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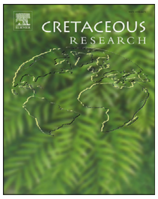

A bioprovince for the Barremian–Aptian charophytes of the Central Tethyan Archipelago

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ABSTRACT

A comprehensive bibliographic compilation of dozens of worldwide records of charophytes from the Barremian to early Aptian interval has been revisited aiming to gather the regional and global distribution data for the clavatoracean family. The compiled data were studied with the palaeontological statistics software PAST (PAleontological STatistics), using a cluster analysis. All analyses of the biogeographic data revealed a consistent separation of the Central Tethyan Archipelago (CTA) from other palaeogeographic areas, mainly the neighbouring Eurasian and American landmasses, based on the species richness of Family Clavatoraceae.

The Central Tethyan Archipelago (CTA) is hence, proposed as a distinct bioprovince for Early Cretaceous charophytes, called the Clavatoracean Bioprovince, based on the abundance and especially the biodiversity of clavatoracean taxa (up to 26 taxa). Within the Archipelago, species distribution primarily shows a latitudinal pattern suggesting that the charophyte floras were subjected to climatic control. However, longitudinal relationships between areas in the eastern or western parts of the CTA were also found. In spite of these internal subdivisions of the Clavatoracean Bioprovince, the flux of populations between the islands must have been sufficiently strong to maintain taxonomic homogeneity within the archipelago throughout the time interval analysed. These biogeographic patterns are compared with those of non-marine ostracods for the same time interval, showing strong similarities and suggesting that they may be equivalent for other non-marine benthic organisms.

1. Introduction

The clavatoraceans (Family Clavatoraceae Pia) are an extinct, mainly Cretaceous group of charophytes that produced complex calcified fructifications called utricles. These biomineralized fructifications bear sufficient vegetative and reproductive characters to determine the species with much more confidence than other fossil charophytes (e.g. Grambast, 1974; Martín-Closas, 2000). Several factors indicate that clavatoraceans represent an excellent group for palaeobiogeographic studies. First, Clavatoraceae utricles are abundant microfossils that are easy to recover from the bearing rocks and to prepare for study. Second, some species show a wide palaeogeographic distribution (continental, sub-cosmopolitan, and cosmopolitan) during the Early Cretaceous (e.g. Martín-Closas and Wang, 2008; Martín-Closas, 2015), coupled

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with a relatively high evolutionary rate, rendering them very useful in biostratigraphy (rock age determination) and stratigraphic correlation worldwide (e.g. Musacchio, 1973; Grambast, 1974; Wang and Lu, 1982; Riveline et al., 1996; Li et al., 2016; Pérez-Cano et al., 2022a). This application in geology, has yielded large quantities of presence data on many continents. Third, some clavatoracean species evolved following anagenetic processes, i.e. gradual evolution of intraspecific lineages (e.g. Grambast, 1974; Martín-Closas, 1996; Vicente and Martín-Closas, 2013; Pérez-Cano et al., 2020), providing significant evolutionary information on the historical biogeography of each species (e.g. Martín-Closas and Wang, 2008). Fourth and lastly, during the Early Cretaceous clavatoraceans thrived in a wide range of non-marine environments such as permanent alkaline lakes, temporary floodplain ponds, and brackish marshes (e.g. Climent-Doménech et al., 2009; Vicente and Martín-Closas, 2013; Pérez-Cano et al., 2022b). In combination, these features provide abundant information about the palaeobiogeographic distribution of clavatoraceans in many parts of the World over this time interval.

Previous studies on clavatoracean palaeobiogeography have mainly focused on the historical biogeography of a few species that attained a sub-cosmopolitan to cosmopolitan distributional range, allowing for inter-continental biostratigraphic correlations (e.g. Martín-Closas and Wang, 2008; Martín-Closas, 2015). Such is the case of *Atopochara trivolvis* Peck and *Clavator harrisii* Peck, which were cosmopolitan during some stages (e.g. the Aptian), at least in a wide tropical to paratropical latitudinal belt in the Northern Hemisphere. In contrast, little is known about the biogeography of most of the other clavatoracean species, which did not expand over large areas of the Cretaceous World but remained confined within the palaeogeographic domain of the present-day Europe, North Africa, and the Middle East. In the Early Cretaceous this palaeogeographic domain was covered by a shallow tropical sea, the Tethys, interspersed with numerous islands of different sizes, forming what is generally known as the Central Tethyan Archipelago (CTA).

