Charophyte communities in Barremian Iberian wetlands

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Abstract

A combined micropalaeontological, taphonomical and sedimentological study was carried out in the non-marine Barremian of the Maestrat Basin (E Iberian Chain) to elucidate the palaeoecology of Barremian charophytes. Understanding the palaeoecology of fossil charophytes is of prime importance for the accurate application of charophyte biozonations, since most species used as biostratigraphic markers and/or biozone index species are restricted to facies formed in a particular environment. Five charophyte biocoenoses were distinguished. (1) Charophyte association from freshwater alkaline lakes receiving low clastic input, mainly composed of \textit{Atopochara trivolvis} var. \textit{triquetra}, \textit{Clavator harrisii}, \textit{Ascidiella stellata}, and \textit{A. triquetra}. The thalli known as \textit{Munieria grambastii}, corresponding to \textit{Clavator utricles}, were extremely abundant in the shallowest facies of the lake margins, and \textit{Hemiclavator}-rich populations were also locally dominant. (2) An association characteristic of freshwater alkaline lakes with high clastic input was mainly composed of \textit{Echinochara lazarii}, \textit{Globator maillardii} var. \textit{trochiliscoides}, \textit{A. trivolvis} var. \textit{triquetra}, \textit{Hemiclavator neimongolensis} var. \textit{neimongolensis}, and locally also \textit{Clavator calcitrapus}. (3) Monospecific populations of \textit{Porochara maestratica} thrived in brackish settings with little clastic influence, whereas (4) monospecific \textit{E. lazarii} populations thrived in clastic-influenced brackish settings. (5) A charophyte association grew in lakes that developed in mudflat to floodplain environments and was mainly constituted by \textit{E. lazarii}, \textit{A. trivolvis} var. \textit{triquetra}, and \textit{C. harrisii} var. \textit{harrisii} and var. \textit{reyi}. Accordingly, the palaeoenvironmental conditions inferred indicate that most of the charophyte species were controlled by (i) bathymetry, (ii) clastic content in the sedimentary environment and (iii) salinity. The stratigraphic succession studied shows an upwards increase in clastic content from the base to the top, which is associated with the more humid period recorded along the margins of the Tethys and the Boreal realm during the early Barremian–early late Barremian. In consequence, those species restricted to clastic-poor settings are constrained to the lower part of the section, whereas those taxa that were able to thrive in clastic-rich settings persisted throughout the entire section. This observation establishes a link between the changes observed in the charophyte floras recognized and the environmental changes that occurred during the Barremian in western Europe.

Keywords Charophyta · Early Cretaceous · Maestrat Basin · Charophyte palaeoecology · Lacustrine carbonate facies · Biostratigraphy

Introduction

Charophyte remains, including thalli and fructifications (utricles and gyrogonites), are among the most abundant components of Early Cretaceous non-marine marls, clays and limestones of the western Tethys (e.g., Martin-Closas and Diéguez 1998; Climent-Domènech et al. 2009; Trabelsi et al. 2016). Three charophyte families coexisted during the Early Cretaceous, the Porocharaceae, Characeae, and Clavatoraceae, with the last being the most common and abundant in the Tethyan Domain (e.g., Martin-Closas and Grambast-Fessard 1986; Schudack 1993; Martin-Closas 2000; Trabelsi et al. 2016; Pérez-Cano et al. 2020). In view
of their high specific diversity and evolutionary rates, clavatoracean fructifications (utricles) found in marls and clays have been extensively used as biostratigraphic markers in the continental record (e.g., Grambast 1974; Riveline et al. 1996; Martín-Closas et al. 2009; Pérez-Cano et al. 2022).

Despite extensive taxonomic knowledge of clavatoracean morphology and its widespread biostratigraphic application in the Early Cretaceous record, the paleoenvironmental distribution of most species is still poorly known or understood. Previous palaeoecological studies of Early Cretaceous charophytes in general and clavatoraceans in particular have usually been limited to a few genera (Martín-Closas and Grambast-Fessard 1986; Schudack 1993) or a few species (e.g., Vicente and Martín-Closas 2013). Palaeoecological studies carried out in the Campanian–Danian of the Pyrenees (Vicente et al. 2015, 2016) and the Eocene–Oligocene of the Ebro Basin (Sanjuan and Martín-Closas 2012) have demonstrated that charophyte palaeoecology is of major importance in charophyte biostratigraphy, as species that are useful for biostratigraphic characterization of the non-marine record may be restricted to particular facies. The aforementioned studies also show that species with a more restricted biostratigraphic distribution usually evidence more stringent palaeoecological requirements, being absent in stratigraphic successions that do not record the particular facies in which the species preferably thrived.

The present study was carried out in a continuous early Barremian to early late Barremian section from the Maestrat Basin (E Iberian Chain) with the aim of determining the palaeoecology of Barremian charophytes. To this end, a combined sedimentological and taphonomical study was performed of charophyte-rich marls and clays, together with a study of charophyte-rich microfacies from limestones. A better understanding of the palaeoecology of Barremian charophyte species, mainly those used as index species and/or as biostratigraphic indicators, will improve the precision and accuracy of Barremian charophyte biozonation. Moreover, a taphonomic and palaeoecological characterization of the Barremian charophyte associations will provide a tool to perform more detailed palaeoenvironmental reconstructions of coeval non-marine settings.

**Geological setting**

The Maestrat Basin is located in the eastern Iberian Chain (Fig. 1A). During the Late Jurassic and Early Cretaceous, basin evolution was mainly controlled by a rifting process, which recorded three discrete rift/post-rift stages (Salas et al. in Martín-Chivelet et al. 2019). These are (1) Kimmeridgian–Berriasian tectonic rifting, mainly related to the opening of the North Atlantic sea floor, (2) late Berriasian–late Hauterivian post-rift, in which the creation of depositional space was mainly controlled by thermal subsidence, and (3) Barremian–early Albian rifting, which was mainly associated with the opening of the Bay of Biscay (Tugend et al. 2015). Listric faults and local uplift shoulders produced a clear division of the Maestrat Basin into several smaller sub-basins (Fig. 1B; Salas and Guimerà 1996; Salas et al. 2001; Salas et al. in Martín-Chivelet et al. 2019). The present-day structure and topographic relief are the result of tectonic inversion of the Mesozoic structures, which occurred during the Alpine Orogeny, lasting from the late Eocene to the early Miocene (e.g., Guimerà 2018; Nebot and Guimerà 2018).

The Herbers-Mas de Petxí section studied here crops out very close to the Herbers Fault, on the northern margin of the Morella Sub-Basin (Fig. 1B, C). The Barremian record in this area is very continuous and thick (ca. 800 m), and can be subdivided into five formations named the Cantaperdius, Artoles, Morella, Cervera del Maestrat and Xert (Fig. 2), which comprise almost all the Barremian deposition in the Maestrat Basin (Bover-Arnal et al. 2016). During the Barremian, the Maestrat Basin was a gulf that opened onto the Tethys Ocean with different depositional settings and palaeoenvironmental conditions (Salas 1987). The base of the Barremian is characterized by the occurrence of lateritic deposits (e.g., Combes 1969; Salas 1987; Yuste et al. 2017) overlying the Hauterivian freshwater limestones of the Herbers Formation or older units (Fig. 2). Above the laterite, the Cantaperdius Formation is mainly built up of lacustrine and palustrine carbonates and reaches a thickness of ~400 m on the northern margin of the Morella Sub-Basin. This lithostratigraphic unit passes laterally and vertically to the shallow-marine marls and limestones of the Artoles Formation (Fig. 2). In the central part of the basin, the Artoles Formation is ~700 m thick, whereas at the margins its thickness decreases to ~200 m (Salas 1987; Salas et al. 2001).

The upper part of the Artoles Formation changes laterally and vertically to the Morella Formation (Fig. 2), which consists of red and grey clays and cross-bedded sandstones and contains abundant dinosaur remains (e.g., Gasulla et al. 2015). These deposits have been attributed to a tidal plain or mudflat environment (e.g., Canérot et al. 1982; Gàmez et al. 2003) and in turn, they pass laterally and vertically to the coastal and shallow-marine deposits of the Cervera del Maestrat Formation (Fig. 2; Salas 1987; Bover-Arnal et al. 2016). Above, the latest Barremian marine carbonates rich in orbitolinids of the Xert Formation occur (Canérot et al. 1982; Bover-Arnal et al. 2016).

The lithostratigraphic units rich in charophyte remains studied here are the Cantaperdius, Artoles, and Morella formations (Fig. 2). The age of this succession is early Barremian–early late Barremian, based on charophyte biostratigraphy and strontium-isotope stratigraphy (Martín-Closas 1989; Martín-Closas and Salas 1994; Pérez-Cano et al. 2022).
Materials and methods

The present study was carried out at Herbers-Mas de Petxí section (base 40º 42’ 39” N, 0º 0’ 36” W; top 40º 42’ 34” N, 0º 0’ 30” E), which is a 690 m thick complete section of Barremian non-marine facies (Supplementary material 1). It crops out on the north-eastern margin of the Maestrat Basin (Fig. 1C). One hundred and twelve limestone beds were sampled from the Cantaperdus, Artoles, and Morella formations for microfacies analysis. For each sample, two 30 µm thick thin sections were made, one parallel and the other perpendicular to the stratification. This methodology enables a better observation of elongate components, such as charophyte thalli. The thin sections were studied under a Motic BA 310 petrographic microscope and photographed using Motic Images Plus 2.0 software.

Marls from the same formations were systematically sampled to study the micropalaeontological assemblages, especially charophytes (Fig. 3). For each interval, around 3 kg of marls were collected. The samples were submerged in a solution of water, sodium carbonate (Na₂CO₃), and hydrogen peroxide (H₂O₂) for several days to disaggregate the marls, deflocculate clay minerals, and eliminate organic matter. Later, the samples were wet-sieved using three different mesh sizes of 1000, 500 and 200 µm. Once the samples were dried, microfossils (charophyte fructifications and thalli, ostracods and other associated microfossils) were handpicked under a Wild M5A binocular microscope using magnifications of × 12 and × 25 at the Departament de Dinàmica de la Terra i de l’Oceà (Universitat de Barcelona). Selected fossil remains were photographed with a Quanta 200 SEM at the Centres Científics i Tecnològics de la Universitat de Barcelona (CCiTUB). The figured specimens and thin sections with figured specimens have been deposited in the Museu Geològic del Seminari Conciliar de Barcelona (MGSCB) with reference numbers MGSCB...
Palaeoecological inferences were drawn following a taphonomic analysis of the charophyte remains and associated microfossils combined with a sedimentological study. This methodology has been demonstrated as useful to infer the palaeoecology of charophyte species (e.g., Sanjuan and Martín-Closas 2012; Vicente et al. 2016). The taphonomic analysis made it possible to distinguish between autochthonous/parautochthonous and allochthonous fossils in the palaeontological association. Two criteria were applied in the taphonomic analysis: (1) fossil abrasion and fragmentation and, in the case of charophytes, (2) the association of fructifications and thalli attributed to the same species, which has been considered as evidence of absence of selection. The relative abundance of fructifications was obtained after analyzing ca. 100 g of sample, ca. 50 g from the > 500 µm–1 mm mesh size sample and ca. 50 g of the > 200–500 µm mesh size sample. Supplementary materials 2 and 3 show the total number of charophyte fructifications collected from each sample and the relative abundance of each taxon in each sample, respectively.

