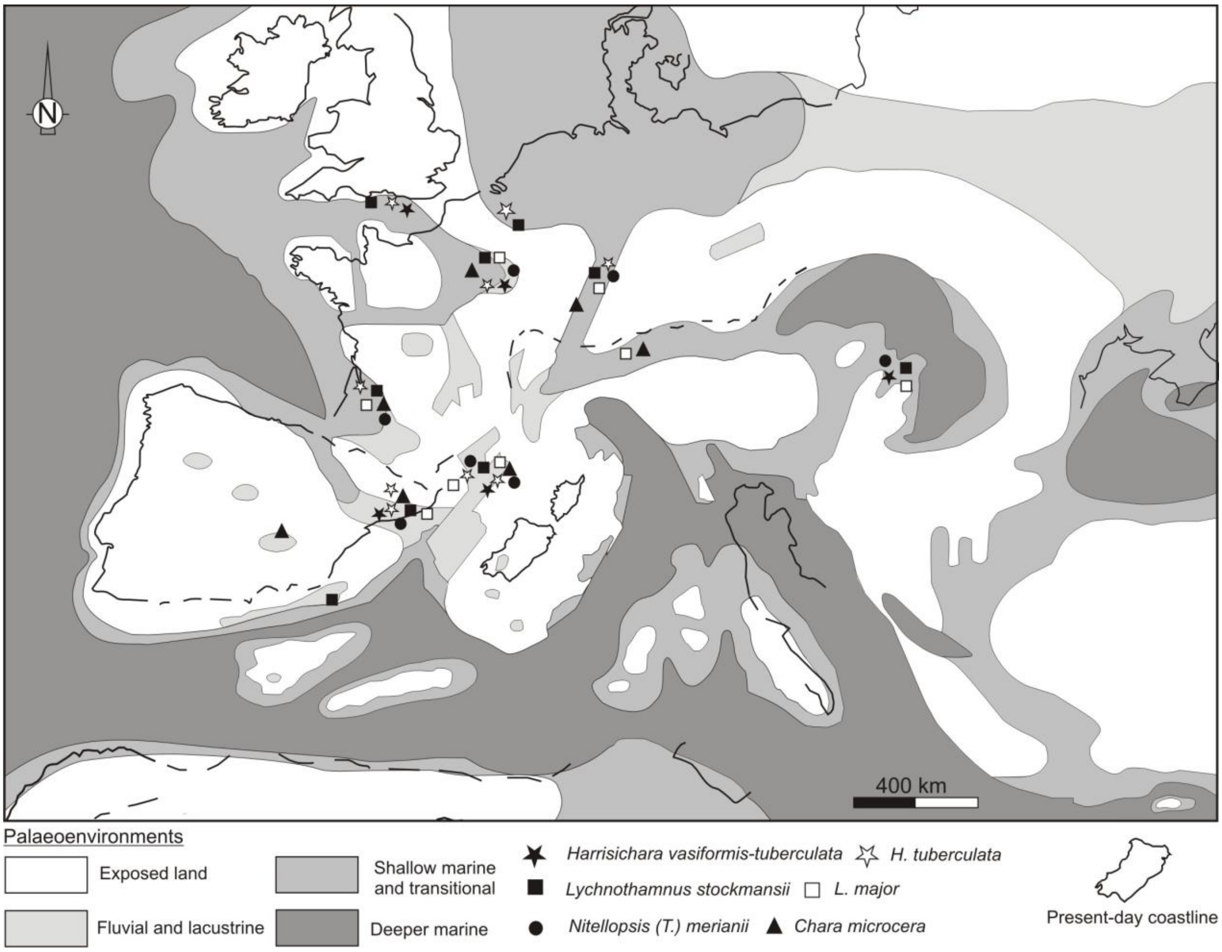


Fig. 10. European bioprovince. Distribution of the *Harrisichara vasiformis-H.tuberculata* and *Lychnothamnus stockmansii-L.major* charophyte lineages and the species *N (T) merianii* and *Chara microcera* during Uppermost Eocene (Priabonian) and Lower Oligocene (Rupelian) on the palaeogeographic map of Europe (modified from Lorenz et al., 1993).

Sphaerochara headonensis (Reid and Groves, 1921) Grambast 1958. On the other hand, the southern basins shared the species *Lychnothamnus grambastii* (Feist-Castel, 1971) nov. comb. Soulié-Märsche, 1989; *Lychnothamnus raibocarpa* (Feist-Castel, 1977b) nov. comb. Soulié-Märsche, 1989 and *Sphaerochara labellata* Feist and Ringeade, 1977, which are not recorded in the north.

Geographically isolated from other well-known European basins, the Upper Eocene-Lower Oligocene deposits of the Transylvanian Basin (Rumania) yield a charophyte flora which has been reported by Baciu & Feist (1999) and is significant from the palaeobiogeographical point of view. The presence of the lineages *Harrisichara vasiformis-Harrisichara tuberculata* and *Lychnothamnus stockmansii-Lychnothamnus major*, along with the occurrence of *Nitellopsis (Tectochara) merianii*, indicates that the charophyte flora from Rumania is closely related to contemporaneous western European basins. In addition, the occurrence of *Sphaerochara headonensis*, *Chara media* and *Chara subcylindrica* suggests an affinity with the north-western European basins (Hampshire, Paris and Rhine Graben) rather than with the south-western European basins

(Aquitaine, Languedoc, Provence and Ebro basins).

A well-marked latitudinal change is observed in the composition of assemblages and in the total number of species of north-western and south-western European basins. The extreme poles in this latitudinal change are the Paris-Hampshire basins and the Ebro Basin, whilst intermediate situations occur in Southern France. Differences in taxonomic composition are illustrated by the abundance of particular species in the north-west (Paris and Hampshire basins), which become scarcer in basins from Southern France (Aquitaine, Languedoc and Provence basins) to disappear altogether in the Iberian Peninsula (Ebro Basin). This is the case of *Gyrogona wrighti* (Salter ex Reid and Groves 1921) Pia 1927, *Gyrogona lemanii* (Brongniart, 1822) Pia, 1927, *Grovesichara distorta* (Reid and Groves, 1921) Horn af Rantzien, 1959, *Psilochara repanda* Grambast, 1958 and *Chara marcoussiensis* Riveline, 1986. In terms of species richness, northern European basins, i.e. Hampshire, Paris and the Rhine basins, display a higher number of charophyte species (mean 31 species) than contemporaneous south-western European basins i.e. Aquitaine, Provence, Languedoc, Ebro (mean 18 species).

DISCUSSION

Charophyte biogeography is a hot topic in the research on extant charophytes. The environmental deterioration of European wetlands in the recent past has resulted in increased government and research interest in determining the distribution and ecology of charophyte species, which contribute significantly to managing water quality and maintaining the biodiversity of European aquatic systems. Unfortunately, biogeographic models are still lacking for extant European charophytes and the available data are devoid of any historical perspective beyond a period of 100 years at most. In this sense, the palaeobiogeography of charophytes over large time-spans of the geological past may provide useful proxies to test hypotheses and interpretations.

Here we provide evidence that during the Eocene-Oligocene boundary, in the context of a global climate change, the charophytes of Europe were sufficiently similar from north to south and from west to east to be included in the same bioprovince. However, some species were restricted to particular basins and a reduced number of species (only *Lychnothamnus stockmansi* in the Ebro Basin) displayed an intercontinental distribution, ranging from Western Europe to China. A striking point that arises from our analysis is that within the European charophyte bioprovince there was a well-defined latitudinal polarity in the distribution of some species. This north to south distribution cannot be attributed to a temperature gradient since by that time, most of Europe belonged to the same climate area, the sub-tropical belt (Scotese 2003). However, the European vascular floras display higher biogeographic complexity than expected from this homogenous thermal situation, showing a latitudinal change. Differences between northern and southern European angiosperm floras during the Late Eocene have been related to the palaeogeographic arrangement of land and sea (Mai & Walter 1985 ; Mai 1989 ; Mihajlović 1993). According to Mihajlović (1993), the northwest-central European floras were dependent on the influence of the North Sea and characterise humid sub-tropical vegetation with a prevalence of oak-laurel forests. In contrast, coeval southern European floras were influenced by the Tethys Ocean and the oak-laurel forests contained abundant xerophytic taxa, such as *Zizyphus*, indicating seasonally drier conditions.

The latitudinal polarity observed in the European Late Eocene-Early Oligocene charophyte flora might also be related to this southward increase in aridity. Thus, charophyte species that are abundant in the north European basins and become scarcer towards the south until finally disappearing would not withstand the effects of seasonal aridity in south European Late Eocene-Early Oligocene wetlands. This biogeographic distribution is also consistent with the distributional pattern of many extant charophytes from Europe. According to Corillon (1972), the species *Tolypella intricata* (Trentepohl ex Roth, 1797) Leonhardi, 1863 displays a marked Atlantic affinity, being abundant in northern Europe and becoming scarcer southwards, to disappear altogether in the Mediterranean region. *Chara rudis* (Braun) Leonhardi 1864 and *Nitellopsis obtusa* (Desvaux in Loiseleur, 1810) Groves, 1919 represent two well-known species mainly distributed in north-central Europe and becoming absent in the Mediterranean region (Corillon 1972). In contrast, *Tollypella hispanica* Nordstedt 1889 displays a Mediterranean distribution and is absent in north-central Europe (Corillon 1972).

Beyond climatic constraints, ecological constraints linked to basin dynamics could also play a significant role in explaining the differences between European Upper Eocene-Lower Oligocene charophyte floras. The hydrological features of each basin, such as the sediment input to aquatic systems or the open vs. closed drainage of a basin, are key factors that might have controlled the distribution of aquatic organisms in the past (Gierlowski-Kordesch 2010). From this viewpoint, the Paris-Hampshire basins were completely different from the Ebro Basin. The former were part of a large cratonic basin related to intracontinental rifting with a permanent connection to the sea, whilst the Ebro Basin was a foreland basin related to interplate collision that evolved into a closed, endorheic system. In general, cratonic basins are large, slowly subsiding and long-lived, and display low sedimentation rates, whilst foreland basins are variable in size, rapidly subsiding and display high sedimentation rates (Einsele 2000). Continuous marine connection and relatively low sedimentary rates favoured the establishment of a wider range of aquatic environments, from freshwater to brackish lacustrine areas, which probably promoted charophyte diversification in the Paris-Hampshire basins. In contrast, the absence of marine influences in the Ebro Basin after the middle part of the Priabonian meant that the basin was dominated by freshwater floodplain environments with high water turbidity and lake bottom instability (Sanjuan & Martín-Closas 2012), limiting the range of ecological niches for charophyte diversification. These environmental constrains are regarded here as the main reason for the low species-richness in charophyte assemblages from the Ebro Basin in comparison to the northern European basins.

The palaeobiogeographic constraints explained above appear to limit the use of certain European charophyte biozones as defined by Riveline et al. (1996). This is the case of *Lychnothamnus pinguis* (Grambast, 1958) Soulié-Märsche, 1989, which occurs mainly in northern European basins but is regarded as the index species of a Lower Rupelian European biozone. In fact, this species only occurs abundantly in the Hamstead beds (Grambast 1958 ; Riveline 1986) of Hampshire, whilst in the Paris Basin the same species is much scarcer, with only three populations recorded (Riveline 1986 ; Riveline pers. communication 2012). In the Rhine Graben, only one locality has been reported (Schwarz 1997). In comparison with these changing northern occurrences, *L. pinguis* has been reported, but not figured, in only one locality from the Iberian Chain, in Teruel province, Spain (Adrover et al. 1982) and is absent altogether in the Ebro Basin. The limited distributional pattern observed in some charophyte species, which are significant from the biostratigraphic point of view, leads us to conclude that it would be more appropriate to consider the Lychnothamnus pinguis biozone as being of regional application rather than of European range.

CONCLUSIONS

Eighteen charophyte species are described and figured from the Upper Eocene-Lower Oligocene of the eastern Ebro Basin, emphasising their palaeobiogeographic distribution. A new charophyte species, very abundant and continuously distributed within the Ebro Basin, *Chara artesica* nov. sp. is defined. The proposal of Riveline (1986) that a European charophyte bioprovince existed in the Lower and Middle Eocene is extended to the Priabonian-Rupelian. This bioprovince is characterised on the basis of two important charophyte lineages, *Harrisichara vasiformis-H. tuberculata* and *Lychnothamnus stockmansii-L.major* along with two more species *Nitellopsis (Tectochara) merianii* and *Chara microcera*. However, differences exist within Europe in the latitudinal distribution of species, mainly as regards the number of charophyte species and the relative abundance of particular species in the assemblages of each basin. In addition, some species were restricted to only one of the basins considered in our analysis.

Latitudinal polarity was probably related to the southwards decrease in seasonal humidity in Europe during the Late Eocene-Early Oligocene period. From this viewpoint, the resulting latitudinal polarity of charophyte assemblages is comparable to the distribution patterns of extant charophytes. In contrast, variations in species richness between European basins appears to be related to ecological parameters such as basin dynamics. The hydrology of the Ebro Foreland Basin i.e., its closed drainage (endorheism) hindering the connection with the sea, and the high water turbidity produced by continuous and abundant terrigenous input within the lacustrine systems, probably limited the number of species. In contrast, the characteristics of the Paris-Hampshire basins i.e., their open drainage leading to a permanent marine connection throughout the period studied, along with a low input of terrigenous materials in the aquatic systems, could have favoured the development of a wider range of ecological niches which resulted in a high number of charophyte species.

The limited biogeographic distribution observed in some charophyte species, such as *Lychnothamnus pinguis*, which are significant from the biostratigraphic point of view, challenges their inclusion in the general biozonation of European charophytes and suggests that these species would be more appropriate for local, basin-wide, biozonations.

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Charophyte palaeoecology in the Upper Eocene of the Eastern Ebro basin (Catalonia, Spain). Biostratigraphic implications

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ABSTRACT

A micropalaeontological study of the non-marine Upper Eocene of the north eastern Ebro Basin (Catalonia, Spain) was carried out to clarify the palaeoecology of well-known charophyte species that are widely recognised as significant in charophyte biostratigraphy. Autochthonous specimens of the biozone index-species *Harrisichara vasiformis-tuberculata* were found in marlstones from the Sant Boi Formation (middle part of the Priabonian), which are associated with brackish water ponds laterally related to paralic marshes. In contrast, laterally equivalent assemblages found in white laminated marls from stable freshwater lakes were devoid of the index species and were dominated by *Harrisichara lineata*. Three more charophyte assemblages are reported from the continental Artés Formation (Stephanochara vectensis biozone, Upper Priabonian). Assemblages dominated by the species *Nodosochara jorbae*, reported only from Iberia at that age, occur in marlstones related to freshwater, temporary and turbid lakes within flood plains in medial fluvial fan environments. However, *Lychnothamnus grambastii* dominates locally in similar environments with higher organic matter content. Laterally equivalent assemblages from freshwater perennial lakes in distal alluvial fan facies were dominated by the biozone index-species *Harrisichara tuberculata*.

These results provide evidence that important charophyte index species of the European charophyte biozonation were controlled by palaeoenvironmental factors such as water salinity, lake level changes or terrigenous input to the lakes. In consequence, these species should be used with caution in biostratigraphic studies, taking into account that their presence or absence may be palaeoecologically driven.

1. Introduction

The fossil record of Charophyta is mainly based on their calcified fructifications (gyrogonites and utricules) known from the Silurian to the present (Feist et al., 2005). Because of their specific morphology and relatively high evolutionary rates, charophyte gyrogonites are among the main biostratigraphic indicators of Tertiary non-marine deposits. Detailed biozonations of the European Palaeogene have been proposed based on the pioneer study of Grambast (1972) on charophytes from the Paris Basin. This first biozonation was followed by a number of local biozonations (Feist and Ringeade, 1977; Feist-Castel, 1977a; Anadón and Feist, 1981; Riveline, 1986; Feist et al., 1994), which were later compiled to build a general European charophyte biozonation (Riveline et al., 1996 and Riveline in Hardenbol et al., 1998). This European charophyte biozonation has been largely accepted by most authors and is still in use, despite some modifications introduced later (e.g. Martín-Closas et al., 1999).

In contrast to the substantial body of knowledge available on the biostratigraphy of European Palaeogene charophytes, these plants have been poorly studied from a palaeoecological point of view. Lyell (1838) considered Eocene charophytes useful palaeoecological indicators of freshwater conditions in sedimentary rocks. However, subsequent applications of Eocene charophytes were mainly concerned with biostratigraphic correlation and rock aging, leaving aside their interest as regards palaeoecology. Massieux and Villatte (1977), Massieux et al. (1981) and Tambareau et al. (1991) are among the few authors who have published on palaeoecological aspects of Lower Eocene charophyte assemblages, mainly from the northern Pyrenees (Languedoc, France).

Charophyte-rich lacustrine intervals are abundant in the non-marine Upper Eocene deposits from the Ebro Foreland Basin. These successions have been the subject of a number of stratigraphic and sedimentological studies (Ferrer, 1971; Puigdefàbregas et al., 1986; Sáez, 1987; Anadón et al., 1989; Sáez et al., 2007) as well as biostratigraphic studies based on mammals (Anadón et al., 1987; Arbiol and Sáez, 1988; Barberà et al., 2001) and charophytes (Anadón and Feist, 1981; Choi, 1989; Anadón et al., 1992; Feist et al., 1994; Sanjuan et al., 2012). The amount of stratigraphic and biostratigraphic data gathered from the non-marine Upper Eocene of the Eastern Ebro Basin provides an excellent basis for performing palaeoecological analyses.

The studied fossil charophytes include representatives of a well-known evolutionary lineage of the Eocene–Oligocene boundary,

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formed by the succession of the three morphotypes *Harrisichara vasiformis* (Reid and Groves, 1921) Grambast, 1957, *H. vasiformis-tuberculata* Feist-Castel, 1977b, and *H. tuberculata* (Lyell, 1826) Grambast, 1957. This lineage represents an excellent example of a biostratigraphically significant set of species, which have never been analysed from a palaeoenvironmental point of view. This evolutionary succession of *Harrisichara* species was first described from the Hampshire Basin (Isle of Wight, England) by Feist-Castel (1977b). Later, Riveline (1986) reported more levels with these species in the same basin, as well as in the Paris Basin, and found that the species' ranges were at times concurrent, showing an overall change through time from *H. vasiformis* to *H. tuberculata*. More recently, Sille et al. (2004) modelled the morphology of these three successive *Harrisichara* morphotypes in the Hampshire basin using the Eigenshape method, and supported the view of a continuous morphological gradation between *H. vasiformis* and *H. tuberculata*. The possibility of facies and environmental control superimposed on the evolutionary trend observed for this *Harrisichara* lineage has been little considered by previous authors, but is not negligible, since in many European successions where this lineage has been recorded there is a parallel facies evolution from transitional to non-marine conditions (Plint, 1984; Pomerol and Premoli-Silva, 1986; Hooker et al., 2004). This sea-level drop is probably glacio-eustatic in origin and driven by global Eocene–Oligocene climate change (Zachos et al., 2001; Xiao et al., 2010).

With the aim of clarifying facies control of the distribution of determined charophyte species significant in the European charophyte biozonation, we carried out a sedimentological, taphonomic and palaeoecological study of the Upper Eocene of the Eastern Ebro Basin (Catalonia, Spain). Sedimentology coupled with taphonomy is a useful tool for characterising the palaeoenvironment in which fossil species thrived (Martin, 1999).

2. Material and methods

Nine stratigraphic sections and one outcrop showing good exposure of transitional to continental and lacustrine facies were sampled systematically in order to palaeoecologically characterise the charophyte assemblages from the Upper Eocene deposits in the eastern part of the Ebro Basin. These sections occur near the villages of Sant Boi de Lluçanès, Sobremunt, Sant Bartomeu del Grau, Oristà, Santa Maria d'Olò and Moià, all located in the Lluçanès and Bages counties, near Vic, about 50 km northeast of Barcelona (Fig. 1 and Table 1).

Fossil remains were obtained from 43 samples of greyish lacustrine mudstones distributed in the aforementioned sections. About 2 kg of sediment per sample were disaggregated in water, oxygen peroxide and Na_2CO_3 solution and later sieved using sieves with mesh apertures of 1.0 cm, 0.5 and 0.2 mm. Gyrogonites were picked out under a light microscope and measured at 40× magnification (hundred gyrogonites per species). Selected gyrogonites were studied and photographed with a scanning electronic microscope Quanta 200 at the Serveis Científico-Tècnics (Universitat de Barcelona). Thin-sections, about 30 μm in thickness, were prepared from 20 selected charophyte limestone beds in order to ascertain the microfacies. The material is housed at the Departament d'Estratigrafia, Paleontologia i Geociències marines, Universitat de Barcelona.

3. Geological setting and stratigraphy

The Palaeogene sedimentary succession in the north eastern part of the Ebro Basin is divided into nine depositional sequences related to the emplacement of the south Pyrenean thrust sheets and linked to two major relative sea-level rises, in the Early and Middle Eocene respectively (Puigdefàbregas et al., 1986). Most of the Palaeogene sedimentary succession in the Eastern Ebro Basin is dominated by siliciclastic and carbonate deposits of marine platforms. During the Late Eocene, tectonic activity led to the restriction of marine influence on the basin and the deposition of an evaporite plug. This evaporitic event (Cardona depositional sequence) is the last marine episode in the southern Pyrenean foreland basin, which subsequently became purely endorheic.

The closure of the Ebro Basin to marine influence is a prominent feature of the basin's evolution, and has been dated as Lower Priabonian, based on calcareous nannofossils, in the eastern part of the basin (Cascella and Dinarès-Turell, 2009). Magnetostratigraphic data from the youngest marine rocks located in the central part of the SE margin of the Ebro Basin (Igualada area) are consistent with these results (Costa et al., 2010). Moreover, a recent biostratigraphic study of charophytes at the easternmost part of the Ebro Basin assigned the marine-continental transition to the middle part of the Priabonian (Sanjuan et al., 2012).

Along the eastern margin of the basin, bordering the Catalan Coastal Chain, the Cardona depositional sequence is represented by the so-called Terminal Complex and its lateral equivalents, the Òdena Gypsum Formation to the south, the Cardona Fm to the west, and the Sant Boi Formation to the north. These units, represent the progressive infilling of the marine basin and its final shift to non-marine conditions. The Terminal Complex, defined by Travé (1992) and Travé et al. (1996), is built up of transitional sandstones of the La Noguera Formation (Reguant, 1967), anoxic marls, lacustrine marl, limestones including freshwater stromatolites, and gypsum. In the south eastern part of the basin, the Terminal Complex passes laterally and is overlain by the Òdena Gypsum Formation. This formation may represent the marginal equivalent of the central basin halite and sylvinite deposits of the Cardona Salt Formation. On the north eastern margin of the Ebro Basin, in the Lluçanès area, the Terminal Complex passes laterally for 15 km and is overlain by the transitional and lacustrine Sant Boi Formation, (Figs. 1 and 2). This formation, recently defined by Sanjuan et al. (2012), is composed of about 15 m of an alternating fine-grained grey sandstone, siltstone and lutite intervals which passes upwards to a characteristic marl interval, frequently rich in lignite and charophytes.

Overlying these latter marine-influenced deposits, the Artés Formation (Ferrer, 1971; Sáez, 1987) corresponds to the Solsona Depositional Sequence and is generally built up by red beds with alternating siltstone and coarse sandstone bodies. This formation shows typical alluvial and fluvial features and represents the first fully terrestrial deposits of the endorheic basin. Intercalated within these terrigenous deposits are lacustrine grey marl and limestone deposits, in some cases rich in charophytes. The present study focuses on the transitional and continental Upper Eocene deposits (Sant Boi and Artés Formations, respectively) in the easternmost part of the Ebro Basin (Fig. 2).

4. Systematic palaeontology (charophytes)

Fourteen characean species have been recognised in the Upper Eocene beds from the studied sections. Although most species have previously been described from the Ebro Basin (Colom et al., 1970; Anadón and Feist, 1981; Choi, 1989; Anadón et al., 1992; Feist et al., 1994; Sanjuan et al., 2012), a brief account of the main features of each species is given below. However, only those species which are significant from a palaeoecological point of view are figured (Fig. 3).

Sphaerochara labellata Feist and Ringeade 1977 gyrogonites occur in the Torre Casanova section (Table 2). They are small in size, averaging 406 μm high and 387 μm wide, oblate or suboblate in shape with a low isopolarity index (ISI = 105). Spiral cells are concave to flat. Eight convolutions are visible laterally. The ornamentation is formed by a midcellular crest, irregularly thickened. The apex is not modified, showing comma-shaped tubercles. Basal plate visible from outside and frequently ornamented with a tubercle.

Chara rhenana Schwarz and Griessemer, 1994 occurs solely but abundantly in the El Perers section (Table 2). Gyrogonites are medium in size, 640 μm high and 392 μm wide (mean values), very elongate, perprolate in shape, with a high isopolarity index (ISI = 164, mean

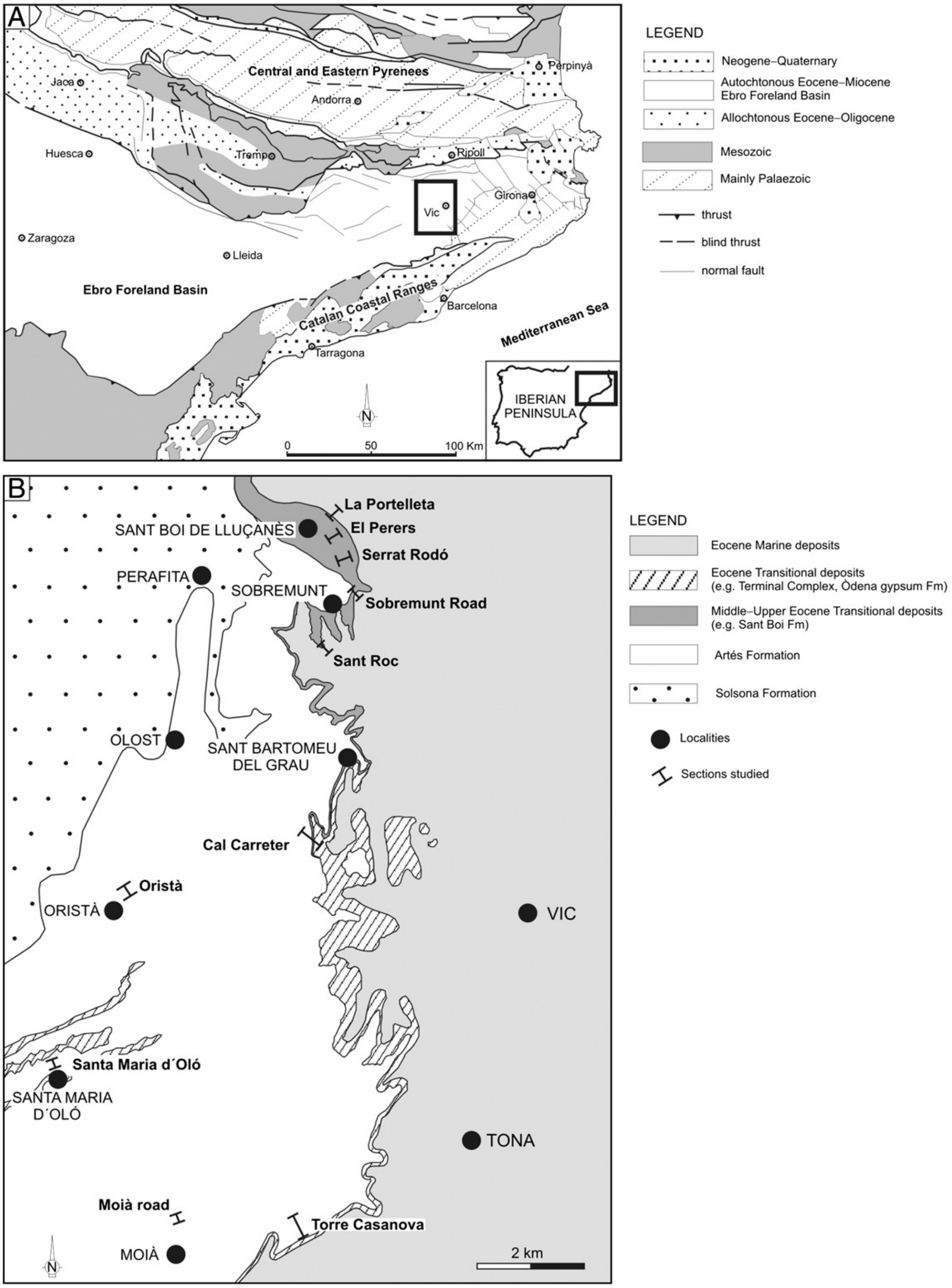

Fig. 1. Geological setting of the study area. A. Geological sketch of the eastern part of the Ebro Foreland Basin showing location of studied area (modified from Vergés et al., 1998). B. Geological map showing the location of the studied sections (modified from Sanjuan et al., 2012).

value). Spiral cells are non-ornamented and concave. Ten convolutions are visible laterally. The apex is psilocharoid and flat. Base progressively tapering to a pointed.

Chara sp. occurs in most samples from the Cal Carreter, Sobremunt road, Oristà, Santa Maria d'Oló, Torre Casanova and Moià sections (Table 2). The gyrogonites are small in size, usually 397 μm high and 304 μm wide, elongate in shape, with an isopolarity index of 129 (mean value). Seven convolutions are visible laterally. Spiral cells are concave to almost flat, with apical endings slightly widening. The base is frequently pointed with a small superficial pentagonal pore.

Lamprothamnium sp. (Fig. 3A–C) occurs in the Cal Carreter section (Table 2). The gyrogonites are medium in size, usually 547 μm high and 434 μm wide, elongate, prolate to subcylindrical in shape, with an isopolarity index of 127 (mean value). Nine convolutions are visible in lateral view. Spiral cells are non-ornamented and flat to convex.

Table 1
Location (coordinates) and lithostratigraphic attribution (formations) of the studied section in the eastern Ebro Basin.

Locality	Sections	Coordinates				Formation
		Base of section		Top of section		
		Latitude	Longitude	Latitude	Longitude	
Sant Boi de Lluçanès	La Portelleta	42°03′39,4″N	02°10′17,2″E	42°03′27″N	02°10′17″E	Sant Marti Xic and Sant Boi Formations
	El Perers	42°03′14,7″N	02°10′E	42°03′27″N	02°10′17″E	Sant Boi Formation
	Serrat Rodó	42°02′49,7″N	02°10′18,4″E	42°02′47,3″N	02°10′10,1″E	Sant Boi Formation
Sobremunt	Sobremunt road	42°02′18,6″N	02°10′21,7″E	42°02′16,4″N	02°10′19,3″E	Sant Boi Formation
	Sant Roc outcrop	42°01′22,8″N	02°09′28,7″E	42°01′22,8″N	02°09′28,7″E	Sant Boi Formation
Sant Bartomeu del Grau	Cal Carreter	41°56′55″N	02°09′34,1″E	41°57′1,1″N	02°09′10,9″E	Terminal Complex and Sant Boi Formation
Moià	Torre Casanova	41°49′11,2″N	02°08′22,4″E	41°49′24,3″N	02°08′7,5″E	Artés Fm
	Moià limestone	41°49′10,4″N	02°05′52,9″E	41°49′11,4″N	02°05′49,8″E	Artés Fm (Moià Limestone Member)
Oristà	Julià Farm	41°56′2,3″N	02°03′56″E	41°56′7,4″N	02°04′5,1,4″E	Artés Fm
Santa Maria d'Oló	Santa Maria d'Oló	41°52′42,3″N	02°02′3,3″E	41°52′35,6″N	02°02′5,1″E	Artés Fm

The apex is truncated, showing a conspicuous periapical depression. The base is rounded and shows a small basal pore.

Gyrogona sp. is only represented by a few specimens in the Sobremunt road section (Table 2). Gyrogonites are large in size, 780 µm high and 822 µm wide (mean values), oblate spheroidal in shape with an isopolarity index of 95. Spiral cells are concave without ornamentation. Five convolutions are visible laterally. The apical area is flat and without periapical modifications. The base is rounded with a small pentagonal shaped basal pore.

Gyrogona caelata (Reid and Groves, 1921) Grambast, 1956 is only represented in the Torre Casanova section (Table 2). Gyrogonites are large in size, 755 µm high and 832 µm wide (mean values), oblate spheroidal in shape with an isopolarity index of 92. Spiral cells are convex and ornamented with a wide midcellular crest. Six convolutions are visible laterally. The apical area is flat or rounded with a well-marked periapical depression. The apex is ornamented with prominent apical nodules elongated following the apical cells. The base is rounded with a small pentagonal shaped basal pore.

Nodosochara jorbae Choi, 1989 (Fig. 3D–F) is an extremely abundant species in many samples from the Sobremunt road, Serrat Rodó, Santa Maria d'Oló, Oristà, Torre Casanova and Moià sections (Table 2). The gyrogonites are large, 758 µm high and 680 µm wide (mean values), generally pear-shaped with an isopolarity index of 112 (mean value). Spiral cells are convex and smooth. Nine convolutions are frequently visible laterally. The apex is nitellopsidoid, and slightly convex, with both a well-marked thinning and narrowing. Periapical depression is frequently well-defined. Apical nodules clustered in an apical rosette. The base is rounded to conical with superficial and small basal pores.

Lychnothamnus longus Choi 1989 is represented in many samples from the Oristà, Santa Maria d'Oló, Torre Casanova and Moià sections (Table 2). Gyrogonites are medium in size, 618 µm high and 464 µm wide (mean values). They are ellipsoidal to ovoidal in shape with an isopolarity index of around 130. The apex is psilocharoid, rounded to truncate, and in some cases pointed in the centre. It displays a conspicuous apical thinning. The base is elongated with a small star-shaped basal pore. Nine convolutions are visible laterally. Spiral cells are non-ornamented, and separated by prominent sutures which are bicarinate in some specimens.

Lychnothamnus stockmansii (Grambast, 1957) nov. comb. Soulié-Märsche (1989) occurs solely in the Torre Casanova section (Table 2). Gyrogonites are large in size, 659 µm high and 561 µm wide (mean values), ellipsoidal in shape with an isopolarity index of around 120. The apex is flat. The base is rounded, showing a star-shaped basal

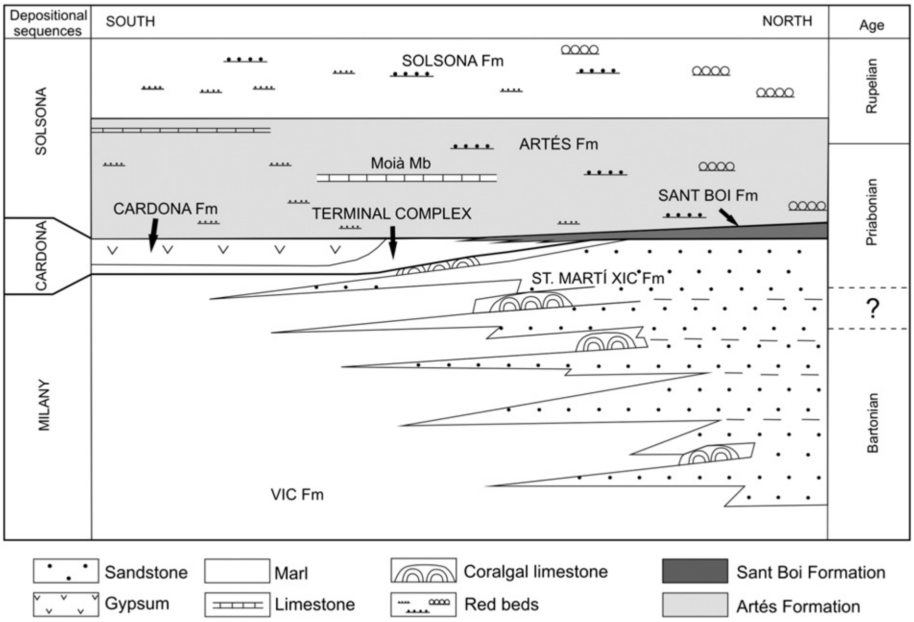

Fig. 2. Stratigraphic framework of the Eocene in the South Pyrenean foreland basin near Vic. (modified from Serra-Kiel and Travé, 1995).

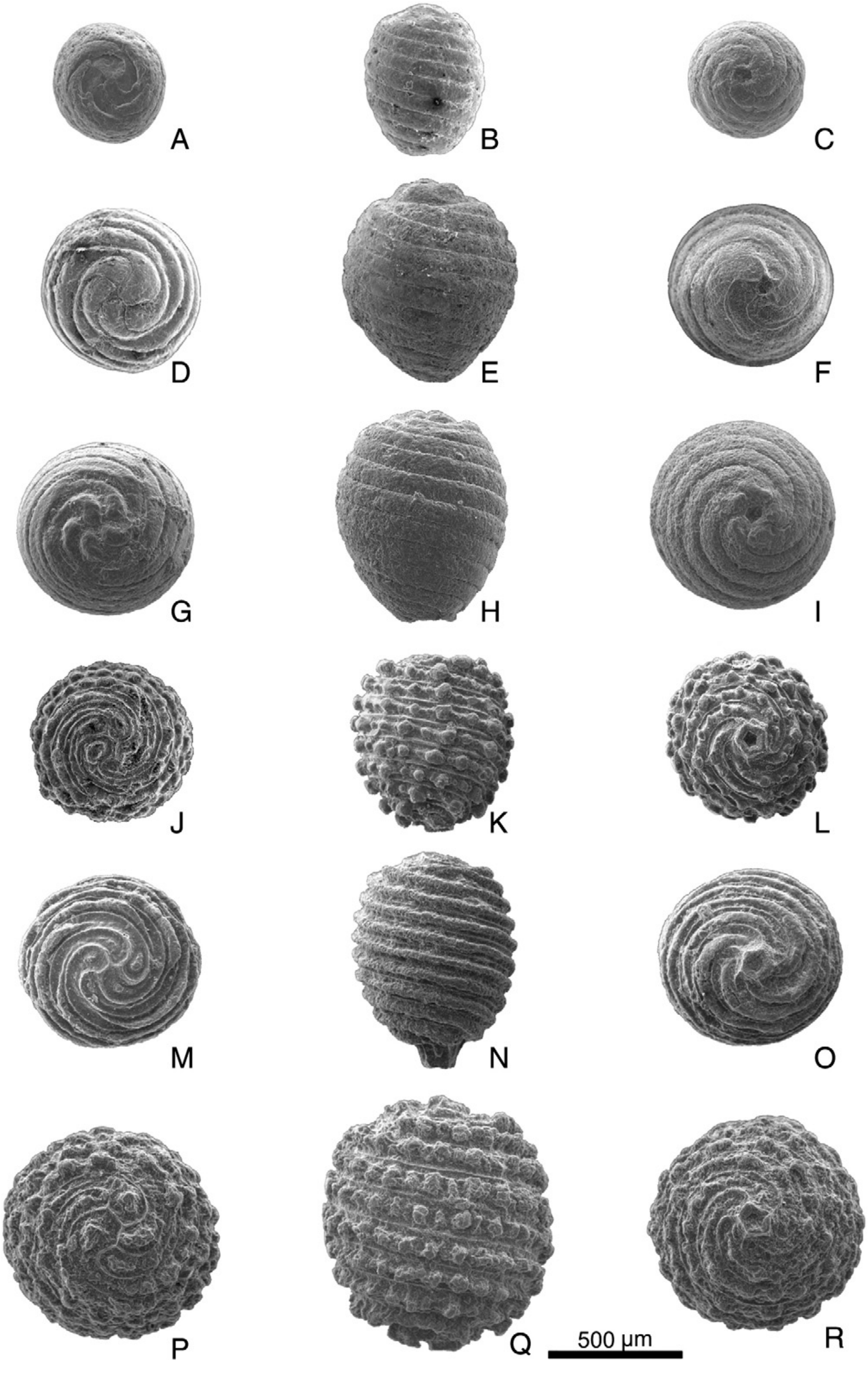

Fig. 3. Charophytes from the Sant Boi and Artés Formation. A.–C., *Lamprothamnium* sp., Cal Carreter section, sample CC-1; A. apex, B. lateral view, C. base. D.–F., *Nodosochara jorbae*, Oristà section, sample O-1; D. apex, E. lateral view, F. base. G.–I., *Lychnothamnus grambastii*, Torre Casanova section, sample TC-9; G. apex, H. lateral view, I. base. J.–L., *Harrisichara vasiformis-tuberculata*, Sobremunt road section, sample Sbr-1; J. apex, K. lateral view, L. base. M.–O., *Harrisichara lineata*, El Perers section, sample Pe-1; M. apex, N. lateral view, O. base. P.–R., *Harrisichara tuberculata*, Moià section, sample Mo-1; P. apex, Q. lateral view, R. base.

pore. Eight convolutions are visible laterally. Spiral cells are non-ornamented and concave, separated by prominent sutures which are bicarinate in some specimens.

