



The charophyte fossil record on the Iberian Peninsula: a synthesis

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ABSTRACT: Iberia was first an island and then a European peninsula during most of the Earth's history. This along with a long-lasting non-marine record has determined that fossil charophytes are well-represented and show significant particularities. As a matter of fact, the Iberian Peninsula is one of the best suited regions of Europe in which to study the charophyte fossil record from the Jurassic to the present. Middle and Late Jurassic charophyte assemblages are represented in the Lusitanian basin (Portugal). They show dominance of the family Porocharaceae in many of the environments available for charophytes. Lower Cretaceous charophytes, dominated by clavatoraceans, have been more studied in the Iberian Chain, where this family achieved high diversity. Also, many European charophyte biozones of this interval are based on Iberian clavatoraceans and have their stratotypes in the Iberian Chain. Upper Cretaceous charophytes of the Iberian Peninsula have been more studied in the Campanian of the Southwestern Iberian Chain (Serranía de Cuenca) and in the Maastrichtian of the south-Pyrenean basins (Catalonia). The floras show important affinity with those from southern France, which is not surprising since both regions were part of the so-called Ibero-Armorican Island. The Upper Cretaceous charophyte record from the southern Pyrenees is significant because it contains a reference section enabling us to define the Cretaceous-Palaeogene boundary based on charophytes in the Åger basin. Palaeogene charophytes from Iberia are best known from studies devoted to the Ebro foreland basin, where a detailed biozonation of the Eocene and Oligocene has been proposed. The charophyte assemblages were composed of a mixture of fossil and present-day genera and included both typical European species as well as endemic taxa. Neogene charophytes from Iberia are poorly known, but a number of studies have been performed, mainly in Central Spain and in the Ebro basin.

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INTRODUCTION

The Iberian Peninsula has been a micro-continent, the Iberian plate, which constituted an island during long periods of the Earth's history, and later a European peninsula. For this reason, the fossil record of non-marine deposits is good and has some peculiarities in comparison with neighbouring areas. Fossil charophytes from the Iberian Peninsula are especially significant from the Upper

Jurassic to the Quaternary. The present study is a review of the state of knowledge about fossil charophytes from the Iberian Peninsula and their biogeographic significance.

Iberian Jurassic charophytes. During most of the Lower and Middle Jurassic, the global sea level was high on the Iberian plate, and non-marine records are scarce worldwide. In contrast, by the Upper Jurassic the opening of the North Atlantic resulted in a generalised distension

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of the Atlantic margins that enhanced rifting processes and the formation of intra-continental sedimentary basins (SALAS & CASAS 1993). By that time the charophyte flora was dominated by two families, the Porocharaceae and the earliest characeans. The porocharaceans are characterised by their generally large gyrogonites, built of five spiral cells coiling clockwise around the oospore, but leaving a large apical germination pore open. This family dominated the charophyte flora in most environments, including lacustrine, fluvial and brackish settings. Such assemblages are finely recorded in the Oxfordian (157-164 million years ago) of the Lusitanian basin, Portugal (Fig. 1), as shown by AZERÊDO *et al.* (2002) and PEREIRA *et al.* (2003). The Kimmeridgian (152-157 million years ago) of the Iberian plate shows more developed non-marine records. By that time, several sedimentary sections with non-marine facies were well developed, especially in the Lusitanian basin (GRAMBAST-FESSARD & RAMALHO 1985) and in the northern Iberian Chain (the Cameros basin) (Fig. 1) (BRENNER 1976; SCHUDACK 1987). The floras were still dominated by porocharaceans, but early clavatoraceans (the genus *Dictyoclavator* Grambast) and early characeans (the genera *Mesochara* Grambast and *Aclistochara* Peck) occurred in particular environments. By the Tithonian (145-152 million years ago), non-marine records became extensive throughout the Iberian plate. These basins showed the first dominance of the clavatoraceans, a fossil family bearing a characteristic vegetative coat, called a utricle, around the oospore and the gyrogonite, when calcified. Interesting floras of the Tithonian (145-152 million years ago) were reported from the Lusitanian basin (Portugal) by PEREIRA *et al.* (2010). Other localities with charophytes were reported in the Cantabrian Mountains by MARTÍN-CLOSAS (2000).

Early Cretaceous Iberian charophytes. During the Early Cretaceous, Iberia was an island forming part of the Tethyan Archipelago located between the European and the African plates in subtropical latitudes. Throughout the whole interval, the formation of rift basins continued actively on the Iberian plate, providing one of the richest sedimentary records of non-marine facies from Europe at this geological time (SALAS *et al.* 2001). In the Early Cretaceous, the clavatoraceans continued their diversification and by the Barremian (126-131 million years ago) achieved dominance in most non-marine environments of the peri-Tethyan domain, relegating the other two families to particular facies, i.e., porocharaceans to brackish water and early characeans to fluvial and floodplain ponds (CLIMENT-DOMÈNECH *et al.* 2009; VICENTE & MARTÍN-CLOSAS 2013).