The aim of the present study was to characterize the biogeographic distribution of all clavatoracean species during the Barremian–early Aptian, paying special attention to the area where they were more abundant and diverse, the CTA, in order to test the hypothesis that this archipelago was home to a particular biota, as suggested earlier for other important groups, such as dinosaurs (Csiki-Sava et al., 2015). To this end, we selected the Early Cretaceous, Barremian–early Aptian (129.4–120 Ma) time interval, which corresponds to the time when the Clavatoraceae family attained their maximum diversification (Martín-Closas and Serra-Kiel, 1991). This time interval is also well constrained biostratigraphically since it corresponds to the Eurasian biozones of Atopochara trivolvis triquetra, Hemiclavator neimongolensis var. neimongolensis, and Clavator gautieri var. jiuquanensis defined by Pérez-Cano et al. (2022a). The results are intended to provide not only a clear picture of the biogeographic distribution of a fossil plant group with an exceptionally rich fossil record (Feist et al., 2005), but also to serve as a proxy for comparison with other less abundant non-marine groups, such as vascular plants (taxa from mega-remains), insects, or vertebrates. Furthermore, it will be useful to test current hypotheses about the spatial relationships between palaeo-landmasses and the effects of climate on very sensitive environments, such as lakes and ponds. Lastly, the biogeographic distribution of charophyte species will provide key data to help to better define the area where current biozonations can be applied.

2. Materials and methods

2.1. Data acquisition

The dataset used in this study consisted of bibliographic references and own data on the occurrence of clavatoracean charophytes during the Barremian–early Aptian. This time interval was selected because of its rich charophyte fossil record worldwide and because it coincides with the maximum species richness of clavatoracean charophytes (Martín-Closas and Serra-Kiel, 1991). The database contains the taxonomy, the age of the deposit, the locality, the geographic area or sedimentary basin, the country, and the bibliographic references used for each entry (Supplementary Data, Table 1). In order to avoid taxonomic misidentifications, only those references with an appropriate description and illustration of the microfossils were considered. Twenty-six taxa (i.e. 16 species and its varieties) were analysed including species and anagenetic varieties within species, enabling better characterization of the species' evolution.

Nine palaeogeographic areas were considered: 1) Asian Mainland (**ASM**), mainly including data from China, but also more sparse data from Kazakhstan, Uzbekistan, Tajikistan, Mongolia, Korea, and Japan; 2) North European landmass (**NE**), including basins from North Germany and the English Wealden; 3) Central Massif Islands (**CM**), including data from the islands located south from the Massif, i.e. the Subalpine Chains in eastern France and the Jura Mountains in Switzerland; 4) Iberian Island (**IB**), including data from Spain, Portugal, and Sardinia (Italy); 5) Moesian-Dacian Island and neighbouring peninsulas (**MD**), including data from present Hungary, Romania, Moldova, southeast Ukraine, and southwest Russia; 6) North American Mainland (**NAM**), including data from the USA (mainly south of the Interior Seaway); 7) South American Mainland (**SAM**), including data from Argentina and Brazil; 8) North African islands (**NAF**), including data from Morocco, Algeria, and Tunisia; and finally, 9) Levantine Island and northeast Africa (**LEA**), including Lebanon, Israel, and the eastern coast of Africa, mainly Somalia. Some areas were excluded from the study due to the absence of data. These correspond to northern South America, central and south Africa, and Oceania (Australia and New Zealand).

2.2. Data analysis

The dataset on clavatoracean occurrences during the Barremian–early Aptian was plotted in a binary matrix, considering the species absence (0) or presence (1) (Table 1). This data matrix was then studied by cluster analysis using the software PAST 4.03 developed by Hammer et al. (2001), in order to identify and test links between species and their palaeogeographic distribution. All cluster analyses used the Pair-Group (UPGMA) algorithm, since it favours joining two groups based on the average distance between all members, which to our understanding is closer to the purposes of the biogeographic similarity between areas. More than 20 similarity indexes were tested and those with the highest correlation coefficients were compared before a final dendrogram was selected to represent the results.

