Taxonomy and palaeobiogeography of charophytes from the Upper Eocene-Lower Oligocene of the Eastern Ebro Basin (Catalonia, NE Spain)

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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* (Grambast, 1957), fourteen species distributed throughout Europe (*Harrisichara vasiformis* form *vasiformis-tuberculata* Feist-Castel, 1977, *Harrisichara lineata* Grambast, 1957, *Harrisichara tuberculata* (Lyell, 1826), *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun ex Unger, 1852), *Lychnothamnus vectensis* (Groves, 1926), *L. grambastii* (Feist-Castel, 1971), *L. major* (Grambast & Paul, 1965), *Gyrogona caelata* (Reid & Groves, 1921), *Psilochara* aff. *acuta* Grambast & Paul, 1965, *Chara* aff. *antennata* Grambast, 1958, *C. rhenana* Schwarz & Griessemer, 1994, *C. microcera* Grambast & Paul, 1965, *Sphaerochara labellata* Feist & Ringeade, 1977, *Lamprothamnium* sp.) and three species restricted to the Ebro Basin during the interval considered (*Nodosochara jorbae* Choi, 1989, *Lychnothamnus longus* Choi, 1989 and *Chara artesica* n. sp., a new species defined by very small gyrogonites and showing a reduced number of convolutions. A biogeographic analysis of the assemblage studied suggests that during Late Eocene and Early Oligocene, Europe represented a bioprovince characterised by the regular and abundant occurrence of species belonging to the lineages of *Harrisichara vasiformis-tuberculata* and *Lychnothamnus stockmansii-major*, along with *Nitellopsis* (*Tectochara*) *merianii* and *Chara microcera* in all Euro-

pean basins. Charophyte distribution in this bioprovince displays a north to south polarity with a reduction in the 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 should be of use only at a regional scale.

KEYWORDS
Charophyta, Biogéography, Eocene, Oligocene, Ebro foreland Basin, Paris Basin, Hampshire Basin, Rhine Basin, new species.

RÉSUMÉ

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

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* (Grambast, 1957), quatorze espèces réparties dans toute l'Europe (*Harrisichara vasiformis* form *vasiformis-tuberculata* Feist-Castel, 1977, *Harrisichara lineata* Grambast, 1957, *Harrisichara tuberculata* (Lyell, 1826), *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun ex Unger, 1852), *Lychnothamnus vectensis* (Groves, 1926), *L. grambastii* (Feist-Castel, 1971), *L. major* (Grambast & Paul, 1965), *Gyrogona caelata* (Reid & Groves, 1921), *Psilochara* aff. *acuta* Grambast & Paul, 1965, *Chara* aff. *antennata* Grambast, 1958, *C. rhenana* Schwarz & Griessemer, 1994, *C. microcera* Grambast & Paul, 1965, *Sphaerochara labellata* Feist & Ringeade, 1977, *Lamprothamnium* sp.) et trois espèces limitées au bassin de l'Ebre (*Nodosochara jorbae* Choi, 1989, *Lychnothamnus longus* Choi, 1989 et *Chara artesica* n. sp.). La nouvelle espèce est caracterisée par 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 matériel terrigènique dans les milieux d'eau douce pendant l'Éocène supérieur-Oligocène, sont opposées aux systèmes carbonatés et avec connexion marine des bassins de Paris, du Hampshire et du Rhin. Ceci implique que la richesse spécifique 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 seraient d'utilisation uniquement régionale.

MOTS CLÉS
Charophyta, biogéographie, Éocène, Oligocène, bassin d'avant-pays de l'Ebre, bassin de Paris, bassin du Hampshire, bassin du Rhin, espèce nouvelle.

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 amount of knowledge obtained on the 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

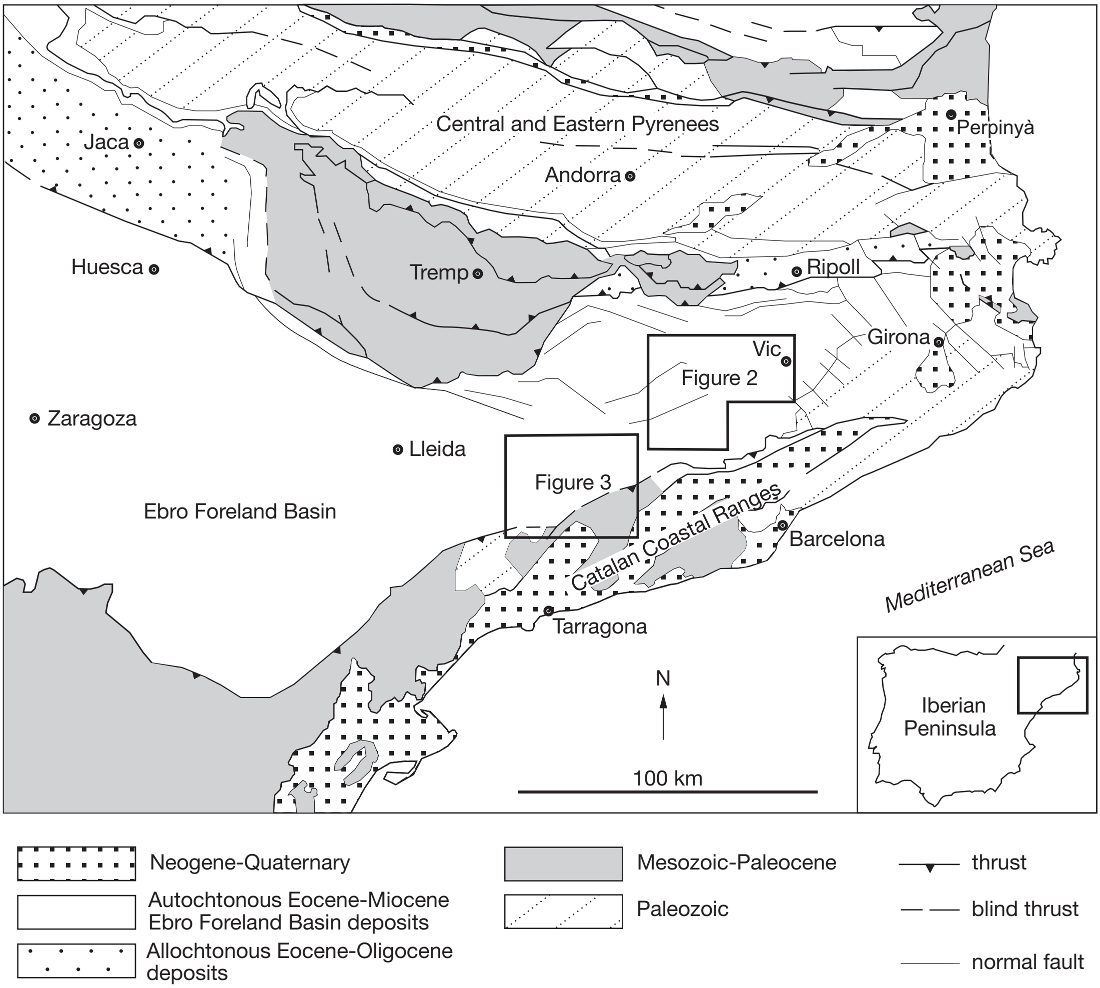

FIG. 1. — Geological sketch of the eastern part of the Ebro Foreland Basin showing location of studied area (modified from Vergés *et al.* 1998).

few authors who have addressed the biogeography of the Paleogene-Neogene 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 Paleogene-Neogene 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 studies on European charophytes have focused on Neogene species, such as *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun *ex* Unger, 1852) Grambast & Soulié-Märsche, 1972 and *Lychnothamnus barbatus* (Meyen, 1827) von Leonhardi, 1863 (Soulié-Märsche *et al.* 1997, 2002; Bathia 1999) or on Jurassic and Cretaceous charophytes (Schudack *et al.* 1998; Martín-Closas & Wang 2008).

The aim of this paper is to describe the charophyte species recorded in the Upper Eocene-Lower Oligocene of the Ebro Basin, and to document their distribution in order to understand the reasons

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

		Coordinates				
		Base of the section		Top of the section		
Locality	**Sections**	**Latitude**	**Longitude**	**Latitude**	**Longitude**	**Formations**
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
	El Perers	42°03'14.7"N	02°10'E	42°03'27"N	02°10'17"E	Sant Boi
	Serrat Rodó	42°02'49.7"N	02°10'18.4"E	42°02'47.3"N	02°10'10.1"E	Sant Boi
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
	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
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
Moià	Torre Casanova	41°49'11.2"N	02°08'22.4"E	41°49'24.3"N	02°08'7.5"E	Artés
	Moià road	41°49'10.4"N	02°05'52.9"E	41°49'11.4"N	02°05'49.8"E	Artés (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
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
Santpedor	Santpedor	41°48'2.8"N	01°51'5"E	41°47'54"N	01°49'46.8"E	Artés
Maians	Maians	41°37'55"N	01°42'22.3"E	41°39'12.8"N	01°40'57.2"E	Artés
Rubió	Rubió	41°38'18.8"N	01°36'3.2"E	41°13'23.5"N	01°36'12.3"E	Artés
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 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
Solivella	Solivella outcrop	41°26'9.2"N	01°11'34.3"E	41°26'9.2"N	01°11'34.3"E	Blancafort
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
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
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

for their biogeographic range. The implications of charophyte biogeography in other fields such as palaeoecology and biostratigraphy, are also considered.

MATERIAL AND METHODS

The charophyte taxa described in this study were obtained from 13 Upper Eocene-Lower Oligocene stratigraphic sections from the eastern margin of the Ebro Basin, which show good exposure of transitional and continental, mainly fluvio-lacustrine, facies (Table 1). For more detailed information about the chronostratigraphy and lithostratigraphy of these sections please refer to Figures 2 and 3 of Sanjuan *et al.* (2014). In the north-eastern sector of the basin, the studied sections are located near the villages of Sant Boi de Lluçanès, Sobremunt,

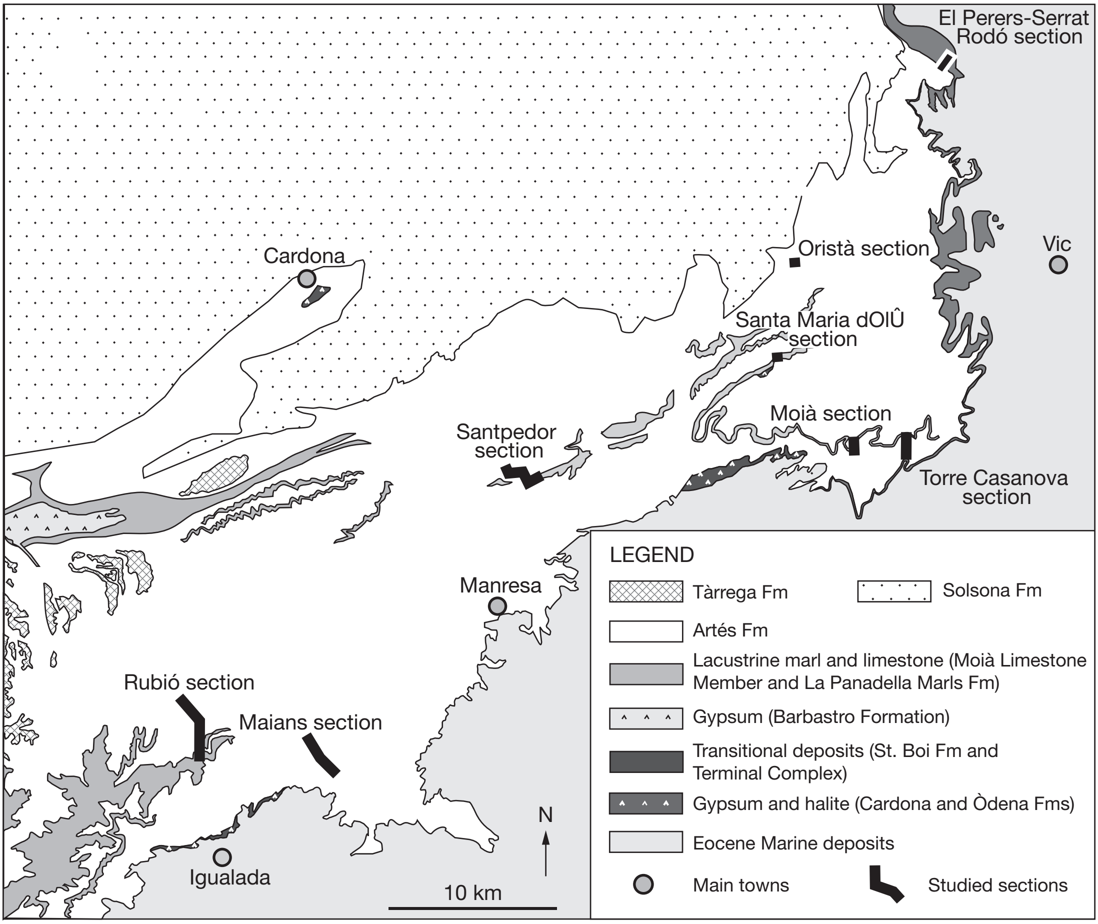

Fig. 2. — Geological setting of the north-eastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Sanjuan & Martín-Closas 2012).