Lychnothamnus grambastii (Feist-Castel, 1971) nov. comb. Soulié-Märsche (1989) (Fig. 3G–I) occurs in some samples from the Torre Casanova section (Table 2). Gyrogonites are medium to large in size, usually 847 μm high and 703 μm wide, normally ovoidal to pear-shaped with an isopolarity index of 119 (mean value). Nine convolutions are visible laterally. Spiral cells are flat to convex. The apex shows a periapical depression and is ornamented by comma-shaped tubercles forming a rosette. The base is tapered and truncated at the end, showing a well-marked funnel.

Table 2
List of charophyte species and gyrogonite abundance in the Sant Boi and Artés Formations in the north eastern part of the Ebro Basin. Vertical position of samples does not represent their relative stratigraphic position, which is indicated in Figs. 4 and 6–8.

Lithostratigraphy	Locality	Species Samples	*H. vasiformis-tuberculata*	*Lamprothamnium* sp.	*Gyrogona* sp.	*Nodosochara jorbae*	*Harrisichara lineata*	*Chara rhenana*	*Harrisichara tuberculata*	*Lychnothamnus longus*	*Lychnothamnus stockmansii*	*Lychnothamnus grambastii*	*Nitellopsis (T) merianii*	*Gyrogona caelata*	*Sphaerochara labellata*	*Chara* sp.
Artés Formation Moià Limestone member	Moià	Mo-20							•	●						●
		Mo-4				•			•							•
		Mo-3				•				•						●
		Mo-2				●				•						●
		Mo-1							⬤		●					⬤
	Torre Casanova	TC-31							⬤	●	⬤				•	●
		TC-30				•				●						⬤
		TC-28							⬤		●		⬤		⬤	●
		TC-27				⬤			•	•	●			•		●
		TC-26				●			•	•		•				●
		TC-25				⬤			⬤			●		⬤		●
		TC-24				⬤			•	●						•
		TC-22				⬤										●
		TC-20				⬤			•							
		TC-19				⬤										●
		TC-18				⬤				●						●
		TC-17														•
		TC-16				•			•	•						•
		TC-15				•				•						●
		TC-14				•										
		TC-13				•				•						•
		TC-12								•						•
		TC-10							•			•				
		TC-9										⬤				
		TC-8				⬤				•						•
		TC-7				●										•
		TC-6				⬤										•
		TC-4				●				•						
	Santa Maria d´Oló	SMO-5				●				•						⬤
		SMO-4				●				●						•
		SMO-3				•				•						●
		SMO-2				⬤			•	•						•
		SMO-1				●			•							
	Oristà	O-4				●				●						●
		O-3				⬤				⬤						•
		O-2														•
		O-1				⬤										•
Sant Boi Formation	Perers	Pe-2					●									
		Pe-1					⬤	⬤								
	Serrat Rodó	SR-2	⬤			●										•
		SR-1	•													
	Cal Car.	CC-1	⬤	⬤												⬤
	Sob. road	Sbr-1	⬤		•	⬤										•

• 1-25 ● 26-100 ⬤ >100

Nitellopsis (*Tectochara*) *merianii* (Grambast and Grambast-Fessard, 1954) Grambast and Soulié-Märsche (1972) occurs in one sample from the Torre Casanova section (Table 2). Gyrogonites are very large, 1084 μm high and 909 μm wide (mean values), normally ovoid in shape with an isopolarity index of around 120. Spiral cells are generally convex, displaying nine convolutions in lateral view. The apex is nitellopsidoid, and slightly convex or sub-rounded, with both thinning and narrowing of the spiral cells in the periapical zone. Apical nodules are more or less prominent. The base is rounded or slightly conical with a large basal pore located within a wide funnel.

Harrisichara vasiformis-tuberculata Feist-Castel, 1977b (Fig. 3J–L) is represented in the Sobremunt road, Serrat Rodó and Cal Carreter sections (Table 2). The gyrogonites are ovoidal or subovoidal in shape, medium to large, 655 μm high and 619 μm wide (mean values) with an isopolarity index averaging 106. Apex flat or rounded without periapical modification but commonly ornamented with tubercles. Ten convolutions are frequently visible laterally. Base rounded or conical and elongated in a small column. The ornamentation is formed by a succession of regularly spaced tubercles, which are arranged along the central line of spiral cells.

Harrisichara lineata Grambast, 1957 (Fig. 3M–O) occurs in the La Portelleta and El Perers sections (Table 2). Gyrogonites are large in size, usually 753 μm high and 659 μm, ellipsoidal or oval in shape with an isopolarity index of 115 (mean value). The apical area is flat to rounded and frequently ornamented with comma-shaped tubercles. Spiral cells are not modified at the apex. Nine convolutions are visible laterally. The base is elongated in a column. The ornamentation is formed by a regular mid-cellular crest along the central line of spiral cells.

Harrisichara tuberculata (Lyell, 1826) Grambast, 1957 (Fig. 3P–R) is represented in the Torre Casanova, Moià and Santa Maria d'Oló sections (Table 2). Gyrogonites are large, usually 901 μm and 802 μm wide, prolate spheroidal in shape with an isopolarity index of 112 (mean value). Spiral cells are flat to concave. Nine convolutions are visible laterally. The apical area is flat to rounded and frequently ornamented with rounded tubercles. Spiral cells are not modified at the apex. The base is elongated, ending in a short column. The ornamentation is typically formed by large, regularly spaced tubercles, which in some cases merge to form an irregular crest.

5. Depositional environments and charophyte palaeoecology

Sedimentological analysis coupled with taphonomy is a powerful tool to infer the palaeoenvironmental distribution of charophytes, as it is for other fossilised sessile organisms (Martin, 1999). In this section, depositional settings of both the Sant Boi Formation and the Artés Formation will be characterised with the help of sedimentological analysis. The autochthony or allochthony of charophyte assemblages in these depositional settings will be then analysed on the basis of taphonomic observations and finally, testable hypotheses on the palaeoecological distribution of these charophyte assemblages will be proposed.

5.1. Sant Boi Formation

5.1.1. Sedimentology and depositional environments of the Sant Boi Formation

5.1.1.1. Description of the lower part of the St Boi Formation. This part crops out at the La Portelleta, El Perers, Serrat Rodó, Sobremunt road and Cal Carreter sections (Fig. 4), is generally formed by a 5–10 m succession of brown rippled and heavily bioturbated sandstones alternating with laminated siltstones. The sandstone bodies, metric in thickness, are largely lenticular in section with a lateral continuity of about 100–300 m and cross-bedded. The laminated siltstones are not bioturbated, and lamination is millimetric. These materials, up to 6 m thick in the Serrat Rodó section pass vertically to a 5 m thick marl interval, green, yellowish or grey in colour. They are diffusely laminated and have a significant presence of organic matter. The fossil content is composed of abundant and well-preserved euryhaline molluscs, such as *Potamides* (*Ptychopotamides*) *cordieri*, *Potamides* (*Exechostoma*) *bonnardi*, *Newtoniella sulcifera* and *Newtoniella textilis* (pers. comm. J. Martinell, 2010), an oyster bank, charophytes and rare marine ornamented ostracods of genus *Bairdia* (pers. comm. J.P. Colin, 2012). Centimetric lignite horizons have been observed at the top of the marls in many sections, such as in the El Perers, La Portelleta and Sobremunt road sections. They may bear small rootlet marks at their base and include permineralised (silicified) plant stems belonging to monocot angiosperms.

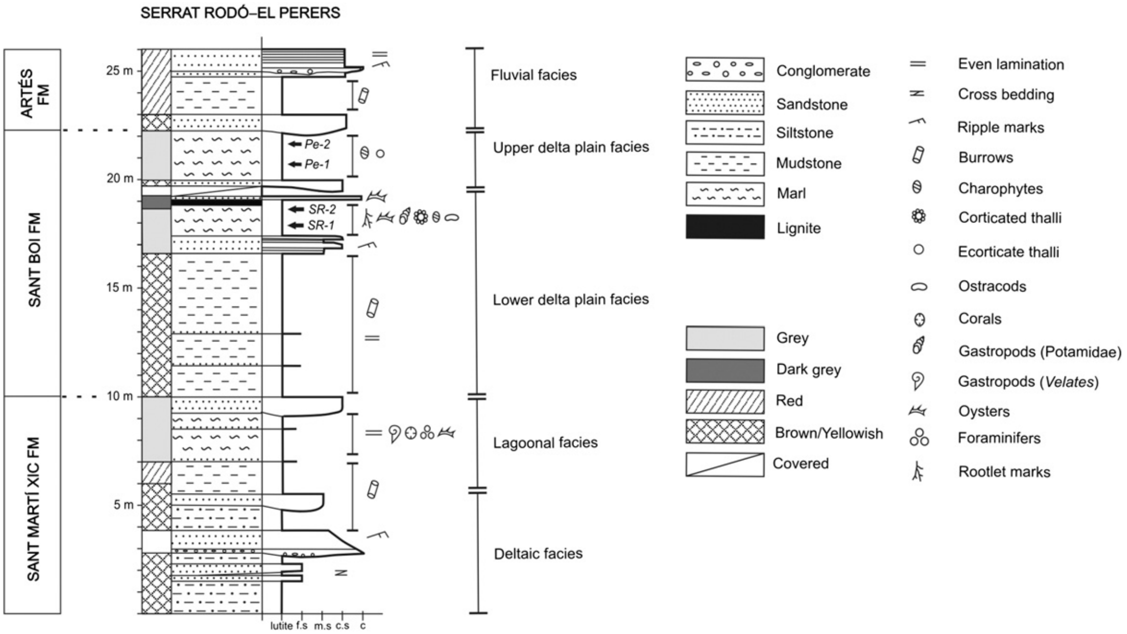

Fig. 4. Stratigraphic logs for the Serrat Rodó-El Perers section, showing the facies associations of the Sant Boi Formation in the Lluçanès area.

5.1.1.2. Interpretation. From a palaeoenvironmental point of view the rippled sandstone bodies are attributed to low-energy river channels in the context of a lower delta plain. Intercalated laminated siltstones represent the overbank flood plain deposits (Sanjuan et al., 2012). Upon these materials, the fossiliferous marl, rich in euryhaline molluscs, oyster shells, charophytes and marine ostracods, would be deposited in shallow ponds close to the shoreline. The mollusc and ostracod assemblage, indicates that brackish conditions prevailed during the sedimentation of the charophyte-bearing marl. Finally, the thin lignite beds with rootlets at the base, suggest autochthonous peat deposition in a coastal marsh surrounding previous ponds.

5.1.1.3. Description of the upper part of the St Boi Formation. This part was studied in the northernmost sections of La Portelleta and El Perers (Fig. 4). It is composed of a succession, about 5 m thick, of brownish sandstones intercalated with decimetric siltstone layers and overlain by a white marl interval which represents a lateral and vertical change from the facies described above for the lower part of the same formation. The sandstone layers are metric in thickness, hectometric in lateral continuity and lenticular in section. They are cross-bedded and show ripples at the top.

5.1.1.4. Interpretation. These sandstone beds are attributed to small channels draining the flood plain in the context of an upper delta plain. The two-metre thick, white laminated marl is very rich in charophyte remains but devoid of other macro- and mesofossils. Preservation of lamination in lacustrine marl may reflect poorly-oxygenated lake bottom conditions with high sedimentation rates, preventing biogenic disturbance to homogenise the lake sediments (Gierlowski-Kordesch, 2010). Similar laminated shallow lacustrine deposits with high terrigenous input have been described in a number of freshwater lake settings such as in the Lower Cretaceous of Las Hoyas (Buscalioni and Fregenal-Martínez, 2012).

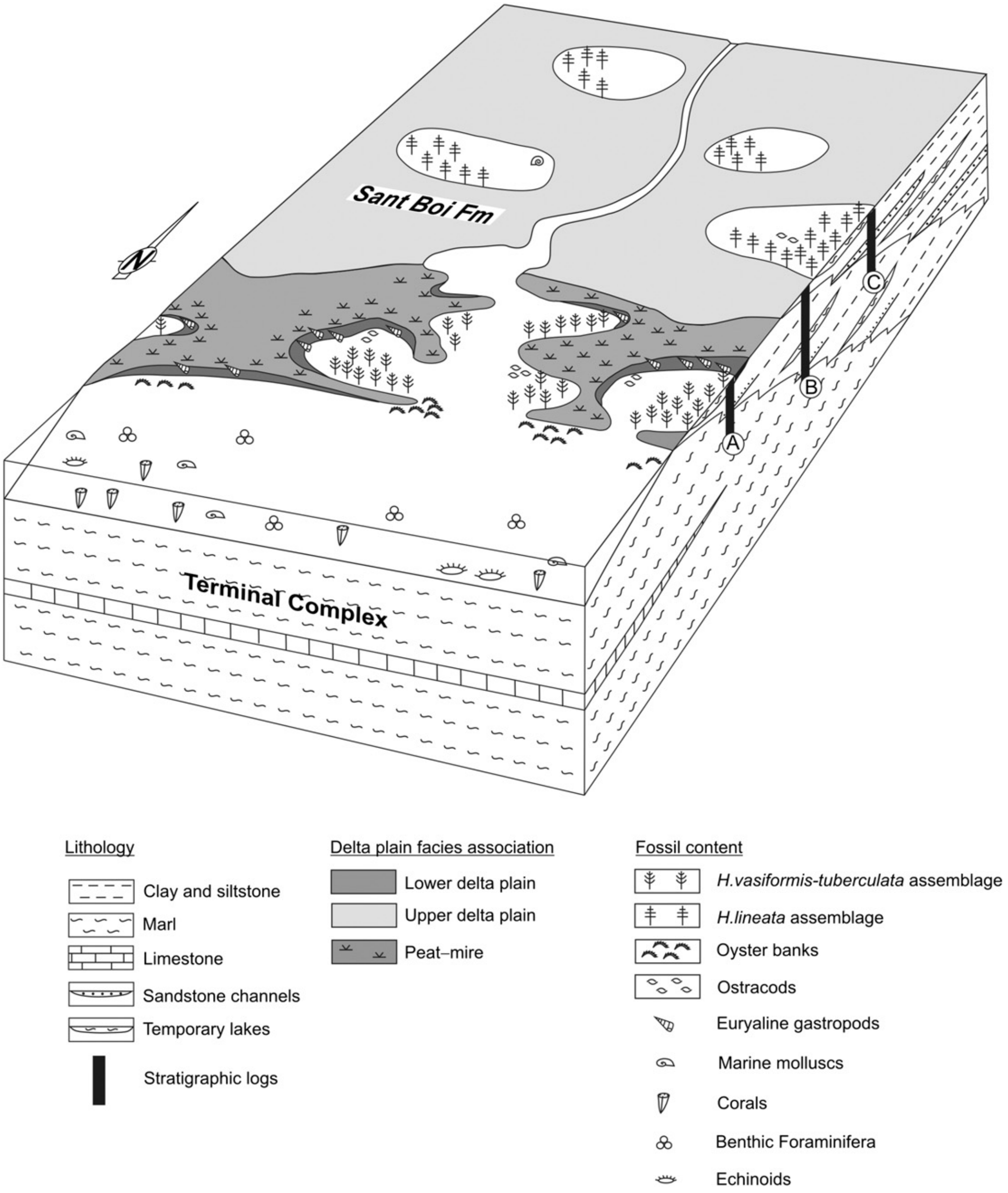

Fig. 5. Palaeoenvironmental model summarising the distribution of the *Harrisichara vasiformis-tuberculata* dominated assemblage and the *Harrisichara lineata* dominated assemblage in the Sant Boi Formation. The main stratigraphic logs represented are: A. Sobremunt Road, B. Serrat Rodó, C. El Perers. Not to scale.

5.1.2. Charophyte taphonomy and palaeoecology in the Sant Boi Formation

Two charophyte assemblages were identified in the St Boi Formation. The assemblage dominated by *Harrisichara vasiformis-tuberculata* occurs in yellowish marlstones found in the lower part of the Sant Boi Formation (Fig. 4 and Table 2). This interval was attributed in the previous section to deposition in shallow brackish coastal ponds (Fig. 5). The charophyte-bearing beds are laterally equivalent with marls, rich in euryhaline gastropods, oysters and marine ostracods, associated with lignite bearing rootlet-marks at the base. This suggests that the charophyte beds were laterally related to paralic marshes.

In most localities, the gyrogonite assemblage is formed by abundant and well-preserved gyrogonites of *Harrisichara vasiformis-tuberculata*, *Nodosochara jorbae* and *Chara* sp. associated with rare ornamented and non-ornamented ostracods. In contrast, *Gyrogona* sp. gyrogonites are rare and poorly preserved. The occurrence of corticated (*Charaxis* sp.) and ecorticate charophyte thalli and the absence of fragmentation or erosion in the gyrogonites of the three first species mentioned indicate that they were buried in situ, whilst allochthony cannot be excluded for *Gyrogona* sp.

In the Cal Carreter section, near Sant Bartomeu del Grau, the assemblage of gyrogonites dominated by *Harrisichara vasiformis-tuberculata* contains *Chara* sp. and abundant *Lamprothamnium* sp. The absence of charophyte thalli and the presence of abrasion in many gyrogonites suggest that they underwent some sort of transport. However, the absence of fragmentation would indicate parautochthony, i.e. only a short lateral shift from their growth site within the same depositional setting. The occurrence of *Lamprothamnium* sp. at the base of the Sant Boi Formation is relevant from a palaeoecological point of view since extant *Lamprothamnium* (*L. papulosum*) is a brackish species that needs seasonal haline salinity changes of below 20‰ to establish a reproductive population (Soulié-Märsche, 1998).

The second assemblage is dominated by *Harrisichara lineata* and occurs in white laminated marl related to deposition in a lacustrine environment from the upper delta plain, at the top of the Sant Boi Formation (Fig. 4 and Table 2). It is composed of *H. lineata* and *Chara rhenana* gyrogonites together with vegetative charophyte remains (corticated and ecorticate thalli). Moreover, gyrogonites do not show any evidence of fragmentation or erosion, indicating that they were buried in situ. The absence of marine or brackish fossils, together with the sedimentological and taphonomic analysis, suggests that this charophyte assemblage grew in shallow freshwater lakes (Fig. 5).

5.2. Artés Formation

5.2.1. Sedimentology and depositional environments of the Artés Formation

The continental Artés Formation, in the sense of Sáez (1987), crops out in a 10 km wide and 15 km long NE–SW oriented band along the eastern margin of the Ebro Basin. These deposits, up to 790 m thick, are mainly composed of red mudstone alternated by sandstones, occasionally conglomerate, grey marls and limestone layers. They are associated with sedimentation in a number of depositional settings related to the Montserrat–Igualada alluvial fan (Sáez, 1987). Thus, the Oristà, Santa Maria d'Oló and most of the Torre Casanova stratigraphic sections are dominated by fluvial fan facies associations, whilst the upper part of the Torre Casanova and Moià sections are dominated by lacustrine facies associations.

5.2.1.1. Fluvial fan facies associations. These are characterised by a succession of sandy channel-fill deposits, thin tabular sandstone beds with high lateral extension, and red mudstones alternating with marls and marlstones. Three facies associations were found: i) medial fluvial fan, ii) terminal lobe, and iii) flood plain facies associations.

i) Medial fluvial fan facies
Description. The medial fluvial fan facies association as described by Sáez et al. (2007) consists mainly of coarse-grained to fine-grained grey or brown sandstones which alternate with red and occasionally grey mudstones. The sandstones are up to 1–3 m thick and have high horizontal continuity reaching hundreds of metres (Figs. 6 and 7). Internally they show multi-storey bedding,

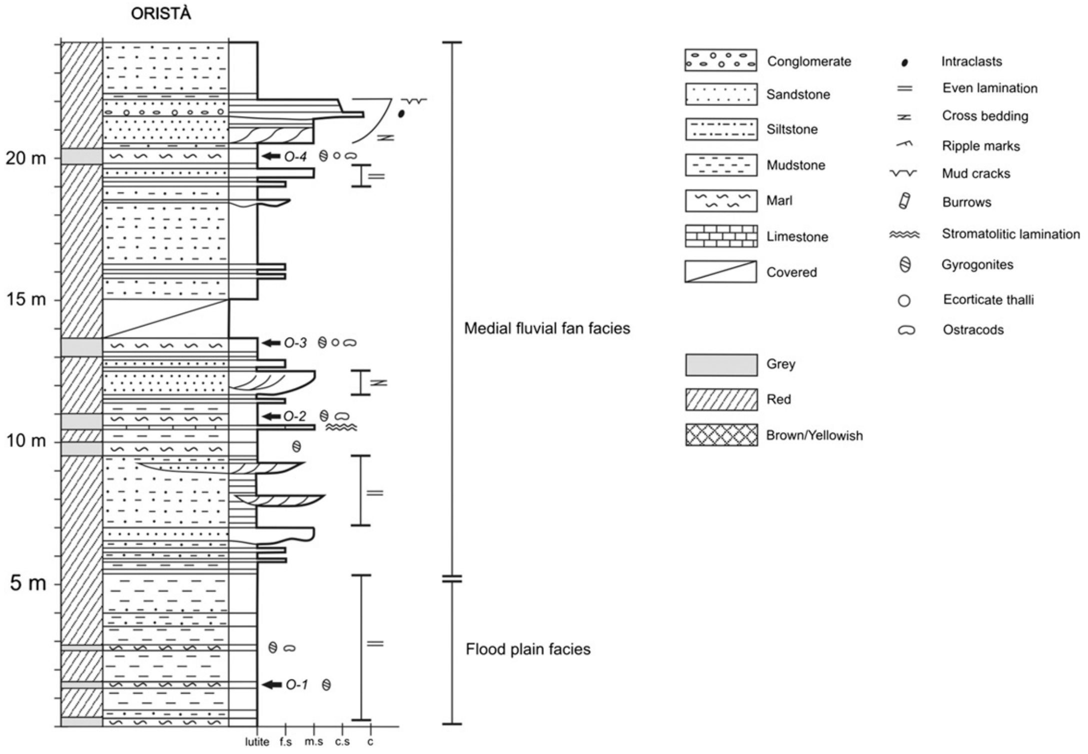

Fig. 6. Stratigraphic log for Oristà in the Lluçanès area, showing facies associations of the Artés Formation.

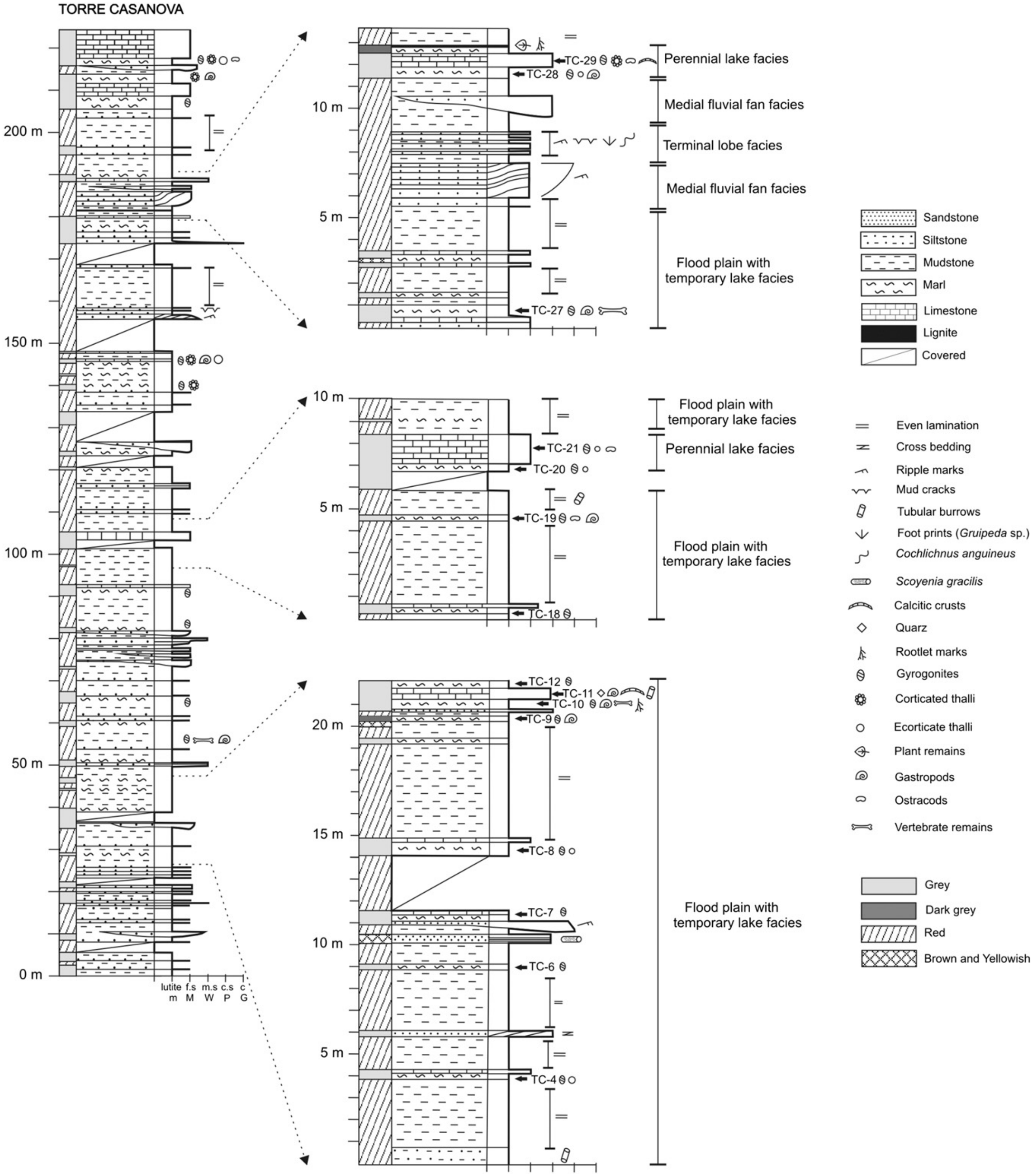

Fig. 7. Stratigraphic logs for Torre Casanova in the Bages area, showing facies associations of the Artés Formation.

formed by structureless, planar or trough-cross bedded sandstones, and mudstones. Commonly, the uppermost part of the channels is composed of siltstones with ripple-marks, desiccation cracks and intense bioturbation consisting of horizontal and vertical tubular burrows with scratch marks attributed to *Scoyenia gracilis*.

Interpretation. These facies were attributed by Sáez et al. (2007) to a medial fluvial fan setting, developed during regionally low lake levels. Red sandstones were attributed to the multi-storey infilling of fluvial channels. In general, the channel bodies from Torre Casanova show poor incision and have a wider lateral extent than similar bodies from the Oristà section. Intense bioturbation at the top of sandstones reflect well-aerated conditions in the last channel infilling phases (Gibert and Sáez, 2009).

ii) Terminal lobe facies

Description. The terminal lobe facies association, as described by Sáez et al. (2007) is dominated by thin grey to brown tabular sandstone beds, 10–30 cm thick, with a lateral extension of 100–500 m. The sandstone beds are commonly amalgamated or occasionally, alternated with laminated red mudstones or grey marlstone with charophytes (Fig. 7). In general, these beds form fining upwards successions. The tabular sandstone beds show very good grain sorting, normal grading from fine sandstone to silt dominated by ripples and planar lamination. Tops of the sandstone beds show mud-cracks, ripple-marks and abundant trace fossils, such as invertebrate burrows (*Cochlichnus anguineus*) and bird tracks (*Gruipeda* sp.).

Interpretation. This assemblage of features was attributed by Sáez et al. (2007) to deposition in spreading lobes under flooding conditions. The presence of some marlstone layers with short lateral extension (~50 m) and rich in organic matter and charophytes suggests that temporary shallow lakes may have formed during these flooding events. The ichnoassemblage mentioned from the top of sandstones has been reported from Oligocene terminal lobe deposits of the Ebro Basin by Gibert and Sáez (2009) and, in the sedimentary context, it indicates sub-aerial exposure soon after deposition and the persistence of wet and soft ground due to fluctuating water tables.

iii) Floodplain facies

Description. They consist of finely laminated red mudstones alternating with grey marlstones. Intervals with red mudstones are several metres thick and may contain thin rippled sandy-silty beds. These facies crop out extensively in the Sta. Maria d'Oló and Torre Casanova sections (Figs. 6 and 7). Marlstones are decimetric to metric in thickness and yield abundant charophyte remains (gyrogonites and thalli), pulmonate aquatic gastropods, rare ostracods and vertebrate remains, i.e. turtle osteoderms, reptile teeth and bone fragments. Decimetric limestone beds occur frequently on top of previous marlstones. From the point of view of microfacies, they are packstones composed of lithoclasts and abundant crusts, made of sparry calcite, several millimetres across, and broadly circular in section, when not collapsed. They were attributed to encrusted stems of submerged macrophytes. Other components are rare and poorly-preserved ostracods, gastropods and charophytes. Many marlstone and limestone beds contain organic matter related to phytoclasts of vascular plants and are intensively burrowed by vertical tubular structures and rootlet marks. Moreover, lignite horizons occur at the top of some limestone beds from the Torre Casanova section.

Interpretation. Red laminated mudstones are interpreted as flood plain deposits, formed by decantation of suspended fine-grained sediments after flooding events (Ricci-Lucchi, 1980). Interbedded fossiliferous marlstones are interpreted as the infilling of temporary lakes with high clastic influx, which would result in lake bottom instability and water turbidity. The limestone beds topping most of the marlstone intervals in the Torre Casanova section represent an upward shift of turbid water conditions due to abundant suspended sediment to clearer water conditions with higher biogenic lime mud production. Similar associations with fine clastic sediments representing deeper lake facies that grade upwards to shallower lake charophyte limestone have been extensively documented in the fossil record (e.g. Gierlowski-Kordesch et al., 1991). Rock fabrics, fragmentation of the skeletal remains and abundant bioturbation suggest very shallow and energetic water conditions with abundant benthic activity (Freytet and Plaziat, 1982). Dark and root-burrowed organic-rich marlstone in a lacustrine context suggests that a palustrine belt occurred in the vegetated lakeshore (Alonso-Zarza and Wright, 2010).

5.2.1.2. Lacustrine facies associations. This group of facies corresponds to the Moià Limestone Member, which presents a progressive increase in carbonates at the top of the Torre Casanova and Moià sections (Fig. 8). The Moià limestone member shows an up to 47 m thick succession of three intervals of lacustrine limestone separated mainly by marls (Sáez, 1987). Three facies associations were found and correspond to (i) marl and marlstones of turbid lake facies, (ii) Wackestones–packstones with abundant biogenic remains and (iii) grainstones of high energy lakeshore facies.

(i) Marl and marlstones of turbid lake facies

Description. Marl and marlstones are organised in up to 1 m thick, grey to yellowish beds commonly showing diffuse lamination and containing abundant disperse organic matter, intraclasts and fossil remains, mainly charophytes and ostracods. They are mainly found in the Moià Limestone Member (Fig. 8).

Interpretation. In the context of a lacustrine environment, this lithology represents deposition by decantation of suspended mud introduced by terrigenous influxes within the lake. Small successions of facies associations were observed, with marls forming the basal bed and grading upwards to marlstones and finally limestones. These successions are interpreted as the increasing activity of lime-producing organisms in the shallower and best-illuminated environments of the lake margins, leading to the view that marls and marlstones were deposited in more distal and deeper lacustrine facies than limestones. Diffuse lamination suggests that the lake bottom was occasionally anoxic, hindering bioturbation (Gierlowski-Kordesch, 2010).

(ii) Wackestones-packstones with abundant biogenic remains

Description. Most of the limestone beds in the Moià Limestone Member are represented by well-stratified and well-cemented wackestone–packstone, generally dark grey in colour, and forming tabular beds, 0.5–2 m thick that may show diffuse lamination(Fig. 8). At the top of some limestone beds, subrounded milimetric micritic intraclasts occur. The most common components of these limestones are non-articulated ostracod shells (Fig. 9B) and calcitic crusts, several millimetres across and commonly collapsed, which are interpreted as lime crusts on submerged macrophytes. Other abundant components are large portions of ecorticate and corticated charophyte thalli, charophyte gyrogonites (Fig. 9A–B), gastropods, vertebrate remains and crusts formed by calcified filaments attributed to skeletal cyanobacterial remains in the sense of Riding (1991) and isolated peloids. At least three charophyte genera, *Harrisichara*, *Gyrogona* and *Chara*, were recognised in thin sections (Fig. 9C–E). Three types of charophyte thalli were also observed, (1) *Charaxis* sp. with contiguous cortication, (2) *Charaxis* sp. with non-contiguous cortication, frequently associated with *Gyrogona* gyrogonites (Fig. 9A), and (3) ecorticate thalli, frequently associated with *Harrisichara* sp. gyrogonites.

Interpretation. The abundant freshwater fossils in these limestone beds correspond to biogenic carbonate producers in well-oxygenated and shallow lake bottoms. Predominance of wackstone and packstone fabrics indicates moderate energy sedimentation. Shallow water and moderate to high energy are also indicated by intraclasts that suggest a reworking of carbonate mud during lake-level oscillations (Freytet and Plaziat, 1982). In sum, these facies are attributed to deposition in freshwater, permanent and shallow lakes with high water alkalinity.

(iii) Grainstones of high energy lakeshore facies

Grain-supported limestone at the upper part of the Moià Member (Fig. 8) are interpreted as high energy lakeshore facies. They are grey to dark grey, massive or cross-bedded packstones–grainstones forming tabular beds, 0.5–1.5 m thick. They include abundant quartz grains, whilst the carbonate components are fragments of gastropods, calcite crusts of millimetric length attributed to incrustations on submerged macrophytes (Fig. 9F), non-articulated ostracod shells, fragments of charophyte gyrogonites and thalli and rare oncoids (Fig. 9H). Well-preserved crusts with local dome-shaped morphologies are found on invertebrate shells. They show abundant calcified filaments, up to 10 μm across, attributed to cyanobacteria (Fig. 9G). Moreover, some layers show abundant sub-angular intraclasts.

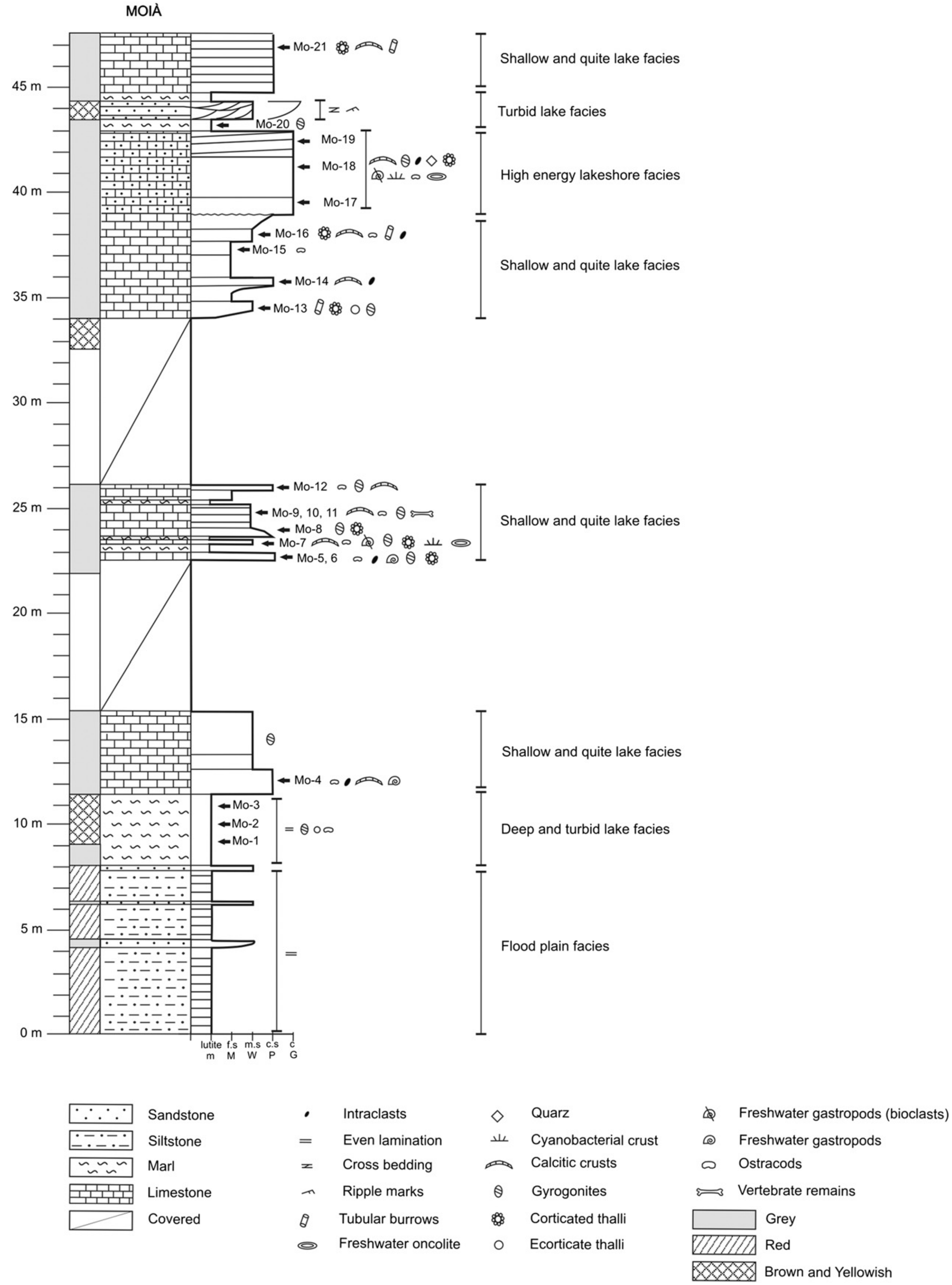

Fig. 8. Stratigraphic log for Moià in the Bages area, showing facies association of the Moià Limestone Member.