One of the most characteristic features of the clavatoracean evolution was the development of gradualistic evolutionary lineages, such as those of *Globator maillardii* (Saporta), *Atopochara trivolvris* Peck and *Clavator grovesii* Harris, which were first characterised

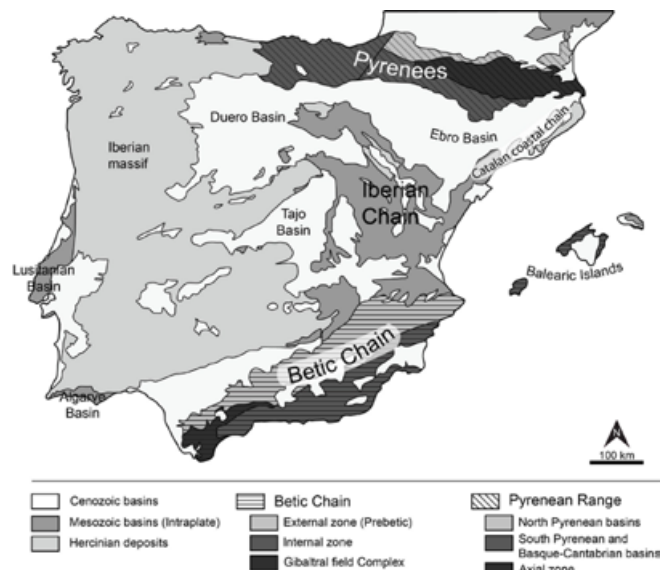


Fig. 1. Geological sketch of Iberia. Modified from VERA (2004).

by GRAMBAST (1966, 1967, 1968, 1970, 1974), mainly based on fossils of the Iberian Chain. All these lineages display a succession of fructifications that changed progressively in time. The lineages developed distinct evolutionary trends, but as a general rule fructifications became progressively larger and the utricle elements more spiralised. From the biomechanical viewpoint, this would enhance the development of larger zygotes and more resistant fructifications, especially in response to internal pressures created by the developing germling (MARTÍN-CLOSAS *et al.* 1999a). Each step in a lineage received a taxonomic name, of either specific or infraspecific rank, depending on the authors [see a discussion in FEIST & WANG (1995) and the reply by MARTÍN-CLOSAS & SCHUDACK (1997)]. The continuous stratigraphic sections of the non-marine Iberian Lower Cretaceous allowed GRAMBAST (1966, 1967, 1968, 1970, 1974) to define the tempo in the gradual evolution of these lineages, making them an excellent tool with which to assign relative ages to the rocks (biostratigraphy). Already in 1974 GRAMBAST proposed the first Lower Cretaceous charophyte biozonation, based mainly on localities from the eastern Iberian Chain. This biozonation was slightly modified in the European consensus biozonation published by RIVELINE *et al.* (1996), which is now the foundation on which datings based on charophytes are performed. Thanks to this tool, important vertebrate palaeontological sites, especially ones rich in plants (including early angiosperms), insects, non-marine fishes, dinosaurs, early birds and early mammals, were given an age.

Many other clavatoracean species were defined later based on Iberian fossils (GRAMBAST 1969, 1970, 1971; GRAMBAST-FESSARD 1980a, 1980b; MARTÍN-CLOSAS & GRAMBAST-FESSARD 1986). An account of these Lower Cretaceous Iberian floras was provided by MARTÍN-CLOSAS

(2000). The richest floras come from the eastern Iberian Chain, especially the Maestrat basin (MARTÍN-CLOSAS & GRAMBAST-FESSARD 1986; MARTÍN-CLOSAS 2000; MOJON 2002), the Cameros basin (SCHUDACK 1987, 1993; MARTÍN-CLOSAS 2000) and the Southwestern Iberian Chain (Fig. 2), especially those from the La Huérguina Formation (VICENTE & MARTÍN-CLOSAS 2013). In the latter unit, a complete assemblage of thalli was described from Las Hoyas Fossilagerstätte. It comprises four species within the genera *Charaxis* Harris, *Clavatoraxis* Martín-Closas & Diéguez and *Palaeonitella* Kidston & Lang (MARTÍN-CLOSAS & DIÉGUEZ 1998), but a lot of work still needs to be done before it is known whether or not these parataxa are equivalent with the species based on fructifications. Beyond the Iberian Chain, abundant charophytes were also found in the south-central Pyrenees (MARTÍN-CLOSAS & LOPEZ-MORÓN 1996), the Prebetic domain in Spain (GARCÍA-CORTÉS *et al.* 1995; MARTÍN-CLOSAS 2000) and the Lusitanian and Algarve basins in Portugal (REY & RAMALHO 1973-74; GRAMBAST-FESSARD 1980b; PEREIRA & CABRAL 2005). Many of these fossil charophytes, first described from Iberia, were also found in other European basins, North Africa and further east in China, as well as in America to the west, indicating that a number of species achieved a cosmopolitan distribution, at least in tropical to subtropical latitudes (MARTÍN-CLOSAS & WANG 2008; MUSACCHIO 2010; MARTÍN-CLOSAS 2015). However, most clavatoraceans shared a similar distribution on islands of the western Tethyan Archipelago, as in present France and North Africa (TRABELSI *et al.* 2010). Rare species would be ones endemic from Iberia.

The excellent fossil record of charophytes in the Lower Cretaceous of the Iberian Chain allowed MARTÍN-CLOSAS & SERRA-KIEL (1991) to define its macroevolutionary trends. In Early Cretaceous times, charophytes showed two main diversification maxima, the first at the beginning (Berriasian, 139-145 million years ago), the second about 20 million years later during the Barremian (126-131 million years ago) to Lower Aptian (116-126 million years ago), coinciding with the palaeogeographic extension of wetlands on the Iberian Island. During Valanginian and Hauterivian times (131-139 million years ago), i.e., between the two periods of maximum diversity, the basins' subsidence decreased and wetlands were limited to particular areas of each basin. With the reduction of space available for the development of charophytes, their diversification decreased too. Finally, during the upper Aptian and Albian (100-116 million years ago), the number of species decreased dramatically, probably coinciding with the diversification of aquatic angiosperms. However, significant records from this age were found in the Algarve (southern Portugal) by REY & RAMALHO (1973-74) and GRAMBAST-FESSARD (1980a) and also in the Iberian Chain (Escucha Formation) (MARTÍN-CLOSAS 1988; TIBERT *et al.* 2013) and Prebetic Chain (MARTÍN-CLOSAS 2000).