Table 1
Data matrix for the cluster analyses of the Clavatoracean distribution during in the Barremian—early Aptian.

Species/Geographic area	MATRIX								
	Worldwide								
	Laurasia						Gondwana		
	ASM	NE	CM	IB	MD	NAM	SAM	NAF	LEA
Subfamily Atopocharoidae (Grambast) emend. Martín-Closas ex Schudack									
***Echinochara* (Peck) emend. Pérez-Cano, Bover-Arnal et Martín-Closas**									
Echinochara lazarii (Martín-Closas) Mojon ex Pérez-Cano, Bover-Arnal et Martín-Closas	0	0	1	1	0	0	1	1	0
***Globator* Grambast**									
Globator maillardii var. *trochilisoides* (Grambast) Martín-Closas	0	0	1	1	1	0	0	1	0
Globator maillardii var. *biutricularis* Vicente et Martín-Closas	0	0	0	1	1	0	0	1	0
***Atopochara* Peck**									
**Atopochara trivolvis* var. *triquetra* (Grambast) Martín-Closas	1	1	1	1	1	0	1	1	1
**Atopochara trivolvis* var. *trivolvis* Peck	1	1	1	1	1	1	1	1	1
Subfamily Clavatoroidae (Grambast) emend. Martín-Closas ex Schudack									
***Clavator* (Reid et Groves) emend. Martín-Closas ex Schudack**									
Clavator grovesii var. *gauteri* and *C. grovesii* var. *combei* (Grambast) Martín-Closas	0	1	1	1	1	0	0	0	0
**Clavator grovesii* var. *jiuquanensis* (Wang) Martín-Closas and *C. g.* var. *jiuquanensis-corrugatus*	1	1	1	1	1	0	0	0	0
Clavator ampullaceus var. *ampullaceus* (Grambast et Lorch) Martín-Closas	0	0	0	0	0	0	0	0	1
Clavator ampullaceus var. *latibracteatus* Sanjuan, Vicente, Pérez-Cano, Stoica et Martín-Closas	0	0	0	0	1	0	0	0	0
**Clavator harrisii* var. *harrisii* Peck	1	0	0	1	1	1	1	1	0
Clavator harrisii var. *reyi* (Grambast-Fessard) Martín-Closas and *C. harrisii* var. *reyi-zavialensis*	0	0	1	1	1	0	0	1	0
**Clavator harrisii* var. *dongjingensis* (Hu et Zeng) Martín-Closas	1	0	0	1	0	0	0	0	0
**Clavator calcitrapus* var. *jiangluonensis* (Wang et Li) Pérez-Cano, Bover-Arnal et Martín-Closas	1	1	0	1	0	0	1	0	0
Clavator calcitrapus var. *calcitrapus* (Grambast) Martín-Closas ex Schudack	0	0	0	1	0	0	0	0	0
***Ascidiella* (Grambast) emend. Martín-Closas ex Schudack**									
Ascidiella stellata var. *stellata* (Martín-Closas et Grambast-Fessard) Martín-Closas ex Schudack	0	0	0	1	0	0	0	0	0
Ascidiella stellata var. *lata* Martín-Closas	0	0	0	1	0	0	0	0	0
Ascidiella triquetra (Grambast) Martín-Closas ex Schudack	0	0	1	1	0	0	0	0	0
Ascidiella cruciata (Grambast) Martín-Closas ex Schudack	0	0	1	1	1	0	0	0	0
Ascidiella iberica var. *iberica* (Grambast) Martín-Closas ex Schudack	0	1	0	1	1	0	0	0	0
Ascidiella iberica var. *inflata* (Grambast-Fessard) Martín-Closas	0	0	0	1	0	0	0	1	0
Ascidiella reticulata var. *reticulata* Grambast et Lorch	0	0	0	0	0	0	0	0	1
***Hemiclavator* Wang et Lu**									
Hemiclavator adnatus (Martín-Closas et Grambast-Fessard) Schudack	0	0	0	1	1	0	0	1	0
Hemiclavator neimongolensis var. *posticecaptus* (Martín-Closas et Grambast-Fessard) Martín-Closas	0	0	1	1	1	0	0	1	0
**Hemiclavator neimongolensis* var. *neimongolensis* Wang et Lu	1	0	1	1	1	0	0	0	0
***Pseudoglobator* Grambast**									
Pseudoglobator fourcadei Grambast	0	0	0	1	0	0	0	0	0
Pseudoglobator paucibracteatus Martín-Closas et Grambast-Fessard	0	0	1	1	1	0	0	0	0