Interpretation. Grain-supported limestone beds of the Moià Member are interpreted as high-energy lacustrine deposits subjected to terrigenous inputs by fluvial inlets. The packstone–grainstone fabrics, the presence of dispersed quartz-grains along with the abundance of fragmented fossil remains and intraclasts are representative of a lakeshore facies association

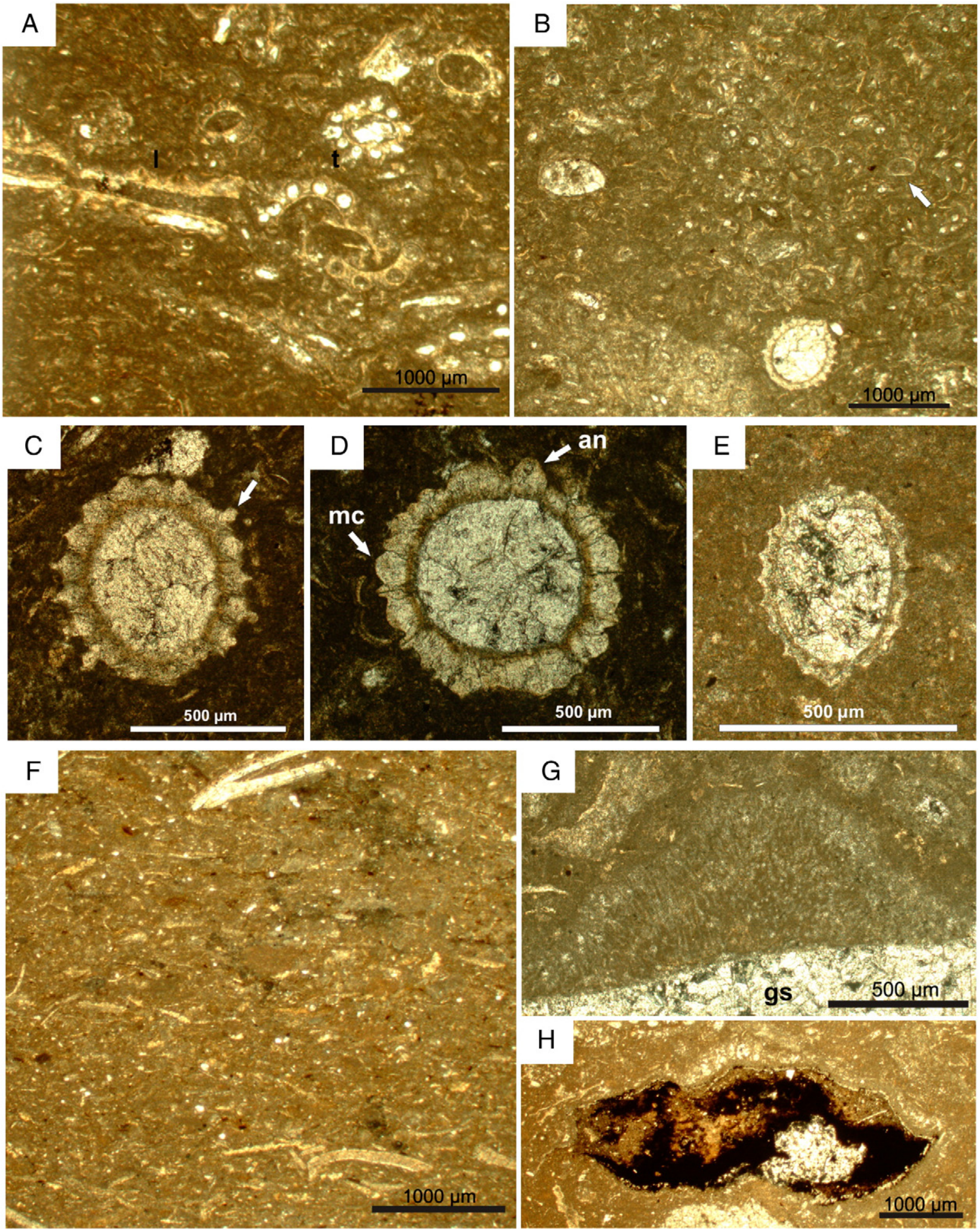

Fig. 9. Microfacies and their components distinguished in limestone from the Moià section. A.–E. Microfacies of wackestones–packstones with abundant biogenic remains. A. *Charaxis* sp. showing non-contiguous cortication in transversal (t) and longitudinal (l) sections; thin section from sample Mo-21. B. Ostracods (arrow) and gyrogonites; thin section from sample Mo-10. C. Near-longitudinal section of *Harrisichara* sp. gyrogonite showing the ornamentation consisting of tubercles (arrow); thin section from sample Mo-5B. D. Longitudinal section of *Gyrogona* sp. gyrogonite showing the apical nodules (ap) and mid-cellular crest (mc); thin section from sample Mo-8B. E. Longitudinal section of *Chara* sp.; thin section from sample Mo-12. F.–H. High energy lakeshore microfacies. F. General view with abundant bioclasts; thin section from sample Mo-18. G. Longitudinal section of cyanobacterial incrustation on a gastropod shell (gs), thin section from sample Mo-18. H. Oncoid with an amber nucleus; thin section from Mo-7.

(Freytet and Plaziat, 1982). Well-preserved cyanobacterial crusts with small domes would be the only autochthonous fossils in this largely transported and allochthonous assemblage. However, the high sedimentation rates probably made difficult the further growth of these microbial structures to form well-developed oncoids, which would generally be expected to appear abundantly in this type of high-energy environment (Arenas-Abad et al., 2010).

5.2.2. Charophyte taphonomy and palaeoecology in the Artés Formation

Three different charophyte assemblages were found to occur in the Artés Formation. (1) An assemblage dominated by *Nodosochara jorbae* along with less abundant *Lychnothamnus longus*, *Harrisichara tuberculata* and *Chara* sp. is particularly frequent in marlstones from flood plain facies associations from the sections of Oristà, Santa Maria d'Oló and most of the Torre Casanova section (Artès Formation), where more than one hundred gyrogonites of *N. jorbae* were found per sample (Table 2). (2) Locally, in one marlstone bed rich in organic matter from Torre Casanova, this assemblage is substituted by an assemblage dominated exclusively by *Lychnothamnus grambastii* (Table 2).

The sedimentological data discussed above indicate that charophyte-rich marlstones represent temporary lakes subjected to abundant terrigenous inputs from neighbouring flood plains, which probably resulted in turbid lake water conditions (Fig. 10). The dominance of *Nodosochara jorbae* or *Lychnothamnus grambastii* in such environments seems to be dependent on the content of organic matter, the latter species also being prone to occur in lacustrine marlstone related to lignite in southern France (Feist-Castel, 1971). In all cases, the excellent preservation of the gyrogonites and their association with thalli, freshwater molluscs and well-preserved non-ornamented ostracods suggest that the assemblage was autochthonous in this depositional setting.

(3) In contrast to previous assemblages, the assemblage dominated by *Harrisichara tuberculata*, along with less abundant *Nodosochara jorbae*, *Lychnothamnus longus*, *Lychnothamnus stockmansii*, *Lychnothamnus grambastii*, *Gyrogona caelata*, *Sphaerochara labellata*, *Nitellopsis* (*Tectochara*) *merianii* and *Chara* sp., occurs in marls from the upper part of the Torre Casanova section and in laterally equivalent beds from the Moià section in the Moià Limestone Member (Table 2).

The assemblage dominated by *Harrisichara tuberculata* was found mainly in grey marl intervals that pass vertically to lacustrine limestones. This succession was characterised in sedimentological terms as representing lake infilling sequences. In general, samples from

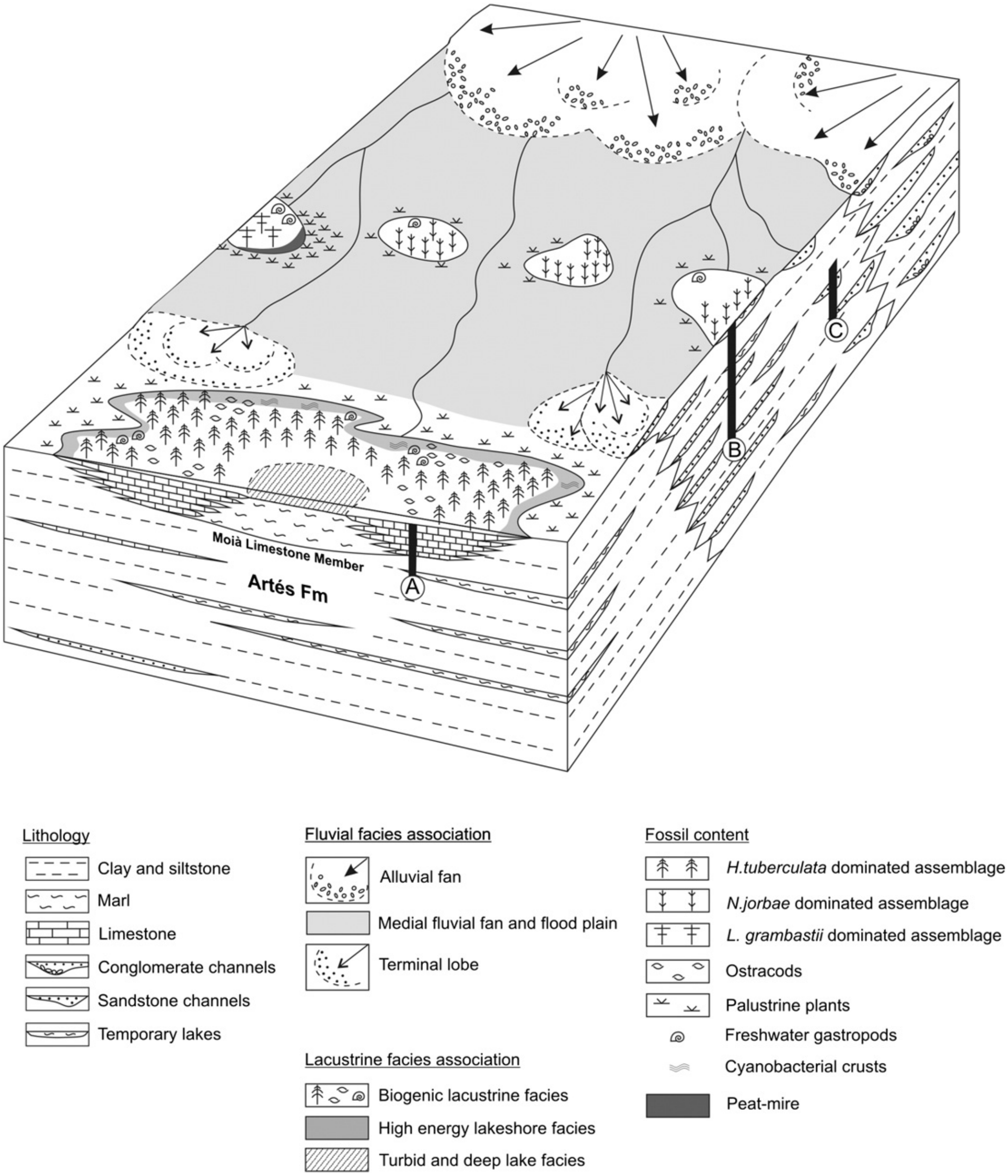

Fig. 10. Palaeoenvironmental model summarising the distribution of the *Nodosochara jorbae*, *Lychnothamnus grambastii* and *Harrisichara tuberculata* dominated assemblages in the continental Artés Formation. The main stratigraphic logs represented are: A. Moià, B. Torre Casanova, C. Oristà. Not to scale.

marls show well-preserved gyrogonites associated with vegetative charophyte remains (ecorticate and corticated thalli), small gastropods and rare non-ornamented ostracods. Many charophyte species identified in marls occur also in limestones representing the shallow lacustrine facies. The components, taphonomy and palaeoecology of these limestones were characterised from thin sections (Fig. 9). The good preservation of both gyrogonites and thalli suggest that they are autochthonous or parautochthonous. In sum, sedimentological and taphonomic analysis of marlstone and limestone intervals from the Moià Limestone Member suggest that the *H. tuberculata*-dominated assemblage grew in freshwater perennial lakes subjected to low terrigenous input and located in distal alluvial fan contexts (Fig. 10).

6. Discussion

Five charophyte assemblages from the Upper Eocene non marine stratigraphic units of the eastern Ebro Basin have been palaeoecologically characterised on the basis of sedimentological and taphonomic evidence. The time interval represented by the Harrisichara vasiformis-tuberculata biozone includes two different palaeoecological contexts in the Sant Boi Formation. The assemblage dominated by *Harrisichara vasiformis-tuberculata* Feist-Castel, 1977b associated with *Nodosochara jorbae* Choi, 1989 *Lamprothamnium* sp. and *Chara* sp. occurs in brackish environments laterally equivalent to paralic marshes. In contrast, in white laminated marls attributed to stable freshwater lacustrine conditions, the charophyte assemblage is composed of abundant *Harrisichara lineata* Grambast 1957 associated with *Chara rhenana* Schwarz and Griessemer, 1994.

Three more charophyte assemblages were found in deposits from the continental Artés Formation and belong to the Stephanochara vectensis biozone. The first assemblage is dominated by *Nodosochara jorbae* Choi, 1989, together with *Lychnothamnus longus* Choi 1989, *Harrisichara tuberculata* (Lyell, 1826) Grambast (1957) and *Chara* sp. as subsidiary species. It occurs in marlstone intervals related to freshwater and temporary lakes located in a middle-distal fluvial fan context and submitted to a high terrigenous input. Another assemblage is exclusively formed by *Lychnothamnus grambastii* and occurs in facies similar to the previous assemblage but with a higher organic matter content. Finally, the assemblage dominated by *Harrisichara tuberculata* Grambast, 1957 is associated with a higher number of species, i.e. *N. jorbae*, *L. longus*, *Lychnothamnus stockmansii*, *L. grambastii*, *Nitellopsis* (*Tectochara*) *merianii*, *Gyrogona caelata*, *Sphaerochara labellata* and *Chara* sp. This species-rich charophyte assemblage occurs in marls and limestones of the Moià Limestone Member, which are related to freshwater perennial lakes located in a distal alluvial fan context.

The palaeoenvironmental distribution of these species suggests that in the Sant Boi Formation the index-species *Harrisichara vasiformis-tuberculata* is to be found only in brackish ponds, whilst in coeval freshwater environments another species, *Harrisichara lineata* occurred. In the Artès Formation it is again evident that another much-used biostratigraphic marker, *Harrisichara tuberculata*, is also palaeoecologically limited. This species is mostly represented in perennial lakes whilst it occurs rarely in temporary lakes.

The palaeoecological restriction of all *Harrisichara* species is in contrast to the wide distribution of the Iberian Priabonian species *Nodosochara jorbae*. This species is equally found in brackish ponds from the Sant Boi Formation and in freshwater temporary and permanent lakes from the Artés Formation. Indeed, this eurytypic ecological nature corresponds much better to what is generally considered the best ecological status for a biostratigraphic marker. However, this wide range of habitats is not supported by a wide geographical distribution or by a short distribution time, which are other important conditions for a species to be useful in biostratigraphy.

7. Conclusions

This study provides new information about the ecology of the Upper Eocene charophyte floras in the north eastern part of the Ebro Basin. In particular, three *Harrisichara* species, significant in the European biostratigraphy, have been shown to display rather restricted ecological distributions. Thus, *Harrisichara vasiformis-tuberculata* grew in brackish ponds whilst the coeval *Harrisichara lineata* appears to have grown in freshwater lakes. Finally, the younger *H. tuberculata* grew mainly in well-developed and perennial freshwater lakes and much more rarely in temporary lakes within an alluvial fan context. Other species appear to be related to specific habitats. Thus, *Nitellopsis* (*T.*) *merianii*, *Sphaerochara labellata*, *Lychnothamnus stockmansii* and *Gyrogona caelata* occur together but not always with *H. tuberculata*, indicating that they were also stenotypic species adapted to perennial freshwater lakes. Another stenotypic species is *Lychnothamnus grambastii*, which was adapted to temporary freshwater lakes with a higher content in organic matter. In contrast, other species displayed a larger range of distributions. This is the case of *Lychnothamnus longus* and *Chara* sp., which occur both within temporary and perennial freshwater lake facies. The so-far Iberian species *Nodosochara jorbae* displays the largest ecological distribution, since it was represented both in brackish environments and in freshwater, temporary and perennial lakes, suggesting that it was a eurytypic species.

The possibility of a facies and environmental control superimposed on the established charophyte biozonation is of prime importance, since it would mean that some biozones are only recognisable provided that particular palaeoenvironmental conditions occurred. Consider for instance the biostratigraphic consequences of the index species *Harrisichara vasiformis-tuberculata* being found exclusively in brackish water deposits whilst coeval freshwater lacustrine deposits bear only the long-lasting *Harrisichara lineata*. The fact that the succession of the three species of the *H. tuberculata* lineage has been recognised in many parts of Europe (Hampshire Basin, Paris Basin, Ebro Basin) is only of regional help since many upper Eocene European basins changed from transitional to non-marine conditions at the Eocene–Oligocene boundary, driven by a relative drop in sea-level due to Antarctic glaciation and global palaeoclimatic aridification and cooling (Zachos et al., 2001; Xiao et al., 2010).

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Biogeographic history of two Eurasiatic Cenozoic charophyte lineages

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ABSTRACT

Long-term biogeographic history of charophytes is a highly relevant, although less-studied topic to understand the distribution of extant species. Two contrasting biogeographic histories of Eurasiatic charophyte lineages are documented and the reasons for such wide distributions are explored. *Nitellopsis (Tectochara) merianii- N. obtusa* is a charophyte lineage ranging from the Uppermost Eocene to the present and displaying Eurasiatic distribution since the Late Oligocene. *Lychnothamnus stockmansii-L. major* lineage is defined here as an Eurasiatic charophyte lineage ranging from the Late Eocene to the Early Oligocene. Both lineages are well documented in the fossil record owing to their applications in rock aging. The historical biogeography of these lineages displays two opposite patterns. Lineage *Lychnothamnus stockmansii-L. major* displays an Eurasiatic distribution from its first occurrence in the Late Eocene, whilst lineage *Nitellopsis (Tectochara) merianii-L. obtusa* underwent a long period of European provincialism ranging from the Late Eocene to the Late Oligocene (ca 10 Million of years, Ma), to begin later, during Late Oligocene and Miocene, an eastwards expansion until reaching its present Eurasiatic distribution. These two different biogeographic patterns appear to be related to the contrasting mechanisms of dispersalin monoecious vs. dioecious charophytes, well known in extant *Chara*, and allow us to identify the time needed by characeans to reach supra-continental distributions.

1. Introduction

Charophyte palaeobiogeography has been poorly explored to date. Although the data about the occurrence of Cenozoic fossil charophytes are rich, they were mainly built for biostratigraphic purposes, without taking into account their biogeographic implications. However, this large amount of biostratigraphic information indirectly provides significant data about the age and distribution of charophytes, which are two important clues for palaeobiogeographic analysis. Previous palaeobiogeographic studies on Cenozoic charophytes were carried out by Riveline (1986) and Anadón et al. (1992) at the European scale. At a supracontinental scale, Soulié-Märsche et al. (2002) analysed the distribution of the well-known Tertiary species

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Nitellopsis (Tectochara) merianii whereas Bhatia (2006) analysed the dispersal routes of the living species *Lychnothamnus barbatus* from the Late Miocene to the present and established an hypothesis about the possible reasons and time needed for this species to achieve its present Eurasiatic distribution.

Distribution of extant charophytes at a supracontinental scale depends on the capability of species to perform sexual reproduction after a colonization event, which is largely related to the arrangement of gametangia (dioecious vs. monoecious) and the role played by migratory aquatic birds in dispersing oospores and gyrogonites (Proctor, 1962; 1980; Proctor et al., 1967). Monoecy and dioecy are difficult to document in fossil species, but they may be inferred if a direct ancestor-descendant relationship can be established between fossil and extant species.

The present study aims to document the biogeographic history of one exclusively fossil charophyte lineage, *Lychnothamnus stockmansii-L.major* and one lineage with both fossil and extant representatives, *Nitellopsis (Tectochara) merianii-N. obtusa,* which depict two constrating ways of reaching a supracontinental biogeographic distribution. We show that such a distribution can be reached independently from the arrangement of gametangia, although at completely different velocities.

2. Material and methods

The dataset of this study results from the revision of the bibliography available to the authors about the world occurrence of the morphotaxa forming the lineages or evolutionary species *Lychnothamnus stockmansii-L.major* and *Nitellopsis (Tectochara) merianii-N. obtusa* (Tables 1-4). The fossil record of these species, shows distributions within Eurasia, but might be increased in the future, when new data will be available from Africa and Australia, which are poorly known from the point of view of Cenozoic fossil charophytes. The dataset shows contrasting qualities of taxonomic data. In most of the references, the taxonomic determinations were checked with the illustrations on hand.

The biogeographic analysis has been performed by plotting the distribution of fossil taxa in palaeogeographic maps obtained from Blakey (2006), for each geological interval. Most of the chronostratigraphic information available allowed for a precision of half a geological stage. This time ressolution is coherent with the temporal ranges of charophyte biozones which are the essential tool for discerning ages. Data with less ressolution are listed in Tables 1-4 for record, but were not plotted on the corresponding palaeogeographical map. The resulting distribution maps show the biogeographic changes through time and allow for a direct interpretation of the species biogeographic history.

3. Characterisation of evolutionary lineages

The study of long term biogeographic patterns in the fossil record is based in evolutionary inferences that relate a chronological succession of fossils with a particular palaeogeographic distribution. From this viewpoint, evolutionary lineages are crucial to characterise the history of one species in long time periods. Evolutionary lineages are understood as uninterrupted gradual successions of the fossil remains of species, which are regarded as continuous lineages of ancestors and

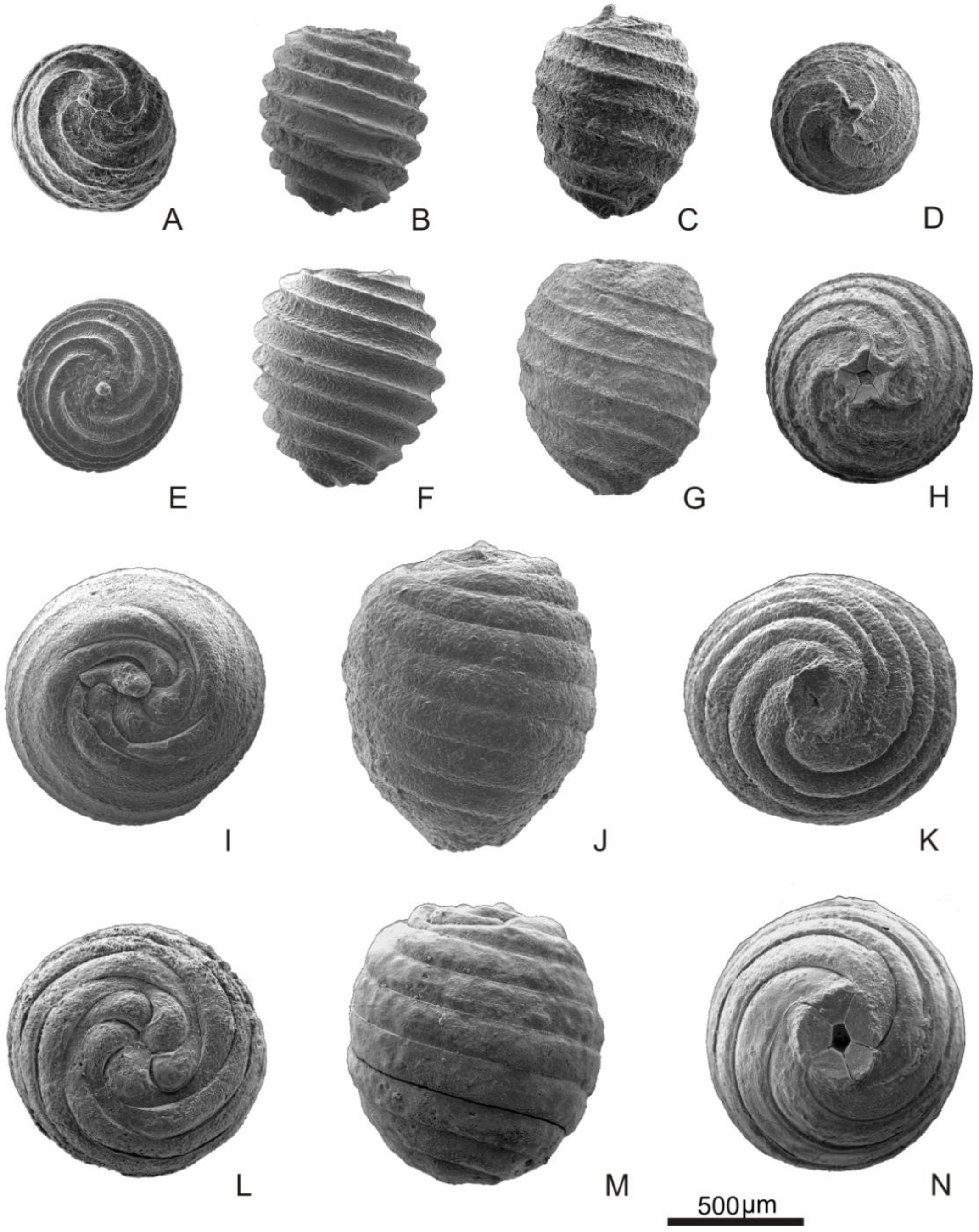


Fig. 1. Charophyte gyrogonites from the eastern margin of the Ebro Basin (Artés Formation and its lateral south-western formations). A-D, *Lychnothamnus stockmansii*, Torre Casanova, Moià, Rubió, Rocafort de Queralt and Sarral sections. A) apex, sample TC-31, B) lateral view, sample TC-31, C) lateral view, sample TC-31, D) basal view, sample TC-31. E-H, *Lychnothamnus major*, Sarral section and El Talladell outcrop, E) apex, sample TA-1, F) lateral view, sample TA-1, G), lateral view, sample SA-19; H) basal view, sample SA-19. I-N, *Nitellopsis (Tectochara) merianii*, Torre Casanova and Vinaixa sections and El Talladell outcrop, I) apical view, sample TC-28 J) lateral view, sample TC-28, K) base, sample TC-28, L) apical view, sample VI-5, M) lateral view, sample VI-5, N) basal view, sample VI-5.

descendants through time. Each step in the gradual succession of morphotypes was termed by Simpson (1961) a chronospecies, due to its use in rock aging (chronostratigraphy), but they are considered now by many palaeontologists to be mere gradual changes within one species (Wiley 1981). The concept of evolutionary species as defined by Wiley (1981) adheres to this idea. In charophyte palaeontology evolutionary lineages were mainly described on the basis of utricles of Cretaceous clavatoraceans by Grambast (1974). These lineages were later redefined as evolutionary species by Martín-Closas (1989, 1996) and Schudack (1993). The recognition of evolutionary lineages in Tertiary characeans is much more complicate, mostly due to the low number of characters preserved in characean gyrogonites in comparison to the characters available in clavatoracean utricles. The two evolutionary lineages studied here were amongst the few characean lineages to be proposed in the past, although with contrasting definition details. Their biogeographic history was never analysed before.

3.1. The evolutionary lineage Lychnothamnus stockmansii-L. major

Two successive chronospecies, initially ranged within the fossil genus *Rhabdochara*, i.e. *R. stockmansii* Grambast 1958 and *R. major* Grambast and Paul 1965, are the base of this lineage. The chronospecies *Rhabdochara stockmansii* was defined by Grambast (1958) in the Priabonian of Southern England (Hampshire basin, Isle of Wight) on the basis of large gyrogonites, 600-950 µm high and 500-825 µm wide, cylindrical-ovoid in shape with a flat apex showing an apical depression and tapered base with a well-marked basal funnel. In lateral view, the gyrogonites showed seven to nine non-ornamented and concave spiral cells ranging between 80 to 160 µm in width. This species was transferred later to genus *Lychnothamnus* as *L. stockmansii* (Grambast 1958) Soulié-Märsche 1989.

Rhabdochara major was described first from the Oligocene of southern France (Saint-Vincent-de-Barbeyrargues, Languedoc) based on large gyrogonites, 800-1150 µm high and 650-1000 µm wide, cylindrical-ovoid in shape. These gyrogonites showed non-modified, flat or slightly rounded apex with an apical depression and a tapered base with a well-defined pentagonal funnel. They displayed in lateral view seven to nine (frequently nine) non-ornamented and concave spiral cells measuring 100-175 µm in width. This species was later transferred to genus *Lychnothammus* as *L. major* (Grambast and Paul 1965) Soulié-Märsche 1989.

According to Grambast and Paul (1965) both *Lychnothamnus* species differed only in the size of the gyrogonite (*L. major* is ~200 µm larger than *L. stockmansii*), the other characters being equal, which mean that they were morphologically very close to each other. Feist-Castel (1977a) mentioned that both species were not only similar in shape but also related to each other by morphotypes of intermediate size, which she found in Lower Oligocene beds from Roque d'Anthéron (Provence, France). Later, Baciu and Feist (1999) mentioned again intermediate gyrogonites between *L. stockmansii* and *L. major* in Lower Rupelian deposits of the Transylvanian basin (Rumania). They proposed first the name "*Lychnothamnus stockmansii-major*" to designate them. These reports implicitly mean that a gradual succession of fructifications occurred between *Lychnothamnus stockmansi* and *L. major*, which would correspond to an evolutionary species in the sense of Wiley (1981).

In order to characterise better the succession of gyrogonites between *L. stockmansii* and *L. major* a number of stratigraphic sections ranging from the Upper Eocene to the Lower Oligocene, and yielding rich gyrogonite assemblages from these two chronospecies, were sampled in the Eastern Ebro basin (Catalonia, Spain). Three gyrogonite assemblages (samples TC-31 from Torre Casanova section, SA-7A and SA-19 from Sarral section), were selected and correspond to three successive and well dated horizons covering the complete time interval when the transition from *L. stockmansii* to *L. major* occurred. The age of these samples was recently provided by Sanjuan et al. (2013) as follows: (1) Gyrogonites from sample TC-31 (Torre Casanova section) were correlated with the MP18 or MP19-20 pre-Grande Coupure European mammal reference level and with the Harrisichara tuberculata - Nodosochara jorbae local charophyte biozone indicating Late Priabonian age. This sample was calibrated with chron C13r providing an absolute age of ~34, 2 Ma (million year ago). (2) Gyrogonites from sample SA-7A (Sarral section) were correlated with MP21 Post-Grande Coupure mammal reference level and with the Lychnothamnus vectensis local biozone (Latest Priabonian-Earliest Rupelian). This sample was calibrated with C13n chron providing an age of ~33, 6 Ma. (3) Finally, gyrogonites from sample SA-19 also from Sarral section, were correlated with MP23 European mammal reference level and with the Lychnothamnus major European biozone (Middle Rupelian). It was calibrated with C12r chron providing an absolute age of ~31, 4 Ma. In conclusion, the three successive gyrogonite assemblages were separated from each other by unequal time intervals, SA-7A being only 0.6 Ma younger than TC-31, whilst the time between SA-7A and SA-19 represents 2.2 Ma. Unfortunately there were no other intermediary samples available between SA-7A and SA-19 to allow for a better characterization of the morphological succession, since the sedimentary facies were inappropriate for charophytes in the succession studied.

The two youngest assemblages, attributed to *Lychnothamnus stockmansii*, (samples TC-31 and SA-7A) displayed similar morphological characters (Figs 1 and 2) except for the size, which was slightly larger in SA-7A, i.e. ~50 µm higher and ~40 µm wider in average. More significant differences were found when comparing these *L. stockmansii* assemblages with the assemblage from sample SA-19 (Fig. 1), assigned to *Lychnothamnus major*, which displayed about ~200 µm larger gyrogonites and a relatively higher number of convolutions, mostly 7-8 convolutions in the chronospecies *L. stockmansii* vs. 8-9 convolutions in *L. major* (Fig. 2A-C). The length/width ratio (Isopolarity Index, ISI) was similar in the three *Lychnothamnus* assemblages studied (Fig. 2D) and the size variation of the three assemblages follows very similar regression line slope (Fig. 2E).

The size shift between the two first assemblages (TC-31 and SA-7A), i.e. 50µm size increase during 0.6 Ma, would roughly correspond to the size increase expected to occur between the second and third assemblages (SA-7A and SA-19). Thus, from 200µm increase in size expected, 183 µm were found for 2.2 Ma, assuming that the change was continuous through time. The number of convolutions shows also a gradual shift in the three assemblages available (Fig 3C). The general tendency of *Lychnothamnus* gyrogonites to increase the size and the convolution number through time, keeping the other gyrogonite characters stable, would support the view of previous authors that there is a continuum of morphological change from Late Priabonian-Early Rupelian *L.*

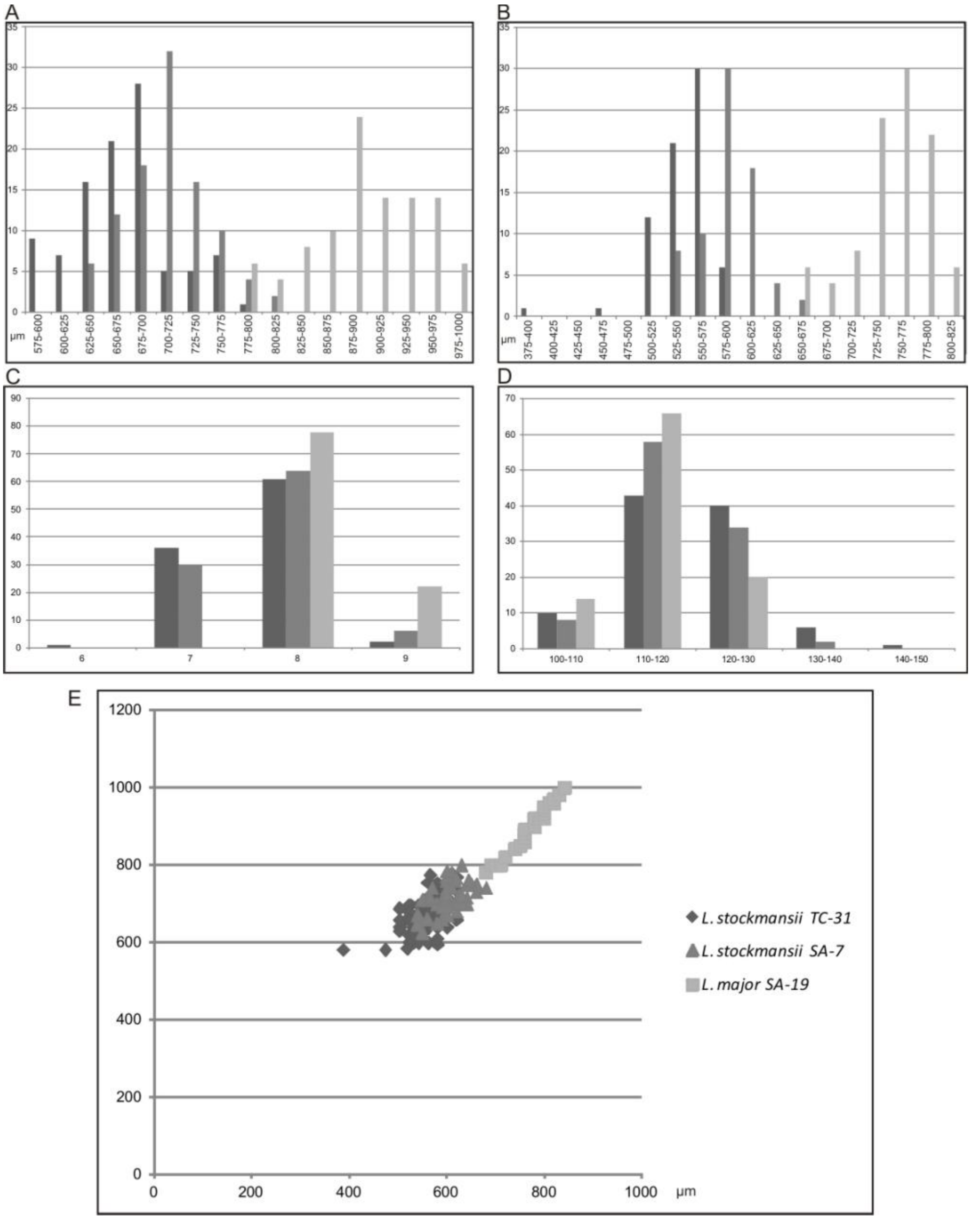


Fig. 2. *Lychnothamnus stockmansii-major* morphometric histograms. A) Distribution of length, B) Distribution of width, C) Number of convolutions, D) length/width ratio (ISI) and E) Dispersion graphic measured on 150 gyrogonites (50 gyrogonites per sample) showing the regression line of each gyrogonite assemblage.

stockmansii to the Middle Rupelian *L. major*.

The morphological trend described (increase in the fructification size and in the convolution number) is very common in other charophyte lineages. Grambast (1974) documented similar trends in a number of Cretaceous clavatoracean lineages, such as *Perimneste-Atopochara* or *Globator*. In the latter case, Martín-Closas et al. (1999) related these trends to a bio-mechanical increase in the fructifications resistance towards internal pressures that would occur during the maturation and germination process of the egg-cell. Focusing on Tertiary charophytes Sille et al. (2004) characterised the same trends through Eigenshape analysis, in two successive Eocene-Oligocene *Harrisichara* chronospecies i.e. *H. vasiformis* and *H.*

tuberculata from the Hampshire basin (Isle of Wight, South of England). These authors interpreted this morphological shift as a functional response of the fructification morphology to the global climate change near the Eocene-Oligocene boundary. In the context of decreasing temperatures and increasing seasonality, larger gyrogonites would be capable of concentrating a larger amount of reserves for germination and be more efficient for reproduction. Soulié Märsche (1989) showed in extant populations of *Lychnothamnus barbatus*, that the gyrogonite size and calcification were mainly controlled by ecological factors, such as the hours of effective sun light upon the plant during the gyrogonite growth, rather than by the plant itself.

3.2. The evolutionary lineage Nitellopsis (Tectochara) merianii-N. obtusa

This evolutionary lineage was proposed by Soulié-Märsche et al. (2002) by comparing the gyrogonite morphology of Late Miocene *Nitellopsis (T.) merianii* from Aït Kandoula basin (Morocco) with a living assemblage of *Nitellopsis obtusa* from lake Uhle Loch (Germany). The authors concluded that the two assemblages showed strong concordance in morphological characters and biogeographical distribution suggesting that they formed two successive chronological terms of the same evolutionary species. The gyrogonites of the first chronospecies, called *N. (Tectochara) merianii* show a characteristic apical morphology, with apical cells displaying well-marked thinning and narrowing in the periapical zone and ornamentation with prominent apical nodules. The base shows a well-marked basal funnel, which is common to all species of subgenus *Tectochara*. In contrast, the second chronospecies of the lineage, *Nitellopsis obtusa,* lacks a basal funnel or has only a shallow depression and often shows a lower degree of calcification and ornamentation.

The oldest occurrence of *Nittellopsis (T.) merianii* has been recently recorded in Late Priabonian bed TC-28 from the stratigraphic section of Torre Casanova near the village of Moià (Eastern Ebro Basin, Catalonia, Spain), which is correlated with pre-Grande Coupure MP18 or MP19-20 European mammal reference level and calibrated to the magnetochron C15n providing an absolute age of ~35 Ma (Sanjuan et al. 2013). The main distribution of this chronospecies occurred during the Oligocene, Miocene and Pliocene. A progressive morphological shift from this morphotype to the *Nitellopsis obtusa* morphotype occurred at the Pliocene-Quaternary boundary (Soulié-Märsche et al., 2002).