Upper Cretaceous Iberian charophytes. At the beginning of the late Cretaceous, in the Cenomanian (93.9-100 million years ago), large parts of Iberia were submerged and the sedimentary record is built up of shallow marine facies. However, rare parts in central Spain remained emerged and allow us to have insight about the charophytes from that time (GRAMBAST 1961). For instance, in Oña (Burgos) the assemblages were still dominated by clavatoraceans, especially *Atopochara trivolvris* var. *multivolvris* Peck.

By the latest Cretaceous, Iberia fused with a large part of present southern France, forming a big island called the Ibero-Armorican Island. The first detailed study about European Upper Cretaceous charophytes in this palaeogeographic domain was undertaken by GRAMBAST (1971) in the Provence, France. This study showed very clearly that the Ibero-Armorican Island contained a unique flora, already dominated by diversified characeans and the last representatives of the porocharaceans and clavatoraceans.

BATALLER (1945) was the first to report Upper Cretaceous charophytes, specifically "*Chara*" *malladae* (now *Feistiella malladae*), from the Iberian Peninsula. Later, two areas were shown to contain a good record: the southern Iberian Chain (València and Cuenca) and the southern Pyrenees (Catalonia). In the southern Iberian Chain, a very diverse flora of characeans and porocharaceans, probably of Campanian age (72.1-83.6 million years ago), occur (GRAMBAST 1974; GRAMBAST & GUTIÉRREZ 1977), while in the Southern Pyrenees mainly Maastrichtian (66-72.1 million years ago) floras were recorded (FEIST & COLOMBO 1983) and the flora showed a combination of characeans (dominant) along with rare porocharaceans and clavatoraceans (Fig. 3). The southern Pyrenean basins were the focus of international attention when the Cretaceous-Palaeogene boundary in the European non-marine realm was to be defined. This objective required detailed sampling and correlation studies performed by a multidisciplinary team whose efforts included the study of charophytes. The results yielded an accurate succession of floras through the Mesozoic-Cenozoic boundary (FEIST & COLOMBO 1983; MÉDUS *et al.* 1988), and a reference section was defined and dated by magnetostratigraphy in the Àger basin, at the so-called Fontllonga section (GALBRUN *et al.* 1993), providing absolute ages of this charophyte fossil record. In recent years, a more detailed insight into the palaeoecology and biogeography of these floras was obtained in a number of studies (VILLALBA-BREVA & MARTÍN-CLOSAS 2011, 2013; VICENTE *et al.*, 2016). From these studies it becomes clear that in the latest Cretaceous each palaeoenvironment was inhabited by distinct charophyte assemblages. For instance, *Peckichara cancellata* Grambast, *P. sertulata* Grambast and *Microchara cristata* Grambast were dominant in shallow but stable belts of permanent lakes, while the extremely small fructifications *Microchara nana* Vicente & Martín-