Abbreviations: ASM, Asian mainland; CM, Central Massif Island; IB, Iberian Island; LEA, Levantine Island and NE Africa; MD, Moesian-Dacian Island and neighbouring peninsulas; NAF, North African islands; NAM, North America; NE, Northern Europe; SAM, South America.
Sub-cosmopolitan to cosmopolitan species are marked with an asterisk (*).

3. Results

The Chord similarity index was selected for cluster analysis because of its higher cophenetic correlation coefficient (0.9094). The dendrogram obtained shows three main separated branches (Fig. 1A). The first of these branches represents the Central Tethyan Archipelago (CTA) which is composed of three different subgroups, one containing the islands bordering the Central Massif Island (CM) to the South, another with the central Iberian (IB) and Moesian-Dacian (MD) islands, and a third group represented by the North African islands (NAF). A second main branch is an heterogenous group that includes the neighbouring mainland from Northern Europe (NE) and the continents North America (NAM), South America (SAM), and Asia (ASM). Finally, the third main branch, includes the Levantine Island and NE Africa (LEA), which is completely isolated from the other groups in the dendrogram (Fig. 1A).

The separation of the CTA (CM, IB, MD, and NAF) from all the other areas is based on the common occurrence of many clavatoracean species and varieties unique to the CTA islands (CTA in Fig. 1B). This branch contains the CTA endemic taxa *Globator maillardii* var. *trochiliscoides* (Grambast) Martín-Closas, *G. maillardii* var. *biutricularis* Vicente et Martín-Closas, *Clavator harrisii* var. *reyi* (Grambast-Fessard) Martín-Closas, *Hemiclavator adnatus* (Martín-Closas et Grambast-Fessard) Schudack, *Ascidiella triquetra* (Grambast) Martín-Closas, *Ascidiella cruciata* (Grambast) Martín-Closas ex Schudack, *Ascidiella iberica* var. *inflata* (Grambast-Fessard) Martín-Closas, *Hemiclavator neimongolensis* var. *posticecaptus* (Martín-Closas et Grambast-Fessard) Martín-Closas, and *Pseudoglobator paucibracteatus* Martín-Closas et Grambast-Fessard (Fig. 2). These taxa represent about one third (ca. 35%) of the 26 clavatoracean taxa reported worldwide.

Within the CTA group, the North African basins are placed in a different branch (Fig. 1A), mainly due to the absence of some taxa (either species or varieties) belonging to genus *Ascidiella* Grambast (e.g. *A. triquetra* and *A. cruciata*), *Clavator* (Reid et Groves) emend. Martín-Closas ex Schudack (e.g. *C. grovesii gautieri* and *C. grovesii-combei*) or *Pseudoglobator* Grambast (e.g. *Pseudoglobator paucibracteatus*). The islands bordering the Central Massif to the south (Subalpine Chains and Jura Mountains) are separated due to the absence of *Globator maillardii* var. *biutricularis, Hemiclavator adnatus*, and *Ascidiella iberica* var. *inflata.* On the other hand, the Iberian Island (IB) and the Moesian-Dacian basins (MD) share a large number of taxa (Fig. 1A-B).

The second group (NE, ASM, SAM, and NAM) observed in the dendrogram (Fig. 1A) is justified by the occurrence of only cosmopolitan and sub-cosmopolitan (Eurasian) species such as *Atopochara trivolvis* var. *triquetra* (Grambast), *A. trivolvis* var. *trivolvis* Peck, *Clavator grovesii* var. *jiuquanensis* (Wang) Martín-Closas, *Clavator harrisii* var. *harrisii* Peck, and *Clavator calcitrapus* var.