4. Palaeobiogeography of *Lychnothamnus stockmansii-L. major*

The biogeographic history of this lineage is subdivided in two different chronological steps, distinct both in terms of palaeogeographic range and gyrogonite morphology.

Late Priabonian–Early Rupelian
Lychnothamnus stockmansii occurred first in numerous sites ranging from Late Eocene (Middle Priabonian) to Earliest Oligocene (Early Rupelian). From the palaeogeographic point of view *L. stockmansii* was reported in many European and Chinese basins (Table 1, Fig. 3). In Europe, the extreme latitudinal occurrences are the Paris-Hampshire basin and Rhine Graben in the North and the island of Menorca and the Ebro basins in the South (Riveline, 1986; Martín-Closas and Ramos, 2005). Intermediate distributions are in the

Taxonomy	Age	Locality	Country	Reference
Rhabdochara stockmansi	Early Oligocene	Les Farges (Haute Loire)	France	Grambast (1958)
Rhabdochara stockmansi	Early Oligocene	Bautersem (Hoogbustel)	Belgium	Stockmans (1960)
Rhabdochara stockmansi	Early Oligocene	Eigalayes (Provence)	France	Montenant (1968)
Rhabdochara stockmansi	Early Oligocene	Bourdas (Provence)	France	Touraine (1971)
Rhabdochara stockmansi	Late Eoc.-Early Olig.	Roque-de Thau (Gironde) Artigues (Gironde) Saint-Aubin-de -Cadelech (Dordogne)	France	Feist and Ringeade (1977)
Rhabdochara stockmansi	Oligocene	Roque-Anthéron (Provence)	France	Feist-Castel (1977a)
Rhabdochara stockmansi	Early Oligocene	Horestone point (Isle of Wight) Whitecliff Bay (Isle of Wight)	England	Feist-Castel (1977b)
Rhabdochara stockmansi	Late Eoc.-Early Olig.	Bohai (Tianjin)	China	Xinlun (1978)
Rhabdochara stockmansi	Late Eoc.-Early Olig.	Paris province (various localities) Horestone point (Isle of Wight)	France England	Riveline (1986)
Rhabdochara stockmansi	Oligocene	Guandong	China	Huang et al. (1988)
Rhabdochara stockmansi	Middle Oligocene	Eastern Zhejiang	China	Liu (1989)
Rhabdochara stockmansi	Late Eocene	Fonollosa (Ebro basin, Catalonia)	Spain	Choi (1989)
Rhabdochara stockmansi	Late Eoc.-Early Olig.	Junggar Basin (Xinjiang)	China	Liu and Wu (1990)
Rhabdochara stockmansi	Late Eoc.-Early Olig.	Tarim basin (Xinjiang)	China	Lu and Luo (1990)
Rhabdochara stockmansi	Early Rupelian	Preluca (Transylvania basin, Cluj)	Roumania	Baciu and Feist (1999)
Lychnothamnus stockmansii	Late Priab.-Early Rup.	Es Macar de sa Llosa (Isle of Minorca)	Spain	Martín-Closas and Ramos (2005)
Lychnothamnus stockmansii	Late Priab.-Early Rup.	Ebro Basin (various localities)	Spain	Sanjuan et al., (2013)

Table 1. Distribution dataset of *Lychnothamnus stockmansii*

Provence and Aquitaine basins, southern France (Riveline, 1986). In Eastern Europe, *L. stockmansii* was found, alone or in mixed populations with *L. major*, in Rumania (Baciu and Feist, 1999). This species has been also documented in many Chinese localities i.e. Bohai Bay basin in NE China (Xinlun, 1978, Huang et al., 1988), Tarim basin in Qianghai and Xinjiang provinces, NW China (Liu and Wu 1990; Lu and Luo 1990) and Yunnan province in southern China (Liu 1989). The biogeographic distribution of this species suggests that *Lychnothamnus stockmansii* was an Eurasiatic species widely distributed throughout the whole continent within the palaeolatitudes ranging between ~20-50ºN.

Middle to Late Rupelian.

This period is characterised by the occurrence of the chronospecies *L. major*, which has been exclusively reported from Europe. This species was recorded in the southern European basins of Aquitaine, Provence and Ebro by Riveline (1986) and references herein (Table 2, Fig. 4). To the north, *L. major* was also reported in Paris basin and in the western sector of the Switzerland Molassic basin (Riveline 1986). Eastwards Baciu and Feist (1999) reported this species from the Transylvanian basin, Rumania (Table 2, Fig. 4).

In consequence with previous data, the historical biogeography of the *Lychnothamnus stockmansii-L. major* lineage comprises two clearly defined periods; 1) origin in Europe and Asia during the Late Priabonian-Early Rupelian and 2) reduction of this biogeographic range to Europe during the Rupelian, leading to extinction in the Latest Rupelian.

Taxonomy	Age	Locality	Country	Reference
Rhabdochara major	Rupelian	Saint-Vincent-de-Babeyragues (Hérault) Fointainebleau, Soisy-sur-École (Paris)	France	Grambast and Paul (1965)
Rhabdochara major	Late Rupelian	Peissy (Satigny)	Switzerland	Kissling (1974)
Rhabdochara major	Late Rupelian	Villebramar (Aquitaine)	France	Feist and Ringeade (1977)
Rhabdochara major	Late Rupelian	Provence (various localities)	France	Feist-Castel (1977a)
Rhabdochara major	Late Rupelian	Itteville, Esclimot, Etrechy, St. Ambroix (Paris)	France	Riveline (1986)
Rhabdochara major	Late Rupelian	Solivella, El Talladell (Ebro basin, Catalonia)	Spain	Feist et al. (1994)
Rhabdochara major	Middle-Late Rupelian	Dâncu (Transilvanian basin, Cluj)	Roumanie	Baciu and Feist (1999)
Lychnothamnus major	Late Rupelian	Sarral, El Talladell (Ebro basin, Catalonia)	Spain	Sanjuan and Martín-Closas (2013)

Table 2. Distribution dataset of *Lychnothamnus major*

The simultaneous appearance of *L. stockmansii* in Upper Priabonian-Lower Rupelian deposits from many European and Chinese basins suggest that this species displayed from the beginning an Eurasiatic distribution, mainly controlled by palaeoclimatic (latitudinal) boundaries, (Fig. 3). This extremely wide biogeographic range was drastically reduced during the Rupelian, when this species became restricted to Europe (Fig. 4). No representatives of this charophyte lineage were found beyond that age, but Soulié-Märsche and Martín-Closas (2003) indicated that the gyrogonite features of the Early Oligocene *Lychnothamnus major* were almost identical to the Late Miocene *Lychnothamnus barbatus* subsp. *megalicarpus* (ancestor of the extant *Lychnothamnus barbatus*) found in La Cerdanya (Catalonia, Spain). The long temporal gap (~ 20 Ma) between both gyrogonite populations makes it difficult to assume that they belong to the same species but regardless of this equivalence, the two were probably very close to each other.

5. Palaeobiogeography of lineage *N. (T.) merianii-N.obtusa*

The occurrence of *Nitellopsis (Tectochara)*. *merianii* in Upper Eocene deposits was doubtful before a population from the Ebro basin was calibrated with the Geomagnetic Polarity Time Scale, GPTS, (C15n chron) providing an absolute age of ~34, 8 Ma (Sanjuan et al., 2013). This result would indicate that the first representatives of this lineage occurred in Europe already in the Latest Eocene (Late Priabonian).

During the Rupelian (Early Oligocene) *N. (T.) merianii* occurred abundantly in many European basins i.e. Paris, Aquitaine, Provence, Languedoc, Swiss Molasse, Rhine Graben and Ebro basins (Feist and Ringeade, 1977; Riveline, 1986; Feist et al., 1994; Schwarz, 1997; Reichenbacher et al., 2004). Moreover, this species has been reported in Eastern Europe (Rumania) and as far East as Turkey (Mädler and Staesche, 1979; Baciu and Feist, 1999) suggesting that by that time it occurred in most subtropical Europe and was beginning its expansion in Asia (Tables 3, 4 and Fig. 5).

In the Chattian (Late Oligocene), *N. (T.) merianii* has been reported in many European and some Chinese basins (Tables 3 and 4, Fig. 6). In Europe, this species occurs in the Provence, Languedoc, Swiss Molasse, Rhine Graben and Slovenia, according to Riveline (1986). In the Iberian Peninsula this species was reported in the Tajo basin (Intermediate Depression) and in many localities from

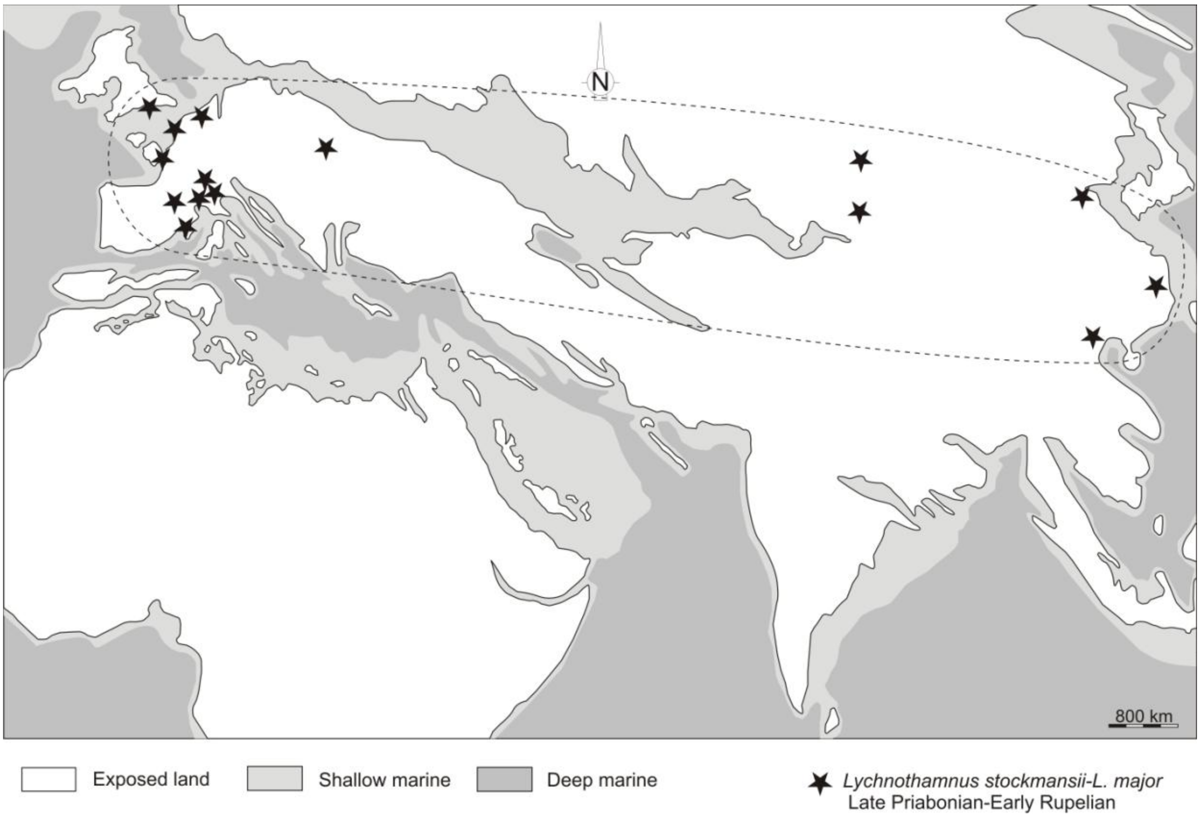


Fig. 3. Biogeographic distribution of *L. stockmansii*-*L. major* lineage showing its earliest Eurasiatic record in Late Priabonian-Early Rupelian (~35-32,5 Ma) and plotted on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent records for a given country or area.

the Ebro basin (Julià de Agar, 1991; Feist et al., 1994; Ortiz et al., 1998). *N. (T.) merianii* was described in China by Wang (1961; 1965) from Tertiary deposits in Chaidamu and Gansu basins. However, due to the lack of further chronostratigraphic information, the age of these Chinese occurrences remains imprecise. Later, Xinlun (1978) and Huang et al. (1988) reported this species in Upper Oligocene deposits from the Bohai Bay Basin (Shandong, Hebei and Henan Provinces, eastern China).

In the Miocene, *Nitellopsis (T.) merianii* reached a larger biogeographic range encompassing Europe, Russia, Eastern Asia and China during the Early-Middle Miocene and extending to Northern India and Northern Africa in the Late Miocene. In more detail, Riveline (1986) and other authors (Iva et al., 1970., Feist and Ringeade, 1977, Feist abundantly in many European Miocene basins such as the Swiss Molasse (Switzerland), the Rhine Graben (Germany), the Aquitaine basin (Southern France), the Velona basin (Northern Italy), Sinj basin (Montenegro), Transylvanian basin (Roumania), the Tajo basin (Central Spain) and the Ebro basin (North-eastern Spain) (Tables 3, 4 and Fig. 7). Mädler and Staesche (1979) and Mazzini et al (2013) identified this species abundantly within Miocene deposits from eastern and central Turkey (Tables 3, 4, Fig. 7). Maslov (1966) reported also *N. (T.) merianii* from many localities of southern Russia. In Asia this species was documented in many localities from China, and some localities from Thailand and India (Tables 3, 4 and Fig. 7). In China *N. (T.) merianii* was reported from Xining and Minhe basins (Qinghai province, North China) by Hao et al (1983), from the

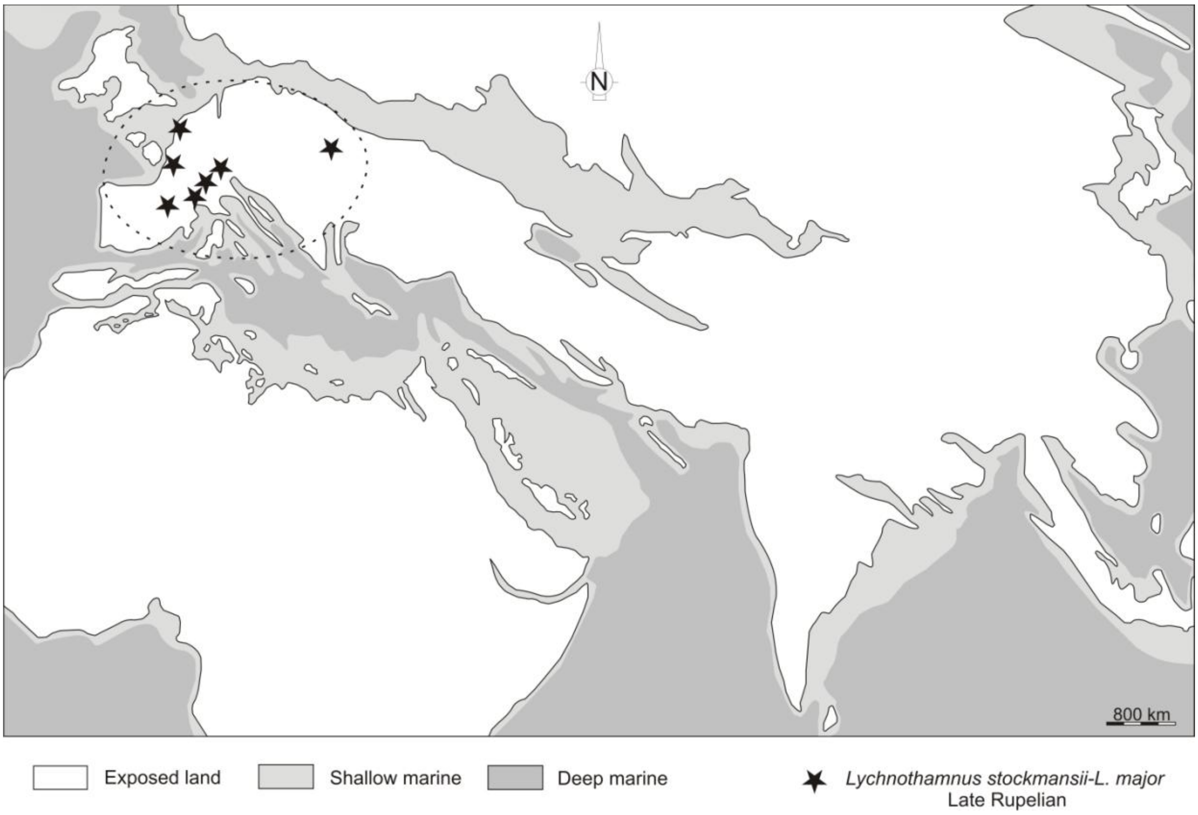


Fig. 4. Biogeographic distribution of *L. stockmansii*-*L.major* lineage showing its restricted western European distribution during Late Rupelian (~32,5-30 Ma) on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent records for a given country or area.

Tarim Basin (Xinjiang province) by Lu and Luo (1990), and from the Qaidam Basin (Qinghai province, Northern China) by Tang and Di (1991). Later Soulié-Märsche et al. (1997) and Berger (1997) identified *N. (T.) merianii* in Middle Miocene lacustrine beds from Northern Thailand. In India this species was recorded within Upper Miocene deposits from Himachal Pradesh (Bhatia and Mathur, 1978; Bhatia, 1999). A further expansion of this species to Africa was noticed by (Soulié-Märsche et al., 2002) who discovered *N. (T.)* gr. *merianii* in Upper Miocene lacustrine deposits in North Morocco (Tables 3, 4 and Fig. 7).

From the Quaternary to the present the lineage *Nitellopsis (Tectochara) merianii*-*L. obtusa* kept largely the same distribution as in the Neogene, extending from western Europe to Japan (Soulié-Märché et al., 2002). Although living *Nitellopsis* were never found in Africa, Early Holocene populations of *N. obtusa* were reported by Soulié-Märshe (1991) from the Sahara below the tropic of Cancer. Moreover, latitudinal distribution of extant *N. obtusa* reach the 65º North (southern Finland). This led Soulié-Märsche et al. (2002, Fig. 5 and Appendix I) to propose that when compared with the biogeography of Miocene representatives, extant *Nitellopsis obtusa* appears to have shifted to the north about 15º.

Despite the large amount of distribution data available from the *Nitellopsis (T.) merianii*-*N. obtusa* lineage, its historical biogeography remained unanalysed until now. It comprises four clearly defined periods; 1) origin in south-western Europe in the Uppermost Eocene (Late Priabonian), 2) expansion through Europe during Early Oligocene

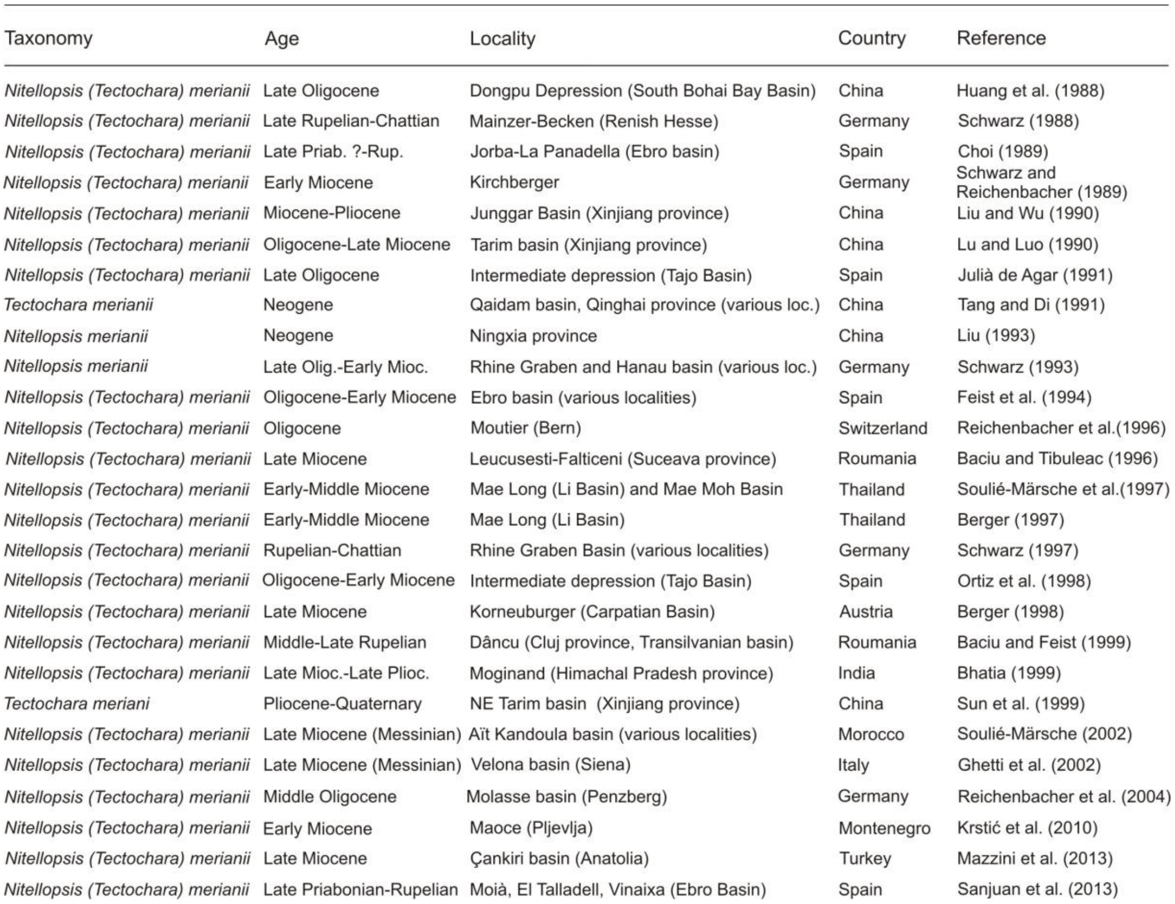
Taxonomy	Age	Locality	Country	Reference
Chara meriani	Tertiary	Oetling (Lörrach)	Germany	Unger (1850)
		KleinKerms (Jetein)		
		St. Jacobum (Basel)	Switzerland	
		Tigurum (Escher)		
		Constantine (Broye-Vully)		
Chara meriani	Tertiary	Sagor (Carniolia)	Slovenia	Unger (1852)
Chara meriani	Tertiary (Miocene)	Molassic Switzerland Basin (various localities)	Switzerland	Heer (1855)
		Konstanz	Germany	
Chara meriani	Tertiary (Oligocene)	Sagor, Savine,Tüffer (Carniola)	Slovenia	Ettinghausen (1872)
Chara meriani	Tertiary	Sagor (Carniolia)	Slovenia	Ettinghausen (1885)
Chara meriani	Tertiary (Miocene)	Oettlingerber (Baden)	Germany	Groves (1933)
		Heggbach, Adelegg, Isny (Württemberg)		
		Molassic Switzerland Basin (various localities)	Switzerland	
		Sta. Giustina (Liguria)	Italy	
		Sagor, Savine (Carniolia)	Slovenia	
Chara meriani meriani	Neogene (Pilocene)	Eichkogel (Mödling)	Austria	Papp (1951)
Chara meriani	Tertiary	Ehinge, Ulm (Donau)	Germany	Straub (1952)
Tectochara meriani meriani	Rup. (?)-Early Mioc.	Höhe (Beiningen)	Germany	Mädler (1955)
Tectochara meriani meriani	Tertiary	Chaidamu basin (Quinghai province)	China	Wang (1961)
Tectochara meriani meriani	Chattian-Tortonian	Tüllingerberg (Weil am Rhein)	Switzerland	Nötzold (1962)
Tectochara meriani meriani	Tertiary	Kansu basin (gansu province)	China	Wang (1965)
Tectochara meriani	Oligocene (Rupelian)	Fontainebleau, Soisy (Paris)	France	Grambast and Paul (1965)
Tectochara meriani	Early Miocene-Pliocene	Southern Russia (various localities)	Russia	Maslov (1966)
Tectochara meriani	Oligocene (Chattian)	Marseille (Provence)	France	Castel (1967)
Tectochara meriani meriani	Oligocene-Miocene	North of Vesul Baxinului (Transilvanian basin)	Roumania	Iva et al. (1970)
Tectochara meriani	Pliocene	Gaber (Belibreg basin)	Bulgaria	Palamarev (1972)
Tectochara meriani meriani	Eocene (?)	Rona-Jibou (Salav)	Roumania	Stoleriu (1973)
Tectochara meriani	Oligocene	Peissy (Genève)	Switzerland	Kissling (1974)
Nitellopsis (Tectochara) meriani	Late Oligocene	Provence (various localities)	France	Feist-Castel (1977a)
Nitellopsis (Tectochara) meriani	Early Olig.-Early Mioc.	Aquitaine Basin (various localities)	France	Feist and Ringeade (1977)
Tectochara meriani	Late Oligocene	Bohai Bay Basin (various localities)	China	Xinlun (1978)
Tectochara meriani meriani	Late Miocene-Pliocene	Daulatpur, Triloknath, Bharil, Kotla	India	Bathia and Mathur (1978)
Nitellopsis meriani	Pilocene-Holocene	Shithatha (Al-Karbala)	Iraq	Knobloch (1979)
Tectochara meriani	Early Oligocene-Pliocene	W and central Turkey (various localities)	Turkey	Mädler and Staesche (1979)
Nitellopsis (Tectochara) meriani	Late Oligocene	Itzac (Midi-Pyrenées)	France	Chellai et al. (1982)
Nitellopsis merianii	Early Miocene (Aquitanian)	Vaud (various localities)	Switzerland	Berger (1983)
		Fribourg (various localities)		
		Berna (various localities)		
Tectochara meriani	Late Miocene	Xianjing and Minhe basins	China	Hao et al. (1983)
Nitellopsis meriani	Pliocene	Jingyuan (Gansu province)	China	Li (1985)
Nitellopsis meriani	Late Olig.-Late Mioc.	Mainzer-Becken (Renish Hesse)	Germany	Shwarz (1985)
Nitellopsis (Tectochara) merianii	Rupelian-Chattian	Itteville, Etrechy, Saint Ambroix (Paris)	France	Riveline (1986)
		Haut-Rhin (various localities)		

Table 3. Distribution dataset of *Nitellopsis (Tectochara) merianii*.

(Rupelian), 3) colonization of Asia and expansion in whole Eurasia in the Late Oligocene (Chattian) and Miocene, when it occurs also in Africa and 4) present Eurasiatic distribution.

5.1 Origin of the lineage in south-western Europe

Upper Eocene deposits from the Ebro basin represent the oldest occurrence of *Nitellopsis (Tectochara) merianii*, suggesting that the original biogeographic area of this species could be restricted to south-western Europe (Fig. 6). The absence of this species in other European basins during Upper Eocene can be justified by



Taxonomy	Age	Locality	Country	Reference
Nitellopsis (Tectochara) merianii	Late Oligocene	Dongpu Depression (South Bohai Bay Basin)	China	Huang et al. (1988)
Nitellopsis (Tectochara) merianii	Late Rupelian-Chattian	Mainzer-Becken (Renish Hesse)	Germany	Schwarz (1988)
Nitellopsis (Tectochara) merianii	Late Priab. ?-Rup.	Jorba-La Panadella (Ebro basin)	Spain	Choi (1989)
Nitellopsis (Tectochara) merianii	Early Miocene	Kirchberger	Germany	Schwarz and Reichenbacher (1989)
Nitellopsis (Tectochara) merianii	Miocene-Pliocene	Junggar Basin (Xinjiang province)	China	Liu and Wu (1990)
Nitellopsis (Tectochara) merianii	Oligocene-Late Miocene	Tarim basin (Xinjiang province)	China	Lu and Luo (1990)
Nitellopsis (Tectochara) merianii	Late Oligocene	Intermediate depression (Tajo Basin)	Spain	Julià de Agar (1991)
Tectochara merianii	Neogene	Qaidam basin, Qinghai province (various loc.)	China	Tang and Di (1991)
Nitellopsis merianii	Neogene	Ningxia province	China	Liu (1993)
Nitellopsis merianii	Late Olig.-Early Mioc.	Rhine Graben and Hanau basin (various loc.)	Germany	Schwarz (1993)
Nitellopsis (Tectochara) merianii	Oligocene-Early Miocene	Ebro basin (various localities)	Spain	Feist et al. (1994)
Nitellopsis (Tectochara) merianii	Oligocene	Moutier (Bern)	Switzerland	Reichenbacher et al.(1996)
Nitellopsis (Tectochara) merianii	Late Miocene	Leucusesti-Falticeni (Suceava province)	Roumania	Baciu and Tibuleac (1996)
Nitellopsis (Tectochara) merianii	Early-Middle Miocene	Mae Long (Li Basin) and Mae Moh Basin	Thailand	Soulié-Märsche et al.(1997)
Nitellopsis (Tectochara) merianii	Early-Middle Miocene	Mae Long (Li Basin)	Thailand	Berger (1997)
Nitellopsis (Tectochara) merianii	Rupelian-Chattian	Rhine Graben Basin (various localities)	Germany	Schwarz (1997)
Nitellopsis (Tectochara) merianii	Oligocene-Early Miocene	Intermediate depression (Tajo Basin)	Spain	Ortiz et al. (1998)
Nitellopsis (Tectochara) merianii	Late Miocene	Korneuburger (Carpatian Basin)	Austria	Berger (1998)
Nitellopsis (Tectochara) merianii	Middle-Late Rupelian	Dâncu (Cluj province, Transilvanian basin)	Roumania	Baciu and Feist (1999)
Nitellopsis (Tectochara) merianii	Late Mioc.-Late Plioc.	Moginand (Himachal Pradesh province)	India	Bhatia (1999)
Tectochara meriani	Pliocene-Quaternary	NE Tarim basin (Xinjiang province)	China	Sun et al. (1999)
Nitellopsis (Tectochara) merianii	Late Miocene (Messinian)	Aït Kandoula basin (various localities)	Morocco	Soulié-Märsche (2002)
Nitellopsis (Tectochara) merianii	Late Miocene (Messinian)	Velona basin (Siena)	Italy	Ghetti et al. (2002)
Nitellopsis (Tectochara) merianii	Middle Oligocene	Molasse basin (Penzberg)	Germany	Reichenbacher et al. (2004)
Nitellopsis (Tectochara) merianii	Early Miocene	Maoce (Pljevlja)	Montenegro	Krstić et al. (2010)
Nitellopsis (Tectochara) merianii	Late Miocene	Çankiri basin (Anatolia)	Turkey	Mazzini et al. (2013)
Nitellopsis (Tectochara) merianii	Late Priabonian-Rupelian	Moià, El Talladell, Vinaixa (Ebro Basin)	Spain	Sanjuan et al. (2013)

Table 4. Distribution dataset of *Nitellopsis (Tectochara) merianii*.

palaeogeographic reasons. At that time Southern Europe was an archipelago of large islands, irregularly connected and climatically influenced by the Tethys Ocean within the subtropical belt (Scotese, 2013), which would enhance allopathric speciation. Palaeoecology appears to be also of prime importance to understand its appearance in the South of Europe. Assuming that the first representatives of this lineage grew in cool freshwater lakes during the Priabonian, as modern representatives do to date, the continuous marine influence that characterised northern European Upper Eocene wetlands (Paris and Hampshire basins) could limit the distribution of this species there.

5.2 Expansion in Europe

From the Early Rupelian on, *N. (T.) merianii* expanded in Europe, from France to Rumania and Turkey (Fig. 5). Palaeoecological constraints linked to basin dynamics during Early Oligocene could play a significant role in this expansion. The closure of European seaways due to the uplift of the Alpine belt and a drop of the sea level resulted in the continentalisation of many European basins (Zachos et al., 2001). The hydrological features of each basin are key factors that might have controlled the distribution of aquatic organisms in the past (Gierlowski-Kordesch, 2010).

5.3 Colonisation of Eastern Asia and expansion in Eurasia

During the Late Oligocene (Chattian), the *Nitellopsis (T.) merianii-N. obtusa* lineage continued its expansion eastwards, reaching China. The occurrence of this species in at least two

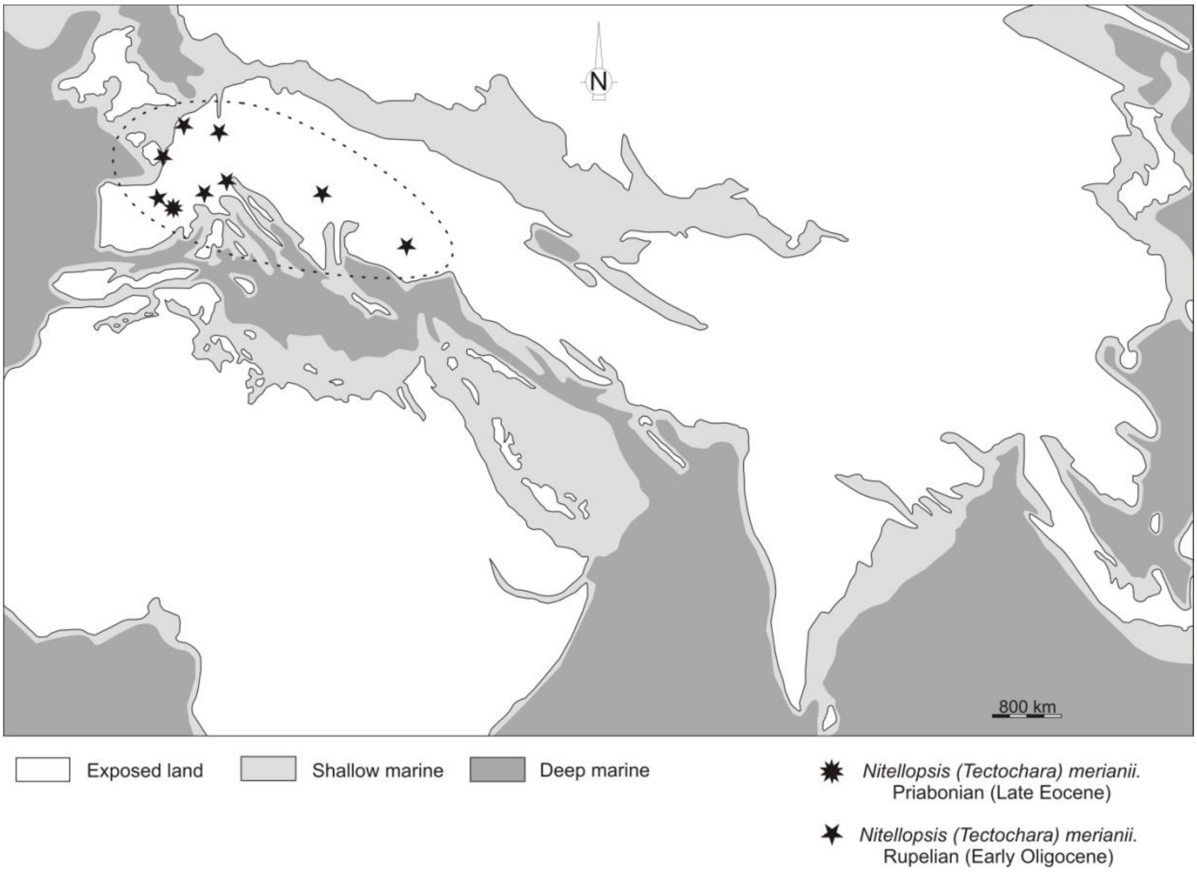


Fig. 5. Biogeographic distribution of *Nitellopsis (Tectochara) merianii-N. obtusa* lineage showing its restricted western European distribution during latest Eocene (Late Priabonian, ~34, 2 Ma) and its European distribution in Early Oligocene (Rupelian, ~33,9-28,1 Ma) on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent records for a given country or area.

Chinese localities in the Late Oligocene, the Bohai Bay basin, to the East, and the Tarim basin, to the West show that this species underwent a rapid migration during this sub-stage. Significantly enough, this expansion is slightly younger than the first fossil record of ducks belonging to the Anatidae (Mayr and Smith, 2001), which occur in the Lowermost Oligocene, and are the main dispersers of charophytes in the present (Fig. 6).

Since the Earliest Miocene, the expansion of *N. (T.) merianii-N. obtusa* in Eurasia remained active. During the Early-Middle Miocene this species expanded in the Chinese provinces of Quinghai, Xinjiang and Ninxia, and colonized new localities in South-east Asia, particularly the Mae Moh basin in Thailand. Also from that time are the first occurrences in southern Russia (Fig. 7). During Late Miocene this already Eurasiatic species continued its expansion southwards reaching the Siwalik Basin (Himalayan Foreland basin) in northern India and the Ait Kandoula basin in northern Africa. Soulié-Märsche et al. (2002) linked the charophyte findings from northern Africa to water birds that were already capable of a transmediterranean flight. The Pliocene record suggests that this species kept its Eurasiatic distribution during this stage (Fig. 7).

5.4. Quaternary and extant biogeographic distribution

The last period in the biogeographic history of *Nitellopsis (T.) merianii-N. obtusa* lineage is represented by *Nitellopsis obtusa* from the Early

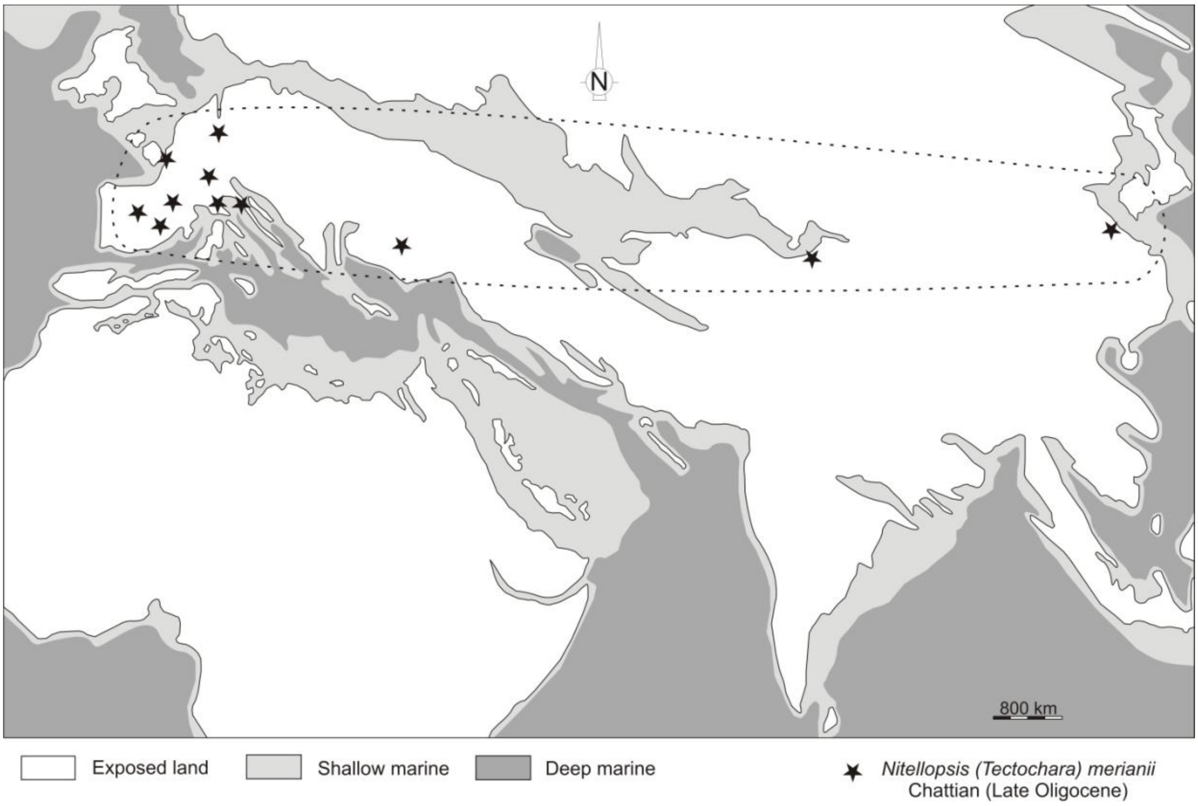


Fig. 6. Biogeographic distribution of *Nitellopsis (Tectochara) merianii-N. obtusa* lineage showing its already Eurasiatic distribution during Late Oligocene (Chattian, ~28,1-23 Ma) on a palaeogeographic map of the world at Lower Oligocene modified from Blakey (2006). Stars represent records for a given country or area.