Results

Based on the lithology, sedimentary features and microfossils, mainly charophytes, 19 different facies (taphofacies and/or biofacies) were identified in four major lithostratigraphic intervals in the Herbers-Mas de Petxí section (Figs. 3, 4A–D; Tables 1, 2). These facies are located above a laterite characteristic of the base of the Barremian in the Maestrat Basin (Fig. 5A) and are arranged into different parasequences (Ps) (Ps1–Ps8). The repetition and alternation of these eight parasequences builds up the studied section. The definition of ‘parasequence’ used here follows Spence and Tucker (2007) who proposed applying this term to all types of meter-scale sedimentary packages characterized by a succession of facies.

Clavatoracean-rich limestones and marls from the Cantaperdius Formation

Description of facies and their charophyte assemblages

1) Clavatoracean-rich marls (cM) contain a micropalaeontological assemblage mainly composed of charophyte thalli and fructifications (utricles and gyrogonites), and ostracods (Table 2).

Neither the charophyte assemblages nor the preservation of charophyte remains within the marls is homogeneous throughout the section, and vertical changes are apparent in the taxonomic composition of charophyte assemblages (Tables 2, 3; Supplementary materials 2–3). In the lower part of the Cantaperdius Formation (11–274 m; Fig. 4A; Table 3), this facies is characterized by the occurrence of thin marl beds with charophyte assemblages composed of abundant, well-preserved utricles of *Atopochara trivolvis* var. *triquetra*, *Clavator harrisii* var. *dongjingensis* and var. *harrisii*, *Ascidiella stellata* var. *stellata* and var. *lata* and *A. triqueta*, and gyrogonites of aff. *Mesochara harrisii* (Fig. 3). The utricles are associated with abundant, long portions of thalli belonging to *Favargerella aquavivae*, *Clavatoraxis* sp., and *Munieria grambastii* (Fig. 3; Table 3). The *Ascidiella* utricles are sometimes found attached to the *F. aquavivae* thalli, while *C. harrisii* var. *dongjingensis* and var. *harrisii* are found attached to *Clavatoraxis* sp. thalli,
Fig. 3 Levigated remains of charophytes from the Herbers-Mas de Petxí section. A, B Porochara maestratica (sample H8). A Lateral view (specimen no. 85579 MGSCB); B Apical view (specimen no. 85580 MGSCB); C aff. Mesochara harrisii. (lateral view; sample H39; specimen no. 85585 MGSCB); D Echinochara lazarii (outer series of utricle; sample H88; specimen no. 85601 MGSCB); E Globator maillardii var. trochiliscoides (lateral view; sample H27; specimen no. 85602 MGSCB); F Globator maillardii var. biitricularis (lateral view; sample H44; specimen no. 85605); G Atopochare trivolvis var. triquetra (lateral view; sample H51; specimen no. 85608 MGSCB); H Atopochare trivolvis var. trivolvis (lateral view; sample H94; specimen no. 85611 MGSCB); I Clavator grovesii var. juquanensis (lateral view; sample H95; specimen no. 85614 MGSCB); J Clavator harrisii var. dongjingensis (lateral view; sample H38; specimen no. 85617 MGSCB); K Clavator harrisii var. harrisii (lateral view; sample H38; specimen no. 85620 MGSCB); L Clavator harrisii var. reyi (lateral view; sample H76; specimen no. 85622 MGSCB); M Clavator calcitrapus var. jiangluoensis (apical view; sample H38; specimen no. 85623 MGSCB); N Clavator calcitrapus var. calcitrapus (apical view; sample H51; specimen no. 85626 MGSCB); O Ascidiella stellata var. stellata (lateral view; sample H6; specimen no. 85677); P Ascidiella stellata var. lata (lateral view; sample H44; specimen no. 85632 MGSCB); Q Ascidiella triqueta (apical view; sample H27; specimen no. 85637 MGSCB); R Ascidiella cruciata (apical view; sample H94; specimen no. 85639 MGSCB); S Hemiclavator adnatus (lateral view; sample H12; specimen no. 85642 MGSCB); T Hemiclavator neimongolensis var. posticecaptus (lateral view; sample H12; specimen no. 85645 MGSCB); U Hemiclavator neimongolensis var. neimongolensis (adaxial view; sample H39; specimen no. 85647 MGSCB); V Pseudoglobator paucibracteatus (lateral view; sample H96; specimen no. 85659 MGSCB); W Charaxis spicatus (sample H124; specimen no. 87440 MGSCB); X Munieria grambastii (sample H5; specimen no. 85656 MGSCB); Y Clavatoraxis sp. (sample H8; specimen no. 85658 MGSCB); Z Favargerella aquavivae (sample H7 specimen no. 85659 MGSCB). Scale bars equal 250 µm.
Fig. 4 A Stratigraphic log of the lower part of the Herbers-Mas de Petxí section (0–280 m), including the facies recognized. Facies codes are explained in the text. See legend in (D). B Stratigraphic log of the middle part of the Herbers-Mas de Petxí section (280–450 m), showing the facies recognized. Facies codes are explained in the text. See legend in (D). C Stratigraphic log of the upper part of the Herbers-Mas de Petxí section (450–690 m), showing the facies recognized. Facies codes are explained in the text. See legend in (D). D Legend for Figs. 4A–C and 8
### Fig. 4 (continued)
indicating autochthony. *Porochara maestratica* is locally abundant (Table 3), and it is interpreted as parautochthonous in this facies. *Globator maillardii* var. *trochiliscoides* is usually rare in the lowermost part of the Cantaperdius Formation, where it locally occurs superficially eroded and thus, is interpreted as paraautochthonous. The larger populations of *G. maillardii* var. *trochiliscoides* are found in the thicker marl beds occurring between 100 and 187 m of the stratigraphic section (Fig. 4A; Table 3), associated with a few utricles of *Echinochara lazarii* and portions of *Charaxis spicatus* (Table 3). The latter two taxa belong to the same charophyte plant (Pérez-Cano et al. 2020). *G. maillardii* var. *trochiliscoides* and *E. lazarii* are interpreted as being autochthonous in these thicker marl beds. Abundant, well-preserved *Hemiclavator adnatus* and *Hemiclavator neimongolensis* var. *posticecaptus* are limited to marls between meters 129 and 130 of the section (Table 3; Supplementary materials 2–3). These utricles are found attached to portions of *Clavatoraxis* sp., suggesting autochthony.

The charophyte assemblage of marls in the upper part of the Cantaperdius Formation (274–366 m; Fig. 4B; Table 4) consists of abundant, well-preserved utricles of *E. lazarii*, *G. maillardii* var. *trochiliscoides* and var. *biutricularis*, *A. trivolvis* var. *triquetra*, *C. harrisii* var. *harrisii*, and
Table 1  Taxonomy list of charophyte species, fructifications and thalli, described in the Herbers-Mas de Petxí section

| CHAROPHYTE FRUCTIFICATIONS                        |
|---------------------------------------------------|
| **Family Pororcharaceae (Grambast) emend. Schudack** |
| Genus Pororcha (Müller) emend. Schudack           |
| *Pororcha maestratica* (Martín-Closas et Grambast-Fessard) nov. comb. Schudack |
| **Family Characeae (Richard ex C. Agardh) emend. Martín-Closas et Schudack** |
| Genus Aclistochara Peck                           |
| *Aclistochara* sp.                               |
| Genus Mesochora Grambast                         |
| aff. *Mesochora harrisii* (Müller) Shaikin        |
| **Family Clavatoraceae Pia**                      |
| **Subfamily Atopocharoidae (Grambast) emend. Martín-Closas ex Schudack** |
| Genus Echinochara (Peck) emend. Pérez-Cano, Bover-Arnal et Martín-Closas |
| *Echinochara lazarii* (Martín-Closas) Mojon ex Pérez-Cano, Bover-Arnal et Martín-Closas |
| Genus Globator Grambast                          |
| *Globator maillardi* var. *trochilisoides* (Grambast) Martín-Closas |
| *Globator maillardi* var. *biotricularis* Vicente et Martín-Closas |
| Genus Atopochora Peck                            |
| *Atopochora trivolvis* var. *triquetra* (Grambast) Martín-Closas |
| **Subfamily Clavatoroidae (Grambast) emend. Martín-Closas ex Schudack** |
| Genus Clavator (Reid et Groves) emend. Martín-Closas ex Schudack |
| *Clavator grovesii* var. *jiuquanensis* (S. Wang) Grambast emend. Martín-Closas |
| *Clavator harrisii* var. *dongjingesis* (Hu et Zeng) Martín-Closas |
| *Clavator harrisii* var. *harrisii* Peck           |
| *Clavator harrisii* var. *reyi* (Grambast-Fessard) Martín-Closas |
| *Clavator calcitrapus* var. *jiangluoensis* (Z. Wang et Z.W. Li) Pérez-Cano, Bover-Arnal et Martín-Closas |
| *Clavator calcitrapus* var. *calcitrapus* (Grambast) Martín-Closas ex Schudack |
| Genus Asciidiella (Grambast) emend. Martín-Closas ex Schudack |
| *Asciidiella stellata* var. *stellata* (Martín-Closas et Grambast-Fessard) Martín-Closas ex Schudack |
| *Asciidiella stellata* var. *lata* Martín-Closas |
| *Asciidiella triquetra* (Grambast) Martín-Closas |
| *Asciidiella cruciata* (Grambast) Martín-Closas ex Schudack |
| Genus Hemiclavator Wang et Lu                     |
| *Hemiclavator adnatus* (Martín-Closas et Grambast-Fessard) Schudack |
| *Hemiclavator neimongolensis* var. *posticecaptus* (Martín-Closas et Grambast-Fessard) Martín-Closas |
| *Hemiclavator neimongolensis* var. *neimongolensis* Wang et Lu |
| Genus Pseudoglobator Grambast                     |
| *Pseudoglobator paucibracteatus* Martín-Closas et Grambast-Fessard |