Sant Bartomeu del Grau, Oristà, Santa Maria d'Oló, Moià, Santpedor, Maians and Rubió (Figs 1, 2; 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 were disaggregated in water, oxygen peroxide and Na_2CO_3 solution and later sieved using sieves with mesh apertures of 1 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 electron 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

MGSCB Museu Geològic del Seminari Conciliar de Barcelona.

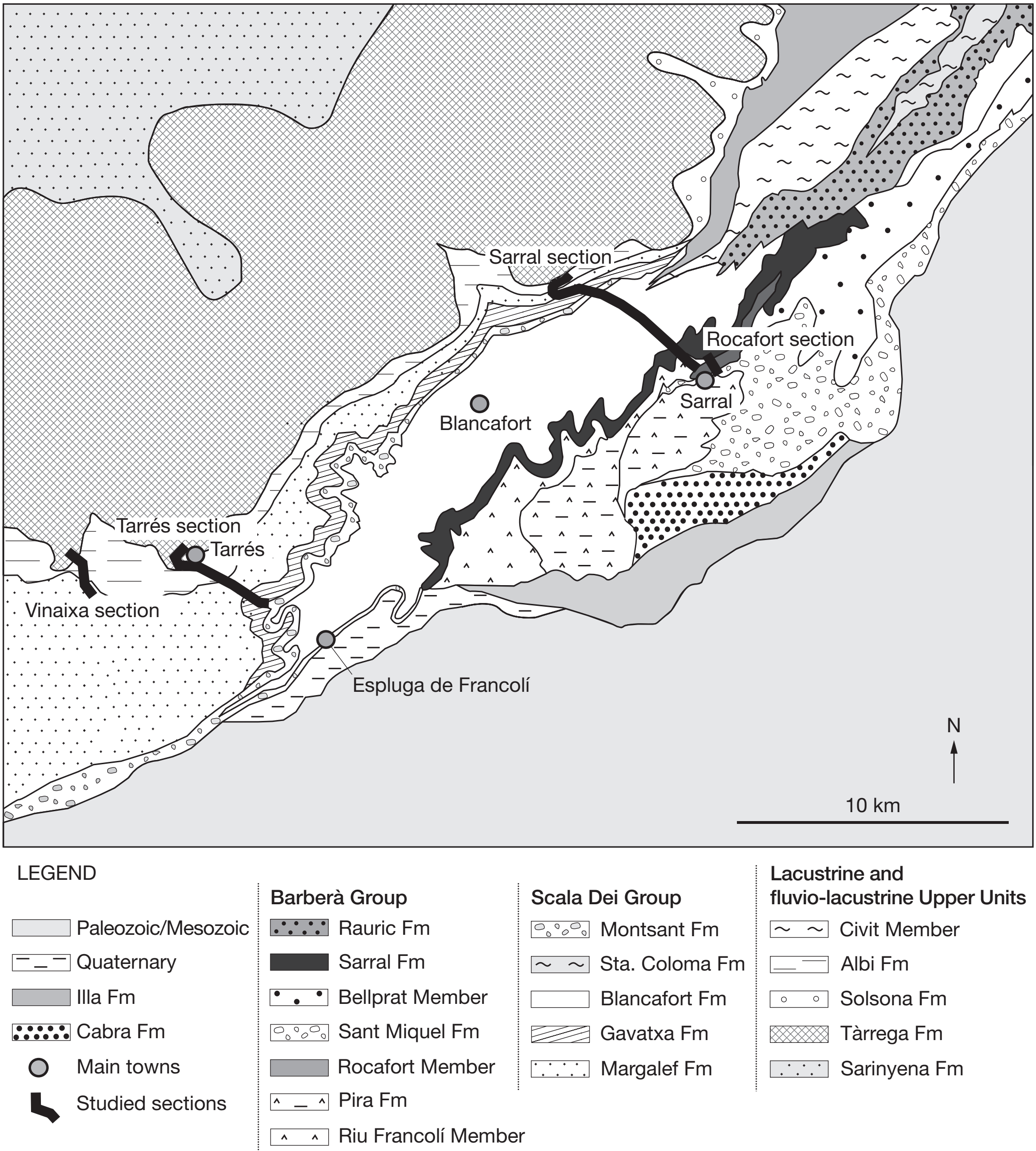

Fig. 3. — Geological setting of the south-eastern part of the Ebro Foreland Basin showing the location of the sampled sections (modified from Barberà 1999).

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 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 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 Complex (Travé *et al.* 1996) and evaporites of the La Noguera, and Òdena Formations (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 the aforementioned Artés Formation, 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)
Horn af Rantzien & Grambast, 1962

Sphaerochara labellata Feist & Ringeade, 1977
(Fig. 4A-D)

Sphaerochara labellata Feist & Ringeade, 1977: 348, pl. 6, figs 1-6.

Distribution. — *Sphaerochara labellata* has been found in Upper Priabonian beds of the Aquitaine Basin (Feist & 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 2-4). The absence of this species in the northern European basins suggests that *Sphaerochara labellata* grew exclusively in southern Europe.

Description

Gyrogonites small, 329-466 µm high (mean 406 µm) and 310-443 µm wide (mean 387 µm), 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.

Subfamily Charoideae
Al. Braun *in* Migula, 1897
Genus *Chara* Vaillant, 1719

Chara aff. ***antennata*** Grambast, 1958
(Fig. 4E-H)

Chara antennata Grambast, 1958: 188, fig. 79.

Distribution. — *Chara* aff. *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, gyrogonites of *Chara* aff. *antennata* do not show any

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. Abbreviations: ·, 1-25; •, 26-100; ●, >100.

Lithostratigraphy	**Locality**	**Samples**	***Harrisichara vasiformis* form *vasiformis-tuberculata* Feist-Castel, 1977**	***Lamprothamnium* sp.**	***Gyrogona* sp.**	***Nodosochara jorbae* Choi, 1989**	***Harrisichara lineata* Grambast, 1957**	***Chara rhenana* Schwarz & Greissemer, 1994**	***Harrisichara tuberculata* (Lyell, 1826)**	***Lychnothamnus longus* Choi, 1989**	***Lychnothamnus stockmansii* (Grambast, 1957)**	***Lychnothamnus grambastii* (Feist-Castel, 1971)**	***Nitellopsis (T.) merianii* (Al.Braun ex Unger, 1852)**	***Gyrogona caelata* (Reid & Groves, 1921)**	***Sphaerochara labellata* Feist & Ringeade, 1977**	***Chara artesica* n. sp.**	***Chara* aff. *antennata* Grambast, 1958**
Artés Fm	Moià (Moià Limestone Member)	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				●										·	

Table 2. — Continuation.

Lithostratigraphy	Locality	Samples	*Harrisichara vasiformis* form *vasiformis-tuberculata* Feist-Castel, 1977	*Lamprothamnium* sp.	*Gyrogona* sp.	*Nodosochara jorbae* Choi, 1989	*Harrisichara lineata* Grambast, 1957	*Chara rhenana* Schwarz & Greissemer, 1994	*Harrisichara tuberculata* (Lyell, 1826)	*Lychnothamnus longus* Choi, 1989	*Lychnothamnus stockmansii* (Grambast, 1957)	*Lychnothamnus grambastii* (Feist-Castel, 1971)	*Nitellopsis (T.) merianii* (Al.Braun ex Unger, 1852)	*Gyrogona caelata* (Reid & Groves, 1921)	*Sphaerochara labellata* Feist & Ringeade, 1977	*Chara artesica* n. sp.	*Chara* aff. *antennata* Grambast, 1958
Sant Boi Fm	Perers	PE-2					•										
		PE-1					●	●									
	Serrat Rodó	SR-2	●			•										·	
		SR-1	·														
	C. Car.	CC-1	●	●												●	
	Sobr.	SBR-2	•		·	●										·	
		SBR-1	●													·	
St. Martí Xic	Portell.	PO-2															•

evidence of fragmentation or erosion, suggesting that they were buried *in situ* or after short transport from the original locality. The sample was collected within a plastic yellowish marl horizon with abundant marine fauna, i.e. foraminifers and ostracods. Taphonomic and sedimentologic evidence, together with the abundance of shallow marine fauna, suggests that *Chara* aff. *antennata* grew in brackish water lagoons close to the shoreline.

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

The 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.

Chara artesica n. sp.
(Fig. 4I-L)

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 (Fig. 4I-L).

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

Type locality. — Torre Casanova (Moià, Catalonia, NE Spain; 41°49'13, 6"N, 02°08'13, 2"E).

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

Age. — Middle Priabonian to Lower Rupelian according to its association with *H. vasiformis* form *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 of spiral 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 the gyrogonites, a low number of convolutions and the concavity of the spiral cells allows the distinction of the new species from similar species. *Chara artesica* n. sp. shows strong similarities with *Chara* sp. 2 from the Ebro Basin described by Choi (1989), especially as regards their biometrical characters. However, *Chara artesica* n. sp. shows concave spiral cells and a flat to slightly convex apex, whereas *Chara* sp. 2 shows a convex shape in the apex and the spiral cells, probably related to the calcification degree.

Chara rhenana Schwarz & Griessemer, 1994
(Fig. 4M-P)

Chara rhenana Schwarz & Griessemer, 1994: 148, pl. 1, figs 1-4.

Distribution. — Previously, this species had only been reported in the Upper Eocene/Lower Oligocene from the Rhine Graben in Germany (Schwarz & 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).

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 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 & 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.