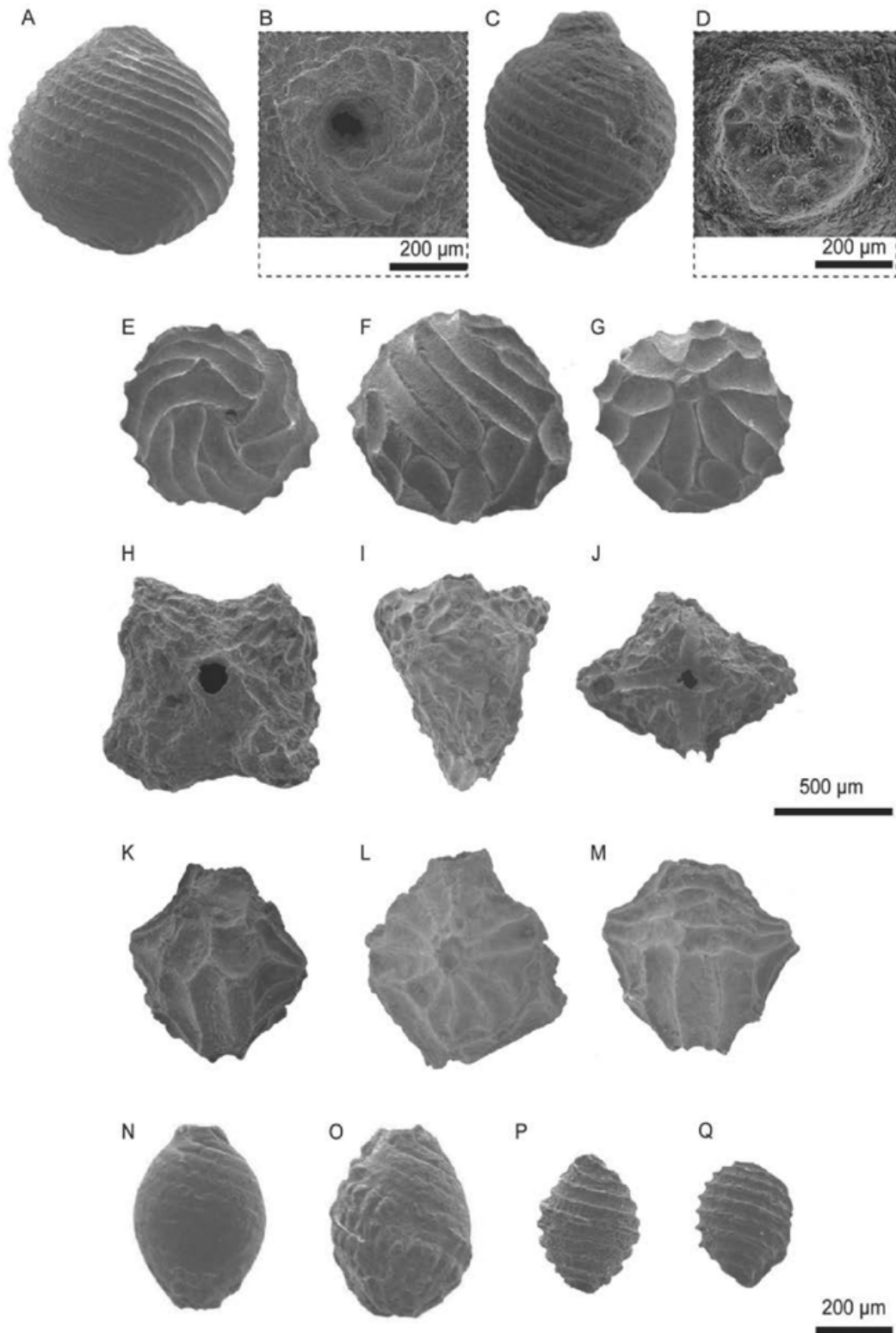


Fig. 2. Most common Lower Cretaceous charophyte assemblages from La Huérguina Formation, Iberian Chain. A, *Globator maillardii* var. *trochiliscoides* Grambast, lateral view. B–H, *Globator maillardii* var. *biutricularis*. Vicente & Martín-Closas B, apical view. C, lateral view and D, basal view. A–B, from sample HUE-32.1, D–C from La Toba (Uña). E–G, *Atopochara trivolis* var. *triquetra* Grambast. E, apical, F, lateral and G, basal views; sample HUE-32.1. H–J, *Ascidiella cruciata* Grambast in H, apical, I, lateral and J, basal view; sample HUE-32.1. K–M, *Clavator grovesii* var. *combei* Grambast in J, lateral, K, abaxial and L, adaxial views; sample HUE-21. N–O, *Clavator harrisii* var. *reyii* Grambast-Fessard, lateral view; sample HUE-3. P–Q, *Mesochara harrisii* Shaïkin, lateral view; sample HUE-3. Figure modified from VICENTE & MARTÍN-CLOSAS 2013.