Quaternary to the present. In general, Quaternary *Nitellopsis obtusa* displays a similar Eurasiatic distribution than *N. (T.) merianii* during the Neogene, ranging from the west coast of Europe to Japan, which is the reason why it *Nitellopsis obtusa* is considered a boreal species (Corillion, 1972; Soulié-Märsche et al., 2002). However, fossil gyrogonites of *N. obtusa* found within Early Holocene deposits from the Sahara suggest that this species displayed a wider distribution to the south, i.e about 15º larger than its present biogeographic range (Soulié Märsche et al., 2002).

6. Discussion and conclusions

Two Upper Eocene-Oligocene charophyte lineages, *Lychnothamnus stockmansii-L. major* and *Nitellopsis (Tectochara) merianii-N. obtusa* reached an Eurasiatic distribution following opposite biogeographic patterns. The origin of *Lychnothamnus stockmansii-L. major* is coeval in Europe and Asia, during the Late Priabonian-Early Rupelian. Later, during the Rupelian this species was restricted to Europe, and became probably extinct at the end of the same period. In contrast, *N. (T.) merianii-N. obtusa* follows the classical dispersal pattern, with origin in south-western Europe during the Latest Eocene (Late Priabonian), expansion through Europe during the Early Oligocene (Rupelian), reaching the extreme East of the Asiatic continent probably during Late Oligocene (Chattian). The expansion of *N. (T.) merianii-obtusa* was intensified in Eurasia during the Miocene and reached Africa in the Late Miocene, with a range slightly wider than in present time.

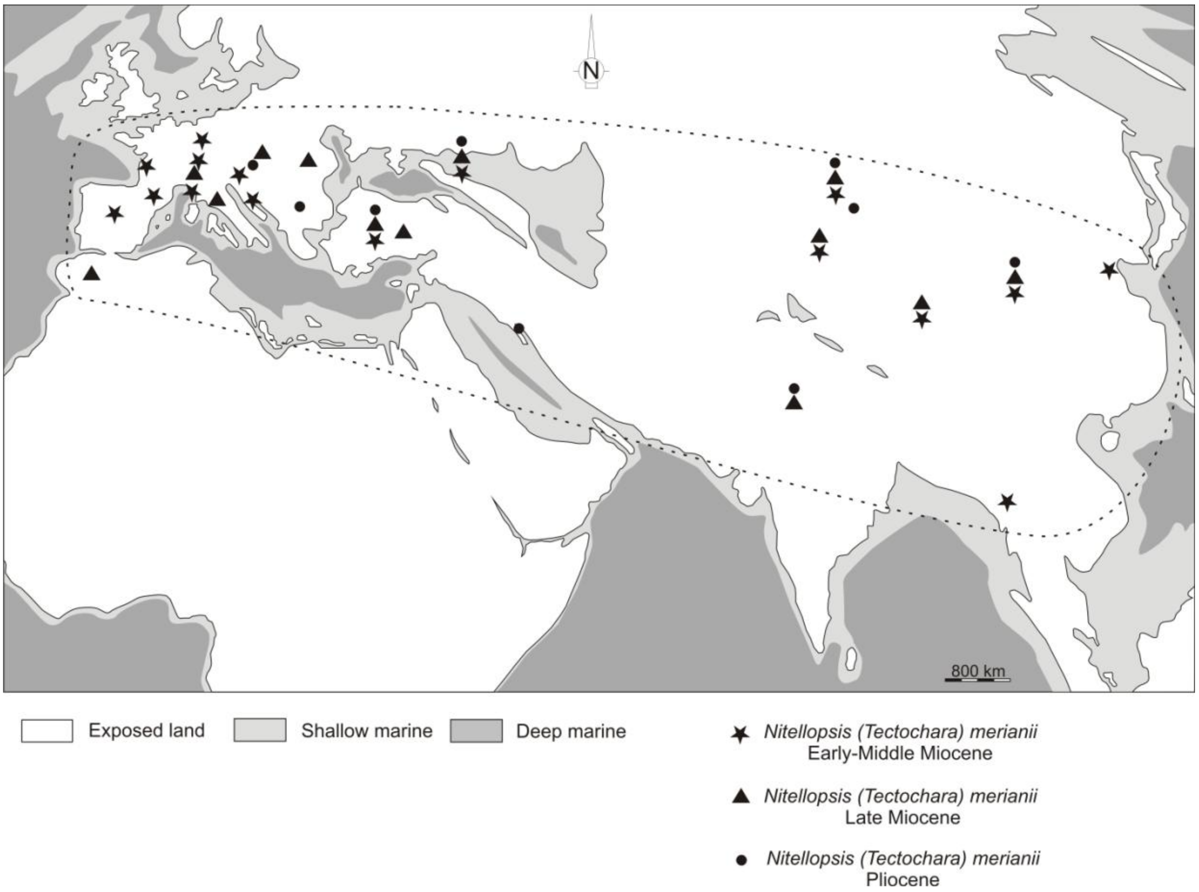


Fig. 7. Biogeographic distribution of *Nitellopsis (Tectochara) merianii*-*N. obtusa* lineage showing its Eurasiatic distribution during the Miocene and Pliocene (~2,5-23 Ma) on a palaeogeographic map of the world at Lower Miocene modified from Blakey (2006). Stars represent records for a given country or area.

In order to explore the reasons governing these contrasting biogeographic patterns it is useful to compare them with the biogeographic patterns and mechanisms of the most diversified extant charophyte genus, *Chara*. According to the study of Proctor (1980) *Chara* displays a dual biogeographic pattern i.e. some species are restricted to a continental area while others grow in large, supracontinental areas or are cosmopolitan. Proctor (1980) hypothesized that biogeography and the arrangement of gametangia were closely related and concluded that cosmopolitan *Chara* species were monoecious, i.e. displaying conjoint male and female gametangia in the same plant, while dioecious species, i.e. with separate male and female plants, were limited to smaller continental areas. The arrangement of gametangia would determine the dispersion mechanism of *Chara*, which is mostly dependent on migratory birds that feed on its meadows, mainly ducks of the Anatidae. Proctor (1980) concluded that monoecious *Chara* species are able to form reproductive populations after a single dispersal event and immediately continue their biogeographic expansion. In contrast, the expansion of dioecious charophyte populations is a rather improbable occurrence since they usually contain very unequal percentages of each sex.

The contrasting dispersal patterns observed in fossil *Lychnothamnus stockmansii*-*L. major* and *Nitellopsis (T.) merianii*-*N. obtusa* suggest that the same patterns that govern the dispersal of living *Chara* would influence the dispersal of other characeans in the past.

Unfortunately, the monoecious or dioecious condition of fossil charophyte species is difficult to ascertain with only the fossil record on hand. In some occasions monoecy or dioecy may be inferred from extant representatives, assuming that a change in the arrangement of gametangia is impossible within in the same species and improbable in species that are thought to have a direct ancestor-descendant relationship. Thus, extant *Nitellopsis obtusa* was surely a dioecious species in the past as it is today (Soulié-Märsche et al., 2002), whilst *L. stockmansii-L. major* is considered by Soulié-Märsche and Martín-Closas (2003) a direct ancestor of extant *L. barbatus*, a monoecious species, and we can hypothesize that this status was the same in both species. Indeed, the geologically instantaneous supra-continental distribution of *L. stockmansii-L. major* at the specie's origin would clearly correspond to the distribution expected from a monoecious species. In contrast, the Eurasiatic range of *N. (T.) merianii-N.obtusa* lineage, which is a dioecious species, would seem to contradict Proctor's hypothesis, based in genus *Chara*. The solution to this apparent contradiction is given by introducing the time dimension which allows concluding that both monoecious and dioecious charophyte species could reach supracontinental distributions although at different velocites. From the case studies analysed, dioecious species would require an expansion up to ten times larger to achieve similar distribution ranges than monoecious species, provided that the palaeo-geographic and palaeoecological conditions were at less as continuous as they were in Eurasia during the Oligocene-Eocene boundary.

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Stratigraphy and biostratigraphy (charophytes) of the marine-terrestrial transition in the Upper Eocene of the NE Ebro Basin (Catalonia, Spain)

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ABSTRACT

The onset of endorheic sedimentation in the Ebro Basin is a prominent feature of the basin's evolution and has recently been characterized as a rapid event occurring in the Early Priabonian. In the north-eastern part of the basin this event coincides with the deposition of the Artés Formation (Fm.), mainly built up by red beds of alluvial origin. The marine-continental boundary has been poorly studied up to now in the so-called Lluçanès area, and what was previously thought to be the base of the Artés Fm. is actually a transitional unit, which we define as the Sant Boi Formation, which covers the underlying marine Milany Depositional Sequence and passes laterally to the Terminal Complex, extending over 15km along the eastern margin of the Ebro Basin. The Sant Boi Fm. is formed by up to 15-20m of alternating siltstones and lutite, grading upwards to brackish and lacustrine marls and lignite, and represents deposition in a brackish to freshwater floodplain. It is characterized biostratigraphically by the fossil charophyte assemblage *Harrisichara lineata*, *Harrisichara vasiformis-tuberculata* and *Nodosochara jorbae*, from the middle part of the Priabonian. In contrast, the overlying red beds of the Artés Fm. are characterized by assemblages containing *Harrisichara tuberculata*, *Nodosochara jorbae* and *Lychnothamnus longus* from the Late Priabonian. These results are largely consistent with recent magnetostratigraphic studies performed south of the studied area, and have enabled us to refine the stratigraphy of the marine-continental transition in the north-eastern Ebro Basin.

KEYWORDS **Charophyta. Biostratigraphy. Ebro Basin. Eocene. Oligocene.**

INTRODUCTION

The continentalization of the Ebro Basin has been a matter of debate in recent years. This event has been described as occurring over a relatively short time, affecting the entire basin at the beginning of the Priabonian (Costa et al., 2010). In the north-easternmost part of the basin (Lluçanès area) the boundary has traditionally been located at the top of the deltaic sandstone with reefal limestones of the Sant Martí Xic Formation (Fm.) (Reguant, 1967). However, new geological mapping, along with stratigraphic and biostratigraphic analyses of an overlying and previously poorly known transitional unit, called here the Sant Boi Fm., led us to revisit previous assumptions on the continentalization of this part of the Ebro Basin.

Not only is the lithostratigraphy of the study area confusing, but the dating of the last marine deposits of the eastern Ebro Basin has also been controversial. Magnetostratigraphy studies by Burbank et al. (1992) and Taberner et al. (1999) assigned the uppermost marine and transitional rocks to Upper Bartonian and Lower Priabonian (chron C17n). Biostratigraphic studies based on foraminifera (Serra-Kiel et al., 2003) also assigned the uppermost marine and transitional rocks to the Upper Bartonian-Lower Priabonian (Shallow Benthic Zones 18 and SBZ 19?). However, recent studies on calcareous nannofossils have revealed that only Priabonian marine rocks occur in this upper part of the stratigraphic record (Zones NP18 and NP19-20) which were correlated with chron C16/16n.2n (Cascella and Dinarès-Turell, 2009). Biostratigraphic studies of continental fossils, mainly charophytes and vertebrate remains, from the central part of the eastern Ebro Basin (Igualada-Jorba area) have attributed the youngest marine units to the Upper Eocene (Anadón et al., 1987, 1992; Choi, 1989; Feist et al., 1994). Furthermore, palaeomagnetic dating has recently been performed in this area, attributing the youngest marine rocks to chron C16 (Costa et al., 2010). In contrast, biostratigraphic markers from the marine-continental transition in the northeastern part of the basin have been poorly studied up to now. In the Lluçanès area fossil charophytes have only been reported by Colom et al. (1970), who found the species *Harrisichara lineata* in the Sant Boi Fm.

Resampling the Lluçanès area has enabled us to document a rich charophyte flora of biostratigraphic interest, which sheds new light on the dating of the continentalization of the Ebro Basin in this area. The new biostratigraphic data are significant in comparison to other margins of the Ebro Basin, where an equivalent stratigraphic situation occurs i.e. in the Riu Boix Fm., south of Igualada (Ramírez et al., 1991) and the Campodarbe Fm., Huesca province (Canudo et al., 1988). The whole of these data will allow us to test the hypothesis of a rapid continentalization of the Ebro Basin in the Priabonian from a biostratigraphic point of view, as drawn from magnetostratigraphic data.

GEOLOGICAL SETTING

The Ebro Basin is the triangular-shaped southern foreland basin of the Pyrenean Range (Fig. 1). The origin of the Ebro Basin is related to flexural subsidence due to the collision between the Eurasian and Iberian plates from the Late Cretaceous to the Miocene. Maximum compression occurred during the Palaeocene and Eocene and resulted in the superposition of a number of thrust sheets in the south Pyrenean central zone. The main structures display an E-W orientation and the deformation progressed south- and westwards in parallel with the basin depositional centres, the lowermost sedimentary sequences being incorporated into the successive thrust sheets (Puigdefàbregas et al., 1992).

The south Pyrenean foreland basin infill includes marine and continental rocks that range from the Upper Cretaceous to the Upper Eocene. Later, exclusively non-marine facies were recorded. During most of the Palaeogene the basin formed an Atlantic gulf. This situation lasted until the Late Eocene, when uplift in the western Pyrenees led to the final isolation from the Atlantic Ocean and the definitive onset of endorheic sedimentation in the Ebro Basin (Puigdefàbregas et al., 1992).

The study area is located in the north-eastern part of the Ebro Basin (Fig. 1). The Palaeogene sedimentary succession in this part of the basin is divided into nine depositional sequences related to the emplacement of the south Pyrenean thrust sheets and linked to two major relative sea level rises, in the Ilerdian (Early Eocene) and Bartonian (Middle-Late Eocene) (Puigdefàbregas et al., 1986). According to these authors, thrust cyclicity and evaporite events allow differentiation of the basin-fill into three main depositional cycles. The first cycle includes the Cadí, Corones, Armàncies and Campdevànol sedimentary sequences and coincides with the submarine emplacement of the upper thrust sheets. The second sedimentary cycle includes the Bellmunt and Milany sequences (Lutetian and Bartonian) and coincides with the development of an antiformal stack of thrust sheets in the central Pyrenees. This structure induced deltaic progradation

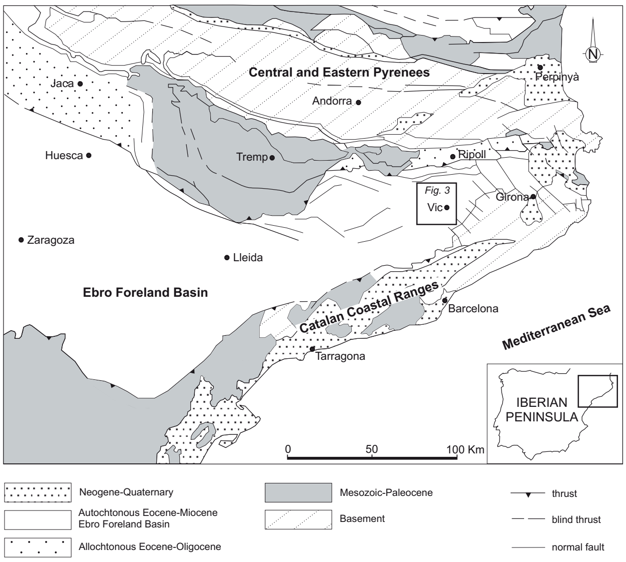

FIGURE 1 | Geological sketch of the eastern part of the Ebro Foreland Basin showing the location of the area studied (modified from Vergés et al., 1998).

and contemporaneous migration of the basin depocentre southwards. At the same time, the Catalan Coastal Chain was tectonically active and contributed to basin infill with well-developed fan delta progradation systems (e.g. Montserrat and Sant Llorenç del Munt fan deltas). This tectonic activity led to the final restriction of the basin and the deposition of the second evaporite plug during the Late Eocene. This evaporitic event (Cardona sequence) is the last marine episode in the southern Pyrenean foreland basin, which became purely endorheic afterwards.

The third cycle includes the Solsona and younger Ebro Basin sequences. It coincides with the southward thrusting and final emergence of the Vallfogona thrust, which carried the former piggyback thrust sheets. These thrust sheets supplied clastic sediments to the alluvial fans that were laterally connected with lacustrine areas in the centre of the basin (Puigdefàbregas et al., 1986).

The closure of the Ebro Basin to marine influence is a significant event of the basin evolution. In the north-eastern part of the basin, where the influence of both the Pyrenees and the Catalan Coastal Chain became superposed, facies related to the definitive onset of the endorheic sedimentation are relatively different to other parts of the basin. In this area, the last fully marine deposits belong to the deltaic sandstones of the Sant Martí Xic Fm., which is composed of low order sequences related to deltaic progradation (Barnolas et al., 1988; Barnolas, 1992). This formation grades basinwards to the prodelta marls of the Vic Fm. (Reguant, 1967) which is equivalent, towards the south, to the Igualada Fm. (Ferrer, 1971). These deposits mark the top of the Milany sedimentary sequence (Fig. 2).

The rocks overlying the Sant Martí Xic Fm. include mainly transitional deposits of diverse sedimentological features, which are bounded by regional unconformities and have been grouped in the so-called Terminal Complex (Fig. 2). This unit, defined by Travé (1992) and Travé et al. (1996), is made up of sandstones of the La Noguera Fm. (Reguant, 1967), anoxic marls, limestones including freshwater stromatoliths, and gypsum, representing the progressive infilling of the basin and its final shift to non-marine conditions. Three carbonate units have been recognized and represent three successive shallowing-upward carbonate platforms interlayered with prograding siliciclastic sediments. Moreover, a characteristic freshwater stromatolithic limestone is abundant in some levels along the entire margin of the basin (Travé et al., 1996). In the south-eastern part of the basin, the Terminal Complex passes laterally and is overlain by the Òdena Gypsum Fm. This formation may represent the marginal equivalent of the central basin halite and sylvinite deposits of the Cardona Fm. The stratigraphic position of these units, intercalated between the marine Milany and the continental Solsona depositional sequences, suggests that the Terminal Complex and the aforementioned evaporites belong to an intermediate sequence which has been controversially considered Late Bartonian or Early Priabonian in age. Recent studies on calcareous nannofossils have revealed the presence of the Lower Priabonian in marine rocks of this part of the basin and these have been assigned to C16/C16n.2n chron (Cascella and Dinarès-Turell, 2009).

Overlying this marine-continental transition, the infill of the Eastern Ebro Basin consists of 1000m thick alluvial and lacustrine deposits. Continental deposits are composed of thick upper Eocene-Oligocene sequences dominated by different lacustrine systems, which developed in the inner basinal zones and were fed by marginal alluvial fan systems. Five lacustrine systems consisting of mudstones and carbonates, evaporite and minor coals, have been recognized in the Upper Eocene to Upper Oligocene sequences of the Eastern Ebro Basin (Anadón et al., 1989). In the studied area, the Artés Fm. defined by Ferrer (1971) is widely represented. This sedimentary unit is generally built up by red beds with alternating siltstone and coarse sandstone bodies, showing typical palaeochannel features. Intercalated in the Artés Fm. there are thin lacustrine grey limestone and marl deposits with abundant charophytes, ostracodes and small limnic gastropods. The sedimentary and stratigraphic features of the Artés Fm. are related to mid to distal alluvial fan systems.

Chronological constraints of the continental sedimentary units overlying the Cardona Fm., i.e. red beds of the Artés Fm. in the Solsona Depositional Sequence, are provided by charophyte and mammal biostratigraphic data and magnetostratigraphy. The oldest known vertebrate fossil assemblage in the easternmost basin area comes from the locality of Sant Cugat de Gavadons, which indicates a Late Eocene age for the basal part of the Artés Fm., according to Anadón et al. (1987). Fossil charophyte flora and vertebrate fauna from the neighbouring locality of Santpedor and the more distant locality of Rocafort de

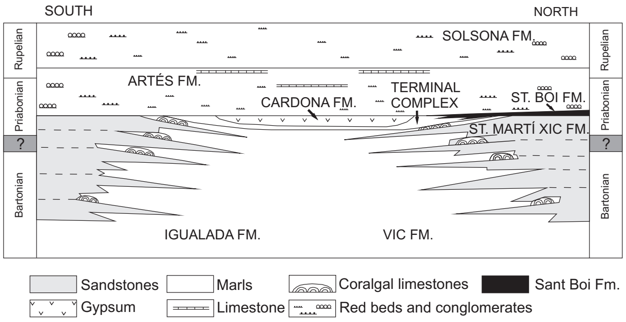

FIGURE 2 | Stratigraphic framework of the Eocene in the South Pyrenean foreland basin near Vic (modified from Serra-Kiel and Travé, 1995).

Queralt also indicate a Late Eocene age (Anadón et al., 1987, 1992; Choi, 1989; Feist et al., 1994). However, Early Oligocene vertebrate fossils have been found in Santpedor as well (Arbiol and Sáez, 1988). Also charophyte flora and preliminary magnetostratigraphic data from the Jorba-La Panadella section indicate an early Late Eocene to Oligocene age (Choi, 1989; Anadón et al., 1992; Feist et al., 1994; Barberà et al., 2001). New magnetostratigraphic data show that the transition from marine to continental sedimentation was a rapid event occurring in the Late Priabonian (Costa et al., 2010). Continentalization of the basin was related to the seaway closure that resulted from the uplift of the western Pyrenees and was coincident with a mid-amplitude eustatic sea-level low with a maximum at 36.2Ma, correlated with chron C16n (Costa et al., 2010).

MATERIAL AND METHODS

Grey mudstones and marls of Palaeogene transitional and lacustrine deposits of six stratigraphic sections were sampled systematically near the villages of Sant Boi de Lluçanès, Sobremunt, Sant Bartomeu del Grau, Oristà and Santa Maria d’Oló (Fig. 3). All sections are located in the Lluçanès area, near Vic, about 60km northeast of Barcelona (Catalonia, Spain). The two sections sampled in Sant Boi de Lluçanès were El Perers and Serrat Rodó. The first section crops out along the BV-4608 road (base coordinates 42º03’14.7’’N and 02º10’E, top coordinates 42º03’26.9’’N, 02º10’12’’E). The Serrat Rodó section is located 500m SE of the previous locality (base coordinates 42º02’49.7’’N, 02º10’18.4’’E, top coordinates 42º02’47.3’’N, 02º10’26.1’’E). These sections cut the marine sandstones from the Sant Martí Xic Fm., the intermediate transitional deposits which are the subject of this study, and the overlying non-marine materials from the Artés Fm. The Sobremunt road section (base coordinates 42º02’18.62’’N and 2º10’21.76’’E, top coordinates 42º02’16.41’’N and 2º10’19.33’’E) is located close to km 1 of the BV-4607 road, 2km SE of the El Perers section and cuts about 10m of marine and transitional deposits. Cal Carreter section, (base coordinates 41º56’55.04’’N and 2º09’34.15’’E, top coordinates 41º57’01.40’’N and 2º09’09.57’’E) is located between km 8 and km 9 from the C-154 road, close to Sant Bartomeu del Grau village and cuts the Terminal Complex and the overlying transitional and continental deposits. The Santa Maria d’Oló and Oristà sections are stratigraphically located at the top of the continental Artés Fm. The first section follows the BV-4315 road at the entrance to the village of Santa Maria d’Oló (base coordinates 41º52’42.3’’N and 02º02’3.3’’E, top coordinates 41º52’35.6’’N and 02º02’5.1’’E) and shows a largely siliciclastic succession passing upwards to lacustrine limestones. The Oristà section is located near the B-433 road, close to the Can Julià farm (base coordinates 41º56’2.3’’N and 02º03’56’’E, top coordinates 41º56’7.4’’N and 02º04’1.4’’). This section is dominated by fluvial red beds with subordinated lacustrine marls containing abundant charophyte gyrogonites and ostracods.

Rock samples were disaggregated in water, oxygen peroxide and Na_2CO_3 solution and later sieved with sieves with mesh apertures of 1.0, 0.5 and 0.2mm. Gyrogonites were picked out under a light microscope and measured at 40x magnification. One hundred gyrogonites were selected and measured for each species. Selected gyrogonites were studied and photographed with a scanning electronic microscope Quanta 200 at the Serveis Científico-Tècnics (Universitat de Barcelona). The material is housed at the Departament d’Estratigrafia, Paleontologia i Geociències marines, Universitat de Barcelona.

RESULTS

Abundant and diverse fossil charophyte floras were found in transitional and non-marine deposits in the Lluçanès area. With the aim of characterizing these deposits, which are covering the last fully marine unit

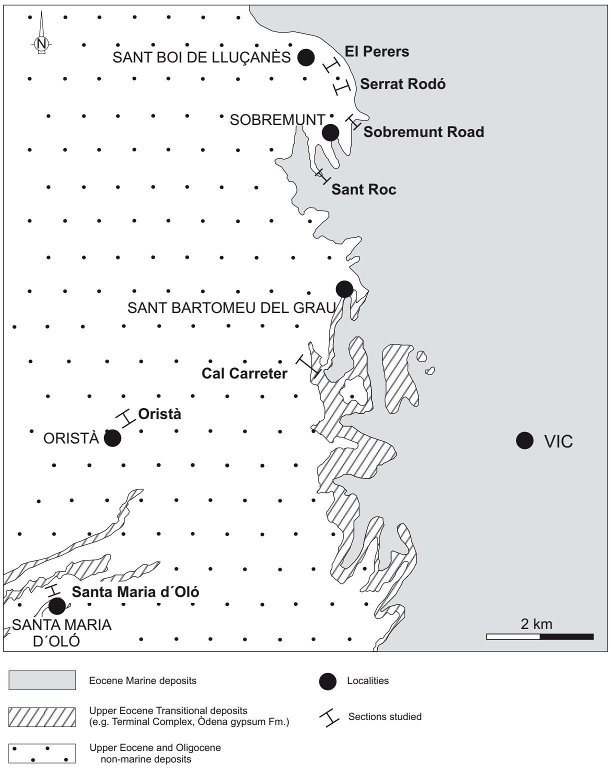

FIGURE 3 | Geological sketch of the northeastern margin of the Ebro Basin showing the location of the studied sections (after Institut Cartogràfic de Catalunya, 2006).

in the north-eastern Ebro Basin, a lithostratigraphic and biostratigraphic study was carried out.

Lithostratigraphy

Sant Boi Formation

Under the name Sant Boi Sandstone, Lignite and Marl Formation we propose a new unit cropping out along 15km on the north-eastern margin of the Ebro Basin, in the Lluçanès area, to the west of the town of Vic. Until now, this unit has been considered to represent the lowest part of the Artés Fm. in this area (Ramírez del Pozo et al., 1975; Barnolas et al., 1983; Barnolas et al., 1994; Mató et. al., 1994) but lithological and biostratigraphic differences have allowed us to characterize it as a new formation. The change of facies has already been reported by Farrés and Staid-Saadt (1964), who described a number of brackish gastropods and inferred brackish conditions for these facies.

The Sant Boi Fm. is generally composed of an alternation of up to 15m of grey to yellowish fine rippled sandstone with yellow to brown lutite to the base, passing upwards to a characteristic interval of up to 5m of grey to yellowish marls, frequently with thin lignite horizons. The base of the unit is defined by a change in facies from the thick, coarse and massive marine sandstones of the Sant Martí Xic Fm. The upper boundary is sharply defined by a sudden change to red arkosic sandstone bodies alternated with red lutite of the Artés Fm. This boundary is proposed here as the base of the continental Artés Fm. (Fig. 4).

The stratotype proposed for the new formation is the so-called Serrat Rodó section, which represents the most complete and well exposed section of the Sant Boi Fm. A supplementary section called El Perers is proposed as another reference section (Figs. 4, 5) in order to characterize the facies variation better. Both sections are located east of the village of Sant Boi de Lluçanès. The Sant Boi Fm. displays marked lateral change in thickness and facies. Sections located to the north, near the type locality (Sant Boi de Lluçanès), cut up to 15m of transitional and lacustrine facies, whilst southwards, from Sobremunt to Sant Bartomeu del Grau, the new formation is only a few meters thick and shows reduced freshwater influence.

In the type locality, the Sant Boi Fm. overlies coarse metric sandstone bodies intercalated with thin lutite horizons of the marine Sant Martí Xic Fm. Decimetric yellow, plastic clays drape some of these sandstone bodies and contain abundant miliolid foraminifera and rare charophytes. The base is composed of 1-2m thick lenticular bodies of fine grained sandstone with ripple marks and heavily bioturbated tops passing laterally to yellow or brown lutite. This succession is attributed to the infilling of low sinuosity channels and their corresponding floodplain deposits. Five meter thick grey marl overlies the previous interval (Fig. 5). At the base it is intercalated with two thin layers of lignite, showing rootlet marks, and banks of oysters. This marl is rich in euryhaline gastropods (e.g. Potamidae) and represents deposition in a brackish marsh. The upper part of the marly interval is rich in charophytes

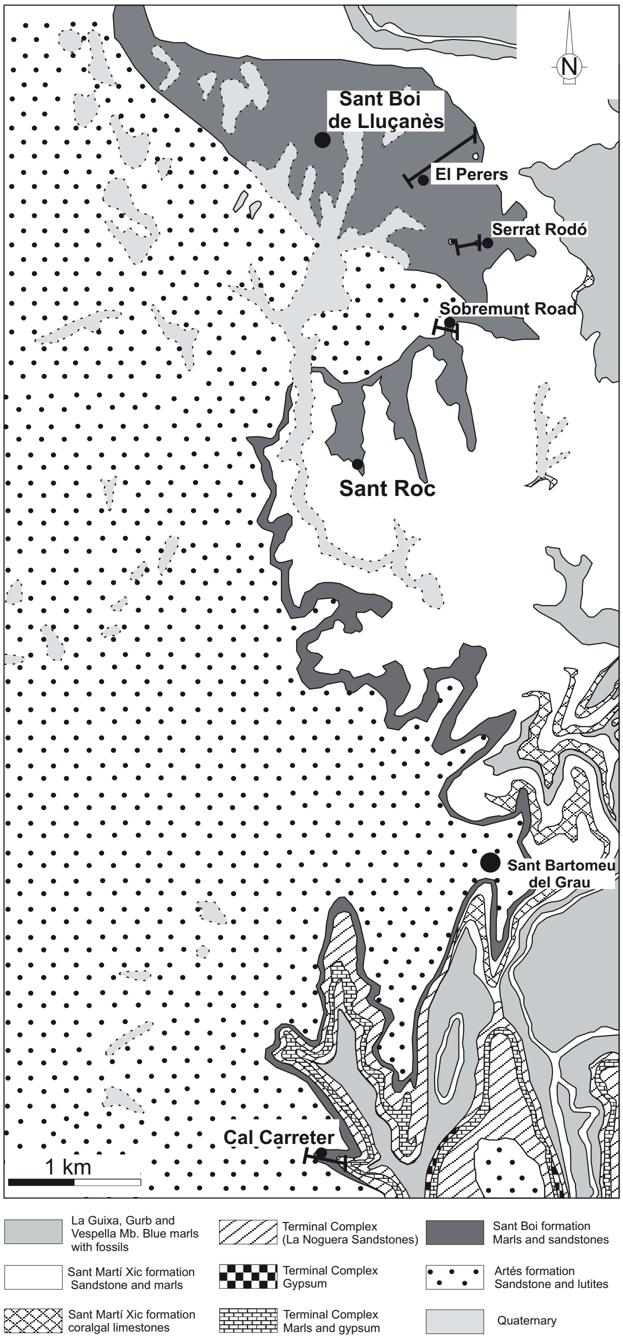

FIGURE 4 | Geological map of the Sant Boi Formation. Studied sections are El Perers, Serrat Rodó, Sobremunt road, and Cal Carreter.

and non-ornamented ostracods, and devoid of brackish fauna which suggest freshwater lacustrine facies.

About 2km southeast of the type locality, near Sobremunt, the Sant Boi Fm. shows a sudden reduction in thickness (Figs. 4, 5). In this locality, the top of the Sant Martí Xic Fm. shows blue marls with abundant marine fossils, such as corals (*Stylophora contorta, Stylophora herzegowiensis, Goniopora elegans, Siderastrea moreti* and *Placosmiliopsis bilobatus*, Álvarez, 2009), marine gastropods (*Velates* sp.), oysters and bioturbations. The overlying Sant Boi Fm. is formed by 6m of yellowish marls with oyster banks (*Saccostrea* sp.) passing upwards to marls with abundant charophytes and topped by a centimetric lignite horizon. This shallowing-upward succession indicates a progressive shift from marine to brackish conditions.

About 9km southwards, near Sant Bartomeu del Grau (Figs. 4, 5), the Sant Boi Fm. is represented at the Cal Carreter section by a 5m thick succession of thin fining-upward, cross-bedded sandstone bodies with bioturbated tops overlain by 3m thick grey marls containing abundant charophytes. Arkosic red sandstones alternated with red mudstones and thin gypsum veins from the Artés Fm. sharply cover the grey siltstones and marls of the Sant Boi Fm. In this locality, the Sant Boi Fm. covers the marine sandstones of the La Noguera Fm. and underlying anoxic

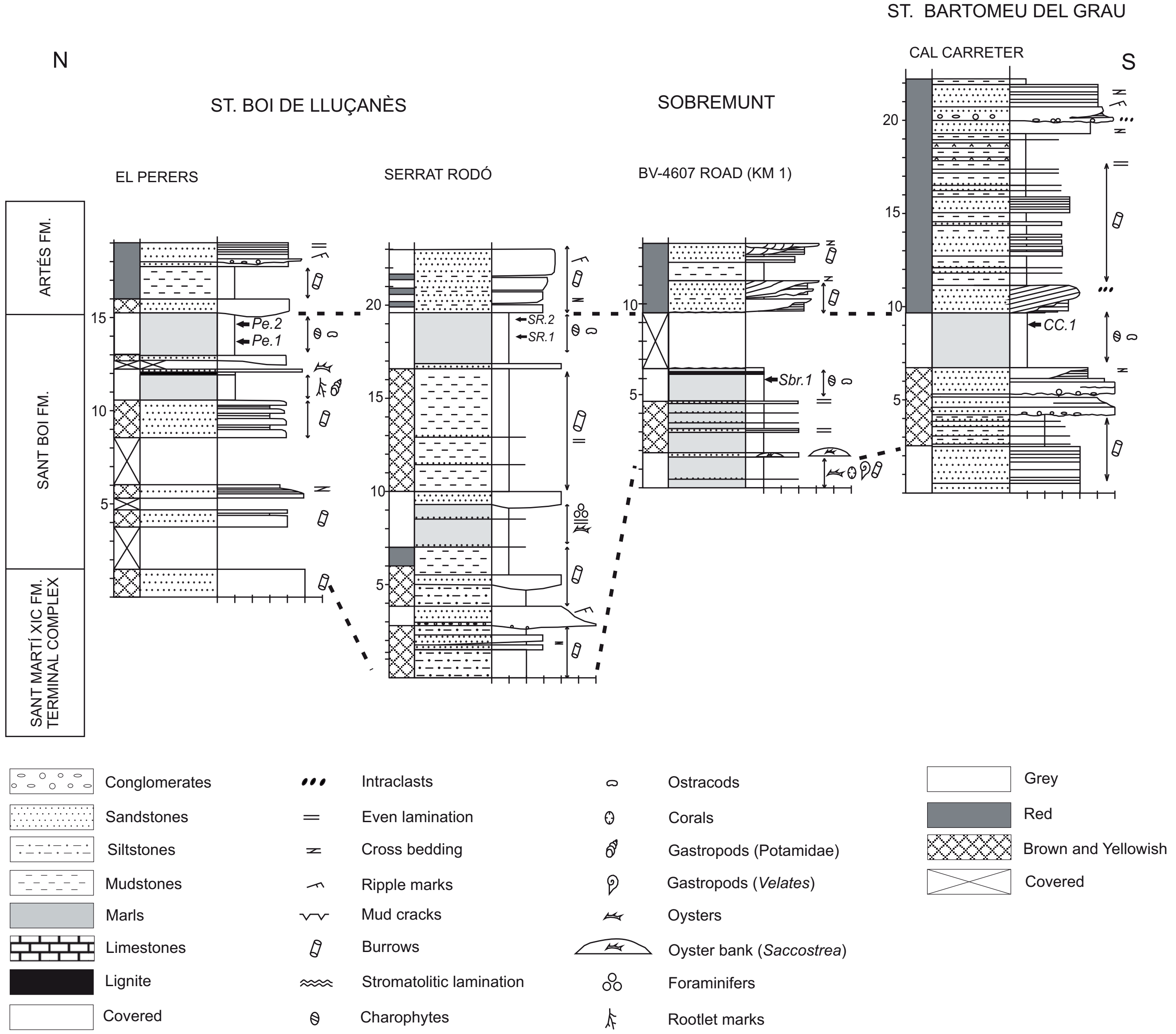

FIGURE 5 | Stratigraphic logs of the Sant Boi Formation.

marls. Both lithologies represent the last marine facies from the Terminal Complex showing an overall upward shallowing. The absence of sedimentary interruption between the marine facies of the Terminal Complex and the transitional Sant Boi Fm. suggests continuous deposition. Therefore, the Sant Boi Fm. is considered to represent a vertical and lateral equivalent of the marine part of the Terminal Complex.

Artés Formation

Facies and age of the Artés Fm. were characterized in two sections, Oristà and Santa Maria d'Oló, representing relatively different facies of the same unit (Figs. 3, 6), the former corresponding to the more proximal facies. The Oristà section is dominated by red beds. The base is composed of red laminated siltstone and clays alternating with minor lacustrine marlstone with abundant charophytes and ostracodes. Overlying materials include thin lenticular layers of lacustrine limestones with stromatolithic lamination. These facies are related to floodplain deposits including temporary lakes. At the top of the section, coarse to medium grained sandstone bodies with erosive base, cross-bedding and large-scale lenticular morphology are related to low energy palaeochannel sequences.

The Santa Maria d'Oló section corresponds to the distal facies of the Artés Fm. (Fig. 6). Thick marls with ferruginous hardgrounds are located at the base of the section. Overlying materials include fine alternating layers of marl, siltstone and sandstone. Lacustrine limestone levels characterize the top of section. Both the lithology and the abundance of charophytes and ostracod remains indicate freshwater lacustrine conditions in a distal alluvial fan context. These lacustrine deposits would mostly correspond to temporary lakes; however, the limestone at the top of the section indicates more perennial lacustrine conditions.