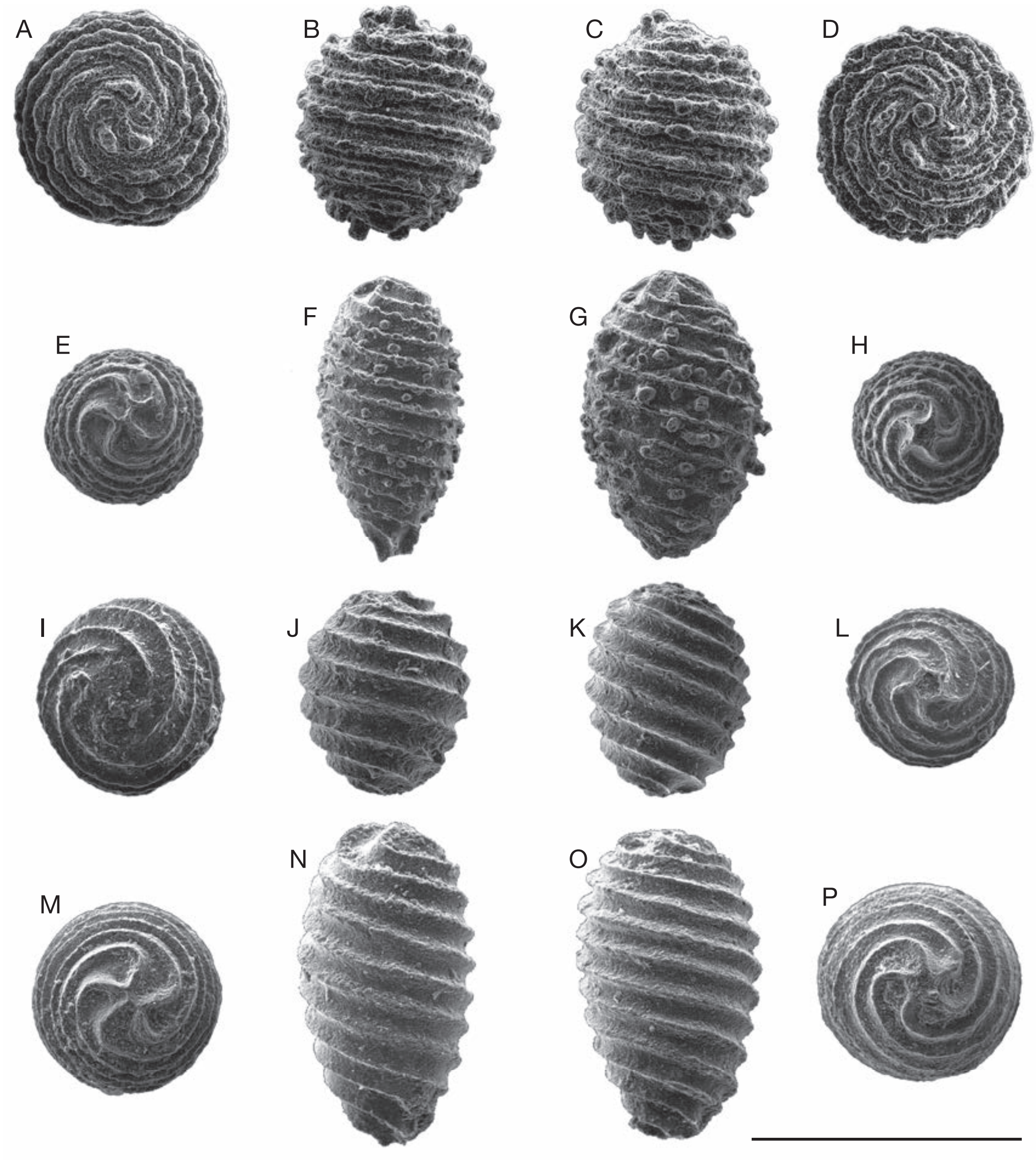

Fig. 4. — Charophytes from the Sant Boi and Artés Fms, Ebro Basin: **A**-**D**, *Sphaerochara labellata* Feist & Ringeade, 1977, Torre Casanova section; **A**, apical view, no. 80063 MGSCB, sample TC-28; **B**, lateral view, no. 80064 MGSCB, sample TC-28; **C**, lateral view, no. 80065 MGSCB, sample TC-28; **D**, basal view, no. 80066 MGSCB, sample TC-28; **E**-**H**, *Chara* aff. *antennata* Grambast, 1958, 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* n. sp., Torre Casanova section; **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* Schwarz & Griessemer, 1994, 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. 80074 MGSCB, sample PE-1. Scale bar: 500 μm.

Chara microcera Grambast & Paul, 1965
(Fig. 6A-D)

Chara microcera Grambast & Paul, 1965: 244, pl. 2, figs 10-14.

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 (Grambast & Paul 1965; Riveline 1986), the Aquitaine Basin (Feist-Castel 1977a; Feist & 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). This species also occurs in many Oligocene localities from the Rhine Graben in Germany (Schwarz 1997). In Spain, this species has been reported in Lower Oligocene beds of the Ebro Basin (Feist *et al.* 1994), and in the Tajo Basin (Juliá 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).

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.

Genus *Psilochara* Grambast, 1959

Psilochara aff. ***acuta*** Grambast & Paul, 1965
(Fig. 6E-H)

Psilochara acuta Grambast & Paul, 1965: 243, pl. 2, fig. 5-9.

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 from the Oligocene of the Rhine Graben (Germany). *Psilochara acuta* was later reported from Upper Eocene (Priabonian) beds in the Transylvanian Basin, Romania by Baciu & Hartenberger (2001). The occurrence of this species in the Ebro Basin (Sarral locality) represents its southernmost record (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* aff. *acuta* starts in the middle part of the Priabonian.

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 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).

Genus *Lamprothamnium* Groves, 1916

Lamprothamnium sp.
(Fig. 6I-L)

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

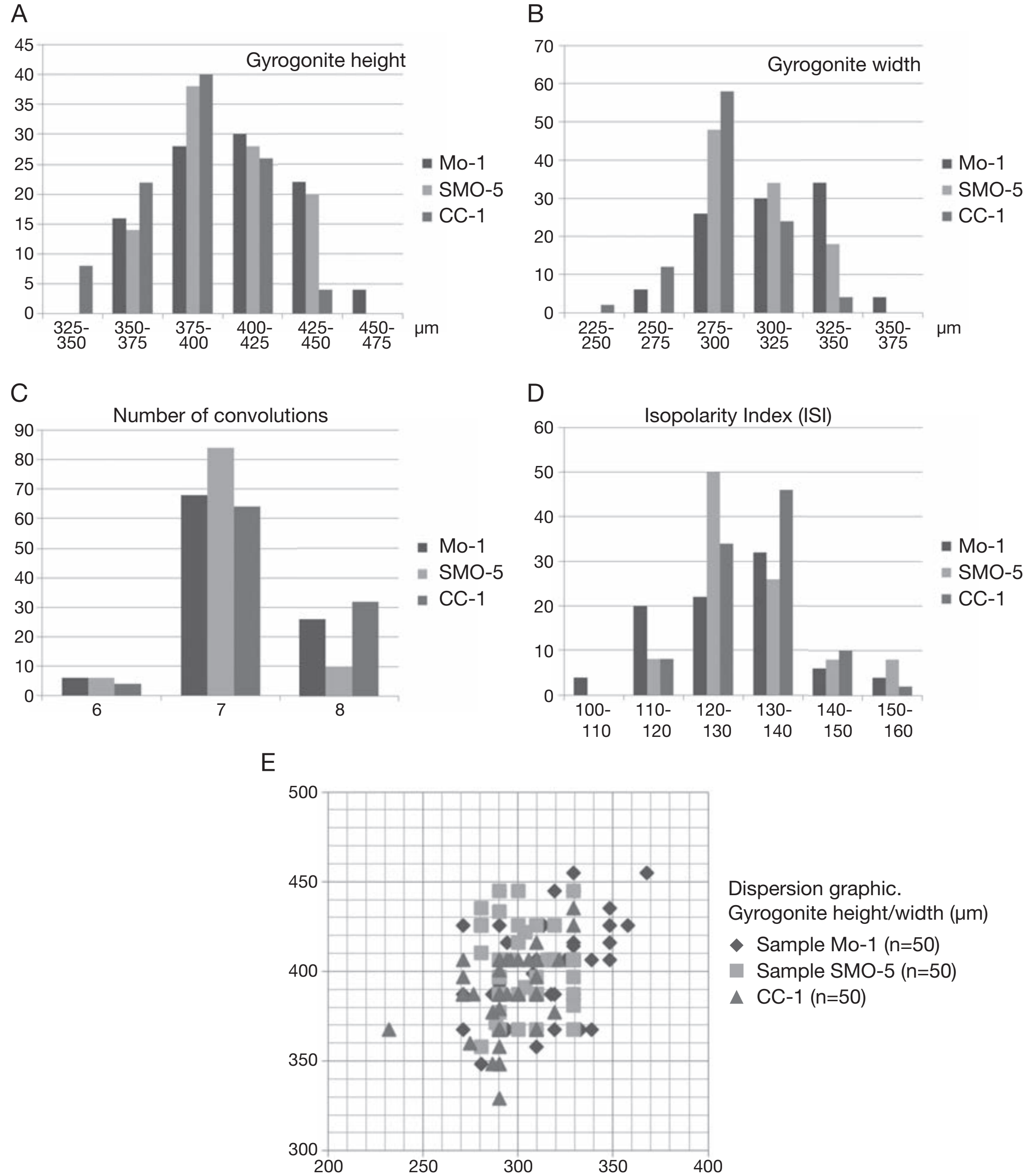

FIG. 5. — Frequency distribution of the length, width, number of convolutions, length/width ratio (ISI) and dispersion graphic of three populations (50 gyrogonites per population) of *Chara artesica* n. sp. Populations from samples CC-1 (El Perers-Serrat Rodó section) SMO-5 (Santa Maria d'Oló section)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

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.

TABLE 3. — Charophyte species and gyrogonite abundances of samples studied from the eastern margin of the Ebro Basin (sections of Santpedor, Maians & Rubió). Vertical position of samples does not represent their relative stratigraphic position. Abbreviations: ·, 1-25; •, 26-100; ●, >100.

Lithostratigraphy	Locality	Samples	*Harrisichara vasiformis* form *vasiformis-tuberculata* Feist-Castel, 1977	*Harrisichara tuberculata* (Lyell, 1826)	*Lychnothamnus longus* Choi, 1989	*Lychnothamnus stockmansii* (Grambast, 1957)	*Lychnothamnus vectensis* (Groves, 1926)	*Sphaerochara* sp.	*Sphaerochara labellata* Feist & Ringeade, 1977	*Gyrogona caelata* (Reid & Groves, 1921)	*Chara artesica* n. sp.
Artés Fm	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		•	·		·	·			●
		SPB-1		•	•	•	•		·		•
Sta. Maria Gr.	Maians	MA-1	·								

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.

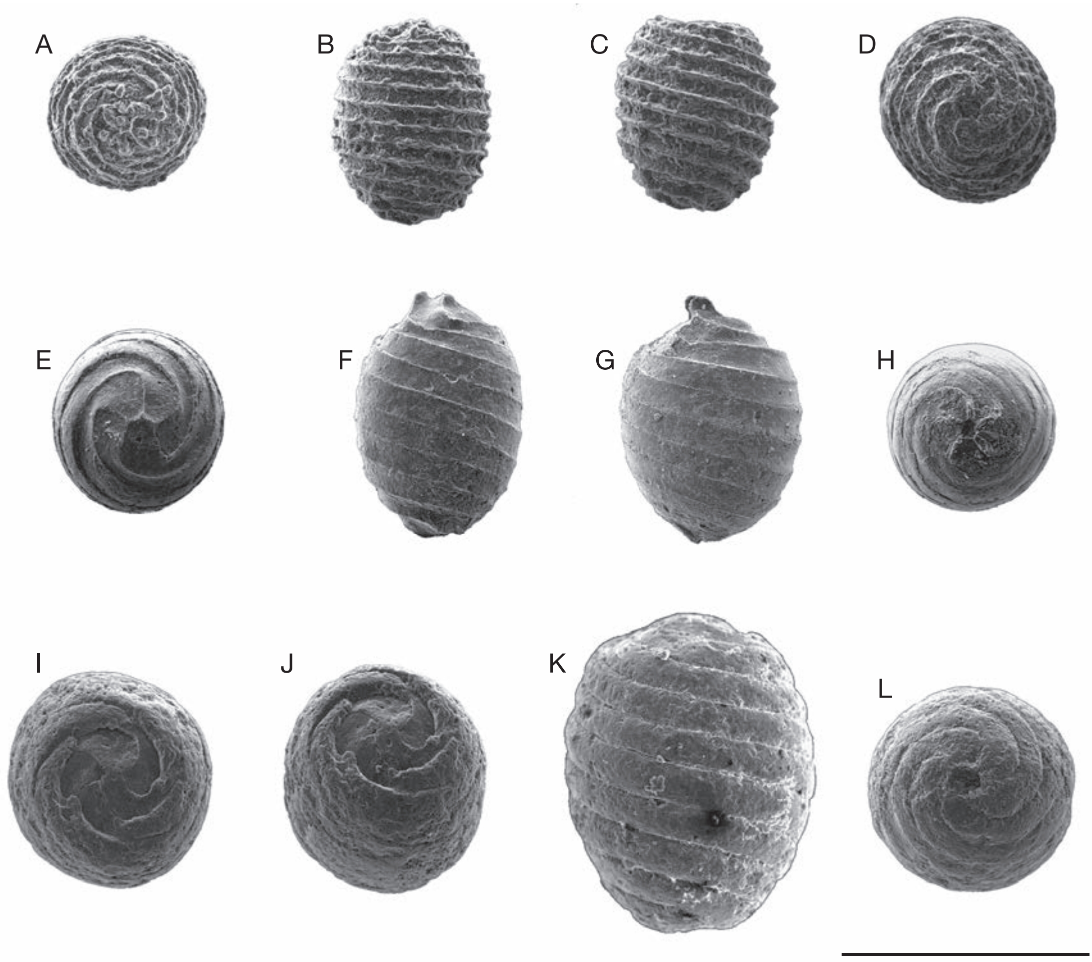

Fig. 6. — Charophytes from Sant Boi, Artés and lateral south-western Formations, Ebro Basin: **A**-**D**, *Chara microcera* Grambast & Paul, 1965, El Talladell outcrop; **A**, apical view, no. 80075 MGSCB, sample BO-2; **B**, lateral view, no. 80076 MGSCB, sample BO-2; **C**, lateral view, no. 80077 MGSCB, sample BO-2; **D**, basal view, no. 80078 MGSCB, sample BO-2; **E**-**H**, *Psilochara* aff. *acuta* Grambast & Paul, 1965, 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 (Cal Carreter locality); **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. Scale bar: 500 µm.