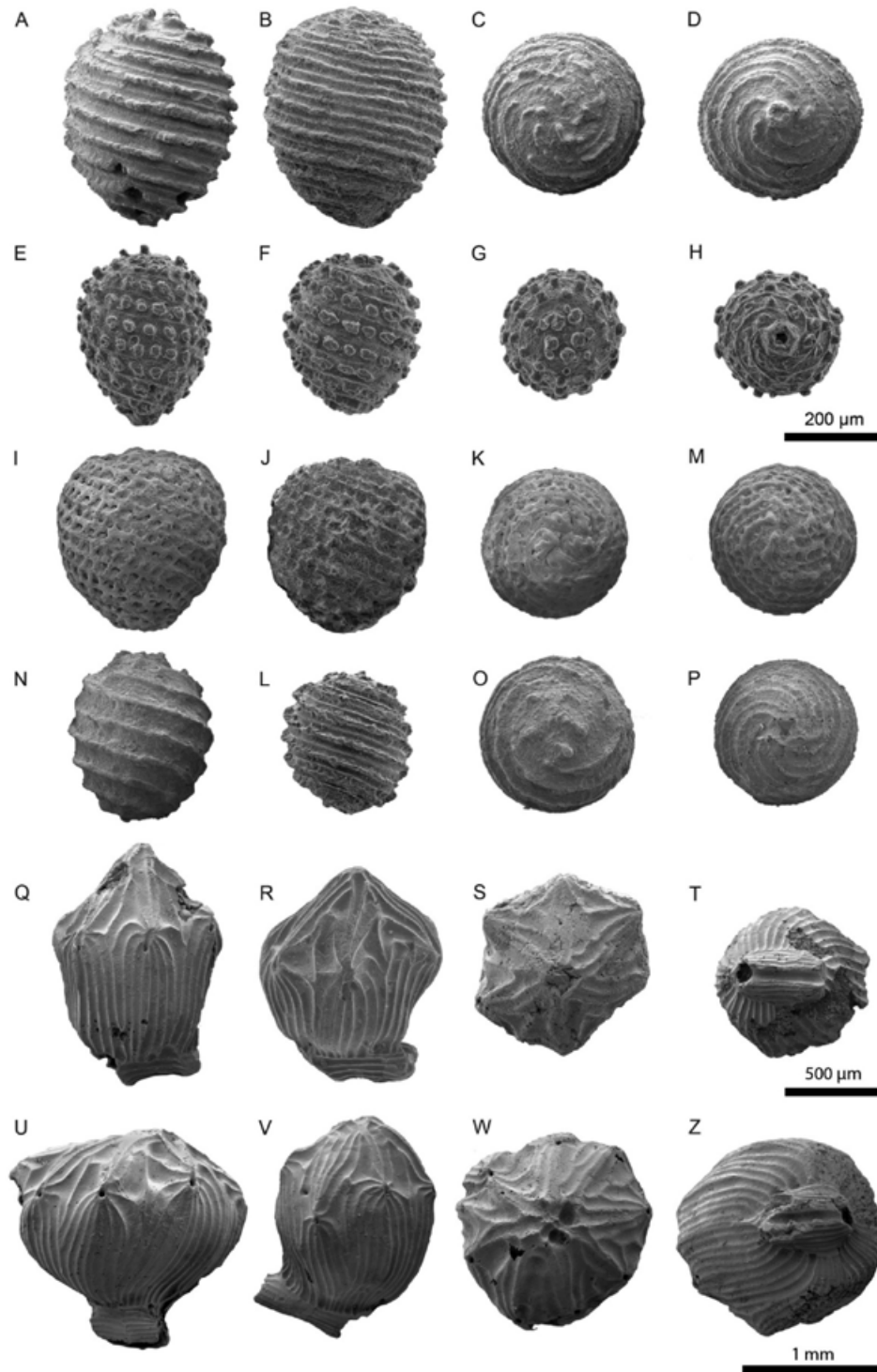


Fig. 3. Most common Upper Cretaceous charophyte assemblages from south Pyrenean basins. A–D, *Microchara cristata* Grambast. A–B, lateral view, C, apical view and D, basal view. Samples A, C and D from Fo-5, Fontllonga section, Àger Basin. Sample B from MSE-14, Santa Eulalia's lignite pit mine, Coll de Nargó Basin. E–H, *Microchara punctata* Feist. E–F, lateral view, G, apical view and H, basal view. Samples from CP-10, Coll de Nargó section, Vallcebre Basin. I–M, *Peckichara cancellata* Grambast. I–J, lateral view, K, apical view and M, basal view. Samples I, K and M from MAC-2, La Maçana section, Àger Basin. Sample J from MT-11, Mina Tumí section, Vallcebre Basin. N–P, *Peckichara sertulata* Grambast. N–L, lateral view, O, apical view and P, basal view. Samples N, O and P from ALZ-2, Alzina-Beniure section, Tremp Basin. Sample L, from EA-2, Gauge Station section, Coll de Nargó Basin. Q–T, *Clavator brachycerus* (Grambast). Q–R, lateral view, S, apical view and T, basal view. Samples Q, S and T from BFo-4, Fontllonga section, Àger Basin. Sample R, from MT-11, Mina Tumí section, Vallcebre Basin. U–Z, *Clavator ultimus* (Grambast). U–V, lateral view, W, apical view and Z, basal view. Samples U, W and Z from BFo-2.2 and V from BFo-5, Fontllonga section, Àger Basin. Figure modified from VICENTE *et al.* 2015, 2016, (in press)

Closas and *Microchara punctata* Feist represent plants thriving mainly in shallow, warm and temporary lakes from floodplains. In contrast, the last clavatoraceans in Europe, *Clavator brachycerus* (Grambast) and *C. ultimus* (Grambast), grew along the shallowest energetic lakeshores and in fluvial ponds, while the last porocharaceans, such as *Feistiella malladae* (Bataller), dominated the brackish environments, sometimes associated with characean species of the genus *Platychara* Grambast. This detailed palaeoecological information strongly influenced the view that charophytes cannot be used in biostratigraphy without a previous analysis of their environmental constraints. Otherwise, the biozone boundaries may be biased, depending on occurrence of the specific facies for each particular species at each particular time interval. This result, along with new biostratigraphic and magnetostratigraphic data, contributed to improving the charophyte biozonation of the uppermost Cretaceous of Iberia (VICENTE *et al.* 2015, 2016).

The impact of the crisis at the end of the Cretaceous on charophyte assemblages has been a matter of debate. The view of GRAMBAST (1974) was that this boundary represented a significant turnover of charophyte floras, since it involved the extinction of one important Mesozoic family, the Clavatoraceae, and renovation in a modern charophyte family, the Characeae, while the Porocharaceae were also strongly affected, since they became extinct shortly after the crisis. FEIST *et al.* (2005) considered that the crisis also represented a significant extinction within the characeans, which these authors evaluated as a loss of 40% of the genera. However, these conclusions need to be modified, mostly because by the end of the Cretaceous the clavatoraceans and porocharaceans were in fact represented by only a few species. Besides, the presumed extinction of genera of the Characeae at the boundary is less significant when we introduce the equivalences of fossil genera with modern characean genera as proposed by SOULIÉ-MÄRSCH (1989).

Palaeogene Iberian charophytes. During the Palaeogene, the collision between the Iberian plate and the European plate associated with the counter-clockwise rotation of Iberia resulted in the progressive rise of the Pyrenees, which probably reached their complete shape by the Oligocene (23-33.9 million years ago). As a consequence, the Iberian floras were separated from other European floras by an orographic barrier (ANADÓN *et al.* 1992). After the Palaeocene (56-66 million years ago) thermal maximum and during the Eocene (23-56 million years ago), the climate was tropical (warm and wet) to become subtropical (cooler and drier) in the Oligocene (ZACHOS *et al.* 2001).

During the Palaeogene (23-66 million years ago), the charophyte floras from Iberia and Western Europe were dominated by a combination of modern characean genera,

Sphaerochara Mädlér, *Chara* Linnaeus, *Lamprothamnium* Groves, *Nitellopsis* Hy and *Lychnothamnus* Ruprecht (sometimes called in the fossil record *Rhabdochara* Mädlér and *Stephanochara* Grambast), with other genera, now extinct, such as *Harrisichara* Grambast, *Maedleriella* Grambast or *Gyrogona* Lamarck ex Lamarck (Fig. 4). All of them display highly mineralised gyrogonites, with thick walls and a wide array of ornamentation features, such as tubercles, crests, nodules or a combination of these types. A second family, the Raskyellaceae, was also abundant in some facies, mainly in coastal lakes. This family first occurs in the Upper Cretaceous but in Iberia is not abundant until the Eocene (23-56 million years ago). It is characterised by presenting gyrogonites similar to the ancestral stock of porocharaceans, but with the apex obturated by a five-celled operculum.