| CHAROPHYTE THALLI                                  |
|---------------------------------------------------|
| Genus Charaxis Harris                              |
| *Charaxis spicatus* (Martín-Closas et Diéquez) emend. Pérez-Cano, Bover-Arnal et Martín-Closas |
| *Charaxis* sp.                                     |
| Genus Clavatoraxis Martín-Closas et Diéquez       |
| *Clavatoraxis* sp.                                |
| Genus Favargerella Mojo                            |
| *Favargerella aquasiva*ae* Martín-Closas et Salas  |
| Genus Munieria Bistrický                           |
| *Munieria grambastii* Bystrický                    |
| Facies name                                                                 | Code | Sedimentary features                                                                 | Fossil assemblages                                                                 | Interpretation                                                                 |
|----------------------------------------------------------------------------|------|-------------------------------------------------------------------------------------|------------------------------------------------------------------------------------|---------------------------------------------------------------------------------|
| **Clavatoracean-rich limestones and marls from the Cantaperdus Formation** |      | Massive, 0.1–2.5 m thick. Color varies between grey and yellow                       | Mainly well-preserved clavatoracean utricles and thalli, and ostracods. Rarely broken or superficially eroded benthic foraminifera, dasycladaleans, molluscs, vertebrate teeth, and eggshells | Relatively deeper parts of freshwater lakes with clavatoracean meadows          |
| **Limestones rich in clavatoracean utricles and thalli**                  | cL   | Massive grey wackestones to packstones (Fig. 6A), 0.5–1 m thick. Locally rootmarks and ferruginous surfaces at top | Abundant and well-preserved clavatoracean thalli (Favargerella sp. and Clavatoraxis sp.) and utricles (Atopochara sp. and Asciella sp.). Occasionally ostracods and molluscs | Shallow freshwater lakes with clavatoracean meadows of *Atopochara* and *Asciella* |
| **Munieria grambastii-rich limestones**                                   | mL   | Massive wackestone and packstone limestones (Fig. 6B), 0.5–2 m thick. Color varies between grey and yellow. Intraclasts 2–5 mm across. Rootmarks and ferruginous surfaces (2 mm thick) at top | Long portions of *M. grambastii* thalli. Occasionally clavatoracean utricles, and small portions of *Favargerella* sp. and *Clavatoraxis* sp. and *Charraxis* sp. surrounded by a periphyton crust. *Only* *M. grambastii* is autochthonous | Lake margins with monospecific meadows of *M. grambastii*                        |
| **Limestones with porocharaceans**                                        | pL   | Massive grey wackestone–packstone limestones (Fig. 6C). Thickness up to 1 m          | Mainly well-preserved *Porochara* sp. gyrogonites. Less abundant utricles of *Echinochara* sp. and portions of *Charraxis spicatus*, ostracods, benthic foraminifera and dasycladaleans | Brackish coastal lakes with porocharacean meadows                               |
| **Limestones with porocharaceans and coated clavatoraceans**              | pccL | Massive packstones (Figs. 6D–F). 0.5–1.5 m thick. The color varies between dark grey to pale grey and red. Up to 2 mm thick ferruginous crusts at top | Mainly well-preserved *Porochara* sp. gyrogonites. Clavatoracean thalli and utricles surrounded by cyanobacterial growths. Less abundant dasycladaleans and miliolids | Shallow freshwater lakes with clavatoracean meadows changing to coastal brackish lakes with porocharacean meadows |
| **Oncoid-rich limestones**                                                | oL   | Up to 0.5 m thick massive dark grey mudstones to wackestones                        | >1 cm large irregular oncoids. Few small portions of charophyte thalli            | Slope areas of shallow lakes                                                    |
| Table 2 (continued) |
|---------------------|

### Sedimentary features

- Porocharacean-rich limestones and marls from the Artoles Formation
- Echinochara lazarii-rich marls and limestones from the Artoles Formation

### Fossil assemblages

- **Porocharacean-rich limestones and marls from the Artoles Formation**
  - Abundant but slightly eroded charophyte remains, few portions of ostracode carapaces, and benthic foraminifera. Less abundant Charophyceae thalli, fructifications, and rare dasycladaleans.
- **Echinochara lazarii-rich marls and limestones from the Artoles Formation**
  - Abundant well-preserved ostracode carapaces, rare portions of Charophyceae thelycormae, and well-preserved dasycladaleans.

### Code

- **pfM**
  - Massive pale grey and brownish marls. Thickness between 0.2 and 3 m.
- **pfL**
  - Massive pale grey wackestones and packstones (Fig. 9A–C), 1–2 m thick.
- **mfL**
  - Massive up to 1 m thick grey mudstones.
- **elGM**
  - Massive 1–3 m thick grey marls (Fig. 4B, C).
- **elRC**
  - Massive up to 1 m thick red clays (Fig. 4C).
- **meM**
  - Up to 14 m thick (commonly 1.5–4 m thick) massive grey marls.
- **tL**
  - 0.5 m thick massive yellowish mudstones (Figs. 4B, 10A). Locally capped by a ferruginous crust.
- **ocL**
  - Up to 2 m thick massive grey marls with intraclasts (Figs. 4C, 10B). Ferruginous crust at top, locally encrusted by oysters (meter 459 of the log, Fig. 4C; Suppl. material 1).

### Interpretation

- Marginal coastal area with low hydrodynamism. *P. maestratica* is parautochthonous. Euryhaline conditions.
- Low-energy areas in coastal marine settings populated by benthic foraminifera, ostracods, and dasycladaleans.
- Coastal brackish marshes with *E. lazarii* meadows exposed to sub-aerial conditions.
- Low-energy, shallow-marine areas with abundant terrestrially derived inputs and dominant infaunal taxa (Heteraster sp.).
- Shallow lakes and ponds in coastal areas populated by *E. lazarii* meadows. Euryhaline conditions.
| Facies name                                                                 | Code  | Sedimentary features                                                                                                                                                                                                 | Fossil assemblages                                                                                                                                                                                                 | Interpretation                                                                                      |
|---------------------------------------------------------------------------|-------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------|
| Finely laminated limestones with benthic foraminifera and cyanobacterial filaments | fcyL  | Up to 0.5 m thick (locally 7 m thick; Fig. 4C) pale grey mudstones. Intercalation of up to 5 mm thick micrite laminas with up to 1 mm thick packstone–grainstone bioclastic laminas                                                                                           | Micrite laminas with relics of calcified microbial filaments (10–20 µm across). Packstone–grainstone laminas include benthic foraminifera and bioclasts of bivalves and echinoids                                      | Microbial mats deposited in intertidal to supratidal settings subjected to storm events             |
| Limestones rich in bivalves and gastropods                                | bgL   | 0.5–4.5 m thick grey packstones and grainstones. Show hectometric lenticular morphologies and cross bedding (Fig. 5E; Supplementary material 1). Indurated top, showing bioerosion and, locally, encrusted oysters (log meters 527 and 534; Fig. 4C; Supplementary material 1) | Reworked mollusc shells (oysters and other bivalves, gastropods), dasycladaleans, benthic foraminifera, echinoid fragments. Intraclasts may contain charophyte thalli | Intertidal to shallow subtidal channels                                                              |
| Clavatoracean-rich clays from the Morella Formation                       | cGC   | Up to 6 m thick (commonly 1–1.5 m thick) massive clays with strong lateral continuity (Fig. 5F)                                                                                                                                 | Abundant and well-preserved to superficially eroded atopocharoid and clavatoroid utricles and long portions of charophyte thalli. Abundant and well-preserved ostracods and benthic foraminifera. Rare bioclasts of marine fossils | Clastic-influenced lakes and ponds near the marine shoreline populated by diverse clavatoracean meadows |
| Red clays with clavatoraceans                                            | cRC   | Up to 6 m thick beds, (commonly 1.5–2.5 m thick) massive red clays with strong lateral continuity (Fig. 5F) that may display mottling and rootmarks at top                                                                                       | Well-preserved to superficially eroded clavatoracean utricles (mainly C. harrisii), short portions of charophyte thalli, ostracods, benthic foraminifera. Rare bioclasts of marine fossils | Tidal flat to fluvial floodplain ponds with clavatoracean meadows temporarily exposed to sub-aerial conditions |
| Limestones with clavatoracean thalli and utricles                         | ctuL  | 0.3–1.5 m thick grey or ochre wackestones and packstones. Thicker beds have hectometric lateral continuity; thinner beds have decametric lateral continuity                                                                                           | Abundant and well-preserved clavatoracean thalli and utricles (mainly E. lazarii–C. spicatus), ostracods, rare benthic foraminifera and dasycladaleans                                                             | Alkaline lakes within floodplain settings populated by clavatoracean meadows sometimes dominated by E. lazarii |
Fig. 5 Field photographs of the Herbers-Mas de Petxí section. A Basal part of the Cantaperdius Formation, showing the basal laterite and the first lacustrine limestones above; B Characteristic marl–limestone succession of a limestone-dominated interval of the Cantaperdius Formation; C Characteristic marl–limestone succession of a marl-dominated interval of the Cantaperdius Formation; D Outcrop of the Artoles Formation showing the characteristic marl–limestone inter-bedding; E Large-scale cross-bedding exhibited by facies bgL (Echinochondra-richer marls and limestones); F Outcrop of the Morella Formation made up of Clavatoracean-rich clays and limestones showing an alternation between grey and red clays. Encircled hammer for scale (E and F).
Table 3  Relative abundance of charophyte species measured in the samples studied

| Lithostratigraphic position (m) | Sample | Charophyte fructifications | Charophyte thalli |
|--------------------------------|--------|-----------------------------|-------------------|
| 172                            | H28    | ![Symbol](image)            | ![Symbol](image)  |
| 171.5                          | H27    | ![Symbol](image)            | ![Symbol](image)  |
| 170–171                        | H26    | ![Symbol](image)            | ![Symbol](image)  |
| 169.5                          | H25    | ![Symbol](image)            | ![Symbol](image)  |
| 168.5                          | H24    | ![Symbol](image)            | ![Symbol](image)  |
| 163.75                         | H23    | ![Symbol](image)            | ![Symbol](image)  |
| 155.25                         | H21    | ![Symbol](image)            | ![Symbol](image)  |
| 147.5                          | H20    | ![Symbol](image)            | ![Symbol](image)  |
| 145                            | H19    | ![Symbol](image)            | ![Symbol](image)  |
| 135.25                         | H18    | ![Symbol](image)            | ![Symbol](image)  |
| 132.75                         | H17    | ![Symbol](image)            | ![Symbol](image)  |
| 131.25                         | H16    | ![Symbol](image)            | ![Symbol](image)  |
| 125.95                         | H15    | ![Symbol](image)            | ![Symbol](image)  |
| 125.85                         | H14    | ![Symbol](image)            | ![Symbol](image)  |
| 125.75                         | H13    | ![Symbol](image)            | ![Symbol](image)  |
| 125.25                         | H12    | ![Symbol](image)            | ![Symbol](image)  |
| 121.5                          | H11    | ![Symbol](image)            | ![Symbol](image)  |
| 101                            | H10    | ![Symbol](image)            | ![Symbol](image)  |
| 97.25                          | H8     | ![Symbol](image)            | ![Symbol](image)  |
| 95.5                           | H7     | ![Symbol](image)            | ![Symbol](image)  |
| 31–31.8                        | H6     | ![Symbol](image)            | ![Symbol](image)  |
| 10.5                           | H5     | ![Symbol](image)            | ![Symbol](image)  |
| 5.25                           | H4     | ![Symbol](image)            | ![Symbol](image)  |
| 1.5–1.75                       | H3     | ![Symbol](image)            | ![Symbol](image)  |
var. reyi, and *H. neimongolensis* var. neimongolensis. In addition, *Clavator calcitrapus* var. *jiangluoensis* and var. *calcitrapus* (Fig. 3) are also common but less abundant (Table 4; Supplementary materials 2–3). *E. lazarii* utricles are attached to their corresponding thalli, *C. spicatus* (Fig. 3), suggesting autochthony. The same interpretation is proposed for the utricles of *C. harrisii* var. *harrisii* and *H. neimongolensis* var. *neimongolensis*, which occur attached to thalli of *Clavatoraxis* sp. Thalli portions of *M. grambastii* are abundant and display up to 4 anatomically attached internodes, and are also interpreted as autochthonous remains. Other species such as *Asciella stellata* var. *lata*, *A. triquetra* and thalli portions of *F. aquavivae* are rare (Table 4; Supplementary materials 2–3), suggesting some type of biostratinomic or palaeoecological selection.