Gyrogona caelata (Reid & Groves, 1921) Grambast, 1956 (Fig. 7A-C)

Chara caelata Reid & Groves, 1921: 184, pl. 4, fig. 4-6.

Gyrogona caelata – Grambast 1956: 280.

Gyrogona caelata forme *fasciata* Grambast & Grambast-Fessard, 1981: 21, fig. 11f.

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 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

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. Abbreviations: ·, 1-25; •, 26-100; ●, >100.

Lithostratigraphy	Locality	Samples	*Harrisichara tuberculata* (Lyell, 1826)	*Lychnothamnus stockmansii* (Grambast, 1957)	*Lychnothamnus vectensis* (Groves, 1926)	*Lychnothamnus major* (Grambast & Paul, 1965)	*Sphaerochara* sp.	*Sphaerochara labellata* Feist & Ringeade, 1977	*Nitellopsis (T.) merianii* (Al.Braun ex Unger, 1852)	*Chara microcera* Grambast & Paul, 1965	*Psilochara* aff. *acuta* Grambast & Paul, 1965
Marqueses Fm	Vinaixa	VI-5							•		
Albi Fm	Vinaixa	VI-2								·	
Tàrrega Fm	El Talladell	FA-2				·					
		BO-2								·	
		BO-1				•			·		
	Tarrés	TA-4					·				
Albi Fm	Saral	SA-19				●					•
Margalef Fm	Saral	SA-18	·								·
		SA-17									•
Gavatxa Fm	Saral	SA-16	·								·
		SA-14	·								•
		SA-13	·								·
Blancafort Fm	Saral	SA-10									•
		SA-9									•
		SA-8									•
		SA-7b									●
		SA-7a		·	·			·			●
		SA-6			·						
Sarral Fm	Saral	SA-5	·	•							•
		SA-3	·								•
		SA-2	●	•							●
	Solivella	SO-2	·								·
Rocafort Member	Rocafort de Queralt	RQ-6									·
		RQ-5		·				·			
		RQ-3		●				•			•
		RQ-2		·				·			
		RQ-1		·				·			

Basin (Anadón & Feist 1981; Choi 1989), with two more records added now, in Torre Casanova (Moià) and Santpedor (Table 2). *Gyrogona caelata* has also been reported by Iva (1987) in Middle Eocene beds from the north-western part of the Transylvanian Basin (Romania). This species has also been found in the central part of the Sahara, Algeria (Mebrouk *et al.* 1997).

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.

Genus *Nodosochara* Mädler, 1955

Nodosochara jorbae Choi, 1989
(Fig. 7D-F)

Nodosochara jorbae Choi, 1989: 33-36, pl. 6, fig. 1-9, pl. 15, fig. 3.

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). *Nodosochara* aff. *jorbae* has also been reported by Mebrouk *et al.* (1997) in the Middle Eocene from the north-eastern Sahara (Algeria).

Description

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

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

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

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

Lychnothamnus longus Choi, 1989: 7-10, pl. 5, figs 1-12.

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 & 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, 3).

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.

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

Rhabdochara stockmansi Grambast, 1957: 355, pl. 8, figs 10-14.

Lychnothamnus stockmansi – Soulié-Märsche 1989: 160.

Distribution. — *Lychnothamnus stockmansii* has been recorded from numerous localities ranging in age from the Upper Eocene (Middle Priabonian) to the Lower Oligocene (Lower Rupelian) (Table 5). In France, this species occurs in the Paris (Riveline 1986), Aquitaine (Feist & Ringeade 1977) and Provence (Grambast 1957; Montenat 1968; Touraine 1971; Feist-Castel 1977a) 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 in Belgium. *Lychnothamnus 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 in the Upper Priabonian-Lower Rupelian from the Torre Casanova (Moià), Moià, Santpedor, Rubió, Rocafort de Queralt and Sarral localities (Table 2-4). Baciu & Feist (1999) reported it from the Lowermost Oligocene of the Transylvanian Basin (Romania). The species is well-represented in many Chinese localities (Table 5). 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 an Eurasiatic species widely distributed from Western Europe to China.

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 from 102-150 (mean 120). The apical zone shows a remarkable constant width of the spiral 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 spiral cells at the apex, 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.

Lychnothamnus grambastii (Feist-Castel, 1971) Soulié-Märsche, 1989 (Fig. 8A-C)

Stephanochara grambastii Feist-Castel, 1971: 166-168, pl. 11, figs. 1-5.

Lychnothamnus grambastii – Soulié-Märsche 1989: 160.

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, reaching now the Upper Priabonian, since it occurs in association with *Harrisichara tuberculata*.

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.

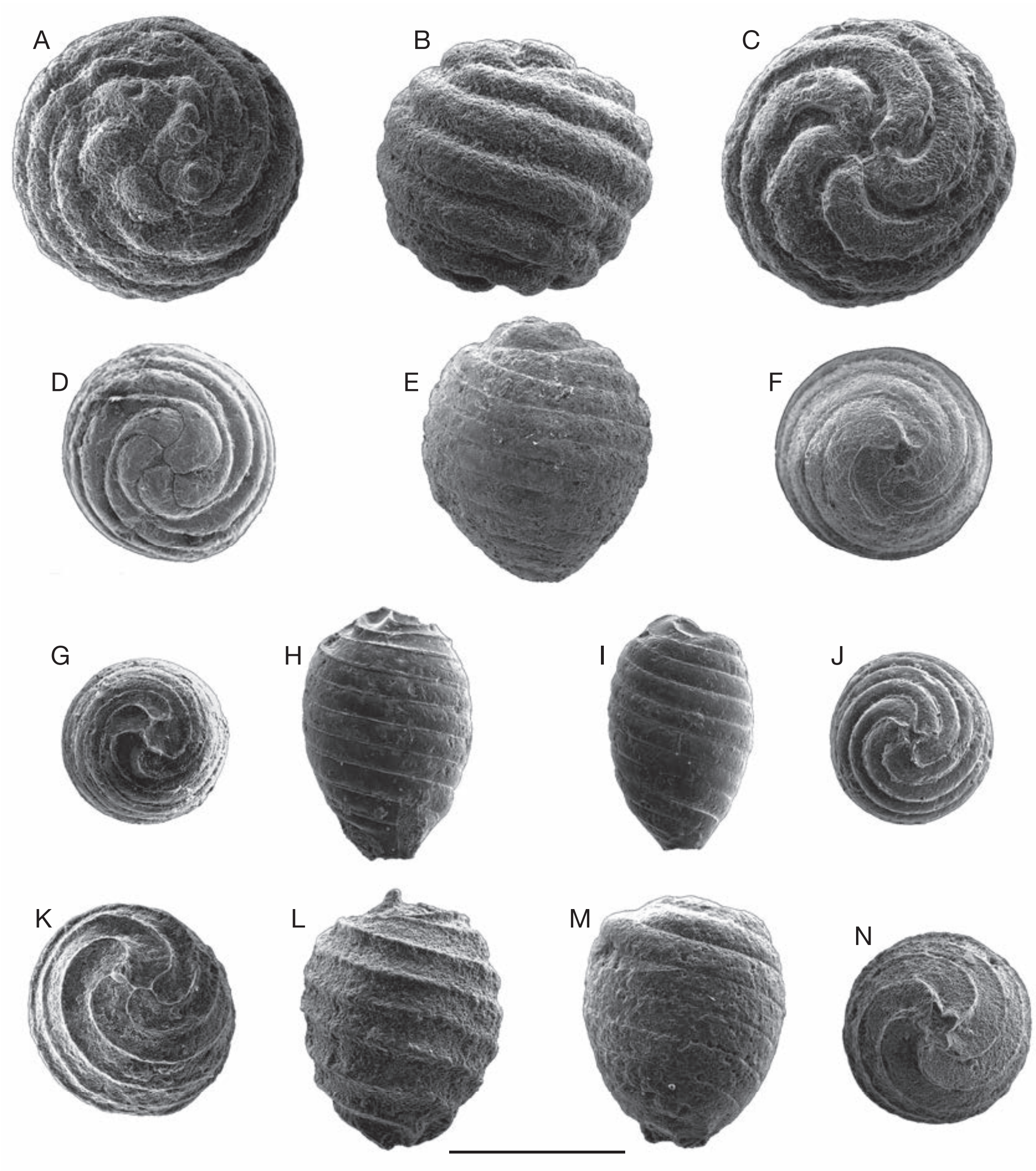

FIG. 7. — Charophytes from Sant Boi and Artés Formations and lateral south-western Formation, Ebro Basin: **A**-**C**, *Gyrogona caelata* (Reid & Groves, 1921), Torre Casanova section; **A**, apical view, no. 80086 MGSCB, sample TC-25; **B**, lateral view, no. 80087 MGSCB, sample TC-25; **C**, basal view, no. 80088 MGSCB, sample TC-25. **D**-**F**, *Nodosochara jorbae* Choi, 1989, El Perers-Serrat Rodó section (Sobremunt locality) and Oristà section; **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* Choi, 1989, Rubió section; **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* (Grambast, 1957), Torre Casanova section; **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. Scale bar: 500 µm.

Remarks

Lychnothamnus grambastii shows similar dimensions and morphology to *Lychnothamnus edwardsii* (Grambast, 1958) Soulié-Märsche, 1989 with both species having 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 edwardsii* shows a rounded base with a superficial basal funnel. Also, *Lychnothamnus grambastii* does not show a periapical constriction which occurs in *Lychnothamnus edwardsii*.

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

Chara vectensis Groves, 1926: 172, pl. 2, figs 2-8.

Stephanochara vectensis – Grambast 1958: 158.

Lychnothamnus vectensis – Soulié-Märsche 1989: 160.

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, 4).

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 biometric parameters (mean values of 715 µm high, 595 µm wide, isopolarity index of 115 and 8 convolutions) similar to the type material. 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.

Lychnothamnus major (Grambast & Paul, 1965) Soulié-Märsche, 1989 (Fig. 8H-K)

Rhabdochara major Grambast & Paul, 1965: 241, 242, pl. 2, figs 1-4.

Lychnothamnus major – Soulié-Märsche 1989: 159.

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 & 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 and Baciu and Feist (1999) from north-western Romania. 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).