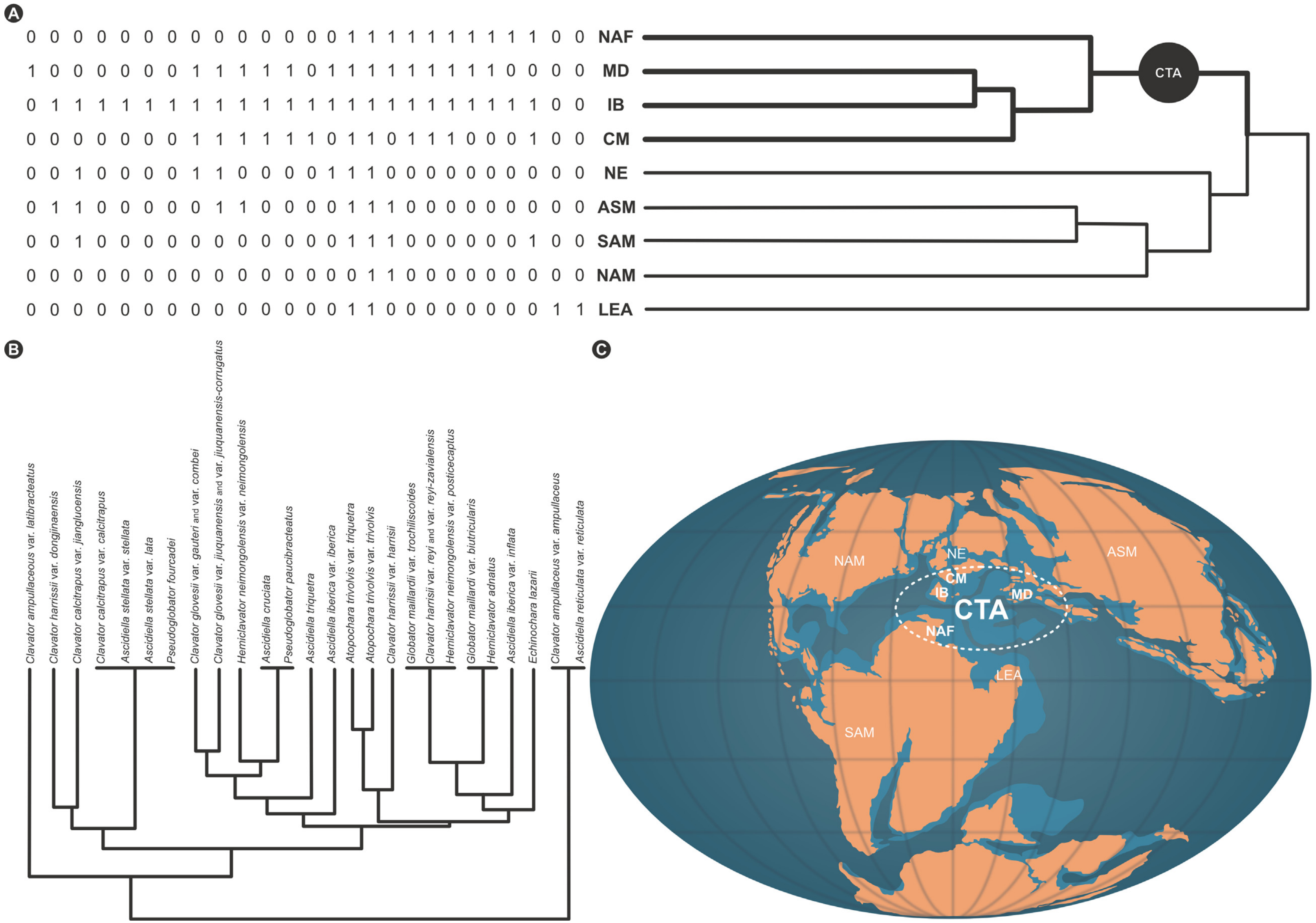