Most of the charophyte floras from the Palaeogene (23-66 million years ago) of the Iberian Peninsula have been recorded in the Ebro basin, but there are many other Eocene records in places throughout the peninsula, such as the Iberian Chain near Teruel (ADROVER *et al.* 1982), the Balearic Islands, at the time connected with the peninsula (MARTÍN-CLOSAS & RAMOS 2005), or the Asturian basin in northern Spain (MARTÍN-CLOSAS 1991). The floras from the eastern margin of the Ebro basin have been studied more intensively, already since the second half of the past century (COLOM *et al.* 1970; ANADÓN & FEIST 1981, CHOI 1989; ANADÓN *et al.* 1992; FEIST *et al.* 1994). From the Palaeocene (56-66 million years ago) to the Miocene (5.3-23 million years ago), the record is almost uninterrupted, providing an excellent base on which to elaborate a biozonation that is only in part similar to that of other European basins, such as the Paris-English basin, and helping to develop the consensus European charophyte biozonation proposed by RIVELINE *et al.* (1996). Parts of this biozonation were modified later (MARTÍN-CLOSAS *et al.* 1999b) and calibrated to the global polarity time scale with the aid of magnetostratigraphy (SANJUAN *et al.* 2014).

From the biogeographic point of view, the Iberian charophytes have been studied in the Upper Eocene-Lower Oligocene interval (28.1-37.8 million years ago). In this period, the charophyte floras were less diversified and showed some differences in the morphology of gyrogonites, which are smaller and less calcified than those from the Paris-English basin (SANJUAN & MARTÍN-CLOSAS 2015). This is thought to be related to the shortness of life cycles in shallow temporary lakes in a relatively more arid environment. Endemism occurs during particular time intervals and is represented by very abundant and well-distributed species, ones such as *Nodosochara jorbae* Choi, in the Upper Eocene and Lower Oligocene, i.e., 28.1-37.8 million years ago (ANADÓN *et al.* 1992; FEIST *et al.* 1994; SANJUAN & MARTÍN-CLOSAS 2012, 2014). Additionally, the Iberian Peninsula contains the first record of *Nitellopsis merianii* (A. Braun ex Unger) worldwide, already in the