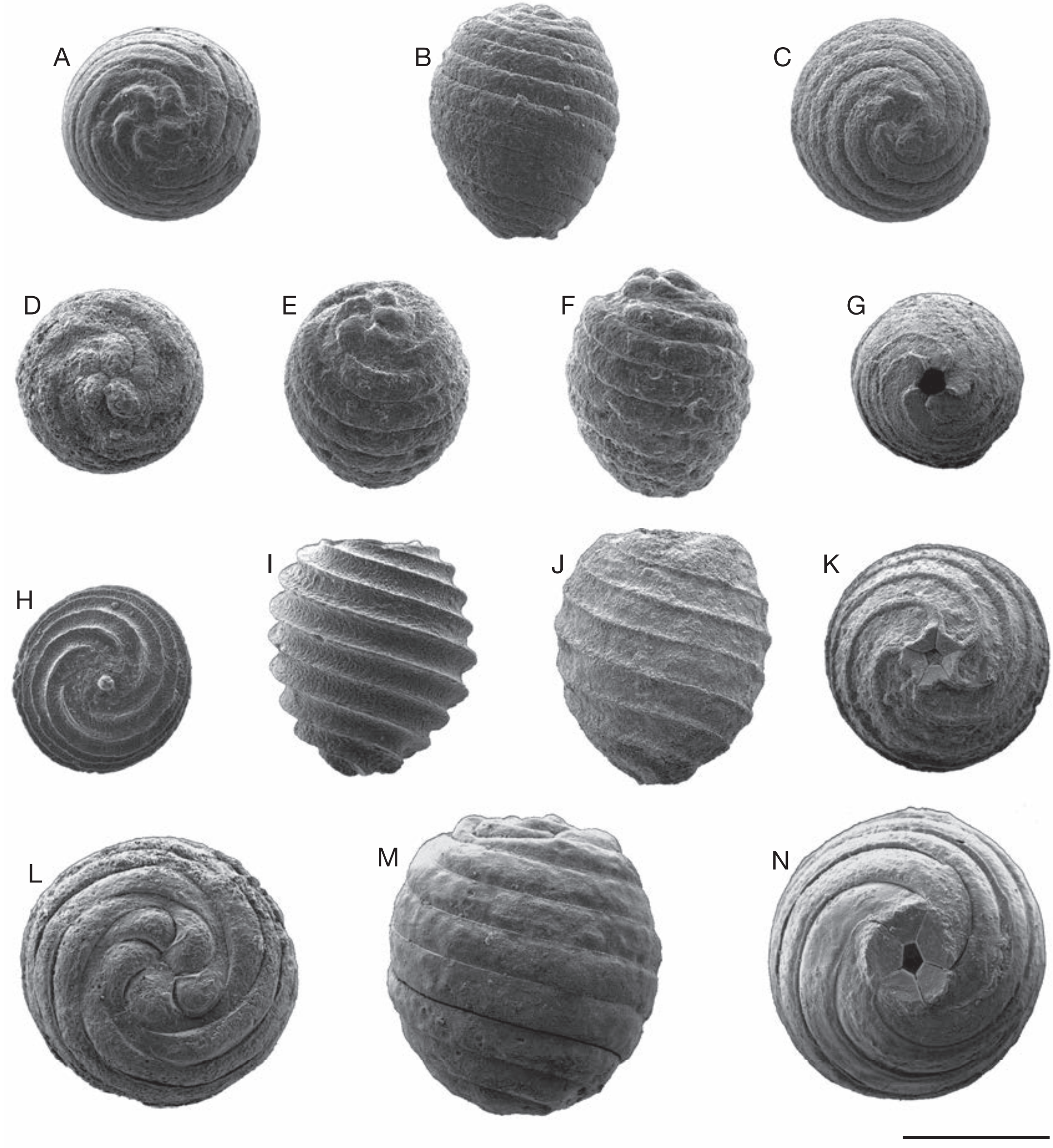

FIG. 8. — Charophytes from the Artés and lateral south-western Formations, Ebro Basin: **A**-**C**, *Lychnothamnus grambastii* (Feist-Castel, 1971), Torre Casanova section; **A**, apical view, no. 80100 MGSCB, sample TC-9; **B**, lateral view, no. 80101 MGSCB, sample TC-9; **C**, basal view, no. 80102 MGSCB, sample TC-9; **D**-**F**, *Lychnothamnus vectensis* (Groves, 1926), Santpedor and Rubió 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* (Grambast & Paul, 1965), 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. 80109 MGSCB 09, sample SA-19; **L**-**N**, *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun *ex* Unger, 1852), Vinaixa section; **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. Scale bar: 500 μm.

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 & Feist 1999).

Genus *Nitellopsis* Hy, 1889
Subgenus *Tectochara*
Grambast & Grambast-Fessard, 1954

Nitellopsis* (*Tectochara*) *merianii
(Al. Braun *ex* Unger, 1852)
Grambast & Soulié-Märsche, 1972
(Fig. 8L-N)

Chara meriani Unger, 1852: 82, pl. 25, figs 10-12.

Tectochara meriani – Grambast & Grambast-Fessard 1954: 668.

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

Distribution. — *Nitellopsis* (*Tectochara*) *merianii* appears to be exclusive to Europe during the Upper Eocene (Upper Priabonian) and Lower Oligocene (Rupelian) (Table 5). It has been reported in Rupelian lacustrine deposits from many French localities, i.e. Paris Basin (Grambast & Paul 1965; Riveline 1986), Aquitaine (Feist & Ringeade 1977), the western sector of Languedoc (Grambast 1962; Feist-Castel 1971) and Provence (Touraine 1971) basins. It was also reported in Lower Oligocene beds in the Rhine Graben in Germany (Mädler 1955; Schwarz 1997) and in Lower Oligocene deposits from the Molassic Swiss Basin (Kissling 1974; Reichenbacher *et al.* 1996). In Spain, this species has been documented in Upper Eocene-Lower Oligocene deposits from the Ebro Basin (Choi 1989; Feist *et al.* 1994) and from Oligocene rocks in the central Iberian Peninsula (Loranca Basin) by Juliá de Agar (1991). Recently, Sanjuan & Martín-Closas (2012) reported the oldest record of the species in the Upper Priabonian of the eastern Ebro Basin, namely at Torre Casanova (Moià), El Talladell and Vinaixa (Tables 2, 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 18°N to 50°N and covering the entire Eurasian landmass (Soulié-Märsche *et al.* 1997 and references therein; Soulié-Märsche *et al.* 2002; Sanjuan & Martín-Closas in press). In Eastern Europe, this species was also recorded in Lower Oligocene deposits from Slovenia (Ettinghausen 1872) and Romania (Iva *et al.* 1970; Baciu & Feist 1999). Mädler & Staesche (1979) reported this species in many localities attributed to Early Oligocene from Turkey (Table 5).

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 subrounded, 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.

Genus *Harrisichara* Grambast, 1957

Harrisichara lineata Grambast, 1957
(Fig. 9D-I)

Harrisichara lineata Grambast, 1957: 27, pl. 4, figs 5-7.

Distribution. — *Harrisichara 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 & Ringeade 1977) and

Provence (Feist-Castel 1977a) basins. In Germany, *H. lineata* occurs in the Rhine Graben Basin (Schwarz & Griessemer 1994). *Harrisichara lineata* has also been reported in the North of Spain. It has recently been documented 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).

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 (Fig. 9G-I). 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.

Harrisichara vasiformis form *vasiformis-tuberculata* Feist-Castel, 1977 (Fig. 9A-C)

Harrisichara vasiformis-tuberculata Feist-Castel, 1977b: 152, pl. 21, figs 2, 3.

Distribution. — *Harrisichara vasiformis* form *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 (Romania) by Baciu & Feist (1999). In Spain, this morphotype has been documented by Martín-Closas & Ramos (2005) in the Island of Mallorca and by Choi (1989), Feist *et al.* (1994) and Sanjuan *et al.* (2012) in the eastern part of the Ebro Basin. In the present study, it has been recorded in Sant Boi de Lluçanès, Sobremunt, Sant Bartomeu del Grau and Maians (Tables 2, 3). Sanjuan & Martín-Closas (2012) showed that in the Ebro Basin, this species grew solely in brackish environments.

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.

Remarks

This taxon was proposed by Feist-Castel (1977) as an informal name to characterise the gradual change from *H. vasiformis* to *H. tuberculata*, rather than as a formal species. Later Sille *et al.* (2004), showed by Eigenshape analysis that these morphotypes are within the variation of *H. vasiformis* rather than being intermediate with *H. tuberculata*.

Harrisichara tuberculata (Lyell, 1826) Grambast, 1957 (Fig. 9J-L)

Chara tuberculata Lyell, 1826: 94, pl. 13, figs 7, 8.

Harrisichara tuberculata – Grambast 1957: 10, pl. 6, figs 1-3, 8-10.

Distribution. — *Harrisichara tuberculata* is widely distributed in the Upper Priabonian to Lower Rupelian of Europe. In France, this species occurs in the Paris Basin (Grambast 1958; Riveline 1986), the north-eastern part of the Languedoc basin (Feist-Castel 1971) and the Aquitaine (Feist & Ringeade 1977) and Provence (Grambast 1958;

Feist-Castel 1977a) basins. *H. tuberculata* was reported in the Isle of Wight, England by Feist-Castel (1977b) and Riveline (1986), and in Belgium (Grambast 1958; Riveline 1986), Germany (Riveline 1986; Schwarz 1997) and Romania (Baciu & Feist 1999). In Spain, Adrover *et al.* (1982) found this species in the locality Barranco de la Calera (Teruel Province), in the Iberian Chain and it is especially common in the eastern Ebro Basin (Choi 1989; 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 2-4).

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.

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 fourteen European species were *Harrisichara lineata, H. vasiformis* form *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*, *Sphaerochara labellata* and *Lamprothamnium* sp.

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 same interval, *Lychnothamnus longus*, *Nodosochara jorbae* and *Chara artesica* n. sp. 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) Soulié-Märsche, 1989; *Lychnothamnus exigua* (Schwarz, 1988) 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, 1977; *Lychnothamnus compta* (Grambast, 1958) 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) Feist & Grambast-Fessard *in* Feist *et al.*, 2005. However, a revision is needed in order to evaluate if these local species do really correspond to endemisms or are rather polymorphs of other species with a wider range.

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

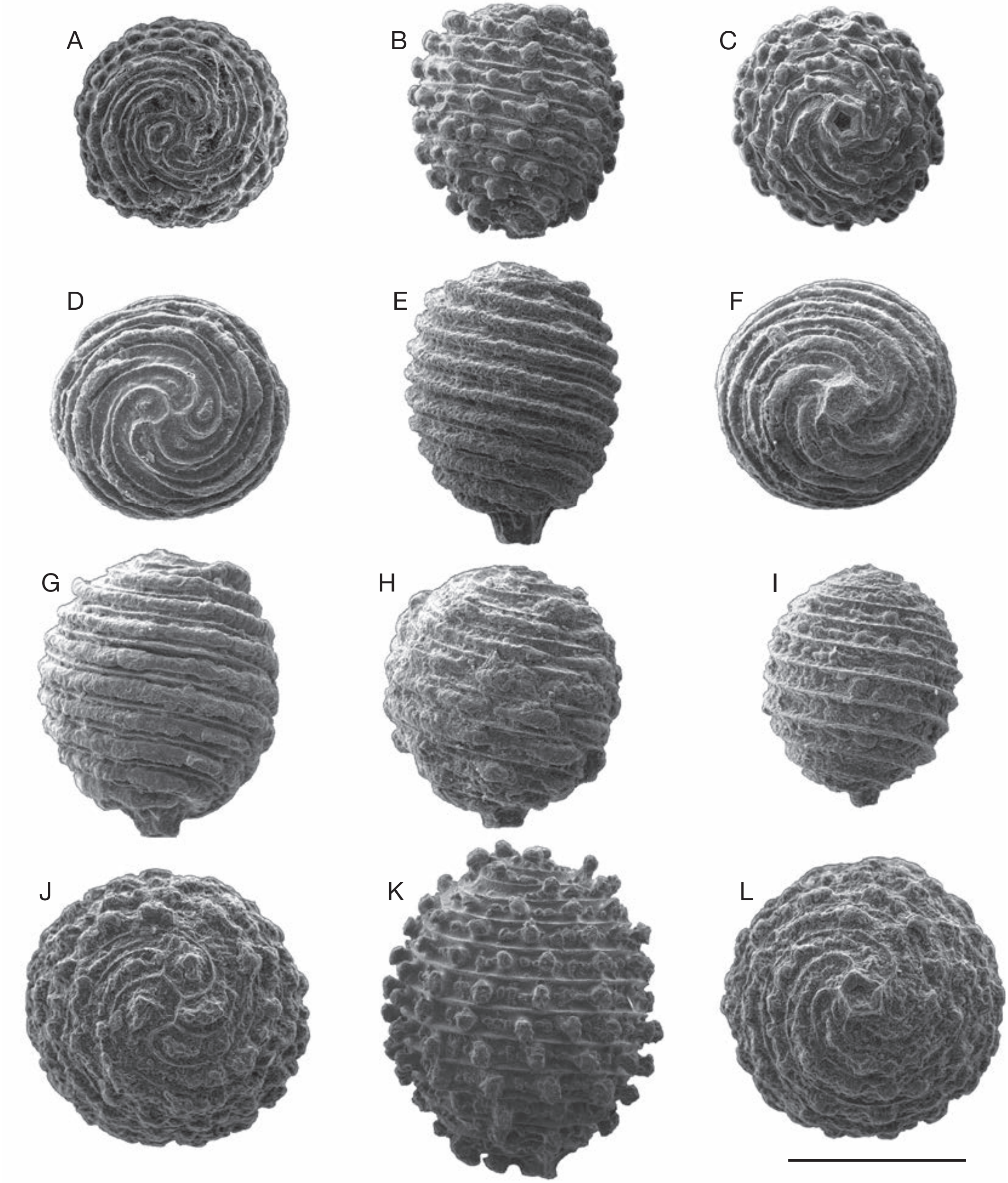

FIG. 9. — Charophytes from Sant Boi, Artés and lateral south-western Formations, Ebro Basin: **A**-**C**, *Harrisichara* vasiformis form *vasiformis-tuberculata* Feist-Castel, 1977, Serrat Rodó, Sobremunt road and Cal Carreter sections; **A**, apical view, no. 80113 MGSCB sample SBR-1; **B**, lateral view, no. 80114 MGSCB, sample SBR-1; **C**, basal view, no. 80115 MGSCB, sample SBR-1; **D**-**I**, *Harrisichara lineata* Grambast, 1957, 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* (Lyell, 1826), 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. Scale bar: 500 µm.