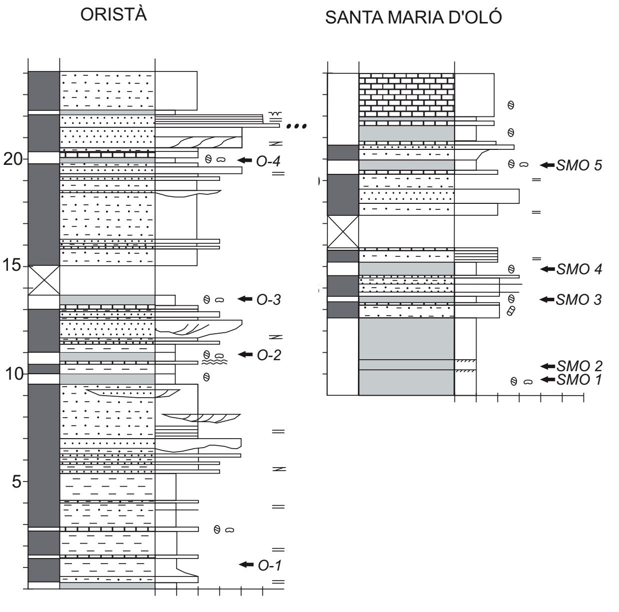

FIGURE 6 | Stratigraphic logs of the Artès Formation. Legend as in Figure 5.

Systematic Palaeobotany (charophytes of biostratigraphic interest)

Division: Charophyta MIGULA, 1897
Class: Charophyceae SMITH, 1938
Order: Charales LINDLEY, 1836
Family: Characeae RICHARD ex C. AGARDH, 1824
Subfamily: Charoideae Al. BRAUN in MIGULA, 1897

GENUS ***Harrisichara*** GRAMBAST, 1957

Harrisichara lineata GRAMBAST, 1957
Fig. 7A-7C

Material. About one hundred gyrogonites per kg of sediment from samples Pe-1 and Pe-2 from El Perers section and tens of gyrogonites from St.Roc-1 sample from the Sant Roc outcrop.

Description. Gyrogonite large in size, 960µm (mean 753µm) high and 520-853µm (mean 659µm) with an isopolarity index of 83-133 (average 115), ellipsoidal or oval in shape. Apical area flat to rounded and frequently ornamented with comma-shaped tubercles. Spiral cells are not modified at the apex. Eight to eleven (frequently 9) convolutions are visible laterally. The base is elongated in a small column. The ornamentation is formed by a regular mid-cellular crest along the central line of spiral cells.

Harrisichara vasiformis-tuberculata FEIST-CASTEL, 1977
Fig. 7D-7F

Material. About hundreds of gyrogonites per kg of sediment from sample Sbr-1 from the Sobremunt road section, 50 gyrogonites from samples SR-1 and SR-2 from the Serrat Rodó section and 300 specimens from sample CC-1 from the Cal Carreter section.

Description. Gyrogonites medium to large in size, 594-756µm (mean 655µm) high and 567-675µm (mean 619µm) wide with an isopolarity index of 96-116 (average 106) ovoidal or sub-ovoidal in shape with a flat or rounded apex, without any periapical modification of the spiral cells. The apex is frequently ornamented with tubercles. Nine to eleven (frequently ten) convolutions are visible laterally. The base is rounded or conical and in some cases

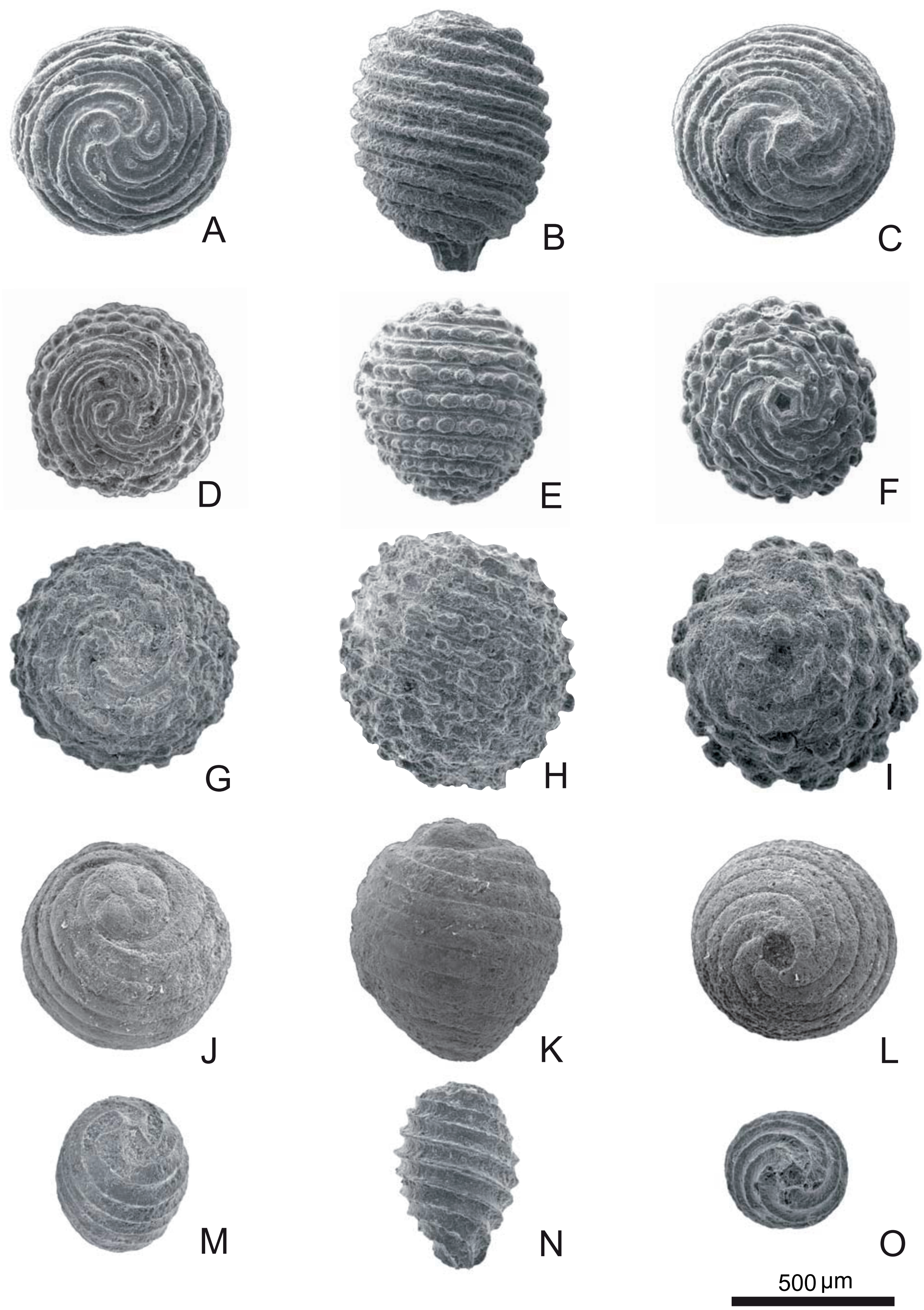

FIGURE 7 | Gyrogonites of biostratigraphic interest from the Upper Eocene of the Northeastern Ebro Basin. A to C *Harrisichara lineata,* El Perers section; A) apex, B) lateral view, C) base. D to F *Harrisichara vasiformis-tuberculata*, Sobremunt and Serrat Rodó sections; D) apex, E) lateral view, F) base. G to I *Harrisichara tuberculata*, Oristà and Santa Maria d'Oló sections; G) apex, H) lateral view, I) base. J to L *Nodosochara jorbae***,** Sobremunt road, Serrat Rodó, Oristà and Santa Maria d'Oló section; J) apex, H) lateral view, L) base. M to O *Lychnothamnus longus***,** Oristà and Santa Maria d'Oló section; M) apex, N) lateral view, O) base.

elongated in a small column. The ornamentation is formed by a succession of regularly spaced tubercules, which are arranged along the central line of the spiral cells and may form an irregular crest.

Harrisichara vasiformis-tuberculata represents an informal taxon created to show the transition between *H. vasiformis* (Reid and Groves, 1921) Grambast, 1957 and *H. tuberculata* (Lyell, 1826) Grambast, 1957. This gradual change was modelized with the Eigenshape method by Sille et al. (2004).

Harrisichara tuberculata (LYELL, 1826) GRAMBAST, 1957
Fig. 7G-7I

Material. A few gyrogonites of *Harrisichara tuberculata* were found in samples O-4 from Oristà section and in SMO-1 and SMO-2 in Santa Maria d'Oló section.

Description. Gyrogonites large in size, high and wide average 862 and 800µm an isopolarity index average 105, spherical in shape, with a flat or slightly convex and ornamented apex. The base is rounded or slightly pointed. Ten to eleven convolutions are visible laterally. The ornamentation is typically formed by large regularly spaced tubercules.

GENUS ***Nodosochara*** MÄDLER, 1955

Nodosochara jorbae CHOI, 1989
Fig. 7J-7L

Material. Hundreds of gyrogonites per kg of sediment from samples Sbr-1 in Sobremunt road and SR-2 in Serrat Rodó sections and in sample O-1, O-3, O-4 from Oristà and SMO-2, SMO-3 from the Santa Maria d'Oló section.

Description. Gyrogonite large, 660-912µm high (mean 758µm) and 540-860µm wide (mean 680µm) with an isopolarity index 90-140 (mean 112), normally pear-shaped but sometimes sub-spherical or ellipsoidal in shape with convex spiral cells, devoid of ornamentation. A characteristic nitellopsidoid apex, i.e. shortening and narrowing of the spiral cells in the periapical zone, along with a small pentagonal basal pore identifies this genus. Periapical depression is well-marked and apical nodules occur in many specimens. Seven to ten convolutions (often 9) are visible in lateral view. The base is rounded or conical.

GENUS ***Lychnothamnus*** (RUPRECHT, 1845) LEONHARDI, 1863 emend. A. BRAUN in BRAUN et NORDSTEDT, 1882

Lychnothamnus longus CHOI, 1989
Fig. 7M-7O

Material. *Lychnothamnus longus* is represented by hundreds of gyrogonites per kg sieved in samples O-3 and O-4 from Oristà section. In contrast, it is represented by dozens of gyrogonites per kg in samples from the Santa Maria d Oló section.

Description. Gyrogonites are medium in size, 450-724µm (mean 618µm) high and 380-580µm (mean 464µm) with an isopolarity index of 104-180 (average 130), ellipsoidal to ovoidal in shape. The apex is psilocharoid, rounded to truncate, in some cases pointed in the centre. It displays a remarkable apical thinning. The base shows a variable morphology, in some cases elongated to form a broad column, and the basal pore shows a small star-shaped funnel. The spiral cells, flat to concave, are devoid of ornamentation and separated by prominent sutures which are bicarinate in some specimens. Seven to ten (frequently 8) convolutions are visible laterally.

Biostratigraphy

This biostratigraphic study focused on the dating of the new Sant Boi Fm. and its chronostratigraphic distinction from the overlying Artés Fm. Taxonomic composition of the samples and relative abundance of gyrogonites is represented in Table 1.

Sant Boi Formation

The charophyte assemblage from the new formation at the El Perers section and at Sant Roc outcrop is composed of *Harrisichara lineata* and *Chara* sp. According to Riveline (1986), *H. lineata* is widely distributed in the Middle Bartonian to Middle Priabonian of Europe. It has been reported in the biozones Chara friteli, Raskyella vadaszi, Psilochara repanda, Gyrogona tuberosa, Harrisichara vasiformis-tuberculata and the basal part of biozone Stephanochara vectensis of Riveline et al. (1996) and Riveline in Hardenbol et al. (1998). *H. lineata* is also present in Biozones 1 (undefined) and 2 (Sphaerochara labellata) of the Ebro Basin biozonation proposed by Feist et al. (1994).

In Sobremunt road and in Serrat Rodó sections, south of the type locality, the charophyte assemblage from the Sant Boi Fm. is composed of *Harrisichara vasiformis-tuberculata*, *Nodosochara jorbae, Gyrogona* sp. and *Chara* sp. The two first species are biostratigraphically significant. In the Cal Carreter section the charophyte assemblage is also represented by *H. vasiformis-tuberculata* and *Lamprothamnium* sp. According to Riveline (1986), *H. vasiformis-tuberculata* is found in the middle part of

TABLE 1 | Charophyte assemblages of non-marine Palaeogene samples from the Lluçanès area. Legend: X) rare, XX) abundant, XXX) very abundant

Lithostratigraphy	Sant Boi Fm.							Artés Fm.								
Locality	El Perers		Serrat Rodó		Sobremunt road	St. Roc	Cal Carreter	Oristà				Sta. Maria d'Oló				
Species / Samples	Pe.1	Pe.2	SR.1	SR.2	Sbr.1	St.Roc.1	CC.1	O.1	O.2	O.3	O.4	SMO.1	SMO.2	SMO.3	SMO.4	SMO.5
Harrisichara lineata	XXX	XX				XX										
H. vasiformis-tuberculata			X	XXX	XX		XXX									
H. tuberculata											X	X	X			
Nodosochara jorbae				XX	XXX			XXX		XX	XX	X	XX	XXX	X	XX
Lychnothamnus longus										XX	XXX		X	X	XX	X
Lamprothamnium sp.							X									
Gyrogona sp.					X											
Chara sp.	XX				XX		XX	XX	X	XX	XX		X	X	X	XX

the Priabonian of Europe. Indeed, it represents the index species of the homonymous charophyte biozone, which has been correlated with biozones NP 19-20 of the marine domain (Riveline et al., 1996; Riveline, 1998). The other biostratigraphically significant species, *Nodosochara jorbae*, has only been found, up to now, in the Upper Priabonian beds of the Eastern Ebro Basin in the Igualada area. This species was included in the Stephanochara vectensis local biozone proposed by Choi (1989) and Feist et al. (1994). Our results indicate that the range of *N. jorbae* must be enlarged at its base to include the middle part of the Priabonian since it occurs in association with *Harrisichara vasiformis-tuberculata*, i.e. in the Harrisichara vasiformis-tuberculata European biozone of Riveline et al. (1996) and Riveline (1998). Summarizing, the Sant Boi Fm. is attributed to the middle part of the Priabonian (H. vasiformis-tuberculata biozone).

Artés Formation

Charophyte assemblages from the Artés Fm., studied in Oristà and Santa Maria d Oló, are homogeneously formed by *Nodosochara jorbae*, *Lychnothamnus longus*, *Harrisichara tuberculata* and *Chara* sp. The association of the three first species is biostratigraphically significant. The biostratigraphic range of *Nodosochara jorbae*, discussed before, suggests that the deposition of the Artés Fm. took place from the middle part of Priabonian to the Eocene-Oligocene boundary. However, this range can be restricted by another chronostratigraphically significant species, common in the Oristà and Santa Maria d'Oló sections, *Lychnothamnus longus*. The total range of *L. longus* extends from the late Priabonian to the middle Rupelian. The first appearance of the species marks the base of the local biozone 3 (Stephanochara vectensis) defined by Feist et al. (1994), which corresponds to the upper part of the Stephanochara vectensis biozone of the European biozonation proposed by Riveline et al. (1996) and Riveline (1998). Finally, *Harrisichara tuberculata* defines a superbiozone that extends from the middle part of the Priabonian to the middle of the Rupelian and includes the two charophyte biozones Stephanochara vectensis and Stephanochara pinguis of Riveline et al. (1996) and Riveline (1998).

In sum, the charophyte assemblages from the Artés Fm. studied in the Lluçanès area can be related to the European superbiozone Harrisichara tuberculata or to the local biozone 3 (Stephanochara vectensis) from Feist et al. (1994). The latter biozone represents the Uppermost Priabonian.

DISCUSSION

The beginning of continentalization in the northeasternmost part of the Ebro Basin has been a matter of controversy. Disagreement exists about the age of the youngest marine sedimentation and the beginning of continentalization. New magnetostratigraphic data from the youngest marine rocks located in the central part of the eastern margin of the Ebro Basin (Igualada area) indicate that continentalization of the basin began in chron 16 (Costa et al., 2010). Moreover, recent studies on calcareous nannofossils of the marine facies of the Terminal Complex and the underlying Milany sequence, document the base of the NP19-20 Zone, Lower Priabonian, in the Vic area (Cascella and Dinarès-Turell, 2009).

The marine-continental boundary has been poorly studied up to now in the Lluçanès area northwest of the town of Vic, where the sedimentary succession shows an intermediate transitional unit, traditionally considered to belong to the continental Artés Fm. This study aimed to show that this unit, defined here as the Sant Boi Fm., covers the underlying marine Milany Depositional Sequence and is a lateral and vertical equivalent, to the south, of the Terminal Complex (Fig. 2). Thus, it represents the last

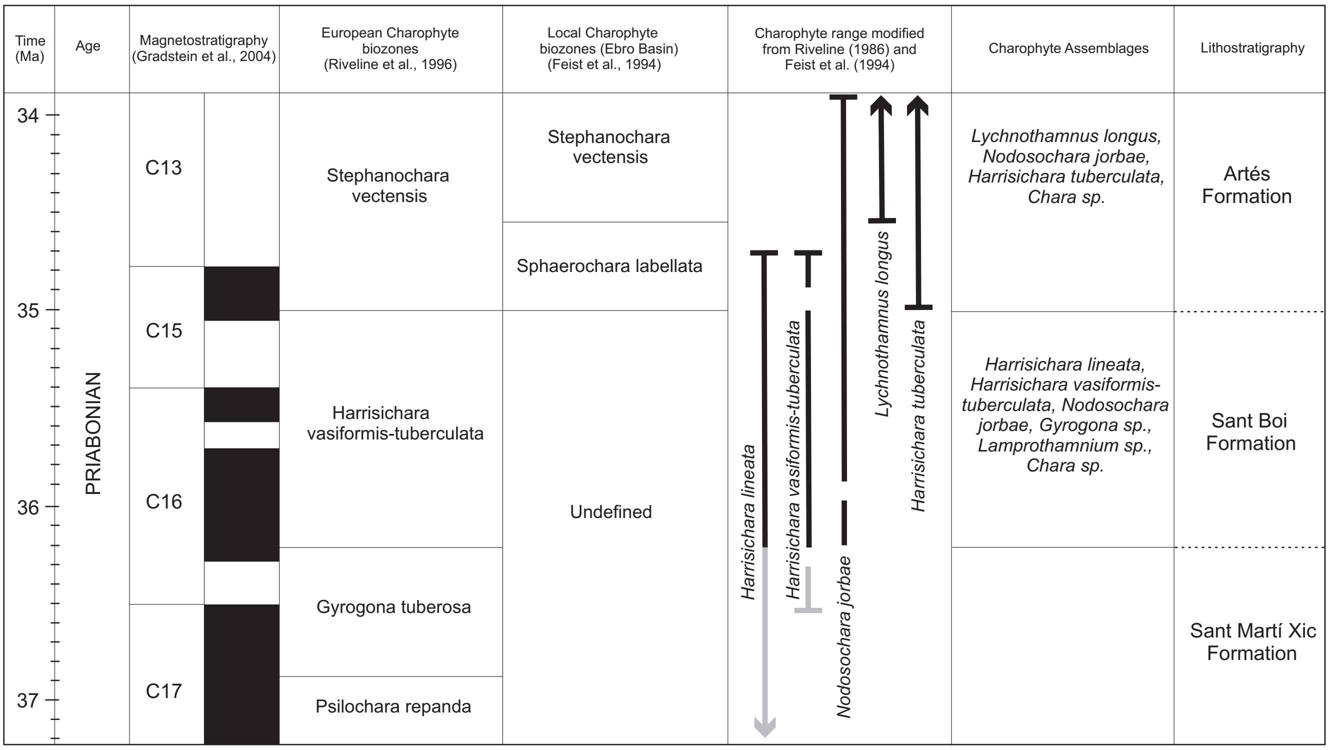

FIGURE 8 | Late Eocene magneto-bio-cronostratigraphy. Geochronological time-scale according to Gradstein et al. (2004), European charophyte biozonations are after Riveline et al. (1996) and Riveline in Hardenbol et al. (1998); local charophyte biozonation (Ebro Basin) after Feist et al. (1994).

marine-linked deposits in this northeasternmost sector of the basin rather than the first terrestrial deposits after continentalization, as previously thought.

Five different charophyte species are reported from Sant Boi Fm. The assemblage is formed by *Harrisichara lineata* Grambast, 1957*, H. vasiformis-tuberculata* Feist-Castel, 1977*, Nodosochara jorbae* Choi, 1989, *Gyrogona* sp., *Lamprothamnium* sp. and *Chara* sp. and belongs to the Harrisichara vasiformis-tuberculata European biozone, which represents the middle part of the Priabonian according to correlations with zone NP 19-20 in the English Basin (Riveline et al., 1996). The overlying Artés Fm. has yielded *H. tuberculata* (Lyell, 1826) Grambast, 1957*, Nodosochara jorbae* Choi, 1989*, Lychnothamnus longus* Choi 1989 and *Chara* sp. from the Harrisichara tuberculata superbiozone of Riveline et al. (1996) and the local biozone 3 (Stephanochara vectensis) from Feist et al. (1994). The latter is Late Priabonian in age (Fig. 8). These results appear to indicate that a small gap exists between the assemblages from the Sant Boi Fm. and those from the overlying Artés Fm., equivalent to the local biozone 2 (Sphaerochara labellata zone) from Feist et al. (1994). This gap would represent part of the Upper Priabonian. Given that the charophyte samples studied from the Artés Fm. are closer to the top of the unit than to the base, this gap could correspond to the non-sampled part of the Artés Fm.

In conclusion, the latest marine-linked deposits of the North-easternmost Ebro Basin (Lluçanès area, near Vic) are transitional and lacustrine siltstones, marls and lignites of the Sant Boi Fm., which cover and are laterally equivalent to the Terminal Complex of Travé et al. (1996). They belong to the mid-part of the Priabonian (Harrisichara vasiformis-tuberculata biozone) and are probably within chron C16 according to the hypothesis of Costa et al. (2010). These data, along with the biostratigraphic data gathered from other parts of the basin by Ramírez et al. (1991) and Canudo et al. (1988) support the conclusion that the continentalization of the Ebro Basin was a rapid and synchronic event throughout the basin.

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Calibration of Eocene-Oligocene charophyte biozones in the Eastern Ebro Basin (Catalonia, Spain)

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ABSTRACT: A charophyte biozonation for the transitional and continental Upper Eocene-Lower Oligocene record in the eastern margin of the Ebro Basin is performed and calibrated using magnetostratigraphic data. This study has been based on intensive sampling collected along five composite sections. The Harrisichara vasiformis-tuberculata European biozone has been renamed to H. lineata biozone, since the former index-species was a poorly characterised morphotype with a non-valid species name. This biozone is represented in the transitional Sant Boi Formation and the lowermost part of the Artés Formation in the northeastern sector of the basin, within the normal part of chron C16. The Harrisichara tuberculata European superzone encompasses most of the continental Artés Formation in the northeastern sector and the Margalef Formation in the southeastern sector of the basin ranging from chron C16n.2n (~35.5 Ma) to chron C12r (~31.5 Ma). Included within the Harrisichara tuberculata superzone, the Lychnothamnus vectensis European biozone was redefined as the interval between the first occurrence of *Lychnothamnus vectensis* and the first occurrence of *Lychnothamnus pinguis*. Redefinition of the Lychnothamnus vectensis biozone implies that its basal limit does not coincide with the basal limit of the Harrisichara tuberculata superzone, as previously believed. The absence of *L. pinguis* in the Ebro Basin, and probably in all Southern Europe, results in a local Lychnothamnus vectensis biozone for that area including the total distribution range of this index species. Magnetostratigraphic correlation suggests that this biozone ranges in the Ebro Basin from chron C13r (~34.5 Ma) to chron C13n (~33.5 Ma) including the Eocene-Oligocene boundary. A new local Harrisichara tuberculata-Nodosochara jorbae assemblage zone was defined at the base of Harrisichara tuberculata superzone coinciding with the base of the Artés Formation in the northeastern sector, ranging between chron C16n.2n and chron C13r. The Lychnothamnus major European biozone encompasses the lower part of the continental Albi Formation in the southeastern sector of the basin within chron C12r. The lower limit of the Chara microcera European biozone is recorded in the Tàrrega Formation. Litho- and magnetostratigraphic correlation suggests that the lower limit of this biozone belongs to the uppermost part of chron C12r (~31 Ma). Comparisons with homologous data from the classical Upper Eocene-Lower Oligocene Solent Group in the Hampshire Basin (Isle of Wight, UK) suggest that the lower limit of the Harrisichara tuberculata superzone is isochronous in Europe but was recorded earlier in the Ebro Basin than in the Hampshire Basin due to more appropriate palaeoecological conditions.

INTRODUCTION

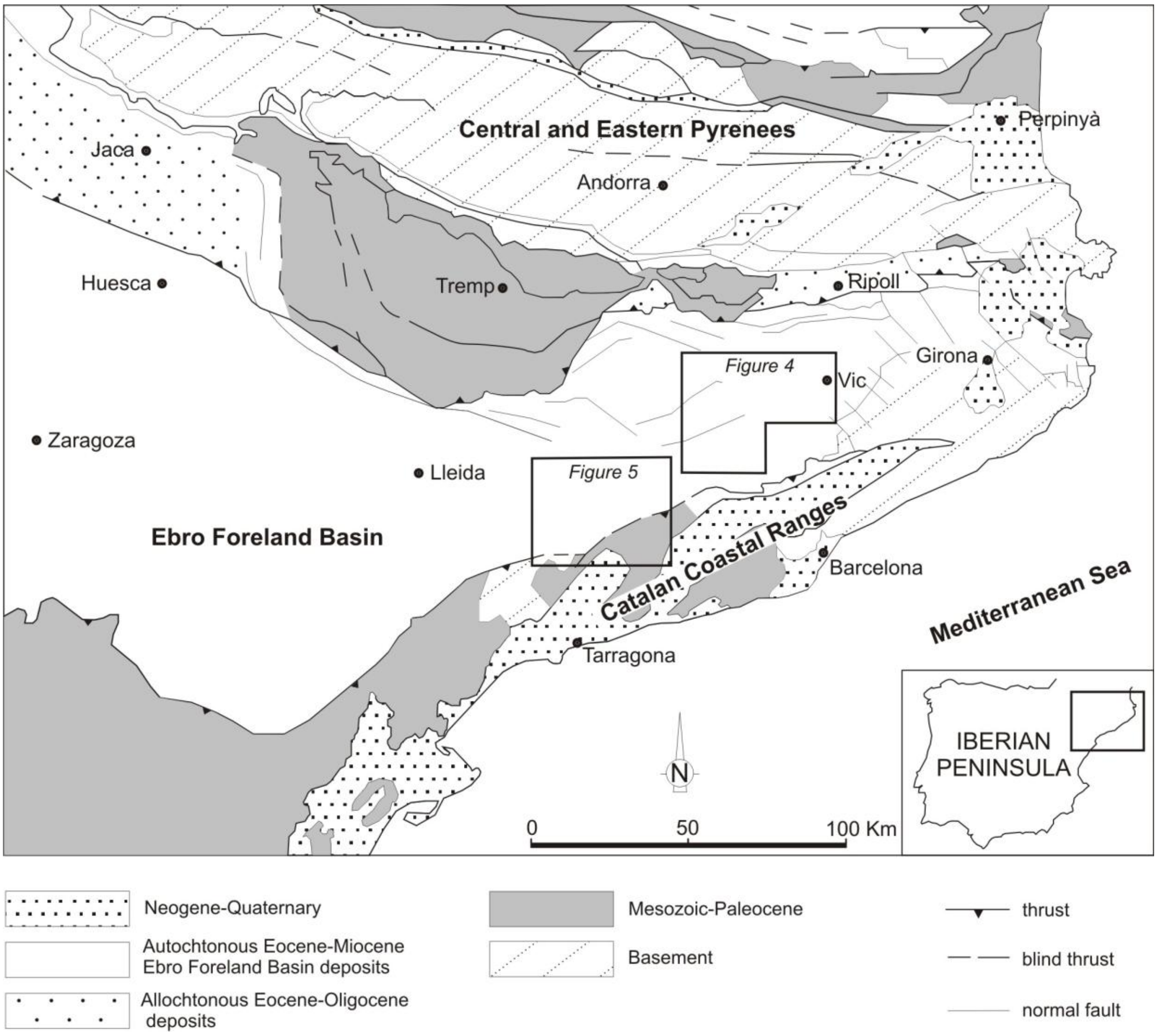
Charophytes are a group of aquatic plants living in brackish and freshwater environments. Their fossil record is mainly based on calcified fructifications (gyrogonites and utricles) known from the Silurian to the present (Feist et al. 2005). Because of their specific morphology and relatively high evolutionary rates, charophyte gyrogonites are, along with mammal remains, the main biostratigraphic indicators of Tertiary non-marine deposits. Biostratigraphy coupled with magnetostratigraphy leads to robust correlations with the Geomagnetic Polarity Time Scale (GPTS), providing the fossil record with absolute ages. Thus, when independent correlations with the GPTS are performed, the resulting magnetostratigraphy-based chronology contributes to the calibration of continental biostratigraphic markers, i.e. charophyte biozones and vertebrate MP mammal reference levels.

Detailed charophyte biozonations of the European Paleogene have been proposed based on the pioneering study by Grambast (1972) in the Paris Basin. This first biozonation was followed by a number of local biozonations (Feist-Castel 1977a; Feist and Ringeade 1977; Anadón and Feist 1981; Riveline 1986; Feist et al. 1994), which were later combined to build a general European charophyte biozonation (Riveline et al. 1996; Riveline in Hardenbol et al. 1998). In the Ebro Basin, a local charophyte biozonation was constructed by Anadón et al. (1992) and Feist et al. (1994) by combining previous biostratigraphic studies in the eastern part of the basin (Dalloni 1930; Rosell et al. 1966; Colom et al. 1970; Anadón 1978; Colombo 1980; Anadón and Feist 1981; Choi 1989; Cabrera 1983). In order to correlate mammal and charophyte biozonations, Feist et al. (1994) sampled charophytes in beds close to those of the classical vertebrate sites, especially the Sant Cugat de Gavadons and Santpedor mammal sites in the northeastern sector and the Rocafort de Queralt, Forés and El Talladell mammal sites in the southeastern sector (Agustí et al. 1987; Anadón et al. 1987; 1992; Sáez 1987; Arbiol and Sáez 1988; Colombo et al. 1995). The magnetostratigraphic record from the southeastern margin of the Ebro Basin provided accurate ages for these and other new mammal sites (Barberà 1999; Barberà et al. 2001) whilst in the northeastern Ebro Basin accurate ages for the Sant Cugat de Gavadons and Santpedor mammal fossil sites were recently provided by Costa et al. (2011).

Unlike the mammal biostratigraphy, Paleogene charophyte biozones have never been calibrated to the GPTS. The Upper Eocene-Lower Oligocene non-marine record along the eastern margin of the Ebro Basin provides several stratigraphic sections rich in red beds and lacustrine-palustrine carbonates. In this study, a charophyte succession in the northeastern sector of the basin was established along two composite sections, located in the Vic-Manresa area (El Perers-Serrat Rodó and Moià-Santpedor sections) and a composite section from the Igualada area (Maians-Rubió section). The charophyte succession in the southeastern sector of the basin was recorded in two composite sections from the La Conca de Barberà area (Rocafort de Queralt-Sarral sections) and from the Garrigues area (Tarrés-Vinaixa section). Charophyte abundance and diversity allowed us to define a new zonal scheme for the Eocene-Oligocene boundary, taking into account the biostratigraphy and paleoecological constraints of charophyte assemblages. The new biozonation, together with new magnetostratigraphic data from the same sampled sections, provides a robust correlation between charophyte biozones and the GPTS of Gradstein et al. (2004), representing the first charophyte biozone calibration for the Eocene-Oligocene boundary.

GEOLOGICAL SETTING

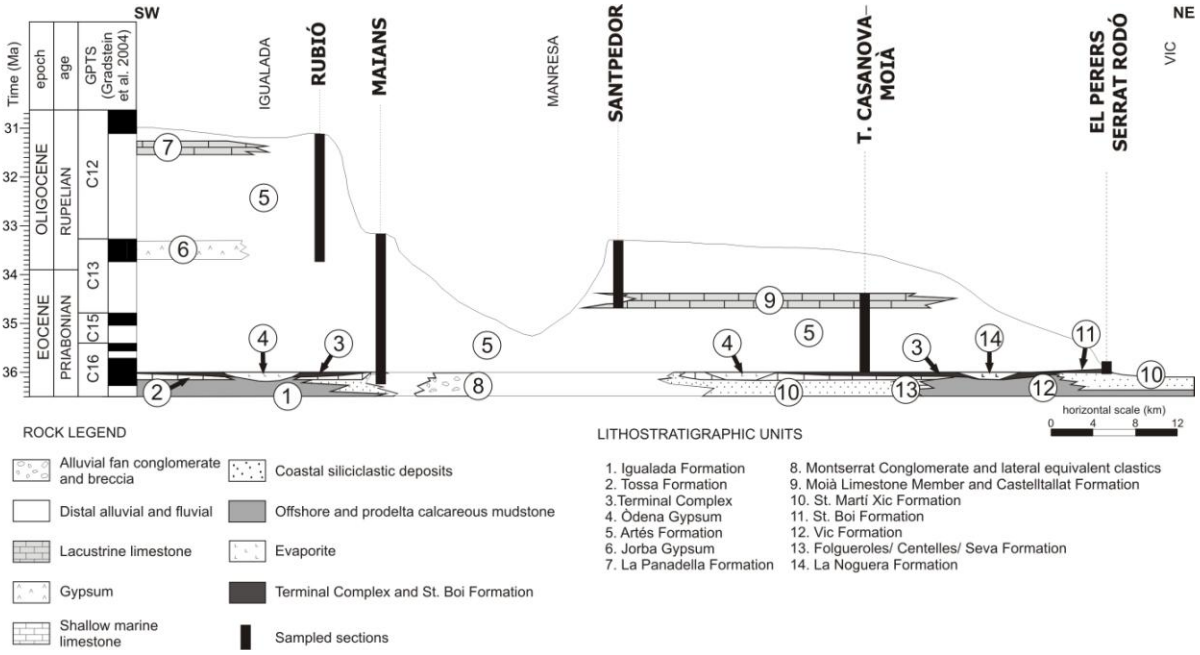
The Ebro Basin is the triangular-shaped southern foreland basin of the Pyrenean Range (Fig. 1). The origin of the Ebro Basin is related to flexural subsidence due to the collision between the Iberian and the European plates from the Upper Cretaceous to the Miocene (Puigdefàbregas et al. 1992). The Paleogene sedimentary record is divided into nine depositional sequences related to the emplacement of the south Pyrenean thrust sheets and linked to two widespread marine transgressions of Ilerdian and Lutetian-Bartonian ages (Ferrer 1971; Riba et al. 1983; Puigdefàbregas and Souquet 1986; Puigdefàbregas et al. 1986; Serra Kiel et al. 2003). During the Late Eocene, tectonic activity in the western Pyrenees led to closure of the basin drainage, restricting the marine influence on the basin and leading to the deposition of an evaporite plug. This evaporitic event represents the last marine episode in the southern Pyrenean foreland basin. Since then, uninterrupted Late Eocene to Middle Miocene continental sedimentation has filled in the resulting endorheic basin (Puigdefàbregas et al. 1992).



TEXT-FIGURE 1.
Geological sketch showing the location of the studied areas (modified from Vergés et al. 1998).

The last completely marine deposits in the eastern Ebro Basin are composed of different lithologies belonging to the Milany depositional sequence (Fig. 2). In the Vic-Manresa area the last marine deposits belong to the deltaic sandstones of the Sant Martí Xic Formation (Barnolas 1992; Barnolas et al. 1988), which grades basinwards to the prodelta marls of the Vic Formation (Reguant 1967) and Igualada Formation (Ferrer 1971). Transitional deposits in the eastern Ebro Basin are represented by the Cardona depositional sequence. North to south, transitional deposits are represented by marls of the Sant Boi Formation, sandstones, marls and limestones of the Terminal Complex, and evaporites of the La Noguera Formation and Òdena Gypsum (Fig. 2).

The overlying non-marine record in the eastern sector of the basin is represented by red beds of the Solsona depositional sequence, the base of which is isochronous along the entire eastern margin of the basin (Ramírez et al. 1991; Canudo et al. 1988; Costa et al. 2010). Recent biostratigraphic data based on calcareous nannoplankton indicate that the uppermost marine deposits of the Ebro basin were deposited in the NP19-20 nannoplankton zone (Cascella and Dinarès-Turell 2009). Moreover magnetostratigraphic data indicate that the transition from marine to continental sedimentation was a rapid and isochronous event occurring within chron C 16n (Costa et al. 2010; Costa et al. in press). Consistent with these results, charophyte assemblages from the Vic area document the Priabonian biozone of Harrisichara



TEXT-FIGURE 2.
Chronostratigraphic framework of the Upper Eocene-Oligocene record in the northeastern Ebro Basin (modified from Costa 2011).

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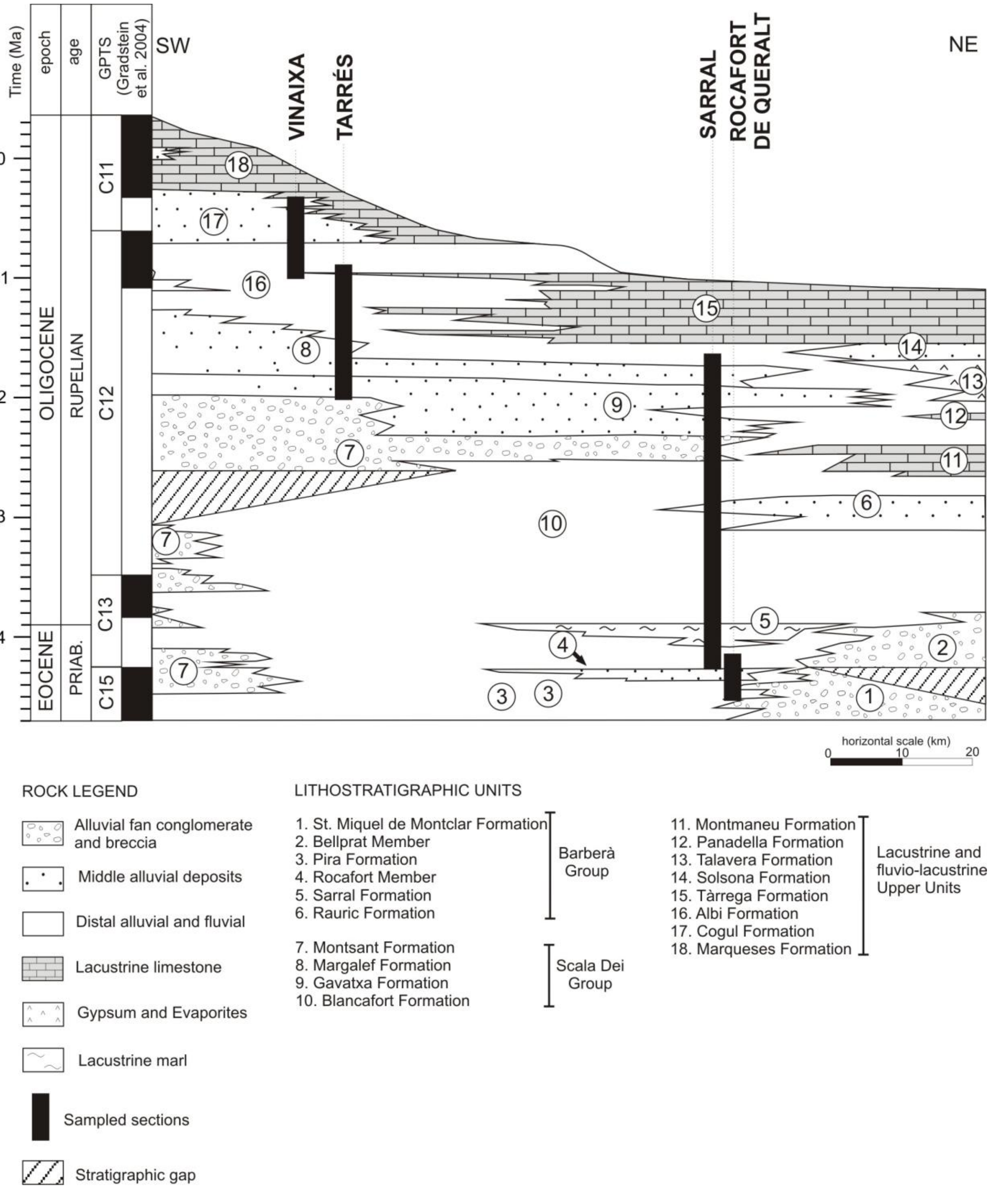
lineata (formerly called H. vasiformis-tuberculata biozone) in the last transitional beds (Sanjuan et al. 2012). In the northeastern sector of the basin, the overlying continental deposits comprise red alluvial and fluvial beds of the Artés Formation (Ferrer 1971; Sáez 1987) with interbedded lacustrine limestone beds e.g. Moià Limestone Member (Sáez 1987) and La Panadella Formation (Colldeforns et al. 1994a) (Fig. 2). Westward of the central areas of the basin, the record consists of lacustrine deposits interfingered with red clastic intervals that correspond to the distal parts of the fluvial fans draining from the basin margins (Sáez et al. 2007).