This facies is interpreted as having been formed by deposition of suspended mud through decantation processes in low-energy, relatively deeper lacustrine settings. The abundance and diversity of charophyte species and the taphonomic evidence suggests that rich clavatoracean meadows developed in these, mostly freshwater, lakes. However, the occurrence of rare and broken and/or superficially eroded dasycladaleans and benthic foraminifera (see Table 2) is interpreted as occasional marine influence, probably during higher tides or storms.

2) Limestones rich in clavatoracean utricles and thalli (*cL*) are characterized by the occurrence of long portions of charophyte thalli belonging to *Clavatoraxis* sp. (Figs. 6A, 7A–C; Supplementary material 4.1, Fig. A–E) and *Favargerella* sp. (Fig. 7D–F; Supplementary material 4.1, Fig. F–H). These thalli are usually associated with well-preserved atopocharoïd utricles (Supplementary material 4.2, Fig. A–C), such as *Atopochara* sp. (Fig. 7G, H), and clavatoroid utricles (Fig. 6A; Supplementary material 4.2, Fig. D–O). Some of these clavatoroid utricles were assigned to *Asciella* sp. based on their characteristic bract cell distribution in cross-section, with 2 bracts and the phylloid arranged 120º around the gyrogonite (Fig. 7I). Thalli and utricles are commonly

| Lithostratigraphy | Stratigraphic position (m) | Sample | Charophyte fructifications | Charophyte thalli |
|-------------------|---------------------------|--------|---------------------------|------------------|
| Porphyroseris aff. Mesoschara harrisii | 274 | H37 | [●●●●] | [●●●●] |
| Asterolophus sp. | 259.75 | H36 | [●●●●] | [●●●●] |
| Echinochara latai | 241 | H35 | [●●●●] | [●●●●] |
| G. milleri var. hochiroticuloides | 219.5 | H34 | [●●●●] | [●●●●] |
| G. milleri var. diffusior | 193.5 | H33 | [●●●●] | [●●●●] |
| A. tortuosa var. taquetia | 189 | H32 | [●●●●] | [●●●●] |
| C. harrisii var. harrisii | 184.5 | H31 | [●●●●] | [●●●●] |
| A. tortuosa var. stellata | 181 | H30b | [●●●●] | [●●●●] |
| A. tortuosa var. lata | 181 | H30a | [●●●●] | [●●●●] |
| F. aquavivae | 178 | H29b | [●●●●] | [●●●●] |
| C. harrisii var. rayi | 173 | H29a | [●●●●] | [●●●●] |

Relative abundance of charophyte fructifications

- [●●●●] > 50%
- [●●●●] 25–50%
- [●●●●] 10–25%
- [●●●●] 1–10%
- [●●●●] 0–1%

Qualitative abundance of charophyte thalli

- [●●●●] Abundant
- [●●●●] Frequent
- [●●●●] Rare

See Fig. 4A for the stratigraphic position of each sample. See supplementary materials 2 and 3 for further detail.
anatomically attached (Fig. 7J, K; Supplementary material 4.2, Fig. M–O), suggesting autochthony. Thalli portions and clavatoroid utricles are locally coated by up to 300 µm thick homogeneous cyanobacterial crusts. This coating is interpreted as having been formed by calcification of the periphyton (Martín-Closas 1999). Rare remains of thalli provisionally attributed to *Palaeonitella* aff. *trifurcata* (Martín-Closas et al. 2021) within cortoids are occasionally found in these limestones (Supplementary materials 4.1, Fig. I–L).
This facies is interpreted as having been formed in shallow lacustrine belts with clavatoracean meadows dominated by Atopochara sp., and clavatoroids, including Ascidiella sp. The utricles of these species are associated with their corresponding vegetative remains, i.e., Clavatoraxis sp. (for Atopochara sp. and many clavatoroids) and Favargerella sp. (for Ascidiella sp.).

3) Munieria grambastii-rich limestones (mL) are characterized by the dominant occurrence of long, well-articulated portions of Munieria grambastii internodes (Fig. 7M), rarely...
Fig. 7 Charophyte components of Clavatoracean-rich limestones from the Cantaperdus Formation. A Tangential section of Clavatoraxis sp. thallus (sample H10c; thin section no. 87447 MGSCB); B Longitudinal section of a Clavatoraxis sp. thallus (sample H7b; thin section no. 85665 MGSCB); C Transversal section through a Clavatoraxis sp. thallus (sample H10c; thin section no. 87446 MGSCB); D Tangential section of a Favargerella sp. branchlet (sample H10c; thin section no. 87449 MGSCB); E Longitudinal section of a Favargerella sp. branchlet (sample H10c; thin section no. 87447 MGSCB); F Transversal section of a Favargerella sp. node (sample H10c; thin section no. 87448 MGSCB); G Longitudinal section of a utricle belonging to Atopochara sp. (sample H6d; thin section no. 87443 MGSCB); H Transversal section of a utricle belonging to Atopochara sp. (sample H7B; thin section no. 85665 MGSCB); I Transversal section of an Asciidiella sp. utricle showing sections of bracts (b) and phylloids (p) (sample H20c; thin section no. 85670 MGSCB); J Longitudinal section of a clavatoroid utricle attached to a Clavatoraxis sp. branchlet (sample H20c; thin section no. 85670 MGSCB); K Clavatoroid utricle (u) attached to a Favargerella sp. branchlet (sample H7c; thin section no. 87444 MGSCB); L Clavatoroid utricle in facies mL (sample H47b; thin section no. 87455 MGSCB); M Longitudinal section of Munieria grambastii (sample H5b; thin section no. 87441 MGSCB); N Longitudinal section of a porocharacean gyrogonite (sample H35b; thin section no. 87453 MGSCB); O Oblique section through the basal part of a porocharacean gyrogonite. The arrow indicates the basal plate (sample H35b; thin section no. 87454 MGSCB); P Transversal section of a Charaxis sp. thallus (sample H35b; thin section no. 87454 MGSCB); Q Transversal section of a Clavatoraxis sp. thallus coated with a microbial crust (sample H20c; thin section no. 87452 MGSCB); R Clavatoroid utricle coated with microbial Thickets (arrowhead) (sample H7c; thin section no. 87445 MGSCB). Scale bar A–R equals 250 µm
associated with clavatoroid utricles (Fig. 7L). A few portions of *Favargerella* sp. and *Clavatoraxis* sp. thalli coated with periphyton crusts are sometimes found in addition to *M. grambastii*.

Facies *mL* is interpreted as having been formed by the deposition of in-situ bioclastified remains of *M. grambastii*, which would have formed almost monospecific meadows. The occurrence of intraclasts and rootmarks (see Table 2) suggests that these meadows occurred near the lake shores.

4) Limestones with porocharaceans (*pL*). This facies is not common in the studied section. The charophyte assemblage is composed of abundant well-preserved porocharaceous gyrogonites (Fig. 7N–O) showing the characteristic multipartite basal plate, which have been attributed to *Porohara* sp. and are associated with their possible thalli, *Charaxis* sp. (Fig. 7P). A few well-preserved utricles of *Echinochorda* sp. and portions of their corresponding thalli, *Charaxis spicatus* (Fig. 6C), also occur. This co-occurrence of thalli and utricles suggests that these charophytes are autochthonous in the depositional setting. Cypridean and non-cypridean ostracods, benthic foraminifera and dasycladalean portions are also present (Fig. 6C; Table 2).

Facies *pL* has been interpreted as formed in brackish lakes, as attested by the occurrence of dominant assemblages of genus *Porohara* (e.g., Martín-Closas and Grambast 1986; Mojon 1989; Schudack 1993; Climent-Domènec et al. 2009). The occurrence of dasycladaleans and benthic foraminifera indicates that these lakes occurred in a coastal area.

5) Limestones with porocharaceans and coated clavatoraceans (*pccL*) are associated with facies *cL* in the same bed, with *pccL* overlying *cL* (Fig. 4A). The fossil assemblage in this facies mainly consists of abundant well-preserved porocharaceous gyrogonites associated with clavatoraceous utricules (Fig. 6E; Table 2). Charophyte thalli are represented by long portions of *Clavatoraxis* sp. and *Favargerella* sp., including several articulated internodes (Fig. 6D, E; Supplementary Material 4.1, Fig. B, D, F), and less-abundant *Charaxis* sp. (Fig. 6F).

Porocharaceous gyrogonites are usually well preserved and associated with portions of *Charaxis* sp. thalli. These remains are interpreted as being parts of the same plant, and are thus considered autochthonous in the depositional setting. The preservation of clavatoraceous remains is similar to that described in facies *cL*, also suggesting autochthony. However, clavatoraceous remains in facies *pccL* are always coated by cyanobacterial crusts (Figs. 6D, 7Q–R). Crusts around thalli (Favargerella sp. and *Clavatoraxis* sp.) are regular in thickness and display calcified entangled filaments (Fig. 7Q), whereas clavatoroid utricules are encrusted by irregular thickets of radially arranged cyanobacterial filaments (Fig. 7R). In contrast, these cyanobacterial coatings are absent on porocharaceous remains.

Monospecific porocharaceous assemblages are commonly associated with brackish conditions in the Lower Cretaceous record (see facies *pL*) and this may also be the case here. The coexistence of clavatoroid charophyte remains encrusted by cyanobacterial coats with non-coated porocharaceous remains suggests some type of ecological separation between the two groups. The growth of cyanobacterial crusts around charophytes has been associated in present and fossil lakes with rapidly changing environmental conditions, leading to the demise of the original charophyte meadows and their substitution by cyanobacteria (e.g., eutrophication in the case documented by Martín-Closas 1999). In facies *pccL*, the absence of cyanobacterial crusts around porocharaceous remains—these charophytes being tolerant to brackish water—suggests that the clavatoroids may correspond to an early condition of the lake, when freshwater conditions prevailed, before it suddenly shifted to more brackish conditions, when porocharaceous thrived. Between the two phases cyanobacteria grew on dying clavatoroid plants. Evidence of episodical marine influence is supported by benthic foraminifera and dasycladaleans (Fig. 6F, Table 2).