TABLE 5. — Distribution dataset of *Harrisichara vasiformis* form *vasiformis-tuberculata* Feist-Castel, 1977 and *Harrisichara tuberculata* (Lyell, 1826) during Late Eocene (Priabonian) (LE) and Early Oligocene (Rupelian) (EO) ordered chronologically by authors.

Taxonomy	Locality	Country	Reference
Harrisichara vasiformis form *vasiformis-tuberculata*	Hampshire Basin, Isle of Wight (various localities) (LE)	England	Feist-Castel (1977b)
	Paris Basin (various localities) (LE)	France	Riveline (1986)
	Hampshire Basin, Isle of Wight (Horestone, Whitecliff Bay) (LE)	England	Riveline (1986)
	Ebro Basin (Moià) (LE)	Spain	Choi (1989)
	Ebro Basin (Moià) (LE)	Spain	Feist *et al.* (1994)
	Transylvanian Basin (Dâncu, Cluj province) (LE)	Romania	Baciu & Feist (1999)
	Alaró (Mallorca) (LE)	Spain	Martín-Closas & Ramos (2005)
	Ebro Basin (Sobremunt, Sant Bartomeu del Grau, Maians) (LE)	Spain	Sanjuan *et al.* (2014)
Chara tuberculata	Hampshire Basin, Isle of Wight (Bembridge) (LE/EO)	England	Lyell (1826)
Harrisichara tuberculata	Louvain (Brabant province) (LE/EO)	Belgium	Grambast (1958)
	Paris Basin (Cormeilles-en-Parisis) (LE/EO)	France	Grambast (1958)
	Provence Basin (Farges, Puy) (LE/EO)	France	Grambast (1958)
	Languedoc Basin (Perignargues) (LE/EO)	France	Feist-Castel (1971)
	Provence Basin (Saint-Cannat) (LE/EO)	France	Feist-Castel (1977a)
	Hampshire Basin, Isle of Wight (Horestone, Whitecliff Bay) (EO)	England	Feist-Castel (1977b)
	Aquitaine Basin (various localities) (EO)	France	Feist & Ringeade (1977)
	Barranco de la Calera (Teruel province) (EO)	Spain	Adrover *et al.* (1982)
	Paris Basin (various localities) (LE/EO)	France	Riveline (1986)
	Velay Basin (Farges, Charentus) (LE/EO)	France	Riveline (1986)
	Hampshire Basin, Isle of Wight (Horestone point, Whitecliff Bay) (EO)	England	Riveline (1986)
	Vleminckx (Bautersem) (LE/EO)	Belgium	Riveline (1986)
	Rhine Graben Basin (Grossalmerode) (EO)	Germany	Riveline (1986)
	Ebro Basin (various localities) (LE/EO)	Spain	Choi (1989)
	Ebro Basin (various localities) (LE/EO)	Spain	Feist *et al.* (1994)
	Rhine Graven Basin (various localities) (LE/EO)	Germany	Schwarz (1997)
	Transylvanian Basin (Dâncu, Cluj province) (EO)	Romania	Baciu & Feist (1999)
	Ebro Basin (various localities) (LE/EO)	Spain	Sanjuan & Martín-Closas (2012)

Riveline (1986) for Middle Eocene charophyte species but has not been explored before for the Upper Eocene and Lower Oligocene. Two well-distributed and abundant charophytes lineages, *Harrisichara vasiformis-H. tuberculata* and *Lychnothamnus stockmansii-L. major,* comprise the main species enabling the characterisation of this bioprovince (Tables 5, 6; 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 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 (Table 7; Fig. 10).

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*,

TABLE 6. — Distribution dataset of *Lychnothamnus stockmansii* (Grambast, 1957) and *Lychnothamnus major* (Grambast & Paul, 1965) during Late Eocene (Priabonian) (LE) and Early Oligocene (Rupelian) (EO) ordered chronologically by authors.

Taxonomy	Locality	Country	Reference
Rhabdochara stockmansi	Provence Basin (Les Farges), Haute Loire (EO)	France	Grambast (1957)
	Boutersem (Hoogbustel) (LE/EO)	Belgium	Stockmans (1960)
	Provence Basin (Eigalayes) (EO)	France	Montenat (1968)
	Provence Basin (Bourdas) (EO)	France	Touraine (1971)
	Aquitaine Basin (Roque-de Thau, Artigues) (LE)	France	Feist & Ringeade (1977)
	Aquitaine Basin (Saint-Aubin-de-Cadelech) (EO)	France	Feist & Ringeade (1977)
	Provence Basin (Roque d'Anthéron) (EO)	France	Feist-Castel (1977a)
	Hampshire Basin, Isle of Wight (Horestone, Whitecliff Bay) (LE)	England	Feist-Castel (1977b)
	Bohai Bay Basin (Tianjin province) (LE/EO)	China	Xinlun (1978)
	Paris Basin (various localities) (LE/EO)	France	Riveline (1986)
	Hampshire Basin, Isle of Wight (Horestone, Whitecliff Bay) (LE/EO)	England	Riveline (1986)
	Guangdong province (LE/EO)	China	Huang *et al.* (1988)
	Eastern Zhejiang province (LE)	China	Liu (1989)
	Ebro Basin (Fonollosa) (LE/EO)	Spain	Choi (1989)
	Junggar Basin (Xinjiang province) (LE/EO)	China	Liu & Wu (1990)
	Tarim Basin (Xinjiang province) (LE/EO)	China	Lu & Luo (1990)
	Transylvanian Basin (Preluca, Cluj province) (EO)	Romania	Baciu & Feist (1999)
Lychnothamnus stockmansii	Es Macar de sa Llosa (Isle of Menorca) (LE/EO)	Spain	Martín-Closas & Ramos (2005)
	Ebro Basin (various localities) (LE/EO)	Spain	Sanjuan *et al.* (2014)
Rhabdochara major	Languedoc Basin (Saint-Vincent-de-Barbeyrargues) (EO)	France	Grambast & Paul (1965)
	Paris Basin (Fontainebleau, Soisy-sur-École) (EO)	France	Grambast & Paul (1965)
	Molasse Basin (Peissy, Satigny) (EO)	Switzerland	Kissling (1974)
	Aquitaine Basin (Villebramar) (EO)	France	Feist & Ringeade (1977)
	Provence Basin (various localities) (EO)	France	Feist-Castel (1977a)
	Paris Basin (Itteville, Esclimot, Etrechy, Saint Ambroix) (EO)	France	Riveline (1986)
	Ebro Basin (Solivella, El Talladell) (EO)	Spain	Feist *et al.* (1994)
	Transylvanian Basin (Dâncu) Cluj province (EO)	Romania	Baciu & feist (1999)
Lychnothamnus major	Ebro Basin (Sarral, El Talladell) (EO)	Spain	Sanjuan *et al.* (2014)

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, 1978 (*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 & 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). However, these numerical data should probably be taken with care until a sound comparison between Chinese and European charophyte floras is carried out.

Table 7. — Distribution dataset of *Chara microcera* Grambast & Paul, 1965 and *Nitellopsis* (*Tectochara*) *merianii* (Al. Braun *ex* Unger, 1852) during Early Oligocene (Rupelian) ordered chronologically by authors.

Taxonomy	Locality	Country	Reference
Chara microcera	Paris Basin (Soysi-sur-École)	France	Grambast & Paul (1965)
	Swiss Molasse Basin (various localities)	Switzerland	Kissling (1974)
	Provence Basin (Prene-les Fontaines, Aix-en-Provence)	France	Feist-Castel (1977a)
	Aquitaine Basin (Massels, Ariey, Saint-Côme)	France	Feist & Ringeade (1977)
	Paris Basin (various localities)	France	Riveline (1986)
	Rhine Graben Basin (Basin Niederentz)	France	
	Ebro Basin (Solivella, Tàrrega)	Spain	Choi (1989)
	Tajo Basin, Intermediate depression. (Montalbo, Montcalvillo)	Spain	Juliá de Agar (1991)
	Ebro Basin (various localities)	Spain	Feist *et al.* (1994)
	Rhine Graben Basin (various localities)	Germany	Schwarz (1997)
	Ebro Basin (El Talladell, Vinaixa)	Spain	Sanjuan *et al.* (2014)
Chara meriani	Sagor, Savine, Tüffer (Carniola)	Slovenia	Ettinghausen (1872)
Tectochara meriani meriani	Molasse Basin (Beiningen)	Germany	Mädler (1955)
Tectochara meriani	Paris Basin (Fontainebleau, Soysi-sur-École)	France	Grambast & Paul (1965)
Tectochara meriani meriani	Transilvanian Basin (various localities North of Vesul Baxinului)	Romania	Iva *et al.* (1970)
Tectochara meriani	Molasse Basin (Peissy, Genève)	Switzerland	Kissling (1974)
Nitellopsis (*Tectochara*) *meriani*	Aquitaine Basin (various localities)	France	Feist & Ringeade (1977)
Tectochara meriani	Western and central Turkey (various localities)	Turkey	Mädler & Staesche (1979)
Nitellopsis (*Tectochara*) *merianii*	Paris Basin (Itteville, Etrechy, Saint Ambroix)	France	Riveline (1986)
	Rhine Graben-Main Basin (Renish Hesse)	Germany	Schwarz (1988)
	Ebro Basin (Jorba, La Panadella)	Spain	Choi (1989)
	Ebro Basin (various localities)	Spain	Feist *et al.* (1994)
	Molasse Basin (Moutier, Bern)	Switzerland	Reichenbacher *et al.* (1996)
	Rhine Graben Basin (various localities)	Germany	Schwarz (1997)
	Transilvanian Basin (Dâncu, Cluj province)	Romania	Baciu & Feist (1999)
	Ebro Basin (Moià, El Talladell, Vinaixa)	Spain	Sanjuan *et al.* (2014)

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 & Groves, 1921; *Chara tornata* (Horn af Rantzien, 1954) Grambast, 1958 and *Sphaerochara headonensis* (Reid & Groves, 1921) Grambast, 1958 (Fig. 11). On the other hand, the southern basins shared the species *Lychnothamnus grambastii* (Feist-Castel, 1971) Soulié-Märsche, 1989; *Lychnothamnus raibocarpa* (Feist-Castel, 1977) Soulié-Märsche, 1989 and *Sphaerochara labellata* Feist & Ringeade, 1977, which are not recorded in the north (Fig. 11).

Geographically isolated from other well-known European basins, the Upper Eocene-Lower Oligocene deposits of the Transylvanian Basin (Romania)

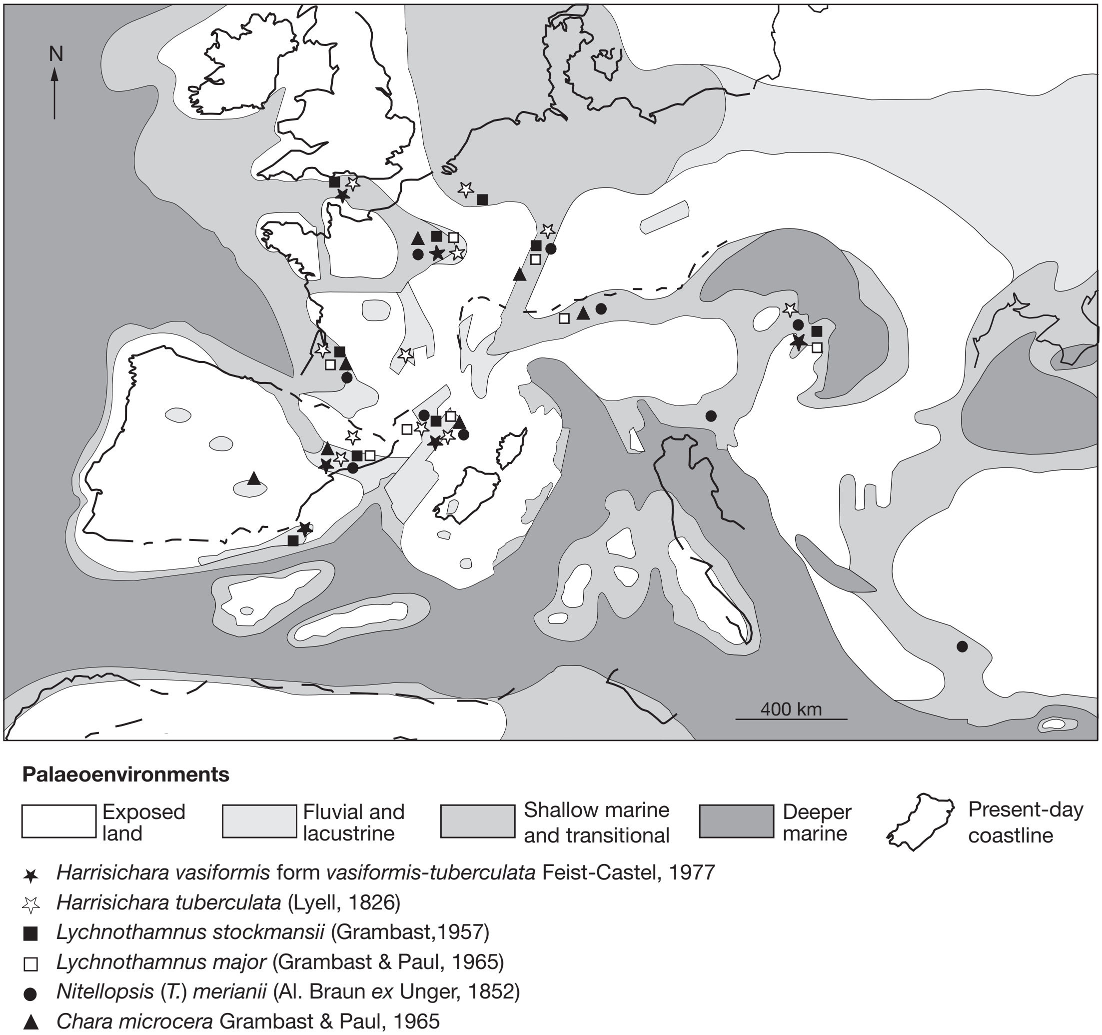

Fig. 10. — European bioprovince. Distribution of the *Harrisichara vasiformis-H.tuberculata* and *Lychnothamnus stockmansii-L.major* charophyte lineages and the species *N* (*T.*) *merianii* and *Chara microcera* during Uppermost Eocene (Priabonian) and Lower Oligocene (Rupelian) on the palaeogeographic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