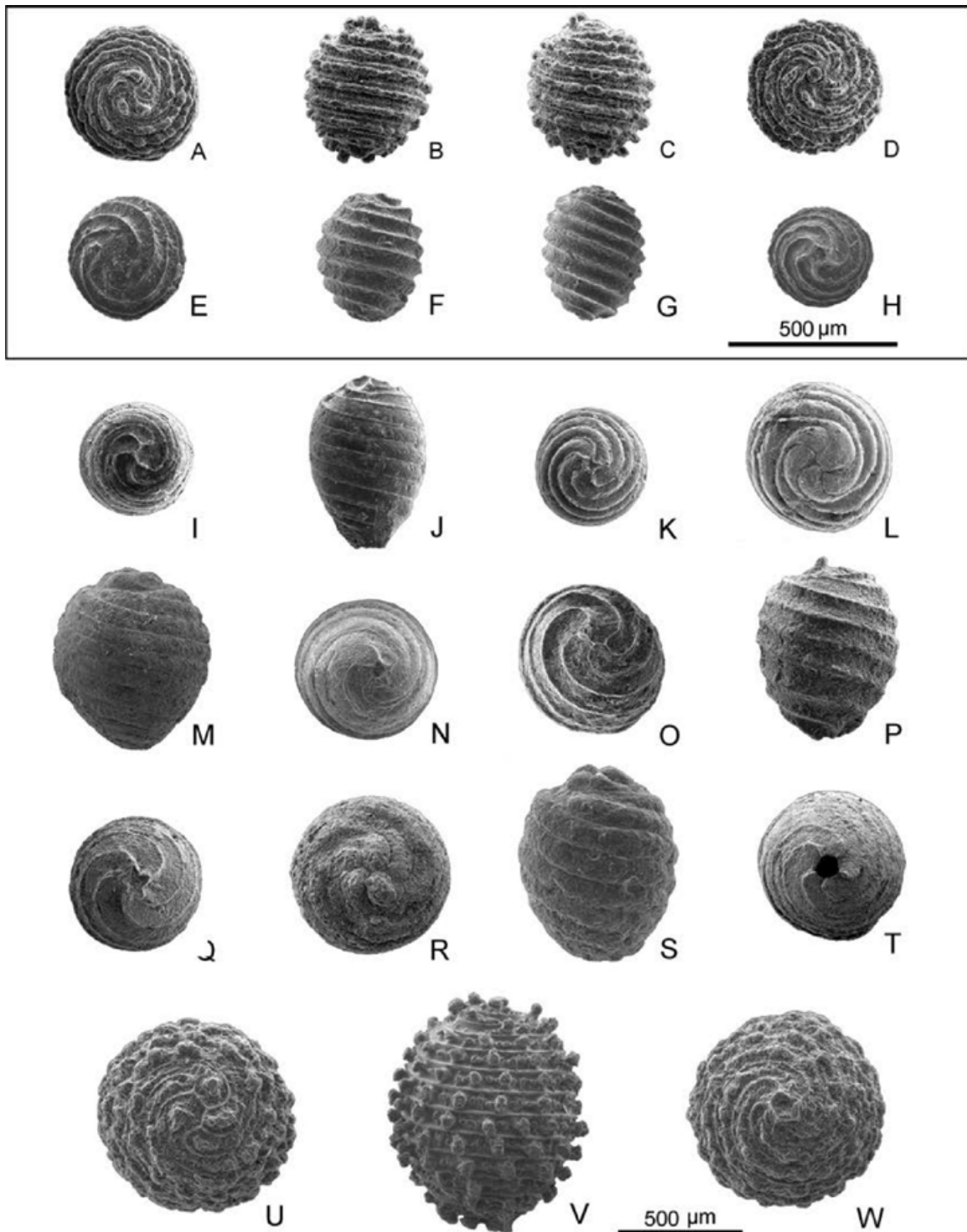


Fig. 4. Most common Upper Eocene charophyte assemblages from the Artés Formation, Ebro Foreland Basin. A–D, *Sphaerochara labellata* Feist & Ringede. A, apical view. B, lateral view, C, lateral view and D, basal view. Samples from TC-28, Torre Casanova section. E–H, *Chara artesica* Sanjuan & Martín-Closas. E, apical view, F, lateral view, G, lateral view and H, basal view. Samples from TC-9, Torre Casanova section. I–K, *Lychnothamnus longus* Choi. I, apical view, J, lateral view and K, basal view. Samples from RB-24, Rubió section. L–N, *Nodosochara jorbae* Choi. L, apical view, M, lateral view and N, basal view. Samples L and N from SBR-2, Sobremunt road section and sample M from Oristà section. O–Q, *Lychnothamnus stockmansii* Grambast. O, apical view, P, lateral view, Q, basal view. Samples from TC-31, Torre Casanova section. R–T, *Lychnothamnus vectensis* Groves. R, apical view, S, lateral view and T, basal view. Sample R from RB-3, Rubió section, sample S from SP-18 and sample T from SP-4, both from Santpedor section. U–W, *Harrisichara tuberculata* (Lyell). U, apical view, V, lateral view and W, basal view. Samples U and W from MO-1, Moià section and sample V from SO-2, Santa Maria d'Oló. Figure modified from SANJUAN & MARTÍN-CLOSAS 2012, 2014.

uppermost Eocene, the indicated species later colonising the whole of Eurasia during the Oligocene and Miocene, i.e., 5.3-33.9 million years ago (SOULIÉ-MÄRSCHÉ *et al.* 1997; SANJUAN & MARTÍN-CLOSAS 2015) and occurring as an exceptional find in North Africa (SOULIÉ-MÄRSCHÉ *et al.* 2002). All these aspects suggest that the isolation of Iberia represented not only a source of endemism, but also a factory of new species that later could enrich the Eurasian charophyte floras.

Neogene and Quaternary Iberian charophytes. The Miocene (5.3-23 million years ago) was marked on the Iberian Peninsula by a renewed development of rift basins, in part due to opening of the Mediterranean seafloor and definition of the present eastern coast of the Iberian plate. The coastal rift basins of Eastern Spain and the Balearic Islands were mainly related to this event. However, the large Ebro, Duero and Tagus basins and the smaller intramontane basins from the Iberian Chain also show a good record of Miocene deposits, mostly in lacustrine facies rich in charophytes. The general climatic evolution during the Neogene (2.6-23 million years ago) was a progressive trend towards an icehouse world, i.e., a decrease of temperatures and of atmospheric pCO₂, with the exception of the lower and middle Miocene (11.6-16 million years ago), when the temperature peaked again. These climatic trends determined that charophyte fructifications became less well-calcified and represented an impoverished flora during the Neogene in comparison with previous geological times. The European Neogene assemblages were mainly composed of extant genera, with rare exceptions, mainly at the beginning of the Miocene.

Studies on the Neogene (2.6-23 million years ago) charophyte flora from Iberia are relatively limited in comparison to what is known from the Cretaceous and Palaeogene, and the conclusions we can draw from this preliminary knowledge are probably biased and provisional. What may be the first fossil charophyte ever reported from Spain was "*Chara*" *aragonensis* A. Braun, from the Miocene (5.3-23 million years ago) of Libros (Teruel), described by UNGER (1850). In any case, this is the first fossil known from Aragon, as recently indicated by MOLINER (2015). The following is intended as a summary of the currently available, relatively scattered publications on Neogene charophytes from the Iberian Peninsula.

a) Catalan Coastal Chain. The charophyte flora from the Mediterranean Neogene depressions has been the subject of short publications mainly presenting the results of stratigraphic and sedimentological studies and geological maps. Unpublished information suggests that lacustrine facies were dominated by *Chara*, while *Lamprothamnium priscum* Castel & Grambast dominated coastal wetlands from the Penedés basin.

b) Pyrenees. In contrast to the coastal basins, an intramontane basin in the Pyrenees, called La Cerdanya

basin, yielded monospecific assemblages of *Lychnothamnus barbatus megalicarpus* (SOULIÉ-MÄRSCHÉ & MARTÍN-CLOSAS 2003) in the upper Miocene (SOULIÉ-MÄRSCHÉ & MARTÍN-CLOSAS 2003). They were shown to be good indicators of the trophic evolution of this lake (MARTÍN-CLOSAS *et al.* 2006)

c) Ebro basin. The basal Miocene of the Ebro Basin was studied by ANADÓN *et al.* (1992) and FEIST *et al.* (1994), mainly from the biostratigraphic viewpoint. However, this basin still has a high potential for the study of Neogene charophytes. For instance, ANADÓN *et al.* (2002) showed charophyte thalli to be of interest for palaeoenvironmental reconstruction of the Pliocene (2.6-5.3 million years ago) Villarroya Lake.

d) Intramontane basins in Central Spain. JULIÁ DE AGAR (1991) described a rich charophyte flora from the upper Oligocene-lower Miocene (16-28.1 million years ago) of the Loranca basin (Cuenca), formed of the genera *Chara*, *Lychnothamnus*, *Nitellopsis*, *Hornichara* Maslov and *Sphaerochara*. In other basins of the Iberian Chain, charophytes have also been reported and appear to be represented by the same genera (LUDWIG 1987; ORTIZ *et al.* 1998).

e) Tagus and Duero basins. Little is known about the fossil record from the two largest Miocene (5.3-23 million years ago) basins of Iberia, the Duero and Tagus (Tajo) basins. SOULIÉ-MÄRSCHÉ (1978) reported a flora from the lower part of the Tagus basin (Póvoa de Santarém, Portugal), consisting of *Nitellopsis (Tectochara) etrusca* (Tongiorgi) and *Lychnothamnus duplicicarinatus* (Papp), that allowed attribution of the studied beds to the middle Miocene. ANTUNES *et al.* (1992) described a nice flora from the upper Miocene of the lowermost part of the Tagus basin. This flora was dominated by *Nitellopsis (Tectochara) etrusca*, *N. (T.) ginsburgi* Riveline and *Lychnothamnus barbatus antiquus* Soulié-Märsché in deposits of a permanent oxbow lake, while the assemblage of *Chara molassica* (Straub) and *L. barbatus antiquus* was more frequent in temporary lakes.

f) Balearic Islands. Charophytes have been reported mainly from the lowermost Miocene of Mallorca by COLOM (1967, 1983) and MARTÍN-CLOSAS & RAMOS (2005). These authors document an assemblage of *Lychnothamnus langeri* (Ettingshausen) and *Nitellopsis* sp. from the Sineu borehole.