6) Oncoid-rich limestones (*oL*). Oncoids are not common facies in the studied section. These limestones are characterized by an abundance of > 1 cm large, irregular oncoids (Fig. 6G), and few short portions of charophyte thalli (*Clavatoraxis* sp., *Favargerella* sp., and *M. grambastii*). The oncoids are formed of laminae, whose thickness varies laterally from 10 to 500 µm, and show filaments with cyanobacterial affinity.

The growth of similar oncoidal structures commonly occurs in low-energy conditions (e.g., Schäfer and Stapf 1978; Lanés and Palma 1998) in lacustrine slope areas (e.g., Tucker and Wright 1990; Platt and Wright 1991). The fragments of charophyte thalli are, thus, interpreted to have been laterally transported from shallower neighboring areas, where the main charophyte meadows grew.

Parasequences and palaeoecology of charophyte assemblages

Two distinct types of parasequence have been distinguished within the Clavatoraceous-rich limestones and marls from the Cantaperdius Formation:

Parasequence 1 (*Ps1*). This parasequence is formed of a succession of the following facies, from base to top: *clavatoraceous-rich marls* (*cM*), *oncoid-rich limestones* (*oL*), *limestones rich in clavatoraceous utricules and thalli* (*cL*), and Munieria grambastii-rich limestones (*mL*) (Fig. 8). The top of the parasequence is characterized by the occurrence of rootmarks and intraclasts attributed to palustrine features (c.f. Alonso-Zarza and Wright 2010). The *clavatoraceous-rich marls* (*cM*) and *oncoid-rich limestones* (*oL*) are locally absent from this type of parasequence. In such cases, the succession of facies is formed solely by limestone facies *cL*.
Fig. 8  Parasequences described in the Barremian of the Herbers-Mas de Petxí section
and m∠L (Fig. 4A). The succession of facies is interpreted as a shallowing-upwards parasequence, formed in shallow, alkaline lakes and ponds (e.g., Murphy and Wilkinson 1980; Strasser 1988; Platt and Wright 1991; Meléndez et al. 2009). This parasequence is dominated by limestone facies in the stratigraphic intervals between 11–100 m and 187–274 m (Figs. 4A, 5B). Meanwhile, marlier parasequences dominated by facies cM occur in the intervals 100–187 m and 274–366 m of the stratigraphic section (Figs. 4A, B, 5C), and indicate higher terrigenous inputs within the lacustrine system.

From a palaeoecological point of view, the clavatoracean-rich limestones (cM) and oncoid-rich limestones (oL) represent deeper and relatively less-vegetated parts of the lake, whereas the limestones rich in clavatoracean utricles and thalli (cL) would correspond to sublittoral areas of the lake. In such facies, charophyte meadows reached the highest diversity and were formed by Atopochara and clavatoroids, including Asciidiella. Finally, the lake margin would have been populated by poorly diverse charophyte assemblages dominated by the thallus M. grambastii, probably belonging in most cases to Clavator plants.

Parasequence 2 (Ps2). This parasequence is formed of a succession of clavatoracean-rich marls (cM), limestones rich in clavatoracean utricles and thalli (cL), limestones with porocharaceans and coated clavatoraceans (pccL), and limestones with porocharaceans (pL) at the top (Fig. 8). Parasequence Ps2 is locally found interbedded with Ps1 (Fig. 4A).

From a palaeoecological viewpoint, the lower part of the parasequence is similar to Ps1. However, the upper part differs substantially since it is characterized by facies rich in Porochara, which suggests that brackish conditions prevailed. In sum, this parasequence records a vertical increase in marine influence. In some cases, the change from a freshwater lake to a brackish environment is captured in facies pccL, in which waning clavatoracean communities are encrusted by cyanobacteria, whereas porocharacean remains are devoid of periphyton, representing the new, succeeding community.

Porochara-trichovitvolis var. trophyetra, Globator maillardii var. trochiliscoides, Asciidiella stellata var. lata, and A. tripqueta (Fig. 3; Tables 3, 4; Supplementary materials 2–3), are superficially eroded or broken and are interpreted as having been deposited after longer transport.

This facies is interpreted as having been developed under low hydrodynamic conditions in a marginal coastal area. The presence of fine siliciclastics within the depositional setting is indicative of continental input. Euryhaline conditions are suggested by the coexistence of brackish (i.e., Porochara maestratica) and marine fossils (benthic foraminifera and dasycladales; Table 2).

2) Limestones with porocharaceans and benthic foraminifera (pfL) are characterized by the occurrence of abundant porocharacean gyrogonites, attributed to the genus Porochara and benthic foraminifera (Fig. 9A–D). Locally, peloids may be abundant (Fig. 9B, C). Most of the porocharacean gyrogonites are well-preserved (Fig. 9D–F) but a few are broken (Fig. 9F, G). Since no thalli were found in association, the charophyte assemblage was interpreted as parautochthonous.

Facies pfL has been interpreted as formed in coastal brackish marshes subjected to wave action. Facies with similar taxonomic and taphonomic features have been documented by Climent-Domènech et al. (2009) and Bover-Arnal and Strasser (2013).

3) Limestones with molluscs and benthic foraminifera (mL) mainly contain well-preserved, agglutinated foraminifera, miliolids, gastropods and bivalves, but rare oyster shells are broken (Fig. 4B). This facies has been interpreted as being deposited in low-energy areas in a coastal marine setting where small benthic foraminifera and molluscs thrived (see, e.g., Colombié and Strasser 2005 for comparison with a similar setting).

Parasequences and palaeoecology of charophyte assemblages

The repeated superposition of the facies described above leads to two parasequence types (Fig. 8):

Parasequence 3 (Ps3). This parasequence is formed of two facies, with marls rich in porocharacean and benthic foraminifera (facies pfM) at the base and limestones with porocharaceans and benthic foraminifera (facies pfL) at the top (Fig. 8). The facies succession reflects an upwards increase in energy and marine influence, passing from a brackish setting with porocharaceans to marginal-marine
conditions relatively rich in benthic foraminifera. The absence of palustrine features, such as rootlet marks, at the top of the parasequence indicates permanent subaquatic conditions (e.g., Osleger 1991).

**Parasequence 4 (Ps4).** This parasequence consists of a succession formed by limestones with molluscs and benthic foraminifera (facies mfL) at the base, followed by limestones with porocharacean gyrogonites and benthic foraminifera (facies pfL) at the top (Fig. 8). The facies succession reflects a transition from low-energy, shallow-marine settings, where matrix-supported textures and exclusively marine components prevail, to higher-energy brackish to euryhaline environments, where grain-supported textures were generated and porocharacean charophytes occurred. Similar parasequences have been associated with shallowing-upwards marginal-marine successions (e.g., Bádenas et al. 2004; Védrine and Strasser 2009), which in the case studied would include a shift towards brackish conditions.

**Echinochara-rich marls and limestones from the Artoles Formation**

**Description of facies and their charophyte assemblages**

1) Echinochara lazarri-rich grey marls (eLGM) are characterized by the occurrence of abundant utricles of *E. lazarri* (Fig. 3D), ostracods and well-preserved agglutinated foraminifera. *E. lazarri* is excellently preserved, showing the two layers of the utricle structure, and fertile whorls in anatomical connection. In addition, calcified portions of the corresponding thalli, *Charaxis spicatus*, are found in anatomical connection with these utricles (Fig. 3W). All these features indicate that this species is autochthonous in the depositional setting. Other clavatoraceans such as *G. maillardi* var. *biutricularis*, *A. trivolvis* var. *triquetra*, *Asciidiella cruciata* and *Pseudoglobator paucibracteatus*...
are rare, and superficially eroded or even broken (Table 5; Supplementary materials 2–3), suggesting parautochthony or allochthony. The ostracod carapaces surveyed usually present anatomically attached valves, which indicates autochthony.

Facies eIGM is interpreted as having been deposited in low-energy marginal-marine environments with significant fine siliciclastic input and populated by charophyte meadows of *Echinochara lazarii*. The co-occurrence of these charophytes and marine organisms (Table 2) suggests brackish to euryhaline conditions.

2) Echinochara lazarii-rich red clays (eIRC) contain a micropalaeontological assemblage largely equivalent to that of eIGM (Table 2). However, with the exception of *E. lazarii* and *C. spicatus* charophytes are generally more fragmented and/or superficially eroded than in the previous facies. Following the aforementioned taphonomic features, only the utricles and thalli of *E. lazarii* are interpreted as autochthonous.

Facies eIRC is interpreted as having been deposited in brackish to euryhaline marginal-marine settings with a higher siliciclastic input than eIGM, and populated by *E. lazarii* meadows. Subsequently these settings were exposed to oxidation under atmospheric conditions (e.g., Kraus and Aslan 1993).

3) Marls with molluscs and echinoids (meM) consist of up to 14 m thick intervals that contain abundant macrofossils (Fig. 4C) such as oysters, internal casts of infaunal bivalves and irregular echinoids (*Heteraster* sp.). All fossils are well preserved, suggesting autochthony.

Marls with a similar fossil assemblage have been associated with deposition in low-energy, shallow-marine areas with abundant terrigenous inputs (e.g., Védrine and Strasser 2009) as it must be the case here.

4) Limestones with rare clavatoracean thalli (tL) contain small portions of charophyte thalli belonging to *Favargerella* sp., *Clavatoraxis* sp. and *Charaxis* sp., and rare clavatoracean utricles and pororachacean gyrogonites (Table 2). The limestone beds of facies tL are locally capped by a ferruginous crust.

This facies is related to deposition in shallow euryhaline ponds and lakes. Low abundance and erosion features suggest that most charophyte remains are parautochthonous in this facies, whereas the association of freshwater, brackish and marine taxa suggest that euryhaline conditions prevailed.

5) Limestones rich in ostracods and charophytes (oCL) may contain intraclasts and are mainly composed of abundant well-preserved ostracod carapaces (generally non-cypriidean and less-abundant cypriidean species; Fig. 10B, C), and charophyte remains. Less abundant are gastropods, foraminifera, and dasycladaleans. The charophyte assemblage mainly consists of *Charaxis spicatus* thalli (Fig. 10D), rare and broken *Clavatoraxis* sp. thalli, utricles of *Echinochara* sp., and clavatoracean utricles (Fig. 10E, F).

Facies oCL is interpreted as having been deposited in coastal, shallow lakes and ponds, where *E. lazarii* thrived. The co-occurrence of charophytes, cypriidean and non-cypriidean ostracods and marine organisms (Table 2) indicates both a freshwater and marine influence. Intraclasts have been related with the wave reworking of the already compacted mud in shoreline lacustrine areas (see, e.g., Freytet and Plaziat 1982).