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 Romania 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 & Groves, 1921) Pia, 1927; *Gyrogona lemanii* (Brongniart, 1822) Pia, 1927; *Grovesichara distorta* (Reid & Groves, 1921) Horn af Rantzien, 1959; *Psilochara repanda* Grambast, 1958 and *Chara marcoussiensis* Riveline, 1986 (Fig. 11). 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 OF THE BIOGEOGRAPHICAL PATTERN

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 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 Late Eocene-Early Oligocene, 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 stockmansii* 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 latitudinal biogeographic complexity than expected from this homogenous thermal situation. 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. Palynological data from Priabonian deposits of the eastern Ebro basin agree with this macrofloral distributional pattern. The presence of palynomoph elements such as *Ephedra*, Chenopodiaceae, *Combrentum*, *Linum*, Plumbaginaceae, Thymalaeaceae and Boraginaceae toghether with large diversity of Caesalpiniaceae and Leguminoseae pollen indicate that dry climatic and seasonal conditions with African influence prevailed during the Priabonian in the Ebro basin and in southern regions of Europe (Cavagnetto & Anadón 1996).

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

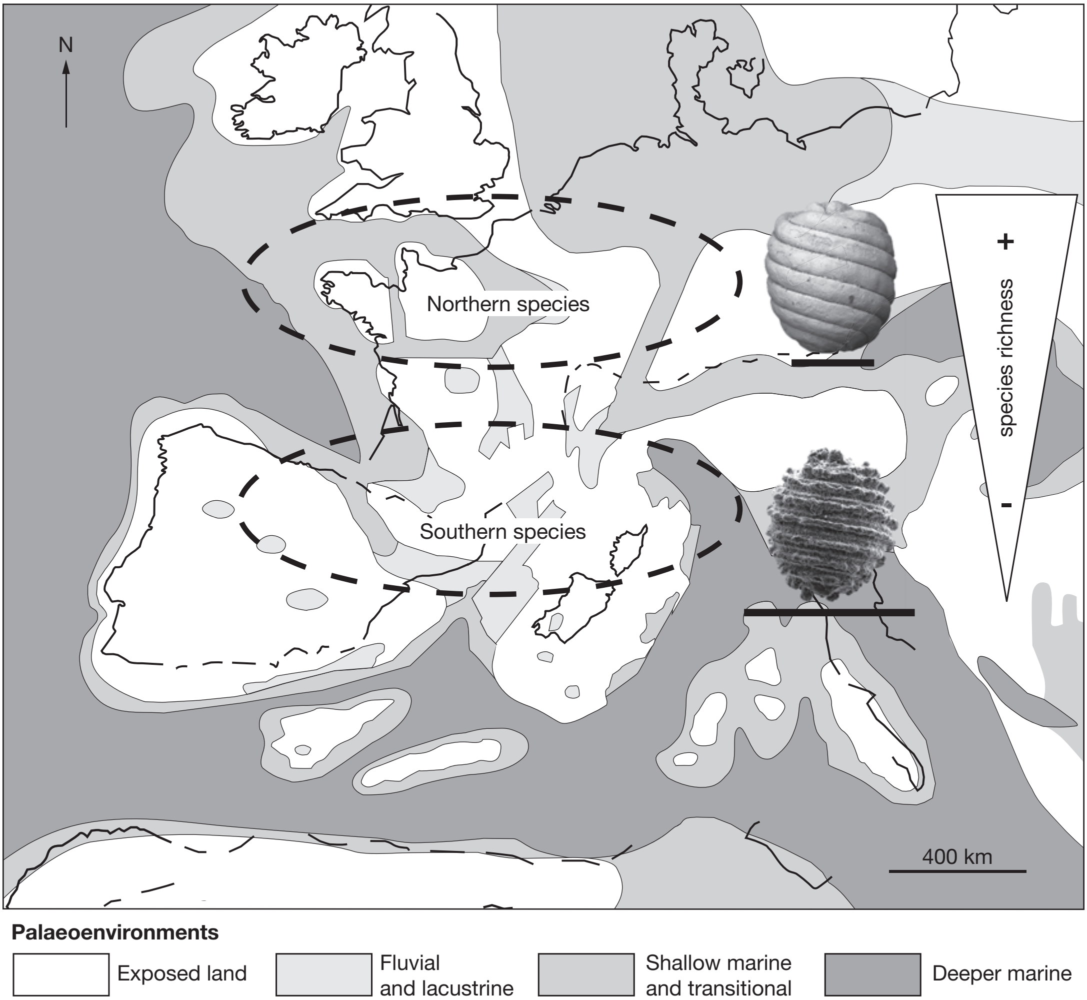

Fig. 11. — Palaeobiogeographic map of Western Europe (Late Eocene-Early Oligocene) showing the latitudinal polarity in distribution of species and species richness (modified from Lorenz *et al.* 1993). Two examples are provided i.e. *Lychnothamnus pinguis* (Grambast, 1957) which represents a characteristic species from northwestern Europe and *Sphaerochara labellata* Feist & Ringeade, 1977 which represents a characteristic species of southwestern Europe. The mean species richness oscillates between 31 species in the North and 18 in the South. Scale bars: 500 µm.

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 Corillion (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, 1857) 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 (Corillion 1972). In contrast, *Tollypella hispanica* Nordstedt, 1889 displays a Mediterranean distribution and is absent in north-central Europe (Corillion 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 and 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 constraints 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 (Fig. 11).

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. comm. 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* n. 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, variation 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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REFERENCES

ADROVER R., FEIST M., HUGUENEY M., MEIN O. & MOISSENET E. 1982. — L'âge et la mise en relief de la formation détritique culminante de la Sierra Pelarda (Province de Teruel, Espagne). *Comptes-rendus de l'Académie des Sciences de Paris* 295: 231-236.

ANADÓN P. & FEIST M. 1981. — Charophytes et biostratigraphie du Paléogène inférieur du Bassin de l'Ebre Oriental. *Palaeontographica* 178: 143-168.

ANADÓN P., CABRERA L., CHOI S. J., COLOMBO F., FEIST M. & SÁEZ A. 1992. — Biozonación del Paleógeno continental de la zona oriental de la Cuenca del Ebro mediante carófitas: implicaciones en la biozonación general de carófitas de Europa occidental. *Acta Geologica Hispanica* 27: 69-94.

BACIU C. & FEIST M. 1999. — Les charophytes oligocènes du nord-ouest de la Transylvanie (Roumanie). *Acta Palaeontologica Romana* 2: 27-29.

BACIU C. & HARTENBERGER J. L. 2001. — Un exemple de córrelation marin-continental dans le Priabonien de Roumanie. Remarques sur la Grande Coupure. *Comptes-rendus de l'Académie des Sciences* 333: 441-446.

BARBERÀ X. 1999. — *Magnetostratigrafia de l'Oligocè del sector sud oriental de la Conca de l'Ebre: implicacions magnetobiocronológiques i seqüencials*. PhD dissertation Universitat de Barcelona, 247 p.

BATHIA S. 1999. — Ecological parameters and dispersal routes of *Lychnothamnus barbatus* (Characeae) in the Early-Middle Holocene from Ganga plain, India. *Cryptogamie, Algologie* 27 (4): 341-356.

CAVAGNETTO C. & ANADÓN P. 1996. — Preliminary palynological data on floristic and climatic changes during the Middle Eocene-Early Oligocene of the eastern Ebro Basin, northeast Spain. *Review of Palaeobotany and Palynology* 92: 281-305.

CHOI S. J. 1989. — Les Charophytes du Bassin Potassique Catalan (Nord-Est de l'Espagne) à la limite Eocène-Oligocène. *Paléobiologie continentale* 26: 1-67.

COLOMBO F. 1986. — Estratigrafía y sedimentología del Paleógeno continental del borde meridional occidental de los Catalánides (Província de Tarragona, España). *Cuadernos de Geología Ibérica* 10: 55-115.

CORILLION R. 1972. — *Les Charophycées de France et d'Europe Occidentale*. Travaux du laboratoire de botanique de la Faculté des Sciences d'Angers, Angers 11-12: 499 p.

COSTA E., GARCÉS M., LÓPEZ-BLANCO M., BEAMUD E., GÓMEZ-PACCARD M. & CRUZ-LARRASOAÑA J. 2010. — Closing and continentalization of the South Pyrenean foreland basin (NE Spain): magnetochronological constraints. *Basin Research* 22: 904-917.

EINSELE G. 2000. — *Sedimentary basins. Evolution, Facies, and Sediment Budget* (2nd edition). Springer, Berlin, 792 p.

Ettinghausen C. 1872. — Die fossile Flora von Sagor in Krain. *Denkschriften der Kaiserlichen Akademie der Wissenschaften/Mathematisch-Naturwissenschaftliche Classe* 32: 159-202.

Feist M. & Ringeade M. 1977. — Étude biostratigraphique et paléobotanique (charophytes) des formations continentales d'Aquitaine, de l'Éocène supérieur au Miocène inférieur. *Bulletin de la Société géologique de France* 7: 341-354.

Feist M., Anadón P., Cabrera L., Choi S. J., Colombo F. & Sáez M. 1994. — Upper Eocene-Lowermost Miocene charophyte in the Ebro Basin (Spain). Contribution to the charophyte biozonation in Western Europe. *Newsletter Stratigraphy* 30: 1-32.

Feist M., Grambast-Fessard N., Guerlesquin M., Karol K., Lu H., Mccourt R. M., Wang Q. & Shenzen Z. 2005. — *Treatise on Invertebrate Paleontology. Part B., Protoctista 1.Charophyta*, The Geological Society of America, Kansas, 170 p.

Feist-Castel M. 1971. — Sur les Charophytes fossiles du Bassin tertiaire d'Alés (Gard). *Geobios* 4: 157-172.

Feist-Castel M. 1977a. — Étude floristique et biostratigraphique des Charophytes dans les séries du Paléogène de Provence. *Géologie Méditerranéenne* 4: 109-138.

Feist-Castel M. 1977b. — Evolution of the charophyte floras in the Upper Eocene and Lower Oligocene of the Isle of Wight. *Palaeontology* 20: 143-157.

Gierlowski-Kordesch E. H. 2010. — Lacustrine carbonates, *in* Alonso-Zarza A. M. & Tanner L. H. (eds), Carbonates in Continental Settings. *Facies, Environments and Processes: Developments in Sedimentology* 61: 1-101.

Grambast L. 1957. — Ornementation de la gyrogonite et systématique chez les Charophytes fossiles. *Revue générale de Botanique* 64: 1-24.

Grambast L. 1958. — *Étude sur les charophytes tertiaires d'Europe Occidentale et leurs rapports avec les formes actuelles*. PhD dissertation Université de Paris, 258 p.