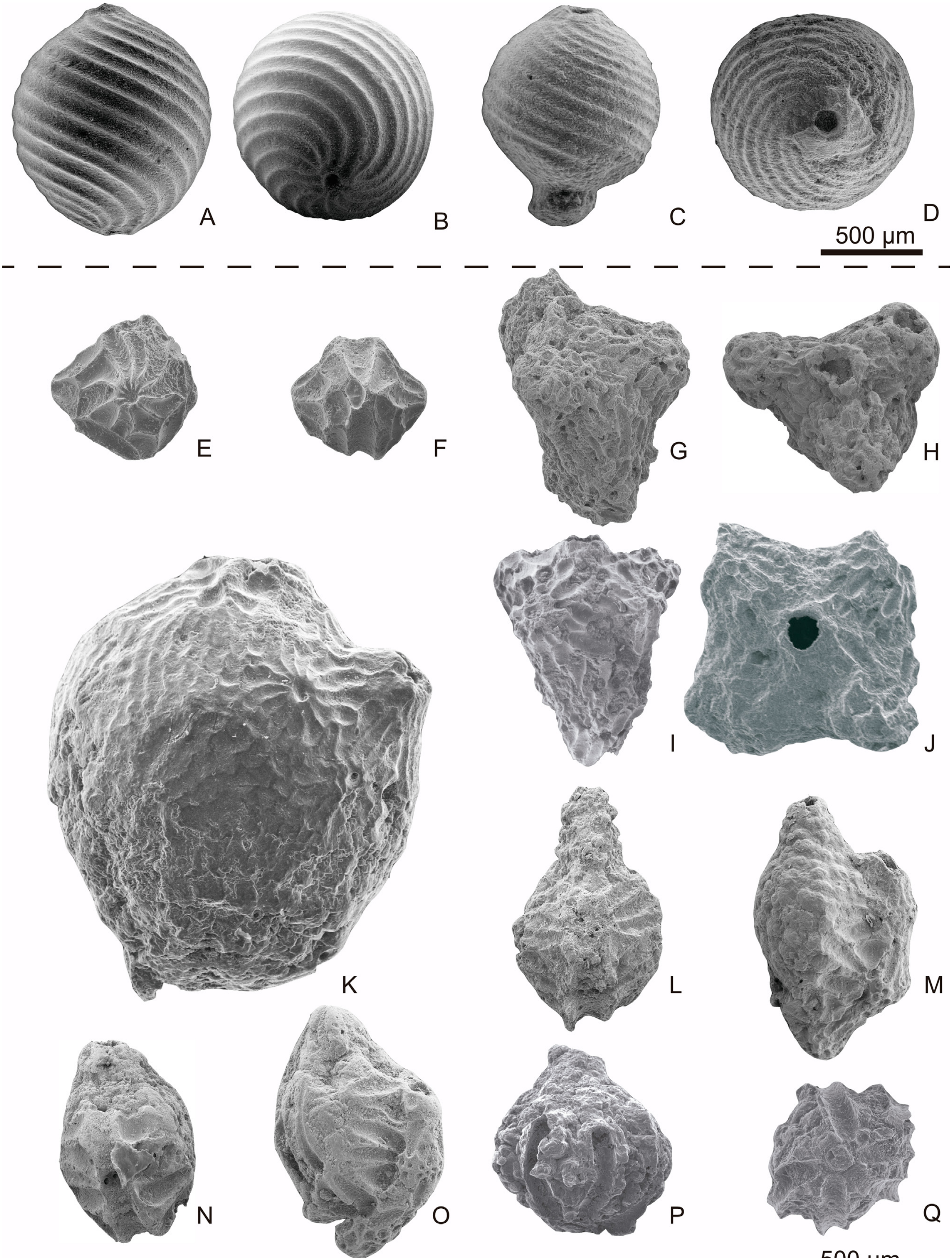