6) Finely laminated limestones with benthic foraminifera and cyanobacterial filaments (fcyL) are formed by an alternation of bioclastic laminae and thicker micrite horizons (Table 2). Skeletal components such as benthic foraminifera and fragments of bivalves and echinoids occur in the bioclastic laminae (Fig. 10M, N). The micritic horizons show relics of calcified microbial filaments (10–20 µm across), rare miliolids, and agglutinated bi- or tri-seriate foraminifera.

Facies fcyL is interpreted as microbial mats formed in an intertidal to supratidal setting (see, e.g., Shinn et al. 1969; Pérez-Valera and Pérez-López 2008; Bover-Arnal and Strasser 2013). Thin bioclastic horizons have similar sedimentary and palaeontological features to the storm-event deposits described within microbial mats (see, e.g., Bover-Arnal and Strasser 2013) and it must be origin of the laminae observed herein as well.

7) Limestones rich in bivalves and gastropods (bgL) are lenticular, cross-bedded limestone beds that contain abundant molluscs (oysters, other bivalves and gastropods; Fig. 10G, H) associated with other marine fossils (Fig. 10I; Table 2). Fossils are usually broken, suggesting that they were transported in the depositional setting. Intraclasts mainly occur at the base of the beds, forming a lag deposit (Fig. 4C). Some of the intraclasts contain portions of charophyte thalli (Fig. 10J–L).

The sedimentary features (Table 2), and the presence of marine fossils indicate that this facies corresponds to channel-fill deposits formed in a marine coastal area. Similar deposits have been associated with intertidal to shallow subtidal areas (e.g., Colombié and Strasser 2005; Védrine and Strasser 2009; Bover-Arnal and Strasser 2013) and it must be the case in this deposit as well.

**Parasequences and palaeoecology of charophyte assemblages**

The previous facies can be arranged into three distinct parasequences.

**Parasequence 5 (Ps5).** This was identified at the base of the Artoles Formation (Fig. 4B). It is characterized by the succession of *Echinochara lazarii-rich grey marls* (facies eIGM) and *limestones with rare clavatoracean thalli* (facies
Table 5  Relative abundance of charophyte species measured in the samples studied

| Lithostatigraphy | Stratigraphic position (m) | Charophyte fructifications | Charophyte thalli |
|------------------|---------------------------|-----------------------------|-------------------|
| Senecio Fm.      | 682 H99                   | Porocladia maestracica      | Citradoxis sp.    |
|                  | 680.5 H98                 | aff. Mesochora haemali     | Cladophoropsis sp.|
|                  | 672 H97                   | Echiocladia friggei        | Fovangerella aquaviva|
|                  | 670 H96                   | G. mollarii var. trochosocoides | Murneria graminifolia |
|                  | 667.5 H95                 | G. mollarii var. bifurcularis | Chara sp. |
|                  | 665.5 H94                 | A. thirovis var. trochosocoides | Chara sp. |
|                  | 661 H93                   | A. thirovis var. friggei   | Chara sp. |
| Morella Formation | 660 H92                   | C. grovesii var. julghentensis | Chara sp. |
|                  | 656 H91                   | C. harrii var. harrii      | Chara sp. |
|                  | 654.5 H89                 | A. cruciata               | Chara sp. |
|                  | 652.5 H88                 | H. neomongolensis var. neomongolensis | Chara sp. |
|                  | 646.5 H86b                | Pseudeuglena pseudoreticulata | Chara sp. |
|                  | 645 H86                   |                            |  |
|                  | 638.5 H85                 |                            |  |
|                  | 635 H82                   |                            |  |
|                  | 621 H76                   |                            |  |
| Morro Fm.        | 614 H75                   |                            |  |
|                  | 494.5 H128b               |                            |  |
|                  | 492 H128a                 |                            |  |
|                  | 488.5 H64                 |                            |  |
|                  | 487.5 H63                 |                            |  |
|                  | 451.5 H124b               |                            |  |

See Fig. 4A for the stratigraphic position of each sample. See supplementary materials 2 and 3 for further detail.
Fig. 10 Microfacies and components of Echinochara-rich marls and limestones from the Artoles Formation. A Facies *tl* (sample H61B; thin section no 87459 MGSCB), scale bar equals 1000 µm; B Facies *ocl* containing abundant carapaces of cypridean and non-cypridean ostracodes (cy), and charophyte thalli (sample H127; thin section no. 87461), scale bar equals 1000 µm; C Non-cypridean ostracod carapace, facies *ocl* (sample H127; thin section no. 87461 MGSCB), scale bar equals 250 µm; D Node with adjacent internodes of Charaxis spicatus, facies *ocl* (sample H127; thin section no. 87461), scale bar equals 250 µm; E Clavatoroid utricle, facies *ocl* (sample H125; thin section no. 87462 MGSCB), scale bar equals 250 µm; F Clavatoroid utricle, facies *ocl* (sample H125; thin section no. 87462 MGSCB) scale bar equals 250 µm; G Facies *bgL* showing abundant bivalve shells (sample H134; thin section no. 87465 MGSCB), scale bar equals 1000 µm; H Complete gastropod, facies *bgL* (sample H130; thin section no 87463), scale bar equals 250 µm; I Tangential section of a dasycladalean thallus, facies *bgL* (sample H71; thin section no. 87468 MGSCB), scale bar equals 250 µm; J Intraclast containing charophyte thalli (sample H133; thin section no. 87464), scale bar equals 1000 µm; K Intraclasts with small portions of charophyte thalli, arrow indicates component enlarged in (L) (sample H135; thin section no. 87466 MGSCB), scale bar equals 250 µm; L Transversal section of a charophyte thallus, (sample H135; thin section no. 87466 MGSCB), scale bar equals 250 µm; M Facies *fcyL*, showing the irregular base of the laminae (storm events) including bioclasts such as bivalve shells (b), and miliolids (m) (sample H68; thin section no. 87467 MGSCB), scale equals 1000 µm; N Detail of the laminae showing micritized benthic foraminifera (f) and fragments of echinoid (e) (sample H68; thin section no. 87467 MGSCB), scale bar equals 250 µm
The top of this parasequence is commonly marked by a ferruginous crust. The parasequence is interpreted as a shallowing-upwards succession, changing from a relatively deeper setting to shallower ponds and lakes, both under brackish to euryhaline conditions. The absence of emergence features such as mudcracks and the presence of ferruginous crusts at the top suggest the persistence of subaqueous conditions throughout the parasequence (e.g., Osleger 1991). From the viewpoint of charophyte palaeoecology, the facies succession is of significance given that it documents the development of charophyte meadows dominated by *E. lazarii* in brackish settings.

**Parasequence 6 (Ps6)**. This parasequence is characteristic of the upper part of the Artoles Formation including an intercalation of the Morella Formation (meters 450–610 of the section studied; Fig. 4C). It is usually composed of a succession of *Echinocarpa lazarii-rich grey marls* (*elGM*) and *E. lazarii-rich red clays* (*elRC*). However, the facies *elGM* is locally overlain by *limestones rich in ostracods and charophytes* (*ocl*).

The succession of lacustrine grey marls to marginal lacustrine limestones and finally to red clays is associated with a shallowing-upwards sequence formed in ponds developed in floodplains and mudflats. The shallowing-upwards trend culminated in sub-aerial exposure and sediment oxidation (e.g., Freytet and Plaziat 1982; Breda and Preto 2011). This parasequence also indicates that *E. lazarii* was able to thrive in temporary ponds exposed to periodic sub-aerial conditions (facies *elRC*), regardless of the amount of clastic input received.

**Parasequence 7 (Ps7)**. This parasequence is intercalated with the previous one between meters 450 and 610 of the stratigraphic section (Fig. 4C). It is mainly formed of the succession of *marls with molluscs and echnoids* (facies *meM*) followed by channelized *limestones rich in bivalves and gastropods* (facies *bgL*) (Fig. 8), which are locally topped by *finely laminated limestones with benthic foraminifera and cyanobacterial filaments* (facies *fcyL*). This parasequence is interpreted as having been formed in a tidal flat to shallow-marine area under normal-marine salinity conditions (facies *meM*) with tidal channels (facies *bgL*). Abandoned channels would have locally evolved into restricted, poorly oxygenated ponds, where microbial mats developed (facies *fcyL*).

**Clavatoracean-rich clays from the Morella Formation**

**Description of facies and their charophyte assemblages**

1) *Clavatoracean-rich grey clays* (*cGC*) mainly contain abundant and diverse clavatoraceans, ostracods and agglutinated foraminifera (*Table 2*). The charophyte assemblage is mainly composed of well-preserved utricles of *E. lazarii* with abundant well-preserved utricles of *A. trivolvis* var. *triquetra* and *C. harrisii* var. *reyi*, and var. *harrisii* (*Table 5*; *Supplementary materials 2–3*), suggesting autochthony. Small populations (usually < 20 utricles; *Table 5*; *Supplementary materials 2–3*) of well-preserved or slightly abraded utricles of *Globator mail-lardii* var. *trochiliscoides* and var. *biutricularis* (Fig. 3E–F), *Clavator grovesii* var. *jiuquanensis* (*Fig. 3I*), *A. cruciata* (*Fig. 3R*), and *P. paucibracteatus* (*Fig. 3V*) and gyrogonites of aff. *Mesochaera harrisii* (*Fig. 3C*) are considered parautochthonous within the assemblage. *H. neimongolensis* var. *nei-mongolensis* is extremely rare in facies *cGC* and the utricles are highly eroded indicating that they represent allochthonous components. Abundant, well-preserved benthic foraminifera, and few echinoid fragments also occur.

This facies is interpreted as having been deposited in permanent lakes and ponds located near the marine shoreline, with abundant terrigenous influence, where charophyte meadows dominated by *E. lazarii, A. trivolvis* var. *triquetra*, and *C. harrisii* var. *harrisii* and var. *reyi* occurred. The presence of abundant, well-preserved agglutinated foraminifera together with charophytes suggests euryhaline conditions with alternating periods of freshwater, brackish and/or marine influence.

2) *Red clays with clavatoraceans* (*cRC*) mainly contain charophyte remains, ostracods and some benthic foraminifera. The charophyte assemblage is mainly composed of abundant, well-preserved utricles of *C. harrisii* var. *reyi* (*Fig. 3L*), which may be associated with a few, locally abraded utricles of *E. lazarii, A. trivolvis* var. *triquetra*, *H. neimongolensis* var. *neimongolensis*, *C. grovesii* var. *jiuquanensis*, and *P. paucibracteatus*, and gyrogonites of aff. *M. harrisii* (*Fig. 3; *Table 5*; *Supplementary materials 2–3*). Thalli are rare, and mainly belong to small portions of *Clavatoraxis* sp. (*Fig. 3V*). As regards utricles, *C. harrisii* var. *reyi* is interpreted as autochthonous, whereas the other species are considered as parautochthonous components, i.e., transported from neighboring areas, where they probably grew.