In the southwestern area of the basin the continental deposits comprise proximal alluvial, fluvial, lacustrine and evaporitic beds of the Barberà and Scala Dei Groups grading upwards to the Upper Units defined by Colombo (1980; 1986). According to Colombo, the Barberà Group is composed of mud flat facies represented by the Montblanc Formation, which contains alternating ponded and lacustrine areas (Sarral Formation). Some distal intervals of alluvial fan bodies (Sant Miquel de Montclar Formation) are interfingered with these fine materials. The Scala Dei Group represents the development of proximal facies (Montsant Formation) and mid mud-flat facies (Margalef Formation) of important alluvial fan bodies. Fluvial to mud-flat facies are represented by the Flix and Blancafort formations, which are located in the marginal-distal areas of the alluvial fan system. The Upper Units defined by Colombo (1986) are represented, in the studied sections, by many lacustrine and fluvio-lacustrine formations such as the Tàrrega Limestone Formation (Fig. 3).

MATERIALS AND METHODS

Location of stratigraphic sections

Eight stratigraphic sections showing good exposure of transitional and continental, mainly fluvio-lacustrine, facies were sampled systematically for biostratigraphic purposes in the Upper Eocene-Lower Oligocene deposits on the eastern margin of the Ebro Basin (Table 1). In the northeastern sector the studied sections are located near the villages of Sant Boi de Lluçanès, Moià, Santpedor, Maians and Rubió (Figs. 1 and 4). In the southeastern sector the sections are located near the villages of Rocafort de Queralt and Sarral, Tarrés and Vinaixa (Figs.1 and 5).

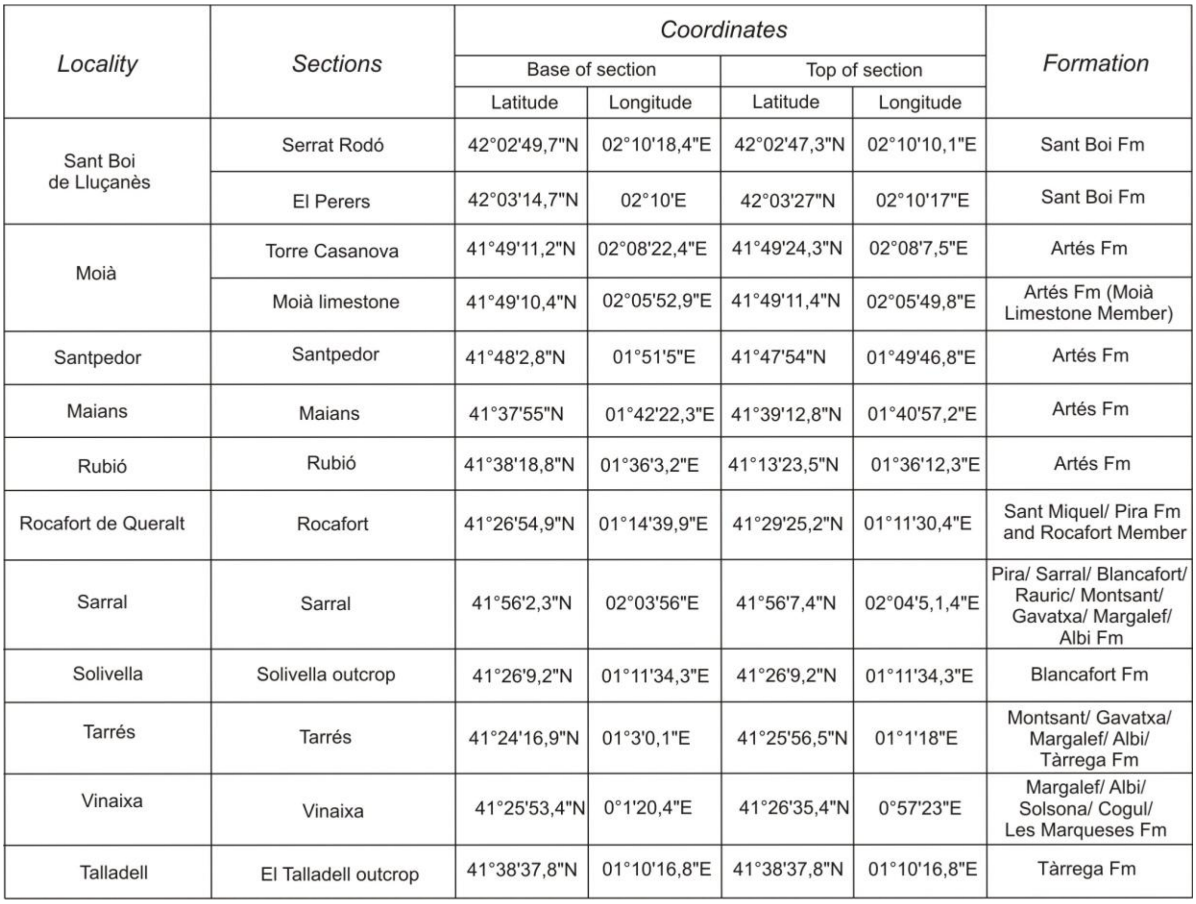


TEXT-FIGURE 3.
Chronostratigraphic framework of the Upper Eocene-Oligocene record in the southeastern Ebro Basin (modified from Barberà 1999).

Processing of samples

Fossil remains were obtained from 87 of 145 samples of greyish lacustrine grey mudstones and marls collected from the aforementioned sections. About 2 kg of sediment per sample were disaggregated in water, oxygen peroxide and Na_2CO_3 solution and later sieved using sieves with mesh apertures of 1.0, 0.5 and 0.2 mm.

Gyrogonites were picked out under a light microscope and measured at 40x magnification (hundred gyrogonites per species). Selected gyrogonites were studied and photographed using a scanning electron microscope Quanta 200 at the Serveis Científico-Tècnics (Universitat de Barcelona). The material is now housed at the



Locality	Sections	Coordinates				Formation
		Base of section		Top of section		
		Latitude	Longitude	Latitude	Longitude	
Sant Boi de Lluçanès	Serrat Rodó	42°02'49,7"N	02°10'18,4"E	42°02'47,3"N	02°10'10,1"E	Sant Boi Fm
	El Perers	42°03'14,7"N	02°10'E	42°03'27"N	02°10'17"E	Sant Boi Fm
Moià	Torre Casanova	41°49'11,2"N	02°08'22,4"E	41°49'24,3"N	02°08'7,5"E	Artés Fm
	Moià limestone	41°49'10,4"N	02°05'52,9"E	41°49'11,4"N	02°05'49,8"E	Artés Fm (Moià Limestone Member)
Santpedor	Santpedor	41°48'2,8"N	01°51'5"E	41°47'54"N	01°49'46,8"E	Artés Fm
Maians	Maians	41°37'55"N	01°42'22,3"E	41°39'12,8"N	01°40'57,2"E	Artés Fm
Rubió	Rubió	41°38'18,8"N	01°36'3,2"E	41°13'23,5"N	01°36'12,3"E	Artés Fm
Rocafort de Queralt	Rocafort	41°26'54,9"N	01°14'39,9"E	41°29'25,2"N	01°11'30,4"E	Sant Miquel/ Pira Fm and Rocafort Member
Sarral	Sarral	41°56'2,3"N	02°03'56"E	41°56'7,4"N	02°04'5,1,4"E	Pira/ Sarral/ Blancafort/ Rauric/ Montsant/ Gavatxa/ Margalef/ Albi Fm
Solivella	Solivella outcrop	41°26'9,2"N	01°11'34,3"E	41°26'9,2"N	01°11'34,3"E	Blancafort Fm
Tarrés	Tarrés	41°24'16,9"N	01°3'0,1"E	41°25'56,5"N	01°1'18"E	Montsant/ Gavatxa/ Margalef/ Albi/ Tàrrega Fm
Vinaixa	Vinaixa	41°25'53,4"N	0°1'20,4"E	41°26'35,4"N	0°57'23"E	Margalef/ Albi/ Solsona/ Cogul/ Les Marqueses Fm
Talladell	El Talladell outcrop	41°38'37,8"N	01°10'16,8"E	41°38'37,8"N	01°10'16,8"E	Tàrrega Fm

TABLE 1
Location (coordinates) and lithostratigraphic attribution (formations) of the studied section on the eastern margin of the Ebro Basin.

Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona.

Systematic paleobotany

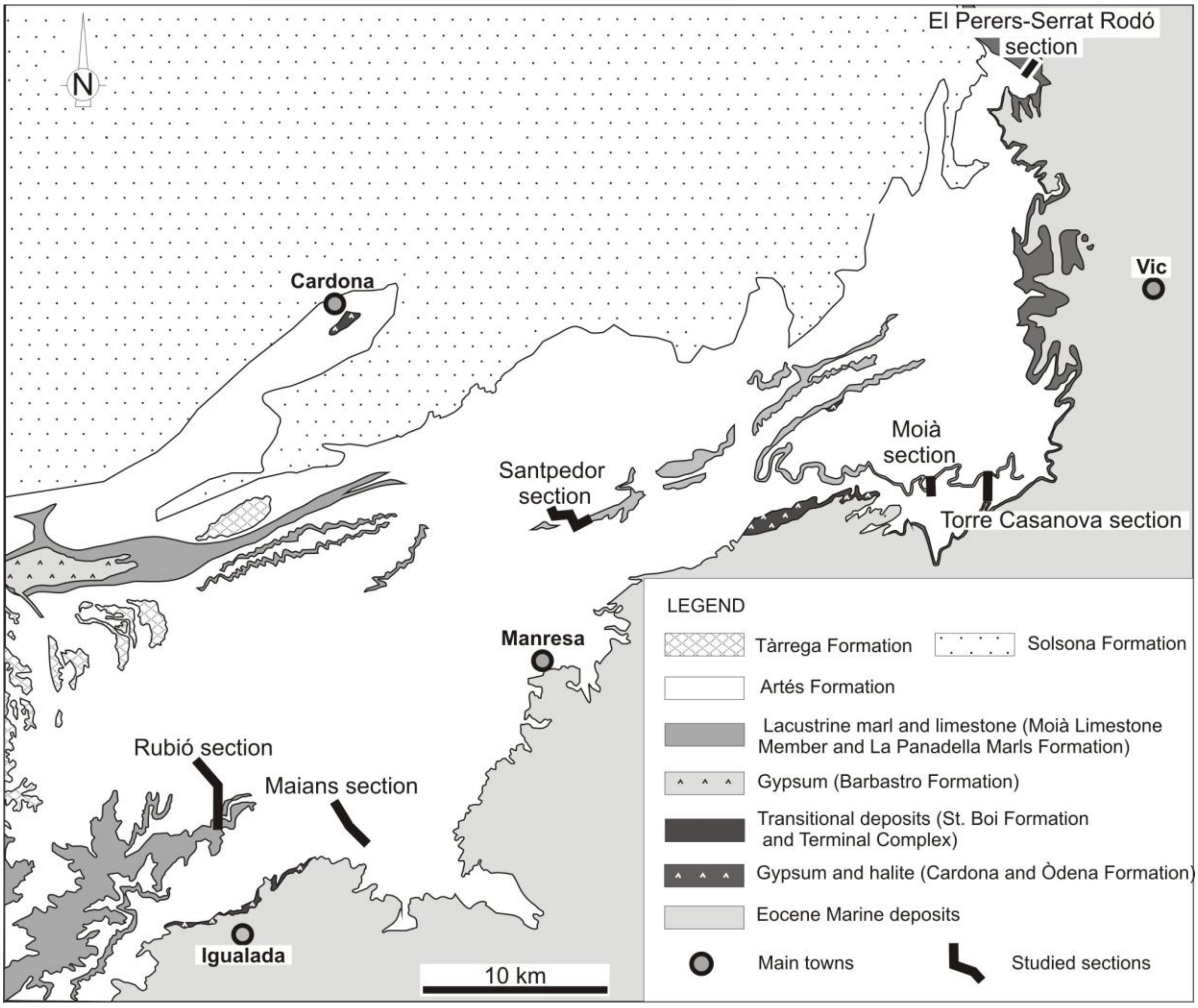
Seventeen characean species were identified in the Upper Eocene-Lower Oligocene sedimentary record in the studied sections. Most species have previously been described in the Ebro Basin (Colom et al. 1970; Anadón and Feist 1981; Choi 1989; Anadón et al. 1992; Feist et al. 1994; Sanjuan et al. 2012; Sanjuan and Martín-Closas 2012), and will not be described here. The main species of biostratigraphic interest were *Harrisichara lineata* Grambast 1957, intermediate morphotypes between *Harrisichara vasiformis* (Reid and Groves 1921) Grambast 1957 and *H. tuberculata* Feist-Castel 1977b, *Harrisichara tuberculata* (Lyell 1826) Grambast 1957, *Nodosochara jorbae* Choi 1989, *Lychnothamnus vectensis* (Groves 1926) nov. comb. Soulié-Märsche 1989 (=*Stephanochara vectensis* Grambast 1958), *Lychnothamnus major* (Grambast 1958) nov. comb. Soulié-Märsche 1989 (=*Rhabdochara major* Grambast 1958) and *Chara microcera* Grambast and Paul 1965.

STRATIGRAPHY OF THE UPPER EOCENE-LOWER OLIGOCENE OF THE EASTERN EBRO BASIN

Northeastern sector

Three composite sections (Serrat Rodó-El Perers, Moià-Santpedor and Maians-Rubió sections) were raised in the Upper Eocene-Lower Oligocene of the northeastern Ebro Basin, containing marls of the transitional Sant Boi Formation and the overlying red beds and limestones of the Artés Formation (Figs. 1 and 4).

Serrat Rodó-El Perers composite section



TEXT-FIGURE 4.
Geological setting of the northeastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Sanjuan and Martín-Closas 2012).

The Serrat Rodó-El Perers composite section records the whole Sant Boi Formation (Fig. 6). It is composed of about 15 metres of alternating fine-grained grey sandstone, siltstone and lutite intervals overlain by a characteristic marl interval, frequently rich in lignite and charophytes (Sanjuan et al. 2012). The Sant Boi Formation displays marked lateral changes in thickness and facies. Both the facies and the fossil content of the Sant Boi Formation suggest sedimentation in shallow brackish to freshwater ponds close to the shoreline, in a delta plain context (Sanjuan and Martín-Closas 2012). Southwards, it passes laterally to the Terminal Complex, which comprises transitional sandstones of the La Noguera Formation, anoxic marls, lacustrine marls, limestones including freshwater stromatolites, and gypsum (Travé 1992; Travé et al. 1996). According to the latter authors, the Terminal Complex passes laterally in the Igualada area, and is overlain by the Òdena Gypsum, which represents the marginal equivalent of the central basin halite and sylvinite deposits of the Cardona Salt Formation.

Moià-Santpedor composite section

The Moià-Santpedor composite section records the whole of the Artés Formation in the easternmost area (Fig. 6). The Artés Formation (Ferrer 1971; Sáez 1987) crops out in a 10 km wide and 50 km long, NE-SW orientated band along the eastern margin of the Ebro Basin. These deposits, up to 1000 m thick, consist of alluvial and fluvial red beds with interbedded lacustrine limestone units (i.e. Moià Limestone Member and La Panadella Formation). They are in part laterally equivalent to the Montserrat-Igualada fluvial fan system (Sáez 1987). The base of the Moià-Santpedor composite section (Torre Casanova subsection) is characterised by a succession of sandy channel-fill deposits, thin tabular sandstone beds with high lateral extension, and red mudstones alternating with marls attributed to fluvial fan, floodplain and lacustrine deposits (Sáez et al. 2007; Sanjuan and Martín-Closas 2012). Overlying this interval, a 100 m-thick lacustrine limestone and marl interval is represented by the Moià Limestone Member. The upper part of the section (Santpedor subsection) is characterised by fine to coarse grained channel-fill deposits alternating with red mudstones and marls related to fluvial and floodplain deposits. The Santpedor subsection contains a continuous and extensive sandstone unit that is 20 m thick (Santpedor Sandstone Unit). This characteristic interval is traceable over most of the eastern margin of the Ebro Basin and represents a key bed for lithostratigraphic correlations close to the Eocene-Oligocene boundary (Sáez 1987; Costa et al. 2011).

Previous biostratigraphic data in the Moià-Santpedor composite section include the Late Eocene mammal site of Sant Cugat de Gavadons and the Early Oligocene mammal site of Santpedor. The Sant Cugat de Gavadons faunal assemblage is included in the Theridomys golpeae biozone of the local biozonation of the Ebro Basin (Agustí et al. 1987; Anadón et al. 1987; 1992; Sáez 1987; Arbiol and Sáez 1988), which was correlated with the MP19–20 European mammal reference level. Recently, Hooker et al. (2009) suggested an alternative correlation with the MP18 mammal reference level, arguing that it does not contain any species diagnostic of the MP19–20. The Santpedor mammal site is included in the Theridomys aquatilis local mammal biozone and was correlated with the MP21 European mammal reference level (Agustí et al. 1987; Anadón et al. 1987; 1992; Sáez 1987; Arbiol and Sáez 1988). This fossil site is directly located in the upper part of the Santpedor section only a few metres above the Santpedor sandstone unit (Fig. 6). Biostratigraphic data based on charophytes were previously provided by Choi (1989), who collected a few, non-contiguous samples that yielded charophyte assemblages attributed to Priabonian ages. Feist et al. (1994) included the Sant Cugat de Gavadons and Moià assemblages in the Sphaerochara labellata local biozone (Upper Priabonian), and the assemblage from Santpedor was attributed to the Stephanochara vectensis local biozone (Upper Priabonian-Lower Rupelian).

Maians-Rubió composite section

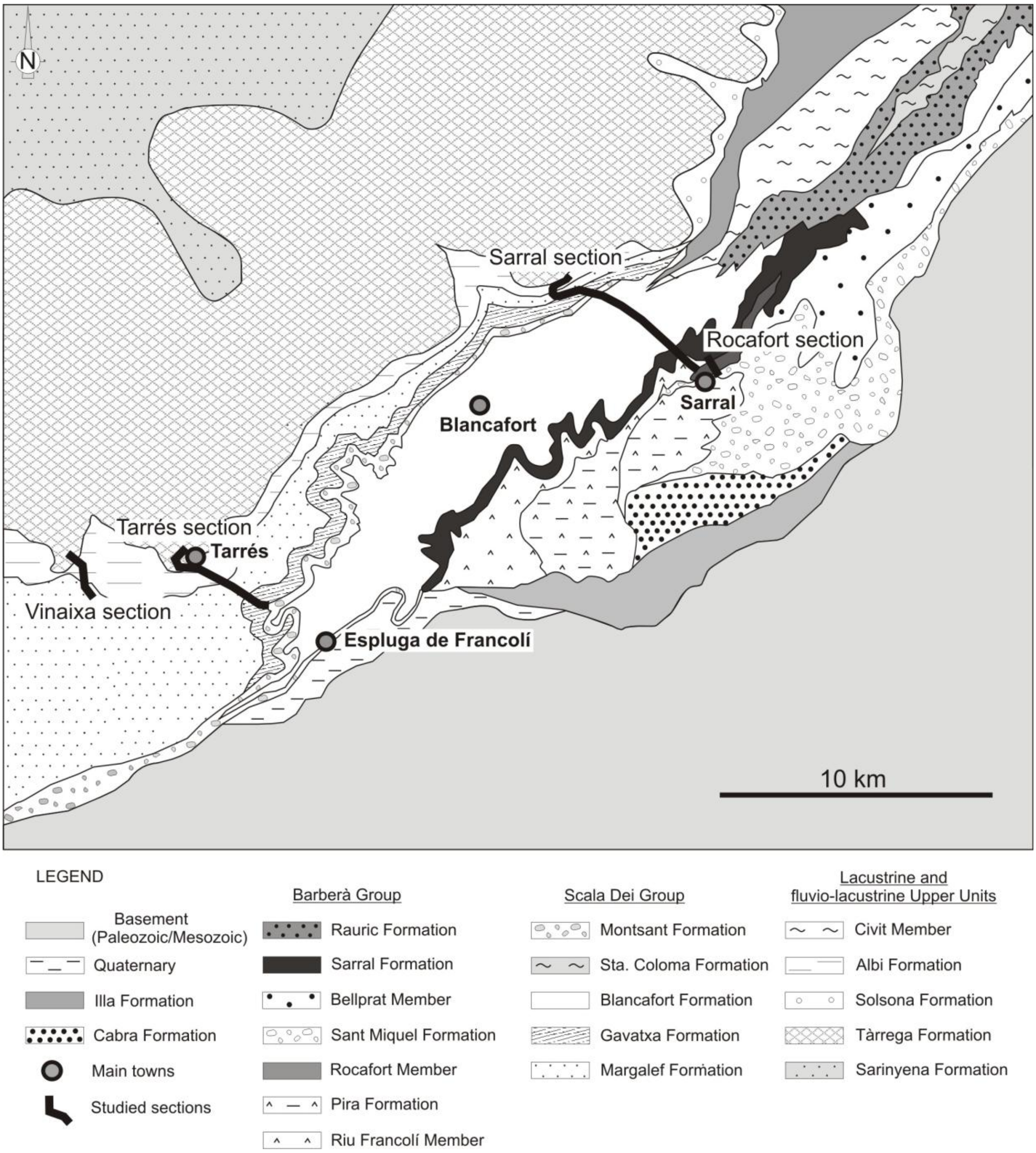
The Maians-Rubió composite section consists of 1135 m-thick red alluvial and fluvial beds with some interbedded lacustrine marlstones of the Artés Formation (Fig. 7) corresponding to the distal parts of the Montserrat-Igualada fluvial fan system (Sáez 1987). The lower part of this composite section (Maians subsection) is represented by a succession of coarse channel-fill deposits, conglomerates, sandstones and red mudstones. The upper part of the Maians-Rubió composite section is represented by the Rubió subsection. The base of the Rubió subsection is formed by 50 m-thick lacustrine marlstones. Interbedded within this interval, the Santpedor sandstone unit stands out. The overlying materials include alternating red mudstones, thin tabular sandstone beds with high lateral extension, and marls attributed to floodplain deposits (Fig. 7). The upper 200 m of the Rubió subsection are dominated by very coarse paleochannel sequences attributed to fluvial deposits (Costa et al. 2010) with few charophyte-rich samples. In contrast to the relatively good knowledge of the biostratigraphy of the Moià-Santpedor composite section, no biostratigraphic data have previously been reported from the Maians-Rubió composite section. However, independent correlation with the GPTS of the local magnetostratigraphy indicated Priabonian to Rupelian ages (Costa et al. 2010).

Southeastern sector

Rocks from this basin sector (Rocafort-Sarral and Tarrés-Vinaixa sections) crop out near the southern borders of the Catalan coastal ranges. According to Colombo (1986) these sections record the Barberà and Scala Dei Groups grading upwards to the ‘Upper Units’ (Tàrrega Formation). These groups are represented by intermediate to marginal facies of the Sant Miquel de Montclar and Montsant alluvial systems and are interfingered by lacustrine facies of the Noguera, Anoia, Segarra, Urgell and Garrigues systems in the sense of Anadón et al. (1989).

Rocafort-Sarral composite section

The lower part of this composite section crops out in the 75 m-thick Rocafort subsection (Fig. 8). The base is characterised by 25 m of conglomerates and sandstones of the Sant Miquel



TEXT-FIGURE 5.
Geological setting of the southeastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Barberà 1999).

de Montclar Formation (Colombo 1980; 1986). The middle part of the subsection is represented by 25 m of mudstones, marls and limestones of the Rocafort Member within the Pira Formation (Colombo 1986; Colldeforns et al. 1994b). Limestone and marls from the Rocafort Member contain a classical mammal and charophyte site (Anadón et al. 1987; Agustí et al. 1987; Choi 1989). Overlying deposits are characterised by sandstones, mudstones, gypsum and limestones of the Pira Formation (Colldeforns et al. 1994b).

Most of the Rocafort-Sarral composite section is composed of the 620 m-thick Sarral subsection, which can be divided into four intervals (Barberà 1999). (1) The lower 95 m-thick interval records the upper part of the Rocafort Member, the Pira and the Sarral Formations. The 70 m-thick Sarral Formation is mainly composed of well-stratified limestone and marlstones, alternating with red and grey mudstone and sandstone layers attributed to a permanent and well-developed lacustrine system (Colombo 1980; 1986). The Sarral Formation has been intensively studied because of its rich macroflora (Fernandez-Marrón 1971; 1973). (2) Overlying these materials is a 240 m-thick interval comprising red mudstones and sandstones with high lateral extension alternating with marlstones and gypsum layers of the Blancafort Formation, which have been attributed to floodplain deposits (Colombo 1986). Interbedded within this interval, the 10 m-thick competent sandstone channel-fill deposit with the strong erosive base of the Rauric Formation stands out (Colldeforns et al. 1994a; Barberà 1999). (3) The base of the third interval is composed of 10 m of red channel-fill deposits attributed to the Montsant Formation (Barberà et al. 2001). Overlying materials are red tabular sandstones and mudstones alternating with some layers of limestone of the Gavatxa Formation, which show a southern provenance (Colldeforns et al. 1994a). (4) The last interval comprises approximately 50 m of channel-fill sandstone deposits alternating with red and grey coloured mudstone that belong to the Margalef Formation (Colombo 1980, 1986). Overlying deposits are mainly composed of grey sandstones and variegated mudstones of the Albi Formation (Colldeforns et al. 1994a) attributed to distal deposits laterally equivalent to the lacustrine deposits of the Tàrrega Formation (Riba 1971).

Previous biostratigraphic data based on mammals from this composite section include the site of Rocafort de Queralt (Anadón et al. 1987; Agustí et al. 1987). According to these authors, the Rocafort de Queralt faunal assemblage belongs to the pre-Grande Coupure mammal reference level (MP18, Middle Priabonian). Later, Barberà (1999) included the Rocafort faunal assemblage in the Theridomys golpeae local Ebro basin biozone. Biostratigraphic data based on charophytes were previously provided by Choi (1989), who collected a few samples from the Rocafort de Queralt mammal site itself and from the Sarral macrofloral site, assigning them to the Priabonian. Feist et al. (1994) included the Rocafort de Queralt and Sarral charophyte assemblages in the local biozones Sphaerochara labellata (Upper Priabonian) and Stephanochara vectensis (Upper Priabonian-Lower Rupelian) respectively.

Tarrés-Vinaixa composite section

The lower part of this composite section is represented by the 290 m-thick Tarrés subsection (Fig. 9). The base of the Tarrés subsection is mainly composed of 80 m of conglomerates alternating with sandstones, red mudstones and pedogenic carbonates of the Montsant Formation (Colombo 1980; 1986). Within this interval is the mammal site of Vimbodí, reported by Colombo et al. (1995). Overlying these materials the section comprises red mudstones, sandstones and pedogenetic carbonates of the Gavatxa Formation overlain by coarse channel-fill deposits of the Margalef Formation. The upper part of the Tarrés subsection comprises 105 m of sandstone layers interbedded with red mudstones of the Albi Formation. The Tarrés subsection is topped by a characteristic 5 m-thick lacustrine interval composed of limestones and marls rich in micromammal remains (Barberà 1999). This lacustrine interval is laterally equivalent to the Tàrrega limestone formation.

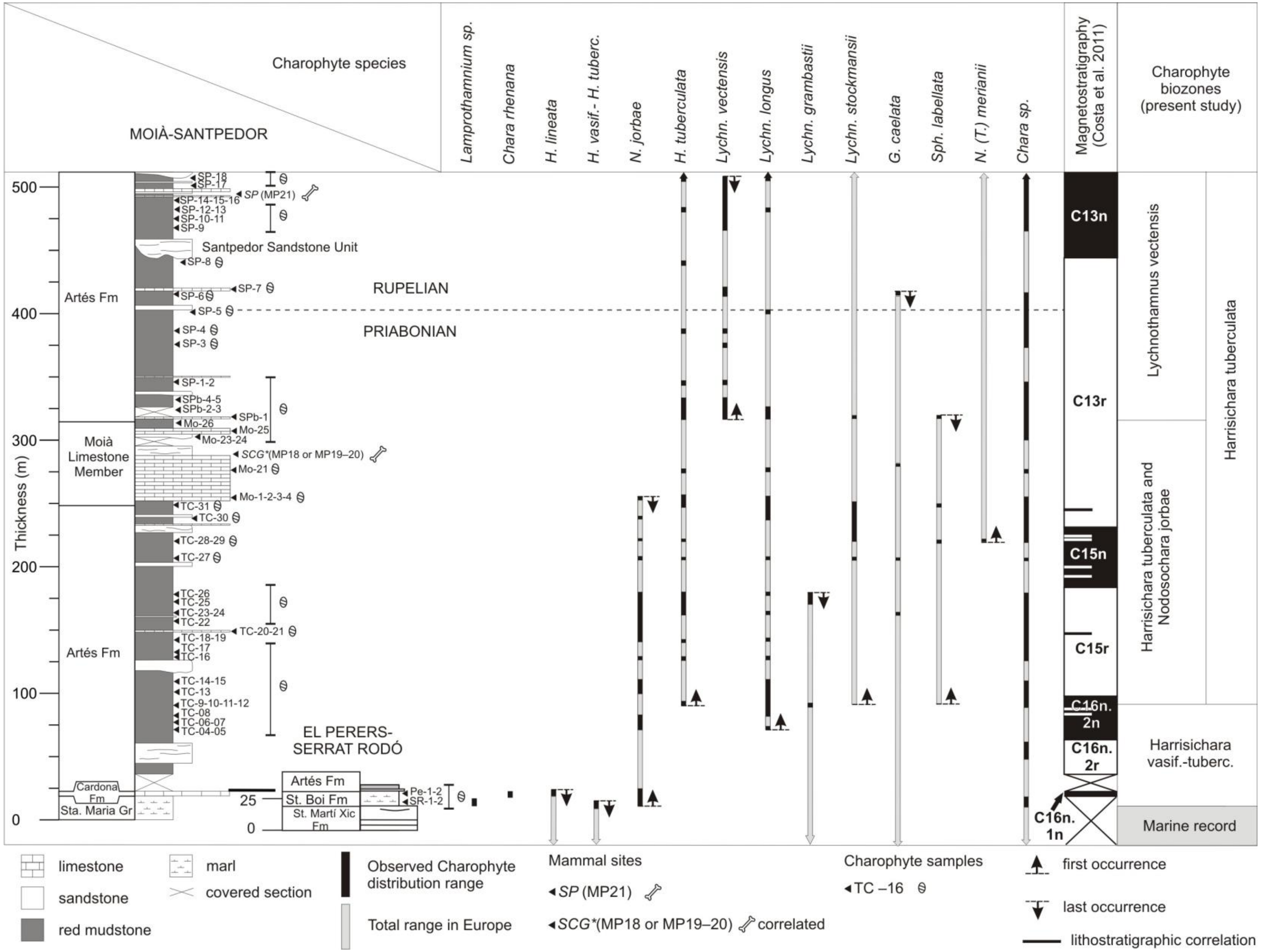
The upper part of the composite section crops out in the 170 m-thick Vinaixa section (Fig. 9). The base is characterised by a 65 m-thick succession of conglomerate and sandy channel-fill deposits with high lateral extension alternating with red mudstones and pedogenic carbonate layers of the Margalef Formation. Overlying these intervals are 35 m of sandstones attributed to the Albi Formation, which is covered by 30 m-thick-arkosic sandy channel-fill deposits of northern provenance related to the Solsona Formation (Riba 1967). The upper part of the Vinaixa subsection comprises limestones, marlstones and gypsum of the Les Marqueses lacustrine Formation, which are interbebbed with sandstone layers of the Cogull Formation (Colldeforns et al. 1994b). Within Les Marqueses/Cogull Formation the mammal site of Vinaixa was reported and dated by Barberà (1999) and Barberà et al. (2001).

To date, biostratigraphic data in the Tarrés-Vinaixa composite section have been based on the micromammals of Tarrés and Vinaixa (Barberà et al. 2001). According to these authors, the Tarrés faunal assemblage is correlated with the MP23 European mammal reference level and the Theridomys major local mammal biozone. The Vinaixa mammal assemblage is attributed to the MP24 European mammal reference level and to the Blainvillimys blainvillei local mammal biozone (Barberà 1999; Barberà et al. 2001).

CHAROPHYTE BIOSTRATIGRAPHY

Biostratigraphy of the Serrat Rodó-El Perers composite section

Sanjuan et al. (2012) reported five different charophyte species from the Sant Boi Formation. The assemblage is formed by *Harrisichara lineata*



TEXT-FIGURE 6.

Stratigraphic logs of El Perers-Serrat Rodó and Moià-Santpedor composite sections showing position of charophyte samples, distribution of charophyte species and magnetostratigraphic data. The location of fossil mammal sites (SCG, Sant Cugat de Gavadons and SP, Santpedor) and their attribution to the mammal MP reference levels are indicated.

Grambast 1957, intermediate morphotypes between *H. vasiformis* (Reid and Groves 1921) Grambast 1957 and *H. tuberculata* Feist-Castel 1977b, *Nodosochara jorbae* Choi 1989, *Gyrogona* sp., *Lamprothamnium* sp. and *Chara* sp. (Fig. 6). The charophyte assemblage was assigned to the Harrisichara vasiformis-tuberculata European biozone of Riveline et al. (1996). This zone represents the middle of the Priabonian according to correlations with zone NP19-20 in the English Basin (Riveline et al. 1996).

Biostratigraphy of the Moià-Santpedor composite section

The Moià-Santpedor composite section contains a charophyte assemblage formed by *Harrisichara tuberculata* (Lyell 1826) Grambast 1957; *Lychnothamnus vectensis* (Groves 1926) nov. comb. Soulié-Märsche 1989; *Lychnothamnus stockmansii* (Grambast 1957) nov. comb. Soulié-Märsche 1989; *Lychnothamnus grambastii* (Feist-Castel 1971) nov. comb. Soulié-Märsche 1989; *Lychnothamnus longus* Choi 1989; *Nodosochara jorbae* Choi 1989; *Gyrogona caelata* (Reid and Groves 1921) Grambast 1956; *Nitellopsis (Tectochara) merianii* (Al. Braun ex Unger 1852) nov. comb. Grambast and Soulié-Märsche 1972; *Sphaerochara labellata* Feist and Ringeade 1977; and *Chara* sp. (Fig. 6). The occurrence of *Harrisichara tuberculata* throughout most of its thickness indicates that it belongs to the homonymous Harrisichara tuberculata superzone of Riveline et al. (1996). However, in the absence of *Rhabdochara major* and associated taxa, the upper limit of this superzone is not recorded. In more detail, the occurrence of *Lychnothamnus vectensis* in samples SPb-1to SP-18 allows us to include the whole composite section in the Lychnothamnus vectensis European biozone. In addition the presence of *Sphaerochara labellata* suggests that at least the lower part of the composite section (Torre Casanova subsection) belongs to the basal part of the Lychnothamnus vectensis European biozone. In summary, the Moià-Santpedor composite section records the lower limit of the European superzone of Harrisichara tuberculata and the lower limit of the European biozone Lychnothamnus vectensis.

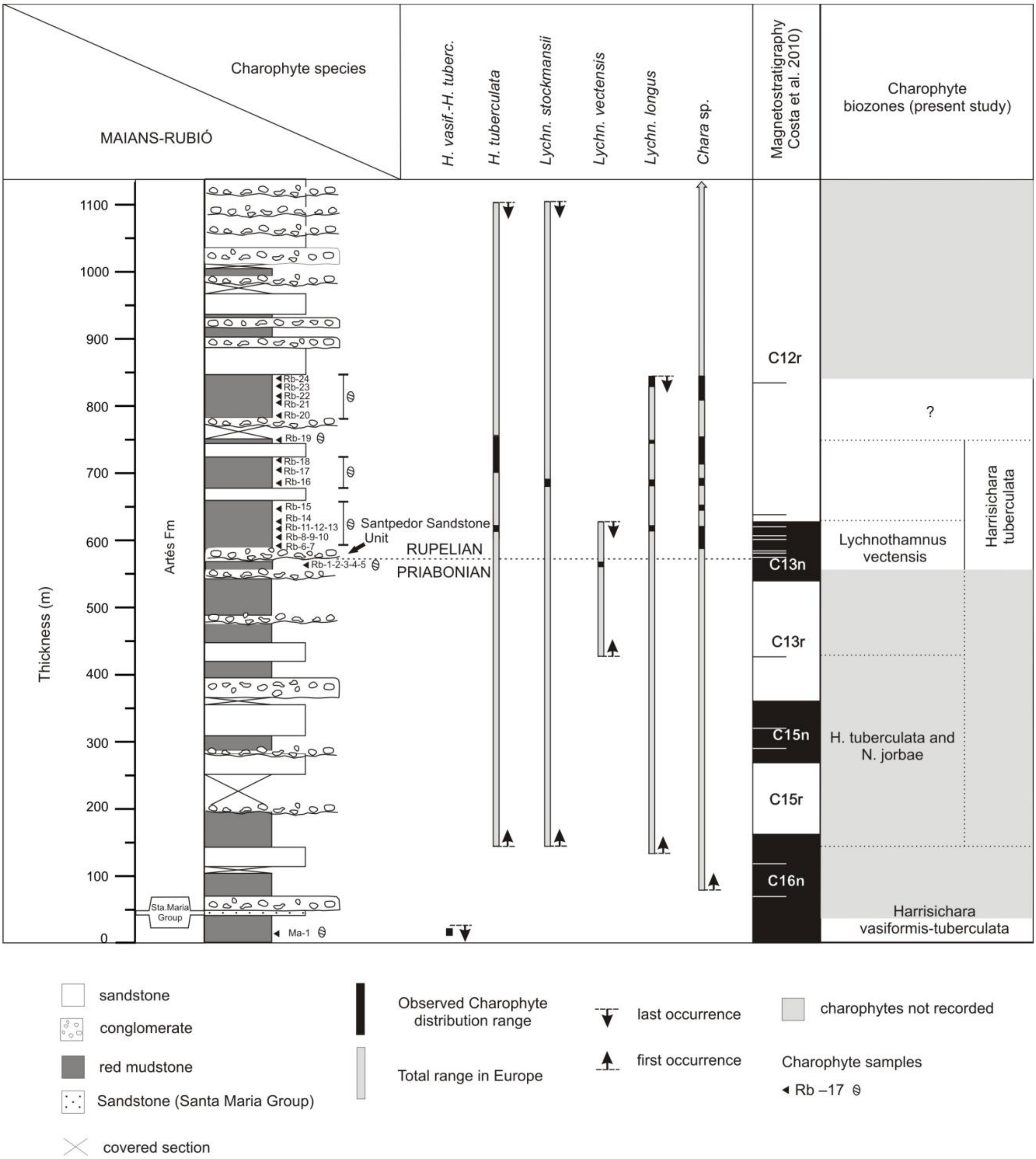
Biostratigraphy of the Maians-Rubió composite section

The dominance of coarse terrigenic deposits in the Maians-Rubió composite section hinders the occurrence of fossil remains. Only one sample located at the base of the Maians subsection (Ma-1) yielded intermediate morphotypes between *Harrisichara vasiformis* (Reid and Groves 1921) Grambast 1957 and *H. tuberculata* Feist-Castel 1977b (Fig. 7). The bed is attributed to the H. vasiformis-tuberculata zone of Riveline et al. (1996). This biozone characterises the middle of the Priabonian (Riveline et al. 1996; Riveline in Hardenbol et al. 1998).