Fig. 1. Biogeographic analysis of the Barremian–early Aptian clavatoraceans in a worldwide context, obtained from a cluster analysis with PAST using the Pair Group algorithm and Chord similarity index. **A**. Dendrogram of area similarity. **B**. Dendrogram of species distribution similarity. **C**. Palaeobiogeographic distribution of the areas represented by the main branches of the dendrogram A on the World palaeomap of the Barremian–Aptian boundary (ca. 121.4 Ma). Palaeogeography modified from Martín-Closas and Wang (2008). See acronyms for areas in the Materials and Methods section.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jiangluonensis (Wang et Li) Pérez-Cano, Bover-Arnal et Martín-Closas. Northern European basins (NE) are ranged in this group of regions due to the relative abundance of cosmopolitan and Eurasian species although they also contain a few taxa characteristic of the CTA; i.e. *Clavator grovesii* var. *combei* (Grambast) Martín-Closas and *Ascidiella iberica* var. *iberica* Grambast.

Lastly, the separation of the Levantine Island and surrounding areas from all previous groups is well justified by the unique occurrence in this region of *Clavator ampullaceus* var. *ampullaceus* (Grambast et Lorch) Martín-Closas and *Ascidiella reticulata* var. *reticulata* Grambast et Lorch (Fig. 1A–B).

4. Discussion

4.1. Definition of a charophyte bioprovince in the Central Tethyan Archipelago

The results obtained herein allow confirming the presence of a separate biogeographic region in the Central Tethyan Archipelago (CTA). It is characterised by the occurrence of unique and abundant clavatoracean charophyte species at least during the Barremian and early Aptian, but probably also throughout the entire Early Cretaceous. This region consists of a core of islands formed by Iberia (Spain and Portugal), the basins surrounding the Central Massif (east France and Switzerland), the Moesian-Dacian platform islands (mainly Bulgaria, Hungary, Romania, Moldova, and parts of Ukraine), and finally, the North African Islands (mainly Tunisia and Morocco). This region differs from most of the surrounding biogeographic regions of the World, including the North and South American mainlands (NAM and SAM respectively), and the Asian Mainland (ASM), because these regions only contain clavatoracean species considered sub-cosmopolitan or cosmopolitan (Fig. 1). Of particular note among the regions within this group is the North European landmass (NE), including English and German basins, because it has transitional floras between the CTA and its neighbouring continents. Finally, the Levantine and NE African (LEA) flora shows an affinity with the CTA in being dominated by clavatoraceans, but also fundamentally differs from them in hosting a significant proportion of its own endemic taxa. This region forms an isolated branch of the dendrogram obtained (Fig. 1A), which may represent a different bioprovince from the CTA, perhaps containing the equatorial charophytes of the Early Cretaceous. However, the absence of data from Central Africa and the north of South America, which formed a single landmass during the Barremian, prevents an assessment of this hypothesis now.

Within the family Clavatoraceae, which was composed of ca. 26 evolutionary species from the Late Jurassic until the latest Cretaceous according to Martín-Closas (1996), at least 2 clavatoracean genera (i.e. *Pseudoglobator* and *Globator* Grambast) and up to 8 species (Table 1; Fig. 1B) belonging to two different subfamilies (i.e. Atopocharoidae (Grambast) emend. Martín-Closas ex Schudack and Clavatoroidae (Grambast) emend. Martín-Closas ex Schudack) are unique to the CTA during the Barremian–early Aptian. In the subfamily Atopocharoidae the monospecific genus *Globator*, with the species *Globator maillardii* (Saporta), has been reported only from the CTA (Figs. 1, 3). This species persists from the Tithonian until the early Aptian, evolving into an anagenetic lineage that has been used intensively for biostratigraphic purposes (e.g. Grambast, 1974; Riveline et al., 1996; Mojon, 2002; Vicente and Martín-Closas, 2013; Pérez-Cano et al., 2022a). This geological application has yielded numerous records from many basins in the CTA. In the subfamily Clavatoroidae two genera, *Ascidiella* Grambast and *Pseudoglobator*, are most typical of the CTA (Figs. 1, 3). The former is a relatively diverse genus that includes *A. stellata, A. triquetra, A. cruciata,* and *A. iberica* in the CTA. However, some species occurred also on neighbouring coasts. Such is the case of *A. reticulata* var. *reticulata,* endemic from the LEA or *A. iberica* var. *iberica* recorded both in the CTA and in the North European landmass. In contrast, genus *Pseudoglobator* is formed by 2 species, *P. paucibracteatus* and *P. fourcadei*, both of which are unique to the CTA. Three more genera, belonging to the family Clavatoraceae (i.e. *Atopochara, Clavator,* and *Hemiclavator*) were present both within and beyond the CTA, some species even attaining cosmopolitanism. However, the species from these genera appeared first on the islands of the CTA (Martín-Closas and Wang, 2008; Martín-Closas, 2015). This is the case, for instance, of *Atopochara trivolvis,* which appeared in the CTA during the Berriasian, and reach cosmopolitanism in a latitudinal belt of the Northern Hemisphere during the Aptian (Martín-Closas and Wang, 2008). *Clavator calcitrapus* was mainly an early Barremian species in Eurasia and South America (Martín-Closas, 2015), but its first representative, *Clavator calcitrapus* var. *jiangluoensis*, occurred in the late Hauterivian of the CTA (Feist et al., 1995). In addition, *Hemiclavator neimongolensis* var. *neimongolensis* is widely represented in Eurasia during the Barremian and early Aptian (Martín-Closas, 2015), but it first appears in the CTA at the end of the Berriasian, where the anagenetic variety *Hemiclavator neimongolensis* var. *posticecaptus* was found on both extremes of the main core islands, i.e. Spain in the Iberian Island (Martín-Closas, 2000) and Romania in the Moesian-Dacian Island (Sanjuan et al., 2021a).