Grambast L. 1962. — Aperçu sur les Charophytes tertiaires du Languedoc et leur signification stratigraphique. *Comptes Rendus Sommaires des Séances de la Société Géologique de France* 10: 313-314.

Grambast L. & Paul P. 1965. — Observations nouvelles sur la flore de charophytes du Stampien du bassin de Paris. *Bulletin de la Société Géologique de France* 7: 239-247.

Grambast L. & Soulié-Märsche I. 1972. — Sur l'ancienneté et la diversification des *Nitellopsis* (Charophytes). *Paléobiologie Continentale* 3: 1-14.

Grambast L. & Grambast-Fessard N. 1981. — Étude sur les charophytes tertiaires d'Europe Occidentale III. Le genre *Gyrogona*. *Paléobiologie continentale* 12: 1-35.

Groves J. 1926. — Charophyta, *in* Reid E. M. & Chandler M. E. J. (eds), *The Bembridge Flora*. British Museum Catalogue, Cainozoicum Plants, London 1: 165-173.

Huang R. J., Zhong Z. Q. & Nie Y. S. 1988. — *Early Tertiary Charophytes from the Dongpu region*, *in* Series on Stratigraphy and Paleontology of Oil and Gas bearing Areas in China. Research Institute of Exploration and Development, Zhongyuan Petroleum Exploration Bureau and Nanjing Institute of Geology and Paleontology, The Petroleum Industry Press, Beijing, 188 p.

Iva M. 1987. — Quelques espèces de charophytes lutétiennes du NO de la Transylvanie, *in* Petrescu I., Ghergari L., Mészáros N. & Nicorici E. (eds), The Eocene from the Transylvanian Basin, Romania. *Geological Formations of Transilvania* 1: 43-48.

Iva M., Margarit M. & Margarit G. 1970. — Asupra citorva caracee din stratele de Turbuta de Pe Valea Hirtoapelor (Nord-Vesul Baxinului Transsilvaniei). *Studiai si cercetari de Geologie, Geofizica, Geografie, Seria Geologie, Bucuresti* 15: 419-430.

Juliá De Agar J. J. 1991. — Contribución al estudio de carófitas fósiles de la Cuenca Terciaria de Loranca (provincia de Cuenca, España). *Coloquios de Paleontologia, Universidad Complutense de Madrid* 43: 57-78.

Kissling D. 1974. — *L'Oligocène de l'extremité occidentale du basin molassique Suisse. Stratigraphie et apercu sédimentologique*. PhD dissertation Université de Genève, 188 p.

Liu J. Y. 1989. — *Cenozoic Paleobiota of the continental shelf of the East China Sea (Donghai)*. Geological Publishing House, Beijing, 324 p.

Liu J. & Wu X. 1990. — *The Study on the Micropaleobotany from Cretaceous-Tertiary of the Oil Bearing Basins in some Regions of Qianghai and Xinjiang*. China Environmental Science Press, 48 p.

Lorenz C., Butterlin J., Cavelier C., Clermonte J., Colchen M., Dercourt J., Guiraud R., Montenant C., Poisson A., Ricou, L. E. & Sandulescu M. 1993. — Late Rupelian (30-28 Ma), *in* Decourt J., Ricou L. E. & Vrielynck B. (eds), *Atlas of Tethys Palaeoenvironmental Maps*. Beicip-Franlab, Rueil-Malmaison, Paris.

Lu H. & Luo Q. 1990. — *Fossil Charophytes from the Tarim Basin. Xinjiang.* Series on Stratigraphy and Palaeontology of oil and gas bearing areas in China. Science and Technical Documents Publishing House, Beijing, 261 p.

Lyell C. 1826. — On a recent formation of freshwater limestone in Forfarshire and some recent deposits of freshwater marl. *Transactions of the Geological Society of London* 2: 72-96.

Mädler K. 1955. — Zur Taxonomie der Tertiären Charophyten. *Geologisches Jahrbuch* 70: 265-328.

Mädler K. & Staesche U. 1979. — Fossile Charophyten aus dem Känozoikum (Tertiär und Quartär) der Türkei. *Geologisches Jahrbuch* B 33: 81-157.

Mai D. H. 1989. — Development and regional differentiation of the European vegetation during the Tertiary. *Plant Systematics and Evolution* 162: 79-91.

MAI D. H. & WALTER H. 1985. — Die obereozänen Floren des Weisselsterbeckens und seiner Randgebiete. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* 33: 1-260.

MARTÍN-CLOSAS C. & RAMOS E. 2005. — Palaeogene charophytes of the Balearic Islands (Spain). *Geologica Acta* 3: 39-58.

MARTÍN-CLOSAS C. & WANG Q. 2008. — Historical biogeography of the lineage *Atopochara trivolvis* Peck 1941 (Cretaceous Charophyta). *Palaeogeography, Palaeoclimatology, Palaeoecology* 260: 435-451.

MEBROUK F., MAHBOUBI M., BESSEDIK M. & FEIST M. 1997. — L'apport des charophytes à la stratigraphie des formations continentales paléogènes de l'Algérie. *Geobios* 32: 171-177.

MIHAJLOVIĆ D. 1993. — Importance of the Upper Eocene flora of the Pčinja-Ovče Polje Group for interregional correlations, *in* PLANDEROVÁ E. KONZÁLOVÁ M. KVA EK Z. SITÁR V. SNOPKOVÁ P. & SUBALLYOVÁ D. (eds), *Paleofloristic and Paleoclimatic Changes during Cretaceous and Tertiary*. Proceeding of international symposium, Bratislava: 99-104.

MOCHALES T., BARNOLAS A., PUEYO E. L., SERRA-KIEL J., CASAS A. M., SAMSÓ J. M., RAMAJO J. & SANJUAN J. 2012. — Chronostratigraphy of the Boltaña anticline and the Ainsa Basin (Southern Pyrenees). *Bulletin of the Geological Society of America* 124 (7-8): 1229-1250.

MONTENAT G. 1968. — Contribution à l'étude des formations tertiaires continentales de Baronnies. *Bulletin du Bureau de Recherches géologiques et minières* 1 (2): 1-18.

PUIGDEFÀBREGAS C., MUÑOZ J. A. & MARZO M. 1986. — Thrust belt development in the eastern Pyrenees and related depositional sequences in the southern foreland basin. *Special Publication of the International Association of Sedimentologists* 8: 229-246.

PUIGDEFÀBREGAS C., MUÑOZ J. A. AND VERGÉS J. 1992. — Thrusting and Foreland Basin Evolution in the Southern Pyrenees, *in* MCCLAY K. R. (ed.), *Thrust Tectonics*. London, Chapman and Hall: 247-254.

REGUANT S. 1967. — El Eoceno marino de Vic (Barcelona). Investigaciones estratigráficas en el borde meridional de la depresión del Ebro. *Memorias del Instituto Geológico y Minero de España* 68: 350 p.

REICHENBACHER B., BERGER J. P. & WEIDMANN M. 1996. — Charophytes et otolithes de la Molasse d'eau douce inférieure oligocène de Moutier (Jura Suisse). *Abhandlungen Neues Jahrbuch für Geologie und Paläontologie* 202 (1): 63-93.

REID C. & GROVES J. 1921. — The Charophyta of the Lower Headon Beds of Hordle (Hordwell) Cliffs (South Hampshire). *Quarterly Journal of the Geological Society of London* 77: 175-192.

RIVELINE J. 1986. — *Les Charophytes du Paléogène et du Miocène inférieur d'Europe Occidentale*. Cahiers de Paléontologie, Centre National de la Recherche Scientifique, 227 p.

RIVELINE J., BERGER J-P., FEIST M., MARTÍN-CLOSAS C., SCHUDACK M. & SOULIÉ-MÄRSCHE I. 1996 — European Mesozoic-Cenozoic charophyte biozonation. *Bulletin de la Société géologique de France* 167: 437-468.

SÁEZ A. 1987. — *Estratigrafía y sedimentología de las formaciones lacustres del tránsito Eoceno-Oligoceno del noreste de la Cuenca del Ebro*. PhD dissertation Universitat de Barcelona, 353 p.

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.

SANJUAN J. & MARTÍN-CLOSAS C. 2014 — Biogeographic history of two Eurasiatic Cenozoic charophyte lineages. *Aquatic Botany*. http://dx.doi.org/10.1016/j.aquabot.2014.05.018

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: 19-31.

SANJUAN J., MARTÍN-CLOSAS C., COSTA E., BARBERÀ X. & GARCÉS M. (2014). — Calibration of Eocene-Oligocene charophyte biozones in the Eastern Ebro Basin (Catalonia, Spain). *Stratigraphy* 11 (1): 61-81.

SCHUDACK M. E., TURNER C. E. & PETERSON F. 1998. — Biostratigraphy, paleoecology and biogeography of charophytes and ostracodes from the Upper Jurassic Morrison Formation, Western interior, USA. *Modern Geology* 22: 379-414.

SCHWARZ J. 1985. — Revision der Charophyten-Flora der Süsswasserschichten und des Kalktertiärs im Mainzer Becken (Oberoligozän-Untermiozän). *Mainzer geowissenschaftliche Mitteilungen* 14: 7-98.

SCHWARZ J. 1997. — Charophyten aus dem Tertiär des Oberrheingrabens (Mitteleozän-Untermiozän). *Palaeontographica Abt. B* 243: 1-84.

SCHWARZ J. & GRIESSEMER TH. W. 1994. — A charophyte flora from the Lower Pechelbronn Formation (?Upper Eocene/?Lower Oligocene) of Malsch south of Heidelberg (SW Germany). *Journal of Micropalaeontology* 13: 147-156.

SCOTESE C. R. 200. — *Paleomap Project*, http://www.scotese.com (accessed May 2013).

SILLE N. P., COLLINSON M. E., KUCERA M. & HOOKER J. J. 2004. — Evolution within the charophyte genus *Harrisichara*, late Palaeogene, southern England; environmental and biostratigraphic implications. *Palaeogeography, Palaeoecology, Palaeoclimatology* 208: 153-173.

SOULIÉ-MÄRSCHE I. 1989. — *Étude comparée de gyrogonites de charophytes actuelles et fossiles et phylogénie des genres actuels*. Millau, Imprimerie des Tilleuls, 237 p.

Soulié-Märsche I., Gemayel P., Chaimanee Y., Suteethorn V., Jaeger J. J. & Ducrocq S. 1997. — *Nitellopsis* (Charophyta) from the Miocene of northern Thailand. *Alcheringa* 21: 141-156.
Soulié-Märsche I., Benammi M. & Gemayel P. 2002. — Biogeography of living and fossil *Nitellopsis* (Charophyta) in relationship to new finds from Morocco. *Journal of Biogeography* 29: 1703-1711.
Stockmans F. 1960. — *Initiation à la Paléobotanique stratigraphique de la Belgique et notions connexes*. Institut Royal des Sciences Naturelles de Belgique, Bruxelles, 222 p.
Touraine F. 1971. — L'Oligocène nord-varois. Sa position stratigraphique et sa signification dans la tectogenèse subalpine (état des connaissances actuelles). *Annales Guébhard* 47: 394-421.
Travé A., Serra-Kiel J. & Zamarreño I. 1996. — Paleoecological interpretation of transitional environments in Eocene carbonates (NE Spain). *Palaios* 11: 141-160.
Unger F. 1852. — Iconographia plantarum fossilium. *Denkschriften Akademie der Wissenschaften, Mathematisch-Naturwissenchaftliche Klasse*, *Wien* 4: 73-118.
Vergés J., Marzo M., Santaeulàlia T., Serra-Kiel J., Burbank D. W., Muñoz J. A. & Giménez-Montsant J. 1998. — Quantified vertical motions and tectonic evolution of the SE Pyrenean foreland basin, *in* Mascle A., Puigdefàbregas C., Luterbacher H. P. & Fernández M. (eds), *Cenozoic Foreland Basins of Western Europe*. Geological Society, Special Publication 134: 107-134.
Wang S. 1961. — Tertiary Charophyta from Chaidamu (Tsaidam) basin, Qinghai (Chinghai) province. *Acta Palaeontologica Sinica* 9: 183-223.
Wang Z. 1978. — Paleogene charophytes from the Yangtze-Han River basin. *Memoirs Nanjing Institute of Geology and Palaeontology, Academia Sinica* 9: 101-120.
Xinlun Z. 1978. — *Early Tertiary Charophytes from Coastal region of Bohai*. Nanjing Institute of Geology and Paleontology. Nanjing, 49 p.

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