The Rubió subsection contains five charophyte species mainly located at its base (Fig. 7). The charophyte assemblage is formed by *Harrisichara tuberculata* (Lyell 1826) Grambast 1957; *Lychnothamnus stockmansii* (Grambast 1957) nov. comb. Soulié-Märsche 1989; *Lychnothamnus vectensis* (Groves 1926) nov. comb. Soulié-Märsche 1989; *Lychnothamnus longus* Choi 1989 and *Chara* sp., which belong to the Harrisichara tuberculata superzone of Riveline et al. (1996). The presence of *Lychnothamnus vectensis* in sample Rb-3 suggests that at least the European charophyte biozone of Lychnothamnus vectensis occurs at the base of the Rubió section.

Biostratigraphy of the Rocafort-Sarral composite section

The Rocafort-Sarral composite section contains the charophyte assemblage formed by *Harrisichara tuberculata* (Lyell 1826) Grambast 1957; *Lychnothamnus vectensis* (Groves 1926) nov. comb. Soulié-Märsche 1989; *Lychnothamnus stockmansii* (Grambast 1957) nov. comb. Soulié-Märsche 1989; *Lychnothamnus major* (Grambast 1958) nov. comb. Soulié-Märsche 1989; *Sphaerochara labellata* Feist and Ringeade 1977 and *Chara* sp. (Fig. 8). The occurrence of *Harrisichara tuberculata* and associated taxa indicates that it belongs to the Harrisichara tuberculata superzone of Riveline et al. (1996). The last occurrence of *Harrisichara tuberculata* in sample SA-18 and the first appearance of *Lychnothamnus major* in sample SA-19 allowed us to place the upper limit of the Harrisichara tuberculata superzone in this section. Also, the last occurrence of *Lychnothamnus vectensis* in sample SA-7 allowed us to assign the lower part of the Rocafort-Sarral composite section to the Lychnothamnus vectensis European biozone. However, its lower limit cannot be defined since charophyte species related to the Harrisichara vasiformis-tuberculata European charophyte zone of Riveline et al. (1996) were absent. The presence of *Sphaerochara labellata* in the Rocafort subsection is significant since it suggests that the lower part of the composite section



TEXT-FIGURE 7.
Stratigraphic log of the Maians-Rubió composite section showing position of charophyte samples, distribution of charophyte species and magnetostratigraphic data.

belongs to the basal part of the Lychnothamnus vectensis European biozone. In summary, the Rocafort-Sarral composite section records the whole European superzone of Harrisichara tuberculata and an imprecise part of the European biozone Lychnothamnus vectensis.

Biostratigraphy of the Tarrés-Vinaixa composite section

The Tarrés-Vinaixa composite section contains an assemblage formed by *Lychnothamnus major* (Grambast 1958) nov. comb. Soulié-Märsche 1989; *Nitellopsis (Tectochara) merianii* (Al. Braun ex Unger 1852) nov. comb. Grambast and Soulié-Märsche 1972; *Psilochara* sp.; *Chara microcera* Grambast and Paul 1965; *Chara* sp. and *Sphaerochara* sp. (Fig. 9). The first occurrence of *Chara microcera* is located in sample TA-1 from the El Talladell mammal site, which Barberà et al. (2001) correlated with the upper part of the Tarrés subsection at ca. 220 m from the section base. The first occurrence of *Chara microcera* in the El Talladell outcrop indicates that the overlying deposits in the uppermost parts of the Tarrés and Vinaixa subsections, belong to the Chara microcera European biozone of Riveline et al. (1996). The absence of *Sphaerochara ungeri* and associated charophyte taxa suggests that the upper limit of this biozone is not recorded in this composite section. Moreover the Lychnothamnus major interval zone was recorded in this section (Fig. 9).

REVIEW OF UPPER EOCENE-LOWER OLIGOCENE CHAROPHYTE BIOZONATION

Intensive sampling of the sections studied provided abundant and well-preserved charophyte assemblages, many of them significant from the biostratigraphic point of view, allowing us to revise the charophyte zonation for the Upper Eocene-Lower Oligocene record of Europe (Fig. 10).

Harrisichara lineata European biozone

Definition.

Interval zone. The Harrisichara lineata European biozone is defined as the interval from the last occurrence of *Gyrogona tuberosa* Grambast 1958 to the first occurrence of *Harrisichara tuberculata* (Lyell 1826) Grambast 1957.

Comments

This biozone is equivalent to the Harrisichara vasiformis-tuberculata biozone as defined by Riveline et al. (1996). The change in the biozone's name is justified because the former index species was never formally defined. Moreover, the Eigenshape analysis performed by Sille et al. (2004) hardly separated the populations named *Harrisichara vasiformis* from those named *H. vasiformis-tuberculata* by Feist-Castel (1977b).

Species assemblage in the Ebro Basin

Intermediate morphotypes between *Harrisichara vasiformis* and *Harrisichara tuberculata, Harrisichara lineata, Nodosochara jorbae, Chara rhenana, Chara* sp.1, *Gyrogona* sp. and *Lamprothamnium* sp.

Biostratigraphic correlations

According to Riveline et al. (1996) this biozone is correlated with the MP18 European mammal reference level and part of the NP19-20 European calcareous nannoplankton biozone (Fig. 10).

Occurrence in the Ebro Basin

This biozone is represented in the Sant Boi Formation and its lateral equivalents from the Terminal Complex. The biozone corresponds approximately to the local undefined biozone 1 of Feist et al. (1994). The lower limit of this biozone has not been recorded in the Ebro Basin due to inappropriate facies. The species *Nodosochara jorbae* appears within this biozone.

Age

Middle part of the Priabonian (Riveline et al. 1996).

Calibration to GPTS

The upper limit of the Harrisichara lineata biozone (former H. vasiformis-tuberculata biozone) is recorded at the base of the Torre Casanova subsection and occurs within a normal magnetozone at the top of chron C16n (C16n.1n), providing an age of ~35.5 Ma.

Harrisichara tuberculata European superzone

Definition

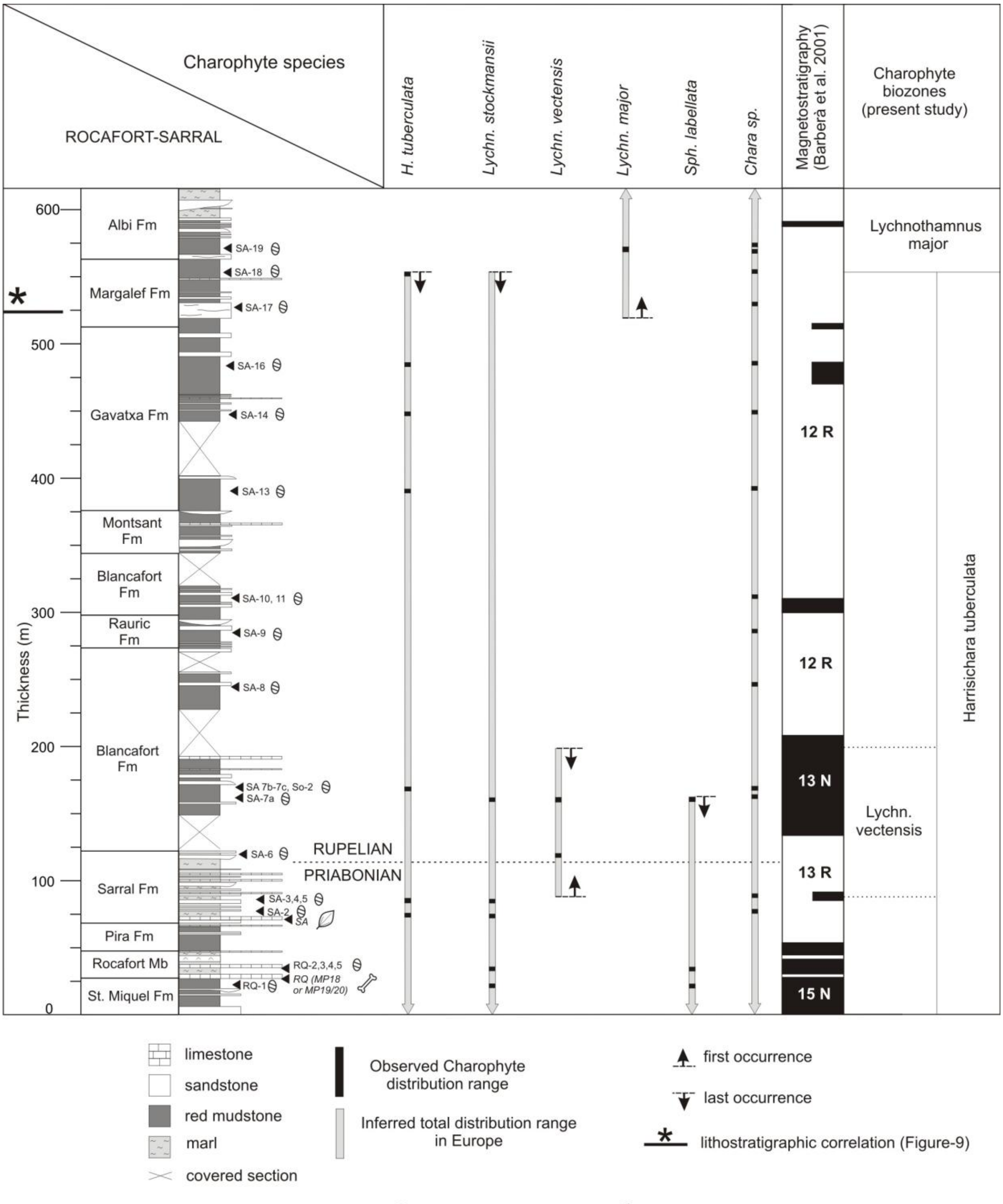
Total range zone. This biozone includes the total distribution range of *Harrisichara tuberculata* (Lyell 1826) Grambast 1957 according to Riveline et al. (1996).

Species assemblage in the Ebro Basin

Harrisichara tuberculata, Nitellopsis (T.) merianii, Sphaerochara labellata, Lychnothamnus stockmansii and *Lychnothamnus vectensis* appear in this zone. Other representative species are *Lychnothamnus longus, Lychnothamnus grambastii, Gyrogona caelata* and *Chara* sp. The species *Nodosochara jorbae* disappears at the base of this superzone.

Biostratigraphic correlations

Data from the Swiss molasse showed that this superzone is older than the MP22 European mammal reference level and NP23 European calcareous nannoplankton biozone (Riveline et al. 1996). In the Ebro Basin, the lower limit of this superzone is even older than the Sant Cugat de Gavadons mammal site (MP18 or MP19-20 European mammal reference level) and correlated with the Theridomys golpeae local mammal biozone of Barberà et al. (2001). The upper limit of this superzone is located above the Vimbodí mammal site, which according to Barberà et al.



TEXT-FIGURE 8
Stratigraphic log of the Rocafort-Sarral composite sections showing position of charophyte samples, distribution of charophyte species and magnetostratigraphic data. The location of the fossil mammal site (RQ, Rocafort de Queralt) and its attribution to the European mammal MP reference levels are indicated. The location of the macrofloral site of Sarral (SA) is indicated

(2001) is correlated with the MP23 European mammal reference level and the Theridomys major local mammal biozone (Fig. 10).

Occurrence in the Ebro Basin

The lower limit of this superzone is located at the base of the Artés Formation in the northeastern sector of the basin. The first occurrence of this species in the Artés Formation was reported by Feist et al. (1994), in their local biozone 2, Sphaerochara labellata. The upper limit of this superzone is located within marlstone layers of the Margalef Sandstone Formation in the upper part of the Rocafort-Sarral composite section (Fig. 8).

Age
Upper Priabonian-Lower Rupelian (Riveline et al. 1996).

Calibration to GPTS
The lower limit of the Harrisichara tuberculata superzone is recorded at the base of Torre Casanova subsection and occurs within a normal magnetozone at the top of chron C16n (C16n.1n), providing an age of ~35.5 Ma. The last occurrence of the species *Harrisichara tuberculata*, according to the definition of this superzone by Riveline et al. (1996), is recorded at the top of the Sarral subsection and is represented in a reversed magnetozone within chron C12 (C12r) with an age of ~31.5 Ma.

Harrisichara tuberculata and Nodosochara jorbae local assemblage zone

Definition
Assemblage zone. This new zone is defined by the co-occurrence of *Harrisichara tuberculata* and *Nodosochara jorbae* in the interval between the first occurrence of *H. tuberculata* and the first occurrence of *L. vectensis*.

Comments
To date the Priabonian records of *Nodosochara jorbae* are limited to the Ebro Basin, which results in an undefined interval corresponding to this local zone in the European charophyte biozonation, in the basal part of the Harrisichara tuberculata superzone (Fig. 10). Although *Nodosochara jorbae* and *Harrisichara tuberculata* are abundant in the Ebro Basin during this interval, they are not always associated in the same sample, since their ecological requirements are slightly different (Sanjuan and Martín-Closas 2012).

Biostratigraphic correlations
The upper limit of this assemblage zone immediately underlies the Sant Cugat de Gavadons mammal site, suggesting that this biozone could be correlated with the pre Grande-Coupure MP18 or MP19-20 European mammal reference levels and the Theridomys golpeae local mammal biozone of Barberà et al. (2001), as indicated in Fig. 10.

Species assemblage in the Ebro Basin
Nodosochara jorbae, *Harrisichara tuberculata*, *Lychnothamnus longus*, *Lychnothamnus stockmansii*, *Lychnothamnus grambastii*, *Gyrogona caelata*, *Sphaerochara labellata*, *Nitellopsis (T.) merianii* and *Chara* sp.

Occurrence in the Ebro Basin
The Harrisichara tuberculata-Nodosochara jorbae assemblage zone is reported from the base of the Artés Formation (e.g. in the Torre Casanova subsection). The presence of *Sphaerochara labellata* within this zone is significant since, according to Riveline (1986), the total range of this species is located within the new zone, i.e. between the base of the Harrisichara tuberculata superzone and the base of the Lychnothamnus vectensis emended biozone. Anadón et al. (1992) and Feist et al. (1994) defined a local Sphaerochara labellata biozone as the interval between the first occurrence of *Sphaerochara labellata* and the first occurrence of *Lychnothamnus longus*. Our results show that *Sphaerochara labellata* occurs stratigraphically much further above the first beds containing *Lychnothamnus longus*. Moreover, according to Sanjuan and Martín-Closas (2012), *Sphaerochara labellata* is extremely restricted from the paleoenvironmental point of view, since it appears to develop only in perennial lake facies. This explains why *Sphaerochara labellata* was not considered as an index species in the present biozonation. *Nodosochara jorbae* has only been recorded in the Priabonian of the Ebro Basin (Choi 1989) and possibly in the Lutetian from Algeria (Mebrouk et al. 1997; 2011). This species is extremely abundant at the base of the Artés Formation and disappears abruptly after sample TC-25 (Fig. 6). Although from the ecological viewpoint it is a species with a wide ecological tolerance, *N. jorbae* never appears associated with *L. vectensis*.

Age
Upper Priabonian.

Calibration to GPTS
The new Harrisichara tuberculata-Nodosochara jorbae assemblage zone was calibrated in the Torre Casanova subsection, where it ranges from chron C16n (C16n.1n) to chron C13 (C13r).

Lychnothamnus vectensis European biozone

Definition

Partial range zone. This biozone is redefined here as the interval from the first occurrence of *Lychnothamnus vectensis* to the first occurrence of *Lychnothamnus pinguis* (synonym: *Stephanochara pinguis*). The absence of *L. pinguis* in the Ebro Basin, and probably in many Southern European basins, results in a local, Lychnothamnus vectensis total range biozone, comprising the interval equivalent to the range of the index species. This definition modifies previous definitions from Riveline et al. (1996) and Feist et al. (1994).

Comments

Riveline (1986) and Riveline et al. (1996) defined this biozone as a partial range zone from the first occurrence of *Harrisichara tuberculata* to the last occurrence of *Lychnothamnus vectensis*, assuming that the lower limits of both the superzone and biozone were equivalent in time. Using the same name but another biozone concept, i.e. an interval zone, Feist et al. (1994) proposed that the local biozone Stephanochara vectensis (synomym of *L. vectensis*) included the interval between the first occurrence of *Lychnothamnus longus* and the first occurrence of *Nitellopsis (Tectochara) merianii*. Our results show that *L. vectensis* appeared after *L. longus*, which invalidates the latter definition. Also, the first occurrence of *Lychnothamnus vectensis* is above the first occurrence of *Harrisichara tuberculata* (Fig. 6). Hence, the Lychnothamnus vectensis biozone is redefined here and implies a detachment of the biozone base from the base of the Harrisichara tuberculata superzone. As a matter of fact, Riveline (1984; 1986) showed that the appearance of *Lychnothamnus vectensis* in the same stratigraphic horizon as *Harrisichara tuberculata* is uncertain in the Hampshire Basin. Moreover, data from the Paris Basin, used by Riveline (1986) and Riveline et al. (1996) to define the biozone, were taken from isolated outcrops (generally quarries) and were of little help in determining the vertical relationships between the two first appearances of these species and biozones.

Species assemblage in the Ebro Basin

Harrisichara tuberculata, *Lychnothamnus vectensis*, *Lychnothamnus longus*, *Lychnothamnus stockmansii*, *Gyrogona caelata* and *Chara* sp.

Biostratigraphic correlations

The lower limit of the Lychnothamnus vectensis biozone, which immediately overlies the Sant Cugat de Gavadons mammal site, is correlated with the MP18 or MP19-20 pre-Grande Coupure European mammal reference level. Due to the absence of *Lychnothamnus pinguis* in the Ebro basin, the upper limit of this European biozone could not be calibrated to the GPTS in this study. In the Ebro basin the upper limit of the local, total range biozone overlies the Santpedor mammal site, which is correlated with the MP21 post-Grande Coupure European mammal reference levels. Moreover this biozone is correlated with the Theridomys aff. aquatilis local mammal biozone of Barberà et al. (2001), as indicated in Fig. 10.

Occurrence in the Ebro Basin

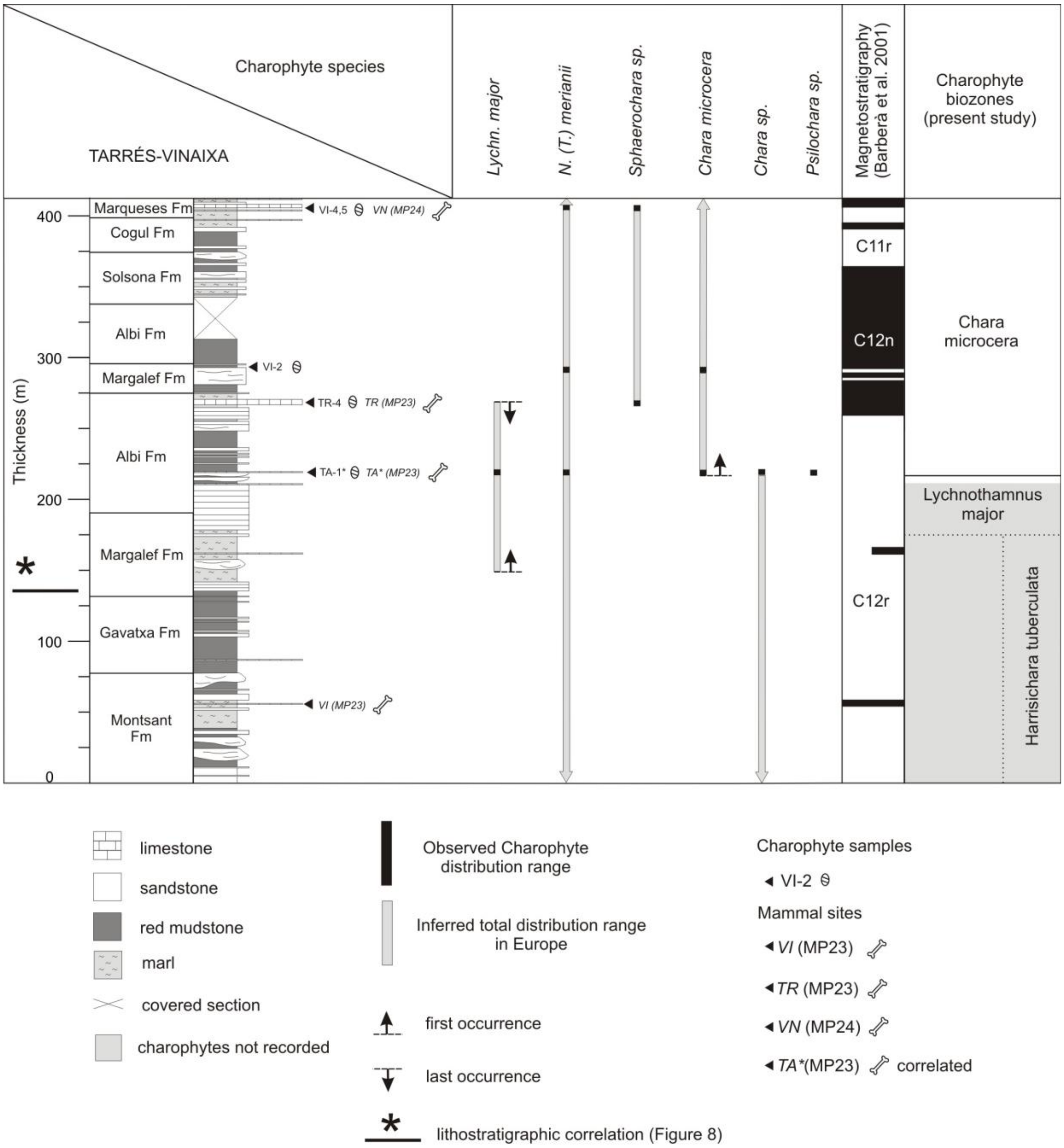
The Lychnothamnus vectensis biozone is mainly represented in the Artés Formation. In the Santpedor subsection the first occurrence is located in sample SPb-1 immediately overlying the Moià Limestone Member, whilst the last occurrence coincides with sample SP-18, which is stratigraphically located at the top of the Artés Formation in this sector of the basin. *Lychnothamnus vectensis* is also represented in one sample from the Rubió section (Rb-3), located immediately underlying the conglomerate reference bed, which, according to Costa et al. (2010), represents a continuous horizon of regional significance for regional lithostratigraphic correlation. Moreover, many samples from the Sarral subsection also yielded *Lychnothamnus vectensis*. These samples were located immediately overlying the Sarral Limestone Formation, which includes the Eocene-Oligocene boundary (Colombo 1986). Hence the total range of *L. vectensis* is considered here to be useful for characterizing the Eocene-Oligocene boundary.

Age

The range of the European biozone (partial range zone) is Uppermost Priabonian, whilst in the Ebro basin the local homonymous zone (total range zone) includes the Uppermost Priabonian-Lowermost Rupelian interval.

Calibration to GPTS

The lower limit of the new Lychnotamnus vectensis biozone is recorded at the base of the Santpedor subsection (sample Spb-1) and occurs within a reversed magnetozone attributed to chron C13 (C13r), providing an age of ~34.5 Ma. The last occurrence of *Lychnothamnus vectensis* is found at the top of the Santpedor subsection (sample SP-18) and is attributed to a normal



TEXT-FIGURE 9.
Stratigraphic log of the Tarrès-Vinaixa composite sections showing position of charophyte samples, distribution of charophyte species and magnetostratigraphic data. The location of fossil mammal sites (VI, Vimbodí. TR, Tarrés. TA, Tàrrega/El Talladell and VN, Vinaixa) and their attribution to the European mammal MP reference levels are indicated. Lateral change between rock formations are represented in Fig. 3.

magnetozone in chron C13 (C13n), which provides an age of ~33.5 Ma (Fig. 6). The lack of the species *L. pinguis* in the Ebro basin hinders the calibration its upper limit of the European L. vectensis biozone.

Undefined interval in the upper part of the Harrisichara tuberculata superzone

In the Ebro basin only three species are represented in this interval i.e. *Harrisichara tuberculata, Lychnothamnus longus* and *Chara* sp. This undefined interval is equivalent to the Lychnothamnus pinguis European biozone defined by Riveline et al. (1996). In contrast, the species *Lychnothamnus pinguis* (synonym *Stephanochara pinguis* Grambast 1958) has not been recorded to date in the Ebro Basin.

Consequently, it is not possible to characterise this interval beyond the range of the Harrisichara tuberculata superzone.

This undefined interval can be correlated with the MP22 or MP23 European mammal reference levels and the Theridomys calafensis or Theridomys major local mammal biozone of Barberà et al. (2001), indicating Lower Rupelian ages (Fig. 10). It is represented in the upper part of the Rubió subsection encompassing the uppermost part of the Artés Formation in the northeastern sector of the basin. In the southeastern sector of the basin, this undefined interval is represented in the Sarral subsection encompassing the Montsant, Gavatxa and Margalef formations.

Lychnothamnus major European biozone

Definition

Interval zone. According to Riveline et al. (1996) this zone is defined by the interval from the last occurrence of *Harrisichara tuberculata* to the first occurrence of *Chara microcera*.

Species assemblage in the Ebro Basin

Lychnothamnus major, Nitellopsis (T.) merianii and *Chara* sp.

Biostratigraphic correlations

According to Riveline et al. (1996) this biozone is correlated with the MP22 European mammal reference level and with the NP23 European calcareous nannoplankton biozone. In the Ebro Basin the duration of this biozone is extremely short since its limits are dependent of occurrence of the adjacent species i.e. *Harrisichara tuberculata* at the base and *Chara microcera* at the top. It can be correlated with the MP23 European mammal reference level and the Theridomys major local mammal biozone of Barberà et al. (2001), as indicated in Fig. 10.

Occurrence in the Ebro Basin

The lower limit of this biozone is located within marlstones of the Margalef Formation in the upper part of the Rocafort-Sarral composite section. The upper limit of this biozone is recorded in the Tàrrega Formation (El Talladell outcrop).

Age

Middle Rupelian.

Calibration to GPTS

The Lychnothamnus major interval zone in the sense of Riveline et al. (1996) is recorded from the top of Sarral subsection to the top of the Tarrés subsection and is represented in the upper part of the reversed magnetozone within chron C12 (C12r).

Chara microcera European biozone

Definition

Partial range zone. According to Riveline et al. (1996) this zone encompasses the interval from the first occurrence of *Chara microcera* to the first occurrence of *Lychnothamnus ungeri*.

Species assemblage in the Ebro Basin

Lychnothamnus major, Nitellopsis (T.) merianii, Psilochara sp., *Chara microcera, Chara* sp. and *Sphaerochara* sp.

Biostratigraphic correlations

According to Riveline et al. (1996) this biozone is correlated with the MP24 and MP25 European mammal reference levels and with the NP24 calcareous nannoplankton biozone. In the Ebro Basin the lower limit of this biozone can be correlated with the MP23 European mammal reference level and with the Theridomys major local mammal biozone of Barberà et al. (2001). These data suggest that the lower limit of the Chara microcera biozone is recorded earlier than in other European basins (Fig. 10).

Occurrence in the Ebro Basin

The lower limit of this biozone is recorded in the Tàrrega Formation (Talladell outcrop). The upper limit of this biozone is not recorded since the species *Lychnothamnus ungeri* and associated taxa were not found in the studied sections.

Age

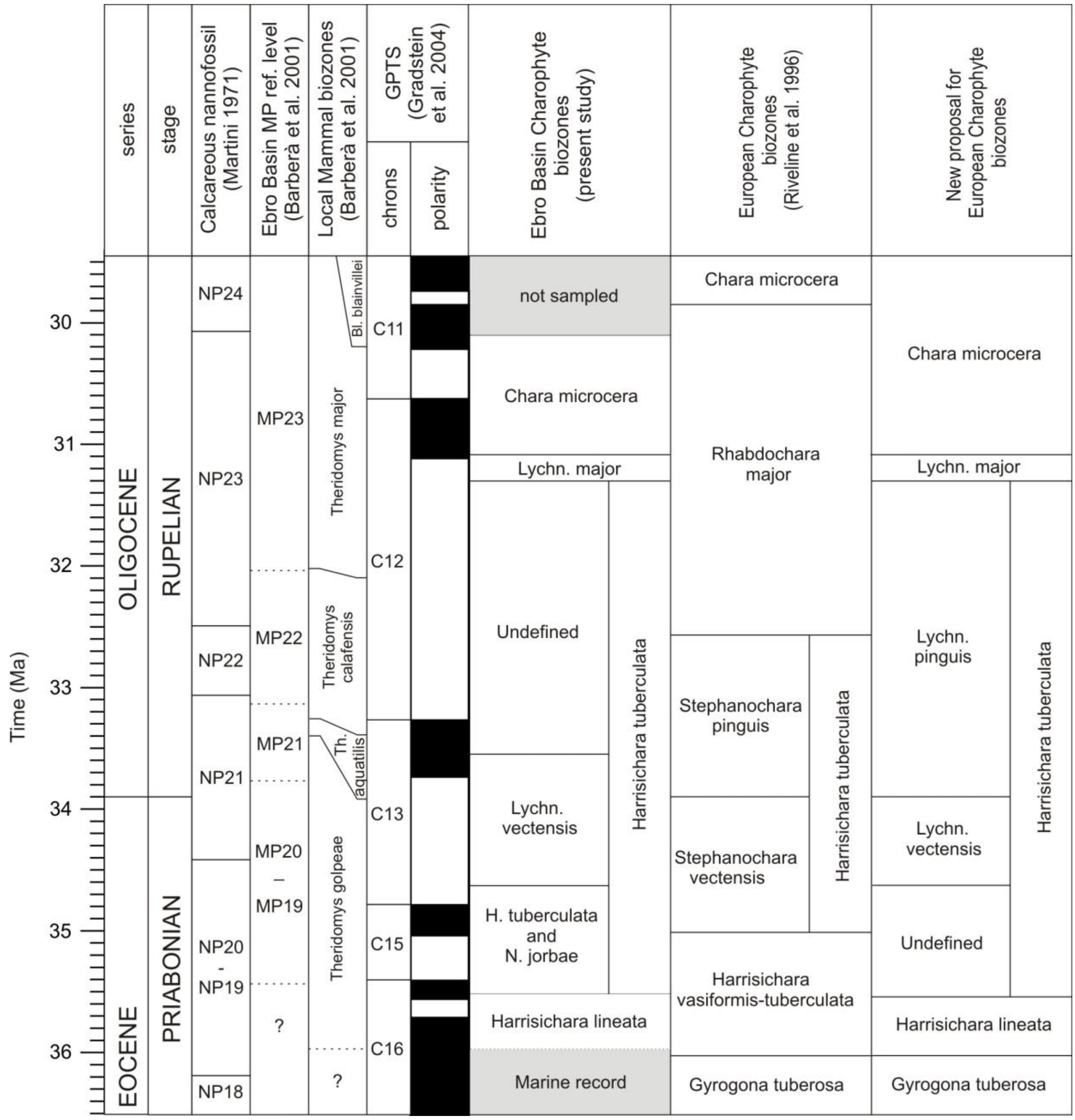
Middle Rupelian.

Calibration to GPTS

The lower limit of the Chara microcera biozone in the sense of Riveline et al. (1996) is recorded in the El Talladell outcrop (Tàrrega Formation) which is laterally equivalent to the upper part of the Tarrés subsection and occurs within the uppermost part of the reversed magnetozone of chron C12 (C12r), providing an age of ~31 Ma.

DISCUSSION

The integration of new charophyte biostratigraphic results with litho- and magnetostratigraphic records provides accurate ages for



TEXT-FIGURE 10.
Calibration of the new Late Eocene-Early Oligocene charophyte biozonation to the GPTS (Gradstein et al. 2004). Previous calibrations of calcareous nannofossil biozones (Martini, 1971), the Local Mammal biozonation of Barberà et al (2001) and the Ebro Basin MP reference levels according to Barberà et al. (2001) and Costa et al. (2011) are also shown. SCG, Sant Cugat de Gavadons. RO, Rocafort de Queralt. SP, Santpedor. CA l., Lower Calaf. CA u., Upper Calaf. PQ, Porquerisses., VI, Vimbodí. FO, Forés. TA, Tàrrega. CI, Ciutadilla. TR, Tarrés. VN, Vinaixa. European charophyte biozonations follow Riveline et al. (1996) and Riveline in Hardenbol et al. (1998).

the Upper Eocene-Lower Oligocene charophyte biozones in the Ebro Basin. These results allow comparison with other European basins that record the Eocene-Oligocene boundary in non-marine facies. Because of its continuous record through the Upper Eocene-Lower Oligocene the Hampshire Basin (Isle of Wight, UK) is of great significance for comparison of magneto- and biostratigraphic data. Previous biostratigraphic studies from the Eocene-Oligocene boundary in the Hampshire Basin based on charophytes were carried out by Reid and Groves (1921), Groves (1926), Grambast (1958; 1972), Castel (1968), Feist-Castel (1971; 1977b) and Riveline (1984; 1986), and were used to define a biozonation for the Solent Group of the Isle of Wight. More recently, biostratigraphic studies based on vertebrates coupled with new magnetostratigraphic data led to the calibration of the mammal zones and the dating of the faunal turnover “Grande Coupure” in the Solent Group (Hooker 1992; Hooker et al. 2004; 2007; 2009; Gale et al. 2006). However the position of the base of the Oligocene in the Solent Group remains a matter of debate, especially regarding the correlation of the Bembridge Normal Polarity Zone with the GPTS (see Hooker et al. 2009, and discussion by Costa et al. 2011).

Calibration of charophyte biozone boundaries on the basis of the magnetostratigraphic attribution of the Solent Group by Hooker et al. (2009) showed that the lower limit of the interval bearing *Harrisichara tuberculata* is represented within chron C13r. According to Riveline (1986) the occurrence of *Lychnothamnus vectensis* is limited to one sample located within the Insect Limestone Unit at the base of the Bembridge Marls Member, which belongs to C13r.1n (Hooker et al. 2009). In contrast, calibration of the Solent Group as proposed by Costa et al. (2011) shows that the first occurrence of *Harrisichara tuberculata* would fall within chron C15r, whilst the first occurrence of *Lychnothamnus vectensis* would correspond to chron C15n. Thus, the lower limits of the Harrisichara tuberculata superzone and Lychnothamnus vectensis biozone are located in different chrons, C13 or C15, depending on which charophyte calibration is followed, i.e. Hooker et al. (2009) or Costa et al. (2011) respectively. Regardless of which calibration is followed the first occurrence of the species *Harrisichara tuberculata* is older in the Ebro Basin (chron C16). This difference is probably reflecting more appropriate palaeoecological conditions for the distribution of this species in the Ebro Basin than a diachronic origin. As a matter of fact the beds that underlie the first occurrence of *H. tuberculata* in the Hampshire Basin would correspond to brackish environments, where this species would not thrive according to present knowledge (Sanjuan et al., 2012; Sanjuan and Martín-Closas, 2012). The possibility of a diachronic origin of *H. tuberculata* within Western Europe would be quite unusual for characeans. Palaeobiogeographic diachronisms have been recorded only between the extremes of large continental scales, such as whole Eurasia (Soulié-Märsche, et. al. 2002; Bhatia, 2006).

The lower limit of the Lychnothamnus vectensis biozone, is represented within chron C13r in both basins if we take into account the calibration of Hooker et al (2009), or would be older in the Hampshire Basin if the calibration of Costa et al. (2011) is followed. These differences are clearly due to different calibration methods and interpretations rather than to palaeobiological facts.

CONCLUSIONS

The European charophyte biozonation has been revised herein on the basis of the Upper Eocene-Lower Oligocene data from the Ebro Basin. Six charophyte zones have been identified and characterised, i.e. Harrisichara lineata (a new name for former H. vasiformis-tuberculata biozone); Harrisichara tuberculata, Harrisichara tuberculata-Nodosochara jorbae, Lychnothamnus vectensis, Lychnothamnus major and Chara microcera. The Harrisichara lineata biozone is represented in the transitional Sant Boi Formation (El Perers-Serrat Rodó section), which encompasses the middle of the Priabonian within chron C16n. The Harrisichara tuberculata European superzone is well represented in the continental Artés Formation in the northeastern sector of the basin and in the Barberà Group) in the southeastern part of the basin. This superzone includes the Upper Priabonian and Lower Rupelian i.e. the Eocene-Oligocene boundary ranging between chron C16n.1n and the upper part of chron C12r. New occurrences allowed us to enlarge the upper part of this superzone. The new Harrisichara tuberculata-Nodosochara jorbae assemblage zone, recorded at the base of the Artés Formation, was calibrated with chrons C16 (C16n.1n) to C13 (C13r). The new European Lychnothamnus vectensis biozone is redefined as an interval zone ranging from the first occurrence of *Lychnothamnus vectensis* to the first occurrence of *Lychnothamnus pinguis*. In the Ebro basin this biozone is redefined as the total range zone of *Lychnothamnus vectensis* and encompasses chrons C13r and C13n, including the upper part of the Priabonian and the basal part of the Rupelian. *L. vectensis* is well represented in the Santpedor, Rubió and Sarral subsections and represents a useful species with which to characterise the Eocene-Oligocene boundary. An undefined interval, equivalent to the Lychnothamnus pinguis European zone, is represented in most of the Rubió and Sarral subsections and coincides with the reversed magnetozone within chron C12r. The Lychnothamnus major European zone is extremely short. Being an interval zone, its range depends on the variation of the range of adjacent zones, and is now included in the upper part of the reversed magnetozone C12 (C12r). Finally, the lower limit of the Chara microcera biozone is recorded in the Tàrrega Limestone Formation and occurs within the lowermost part of the normal magnetozone attributed to chron C12 (C12n), providing an age of ~31 Ma.

Comparisons with homologous data from the classical Upper Eocene-Lower Oligocene Solent Group in the Hampshire Basin (Isle of Wight, UK) show that the chronological attribution of the lower limit of the Harrisichara tuberculata superzone differs in the two basins. This suggests that *Harrisichara tuberculata*, which represents a common charophyte species recorded from numerous sites from the Upper Priabonian to the Lower Rupelian, appeared first in the Ebro Basin due to favourable palaeoecological conditions.

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