Red clays are interpreted as tidal flat to fluvial floodplain deposits oxidized under sub-aerial conditions (see, e.g., Kraus and Aslan 1993; Abdul-Aziz et al. 2003; Vicente et al. 2016). The occurrence of abundant charophyte remains associated with benthic foraminifera indicates sedimentation in temporary coastal lakes and ponds exposed to euryhaline conditions. The presence of rootmarks and mottled features suggests the development of hydromorphic soils within a floodplain setting (e.g., Kraus and Aslan 1993).

3) *Limestones with clavatoracean thalli and utricles* (*ctuL*) contain abundant charophyte remains, thalli portions and utricles (*Supplementary material 5*). The thalli are usually encrusted by an up to 400 µm thick cyanobacterial coat (*Supplementary material 5, Fig. G–H*). Long portions of...
the thallus *C. spicatus* (Fig. 11C, E) and the corresponding *E. lazarii* utricles are common (Fig. 11D, E; Supplementary material 5, Fig. F–H). Both plant organs (*C. spicatus* and *E. lazarii*) are locally found in anatomical connection (Fig. 11E), indicating that the species bearing them was autochthonous in this setting. In some cases, *E. lazarii*-*C. spicatus* may form monospecific assemblages (Fig. 11B). Other well-preserved charophyte thalli are *Clavatoraxis robustus* (Fig. 11G–I) and *Favargerella* sp. The thallus *Clavatoraxis* sp. can also form monospecific assemblages.

**Fig. 11** Microfacies and components of Clavatoracean-rich clays and limestones from the Morella Formation. **A** Facies *ctuL* showing the co-occurrence of *Clavatoraxis* sp. (cl), *Charaxis* sp. (ch) and a *Globator* sp. utricle (u) (sample H77-79; thin section no. 87469 MGSCB); **B** Another view of facies *ctuL* dominated by *Charaxis spicatus* (sample H90b; thin section no. 87477 MGSCB); **C** Transversal section of *C. spicatus* internode (sample H90; thin section no. 87473 MGSCB); **D** Complete fertile whorl of *Echinochara* (sample H90; thin section no. 87475 MGSCB); **E** *Charaxis spicatus* anatomically connected to *Echinochara* (sample H90b; thin section no. 85676 MGSCB); **F** Facies *ctuL*, showing predominant *Clavatoraxis* sp. thalli (sample H87; thin section no. 87472); **G** Transversal section of *Clavatoraxis* sp. (sample H90; thin section no. 87473); **H** Longitudinal section of *Clavatoraxis* sp. and a clavatoroid utricle (sample H87; thin section no. 87475 MGSCB); **I** Transversal section of *Clavatoraxis* sp. with poorly calcified cells (sample H90; thin section no. 87476 MGSCB); **J** Clavatoroid utricle showing the apical neck (arrow) (sample H90; thin section no. 87476 MGSCB); **K** Clavatoroid utricle with a thick nodular layer (sample H87; thin section no. 87471 MGSCB); **L** Transversal section of a clavatoroid utricle (sample H90; thin section no. 87474 MGSCB); **M** *Ascidiella* sp. utricle (sample H77-79; thin section no. 87469 MGSCB); **N** *Atopochara* sp. utricle (sample H78; thin section no. 87470 MGSCB); Scale bar **A**, **B**, **F** equals 1000 µm; **C–E**, **G–N** equals 250 µm
in these limestones (Fig. 11F). Clavatoroid utricles are very abundant but their taxonomic determination from thin sections was not generally possible (Fig. 11J–L; Supplementary material 5, Fig. A–C, E). An exception is Ascidiella sp. that was recognized on the basis of its 3 bract cells and the phyllloid arranged around the gyrogonite in transversal sections (Fig. 11M, Supplementary material 5, Fig. C). Atopocharoid utricles belonging to Atopochara sp. (Fig. 11N) are common. These charophytes are associated with ostracods, and locally also with benthic foraminifera and dasyycladales.

The deposits in this facies are interpreted as being the result of sedimentation in alkaline lakes (e.g., Freytet and Plaziat 1982; Bardenas et al. 2018), where diverse clavatoroid and atopocharoid charophyte meadows thrived, locally dominated by E. lazarii.

4) Limestones with bivalves and gastropods (bgL). This facies has similar features to those in the Echinochara-rich marls and limestones of the Artoles Formation.

Parasequences and palaeoecology of charophyte assemblages

Parasequence 8 (Ps8). The repetition of this basic accretional unit mainly gives rise to the base of the Morella Formation (Fig. 4C). It is formed by the succession of (1) limestones with clavatoracean thalli and utricles (ctul), (2) clavatoracean-rich grey clays (cGC) and (3) red clays with clavatoraceans (facies cRC) (Fig. 8). It is interpreted as a shallowing-upward succession recording a depositional change from sedimentation in an alkaline lake to ponds with significant clastic input, finally leading to temporary ponds subjected to sub-aerial exposure (e.g., Freytet and Plaziat 1982; Abdul-Aziz et al. 2003; Abels et al. 2009; Breda and Preto 2011; Bardenas et al. 2018). Euryhaline conditions prevailed throughout the parasequence. Regarding the charophyte palaeoecology, the shallowing-upwards process recorded a charophyte species shift from a diverse assemblage including E. lazarii, Atopochara trivolvis var. triqueta and var. trivolvis, and C. harrisii var. harrisii and var. reyi, which developed in both alkaline and clastic-influenced lakes, to a poorly diverse assemblage containing only abundant C. harrisii, developed in floodplain ponds.

A variation of this parasequence occurs at the boundary between the Morella Formation and the overlying marine facies of the Cervera Formation (Fig. 4C), where only the two end types occur intercalated with tidal channels formed by limestones rich in bivalves and gastropods (facies bgL).

Discussion

Palaeoenvironmental evolution

The Herbers-Mas de Petxí section contains a thick and continuous sedimentary record, which is representative of the vertical and lateral evolution of the Barremian depositional environments established on the north-western margin of the Morella Sub-Basin in the northern Maestrat Basin. Based on the facies and parasequences recognized, and on the taphonomy and palaeoecology of their charophyte assemblages (Fig. 4A–C), three different stages of palaeoenvironmental evolution can be interpreted (Figs. 12, 13, 14).

1) The first stage is mainly represented by the early Barremian clavatoracean-rich limestones and marls of the Cantaperdius Formation. It is characterized by the inter-bedding of parasequences Ps1 and Ps2, which are laterally equivalent to one another, forming a patchwork of freshwater to brackish lakes and ponds (Fig. 12A). Parasequence Ps1 was the most common type of succession that developed in these alkaline palaeoenvironments, whereas Ps2 represents freshwater lakes that received marine influence and were thus located closer to the coast. Similar freshwater alkaline environments receiving intermittent or sporadic marine influence have been reported in other ancient coastal wetlands (e.g., Armenteros and Edwards 2012; Suárez-González et al. 2015) and in extant coastal wetlands, such as the Everglades National Park (Florida) (e.g., Platt and Wright 1992; Marshall et al. 2009; Fig. 12B).

Charophyte assemblages in these wetlands are distributed according to depth, alkalinity, salinity and clastic influence (Fig. 12A). Charophyte floras in freshwater alkaline lakes with low clastic inputs were composed of Atopochara trivolvis var. triqueta, Clavator harrisii var. harrisii, Ascidiella var. stellata var. stellata and var. lata, and A. triqueta. Locally, Hemiclavator-dominated populations (H. adnatus and H. neimongolensis var. posticecaput) occur. These charophyte assemblages would have grown in relatively deep areas of the lake, passing to almost monospecific assemblages of Munieria grambastii at the lake margins (Fig. 12A). These types of lake are better represented in the limestone-dominated intervals of the lower part of the Cantaperdius Formation (between meters 0 and 100 of the section in Fig. 4A). Meanwhile, under higher clastic inputs (mainly in marly intervals between meters 100 and 187 of the section; Fig. 4A), previous charophyte assemblages were rich in Globator maillardii var. trochiliscoides. Otherwise, brackish floras from this interval were mainly composed of Porochara maestratica and occasionally, E. lazarii.

2) The second palaeoenvironmental stage is late early Barremian in age and corresponds to the upper part of the Cantaperdius Formation and the lower part of the Artoles Formation (Fig. 4B). It is formed by three depositional belts ranging from lacustrine to shallow-marine facies (Fig. 13A). The most proximal belt is formed by freshwater lakes and ponds of Ps1, showing a dominance of clavatoracean-rich assemblages with E. lazarii, A. trivolvis var. triqueta, G. maillardii var. trochiliscoides C. harrisii var. harrisii, C. calcitrapus var. jiangluoensis and var. calcitrapus, and
Fig. 12 Palaeoenvironmental reconstruction of the first depositional stage recorded in the Herbers-Mas de Petxi section, corresponding to carbonate-dominated wetland environments of the Cantaperdus Formation. A Palaeoecological model including the parasequences and charophyte distribution interpreted and discussed in the text for the Cantaperdus Formation. B Google Earth photograph of wetlands in the Everglades National Park (Florida, United States of America), which are considered a modern analogue of (A)

**Hemiclavator neimongolensis** var. **neimongolensis**, changing to **Munieria**-rich meadows at the lake margins. The second depositional belt was formed by supratidal brackish lakes and ponds (**Ps3** and **Ps5**) interspersed with tidal channels, represented by **Ps6**. **Echinochara lazarii** inhabited the deeper areas of the lakes, whereas other clavatoraceans predominated at the lake margins (**Ps5**). The third depositional belt included coastal brackish lakes, exclusively colonized by porocharacean-rich meadows (**Ps3**) that changed seawards to benthic foraminifera and molluscs in shallow-marine conditions (**Ps6**). Based on the facies descriptions, their lateral relationships and the fossil organisms identified, the more heavily clastic-influenced areas of the Everglades National Park would constitute a modern analogue of the depositional environments recorded in the upper part of the Cantaperdus Formation and the lower part of the Artoles Formation (Marshall et al. 2009) (Fig. 13B).

In comparison with the previous stage, the wider development of brackish facies in this second depositional stage was related to the early phase of the marine transgression of late early Barremian age recorded in the Maestrat Basin (e.g., Bover-Arnal et al. 2016). This transgressive pulse is best characterized in the more depocentral areas in the Maestrat Basin such as in the Salzedella Sub-Basin (Fig. 1B), where the Artoles Formation is fully marine (Salas et al. 2001). In the section studied, the increase in clastic content in the sedimentary system during this second depositional stage is interpreted to indicate enhanced rainfall and clastic run-off (see e.g., Pasquier and Strasser 1997; Strasser and Védrine 2009) during the late early Barremian in the northern Maestrat Basin.