The Quaternary charophytes (0-2.6 million years ago) from Iberia have been even less studied than their Miocene and Pliocene counterparts. The modern species *Lamprothamnium papulosum* (Wallroth) was reported from several Plio-Pleistocene brackish-water habitats in the province of Murcia (SOULIÉ-MÄRSCHÉ 1989). One paper useful for reference purposes is the study by ANADÓN *et al.* (1987) of the Pleistocene (0.01-2.6 million years ago) of the Guadix-Baza basin, in southern Spain, indicating charophytes to be of interest in determining oscillation of the lacustrine water table during important climatic changes.

CONCLUSIONS

The Iberian Peninsula contains a very rich fossil record of the interval from the Upper Jurassic to the Neogene. However, up to now only the Cretaceous and the Palaeogene charophytes have been studied in detail. For this time interval, the charophyte fossil record provides an international reference from the viewpoint of taxonomy, palaeoecology and biostratigraphy.

Upper Jurassic charophytes are best known from the Lusitanian basin in Portugal. The floras were dominated by porocharaceans, along with rare early characeans and clavatoraceans. Porocharaceans colonised almost all environments available, in contrast to later times, when they became relegated to brackish water.

The Lower Cretaceous of the Iberian Chain shows the greatest diversity of clavatoraceans worldwide and has allowed definition of gradualistic evolutionary lineages, which were the base of the Berriasian-Albian biozonation. As a matter of fact, during the Lower Cretaceous, the Iberian Island and other islands of the Mesogean Archipelago were the places of origin of most clavatoracean charophytes that later emigrated far away, sometimes becoming cosmopolitan.

Upper Cretaceous Iberian charophytes have been most studied in the south-central Pyrenean basins. They are of international interest in defining the non-marine Cretaceous-Palaeogene boundary based on charophytes. The floras show considerable palaeoenvironmental differences, allowing for the distinction of assemblages from brackish lagoons, permanent lakes or temporary ponds. In contrast, they exhibit great biogeographic homogeneity, being confined within the so-called Ibero-Armorican Island.

Palaeogene floras from Iberia have been extensively studied in the Ebro foreland basin. After the extinction of porocharaceans and clavatoraceans near the Cretaceous-Palaeogene boundary, rich characean assemblages dominated the non-marine environments. They already contained some modern genera such as *Chara*, *Nitellopsis*, *Lychnothamnus* and *Lamprothamnium*, along with many other genera that are now extinct, like *Maedleriella*, *Harrisichara*, *Nodosochara* or *Gyrogona*. The Eocene-Oligocene flora seems to be subject to latitudinal and facial control, with the presence of endemism and intraspecific polymorphism. However, some taxa achieved a progressive cosmopolitan distribution starting from the Iberian Peninsula during this period of time.

Neogene floras from Iberia have been most studied in small intramontane basins in the Iberian Chain and the Ebro foreland basin. They show for the first time a strong affinity with extant genera and species. However, conclusions are provisional, since only an extremely small part of the Neogene charophyte record from Iberia has been studied.

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 REZIME

Fosilni nalazi harofita na Iberijskom poluostrvu: sinteza

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Iberija je najpre bila ostrvo, a zatim, tokom najvećeg dela istorije Zemlje, poluostrvo Evrope. Ovo, zajedno sa dugotrajnim nemarinskim nalazima, čini da su fosili harofita dobro prezentovani i pokazuju značajne osobenosti. Zapravo, Iberijsko poluostrvo je jedan od naboljih regiona Evrope za proučavanje fosilnih nalaza harofita od jure do danas. Skupine harofita srednje i kasne jure su predstavljene u Lusitanijskom basenu (Portugal). One omogućavaju uočavanje dominacije familije Porocharaceae u mnogim sredinama pogodnim za harofite. Harofite iz donje krede su više istraživane u Iberijskom masivu, gde familija dostiže visoki diverzitet. Takođe, mnoge biozone evropskih harofita ovog perioda se baziraju na iberijskim klavatoraceama i imaju svoje stratotipove u Iberijskom masivu. Harofite gornje krede Iberijskog poluostrva su više proučavane u jugozapadnom delu Iberijskog masiva (Serranía de Cuenca) i u južnom delu Pirinejskog basena (Katalonija). Flore pokazuju značajnu sličnost sa onima iz južne Francuske, s obzirom da su oba regiona bila deo istog ostrva. Dokazi o harofitama gornje krede sa južnih Pirineja su značajni s obzirom da doprinose definisanju granice kreda-paleogen, zasnovane na harofitama iz Ager basena. Harofite iz paleogena sa Iberijskog poluostrva su najviše poznate iz studija posvećenim Ebro basenu, gde je predložena detaljna biozonacija eocena i oligocena. Skupine harofita su sastavljene od mešavine fosila i recentnih rodova i uključuju tako tipične evropske vrste, tako i endemične taksone. Neogene harofite sa Iberijskog poluostrva su slabo poznate, ali su brojne istraživanja urađena uglavnom u centralnoj Španiji i u Ebro basenu.

KLJUČNE REČI: harofite, Španija, Portugal, mezozoik, kenozoik