(3) The third depositional stage was reconstructed based on the lateral and upwards change from the **Echinochara**-rich marls and limestones of the upper Artoles Formation to the clavatoracean-rich clays and marls of the Morella Formation (Fig. 4C), which recorded a regression of early late Barremian age. Three palaeoenvironmental belts were distinguished (Fig. 14A). The most distal belt is represented by shallow-marine subtidal areas with abundant infaunal bivalves and irregular echinoids, and tidal channels (**Ps7**). The latter may become abandoned and develop into restricted and microbially dominated ponds. This belt graded landwards to a second depositional belt formed by brackish supratidal lakes and ponds. These were rich in **Echinochara lazarii** and passed laterally either to lakeshore areas or to exposed, oxidized flood plain areas (**Ps6**; Fig. 14A). Finally, the most proximal depositional belt corresponds to floodplains with freshwater alkaline lakes populated by **Echinochara** sp., **Atopochara** sp., **Ascidiella** sp., and other clavatoroidean charophytes, and clastic ponds where **Echinochara lazarii**, **Atopochara trivolvis**, and **Clavator harrisii** thrived. These lakes contained more diverse charophyte assemblages than the brackish belt (**Ps6**). In some areas, small tidal channels drained the floodplain. Modern analogue environments with similar facies and sedimentary features are found in non-marine areas around Buckingham Bay in Northern Australia (Fig. 14B) (Short 2020).

In this last depositional stage, the sedimentary system shows an increase in clay content (Fig. 14A), suggesting greater terrigenous run-off than in the previous stage (Fig. 13A). Evaporitic and dolomitic beds, which are very frequent in arid or strongly seasonal tidal flats (e.g., Breda and Preto 2011; Bádenas et al. 2018), are absent, indicating that humid conditions prevailed in the Maestrat Basin during the early late Barremian. In a more general context, humid conditions have been reported in the Tethyan and Boreal domains during the mid Barremian (= late early Barremian and early late Barremian) (e.g., Ruffell and Batten 1990; Godet et al. 2008; Mutterlose et al. 2014).

**Charophyte palaeoecology**

The palaeoenvironmental reconstruction proposed in the previous section allows a precise characterization of the palaeoecological constraints of the most representative charophyte species from the Barremian of Iberia. These species were mainly distributed according to lake bathymetry, salinity (ranging from freshwater to brackish or euryhaline), and clastic inputs into the lakes.

**Charophytes from freshwater lakes with different degrees of clastic influence**

Freshwater settings contain the richest and most diverse charophyte assemblages, with most species living in shallow water, whereas only one species usually prevailed in the shallowest margins (**Munieria grambastii**, probably representing the thalli of some **Clavator** species). Only two species, **Atopochara trivolvis** var. **triquetra** and **Clavator harrisii**, were capable of growing in these Barremian lakes regardless of the amount of clastic input received. Another species, **Echinochara lazarii**, was limited during the early Barremian to clastic-influenced lakes, whereas later, by the late Barremian, it had colonized freshwater settings with low clastic input, such as the alkaline lakes recorded in the Morella Formation, indicating that its palaeoecological requirements expanded over time. In this regard, **Charaxis**
spicatus, which represents the thallus of E. lazarii, was first described in freshwater lacustrine limestones from Las Hoyas in the south-western part of the Iberian Chain (Martín-Closas and Diéguez 1998) where it occurs attached to non-calcified gyrogonites, latter attributed to E. lazarii (Pérez-Cano et al. 2020).

Charophytes that preferred freshwater lakes with low clastic inputs, include two species, Ascidiella stellata and A. triqueta, which are more abundant in the lower part of the Cantaperdius Formation (Figs. 4A and 12A). The abundance of these latter species wanes as clastic content increases in the depositional systems. The palaeoenvironmental distribution of A. cruciata shows a greater tolerance to clastic influence than its ancestor. A. triqueta, since it has been found in facies of temporary alkaline lakes with low clastic influence in floodplains of the Morella Formation (Fig. 14A) and in palustrine areas with higher clastic influence in floodplains of the La Huérguina Formation in the south-western part of the Iberian Chain (Vicente and Martín-Closas 2013; Buscalioni et al. 2018).

Globator maillardii var. trochiliscoides and var. biarticulata, Clavator harrisi var. reyi, and C. calcitrapus var. jiangluoensis and var. calcitrapus were largely limited to clastic-influenced settings, either lakes or floodplains. This palaeoecological preference has already been reported in other sedimentary basins in Eurasia (e.g., Martín-Closas 2000, 2015; Vicente and Martín-Closas 2013).

In contrast to the previous species, Hemiclavator neimongolensis was able to change its palaeoecological requirements during the Barremian. In the early Barremian, the older anagenetic stage of this species, H. neimongolensis var. posticecaptus, dominated in particular charophyte assemblages in alkaline lakes with low clastic influence (Fig. 12A), whereas the younger variety, H. neimongolensis var. neimongolensis, shifted its habitat to coastal lakes with high clastic inputs. In the latter, it formed part of diverse charophyte assemblages that include Echinocchara lazarii, Atopochara trivolvis var. triqueta, Clavator harrisi var. harrisi, and C. calcitrapus (Fig. 13A). In Chinese basins, H. neimongolensis var. neimongolensis has also been found in clastic-influenced lakes in a fluvial context (pers. comm. Q.F. Wang in Martín-Closas 2015). The expanding palaeoenvironmental distribution of this latter species may account for its wide biogeographic distribution across all Eurasia in the late early Barremian and late Barremian (see Martín-Closas 2015).

Charophytes from brackish lakes with different degrees of clastic influence.

The Early Cretaceous brackish charophyte assemblages have long been known to have been dominated by species of Porochara sp. (family Porocharaceae), commonly forming monospecific assemblages (e.g., Martín-Closas and Grambast-Fessard 1986; Mojon 1989; Climent-Doménech et al. 2009). In a comparison with ostracods, Schudack (1993) suggested that the clavatoracean genera Echinocchara, Atopochara, Globator and Clavator may also have grown in brackish conditions. In particular, he concluded that the genera Porochara and Echinocchara showed similar tolerances to high salinity (from oligohaline to brachyhaline). The data presented here show that these genera differed palaeoecologically in their tolerance to the input of clastic sediments in such brackish settings. Thus, autochthonous populations of Porochara maestratica were restricted to limestone-dominated intervals, whereas Echinocchara lazarii meadows were abundant in marl-dominated intervals, suggesting that this latter species preferred settings with higher clastic influence.

The palaeoecological analysis has also shown that, as already suggested by Schudack (1993), Atopochara trivolvis var. triqueta, and var. trivolvis, and Clavator harrisi var. harrisi, and var. reyi also grew in brackish settings, but they never formed large or monospecific populations there, in contrast to E. lazarii. These differences may indicate different degrees of salinity, with the assemblages composed of E. lazarii, A. trivolvis, and C. harrisi corresponding to a lower degree of salinity and the monospecific assemblages of E. lazarii representing a higher salinity degree.

Did climatic cyclicity control the evolution of charophyte communities in the Barremian?

In the Herbers-Mas de Petxí section, at least three different types of sedimentary cycle were recognized. These are superimposed on one another and present different frequencies.

(1) The highest frequency sedimentary cycles correspond to parasequences (Ps1–Ps8). Such small-scale cycles are usually associated with Milankovitch-driven climatic variations (e.g., Strasser et al. 1999; Bádenas et al. 2004). However, the occurrence of channel deposits (Ps7, which is mainly observed in the upper part of the stratigraphic section; Fig. 4B, C) suggests that autocyclic processes, such as lateral channel migration or a sudden increase in tectonic subsidence, played a role in this type of cycle (e.g., Kindler 1992; Drummond and Wilkinson 1993).
Morella Formation in the early late Barremian (Figs. 2 and 4). The second transgressive cycle is of late early Barremian age and corresponds to the progradation of the marine Artoles Formation over the non-marine Cantaperdius Formation (not studied here) over the non-marine Morella Formation in the early late Barremian (Figs. 2 and 4C). This type of cyclicity is usually associated with large-scale eustatic changes, which are well-documented in the Barremian (e.g., Hardenbol et al. 1998; Haq 2014). In fact, these two longer-term transgressions recorded in the Morella Sub-basin had regional significance in the Maestrat Basin (Bover-Arnal et al. 2014) and seem to be correlatable with the global transgressive events that occurred between sea-level events KBa3 and KBa5 of Haq (2014). Accordingly, variations in the relative sea level favored the expansion or contraction of freshwater and brackish biotopes, and, as a consequence, they governed the development of halphobic or halophile charophyte species.

Conclusions

A palaeoecological study of the Herbers-Mas de Petxí section has provided new information about the palaeoenvironmental distribution of Barremian charophyte species in coastal wetlands. This study shows that the occurrence of most charophyte species was mainly controlled by the following interrelated factors: (1) amount of clastic supply, (2) waterbody salinity and (3) water depth. In this regard, the species used as index species of a biozone were restricted to particular environments, as in the case of *Globator maillardii* var. *trochiliscoides*, which was restricted to clastic-influenced freshwater lakes. Moreover, species used as biostratigraphic markers for the early Barremian were restricted to freshwater lakes with low clastic influence, as in the case of *Ascidiella stellata* var. *lata* and *Ascidiella triquetra*, or to clastic-influenced freshwater lakes, as in the case of *Clavator calcitratus* var. *lata* and *Ascidiella triquetra*, or to clastic-influenced freshwater lakes. In contrast, in the late Barremian record, this distinction between the species restricted to freshwater lakes with low clastic influence and those restricted to freshwater lakes with high clastic influence becomes less clear, since the former were rare.

In the late Barremian, salinity seems to be a significant palaeoenvironmental parameter controlling the distribution of charophyte species. Only three species, *Atopochara trivolvis* var. *triquetra*, *Clavator harrisii* var. *harrisii*, and *E. lazarii* (the latter only during the late Barremian) were able to thrive in clastic-influenced and non-clastic freshwater settings alike. These species are also the only clavatoraceans that were able to thrive in brackish settings. However, the occurrence of monospecific populations of *E. lazarii* in late Barremian brackish limestones and marls indicates that this species was better able to thrive in environments with higher salinity than *A. trivolvis* or *C. harrisii*. Future research may enhance these results by comparison with other palaeobiological indicators, such as ostracods, or with geochemical data, such as stable isotopes and clay mineralogy.
Three different types of sedimentary cycle with distinct ranks were distinguished in the stratigraphic section studied. In decreasing cyclicity frequency, these are (1) the parasequences, with a metric thickness, (2) the clastic-rich and clastic-poor intervals with decametric thickness, and (3) the transgressive–regressive cycles, of hectometric thickness. The inter-bedding of limestone- and clastic-dominated intervals together with the marine/non-marine influence governed by transgressive–regressive cycles, exerted a strong control over the distribution of charophytes in the Barremian record of the Maestrat Basin. This suggests that large-scale climatic parameters determining environmental changes such as humidity, clastic run-off or changes in the relative sea level were the main drivers of charophyte diversity, distribution, and evolution during the Barremian.

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