Beyond the CTA the Barremian–early Aptian charophyte floras were dominated by two other families, the family Characeae, represented mainly by the genera *Aclistochara* (Peck) Schudack, *Mesochara* Grambast, and *Sphaerochara* (Mädler) Soulié-Märsche, and the family Porocharaceae (Grambast) emend. Schudack, characterized mainly by the genera *Porochara* Grambast and *Feistiella* Schudack, only associated with the cosmopolitan or sub-cosmopolitan (i.e. Eurasian) representatives of the Clavatoraceae (Martín-Closas and Wang, 2008; Martín-Closas, 2015). Some examples of this type of floras have recently been described in China (Li et al., 2020) and in South America (De Sosa Tomás et al., 2022) for the interval studied (Barremian–early Aptian).

In sum, all the available data suggest that a particular charophyte bioprovince can be proposed for the Barremian–early Aptian Central Tethyan Archipelago (CTA), and that it probably persisted throughout the entire Early Cretaceous. Based on the abundance and biodiversity of clavatoracean charophytes endemic to this archipelago, this bioprovince can be called the “Clavatoracean Bioprovince”.

4.2. Climatic constraints of the Clavatoracean Bioprovince

The results obtained reveal that the Clavatoracean Bioprovince is separated from neighbouring areas by latitudinal boundaries. The northern boundary is represented by the North European landmass, which is located at a palaeo-latitude of ca. 35–45°N (Fig. 3). The main core of islands of the CTA ranges in latitude from 10 to

Fig. 2. Utricles of clavatoracean species characteristic of the Central Tethyan Archipelago. **A**–**B**. *Globator maillardii* var. *trochiliscoides* (Southern Dobrogea, Romania; from Sanjuan et al., 2021a). **A**. Lateral view; **B**. basal view. **C**–**D**. *Globator maillardii* var. *biutricularis* (Southern Dobrogea, Romania; from Sanjuan et al., 2021a, b). **C**. Lateral view; **D**. Basal view. **E**–**F**. *Clavator grovesii* var. *gautieri* (Iberian Chain; Spain; from Pérez-Cano et al., 2022a). **E**. Lateral view; **F**. Adaxial view. **G**–**H**. *Ascidiella triquetra* (Iberian Chain, Spain; from Pérez-Cano et al., 2020). **G**. Oblique-abaxial view; **H**. Apical view. **I**–**J**. *Ascidiella cruciata* (Iberian Chain, Spain; from Vicente and Martín-Closas, 2013). **I**. Lateral view; **J**. Apical view. **K**. *Ascidiella iberica* var. *inflata* (lateral view; Iberian Chain, Spain). **L**–**M**. *Hemiclavator adnatus* (Iberian Chain; Spain; from Pérez-Cano et al., 2020). **L**. Abaxial view; **M**. Lateral view. **N**–**O**. *Hemiclavator neimongolensis* var. *posticecaptus* (Iberian Chain, Spain; from Pérez-Cano et al., 2020). **N**. Abaxial view. **O**. Lateral view. **P**–**Q**. *Pseudoglobator paucibracteatus* (Subalpine Chains, France; from Martín-Closas et al., 2009). **P**. Lateral view; **Q**. Basal view.

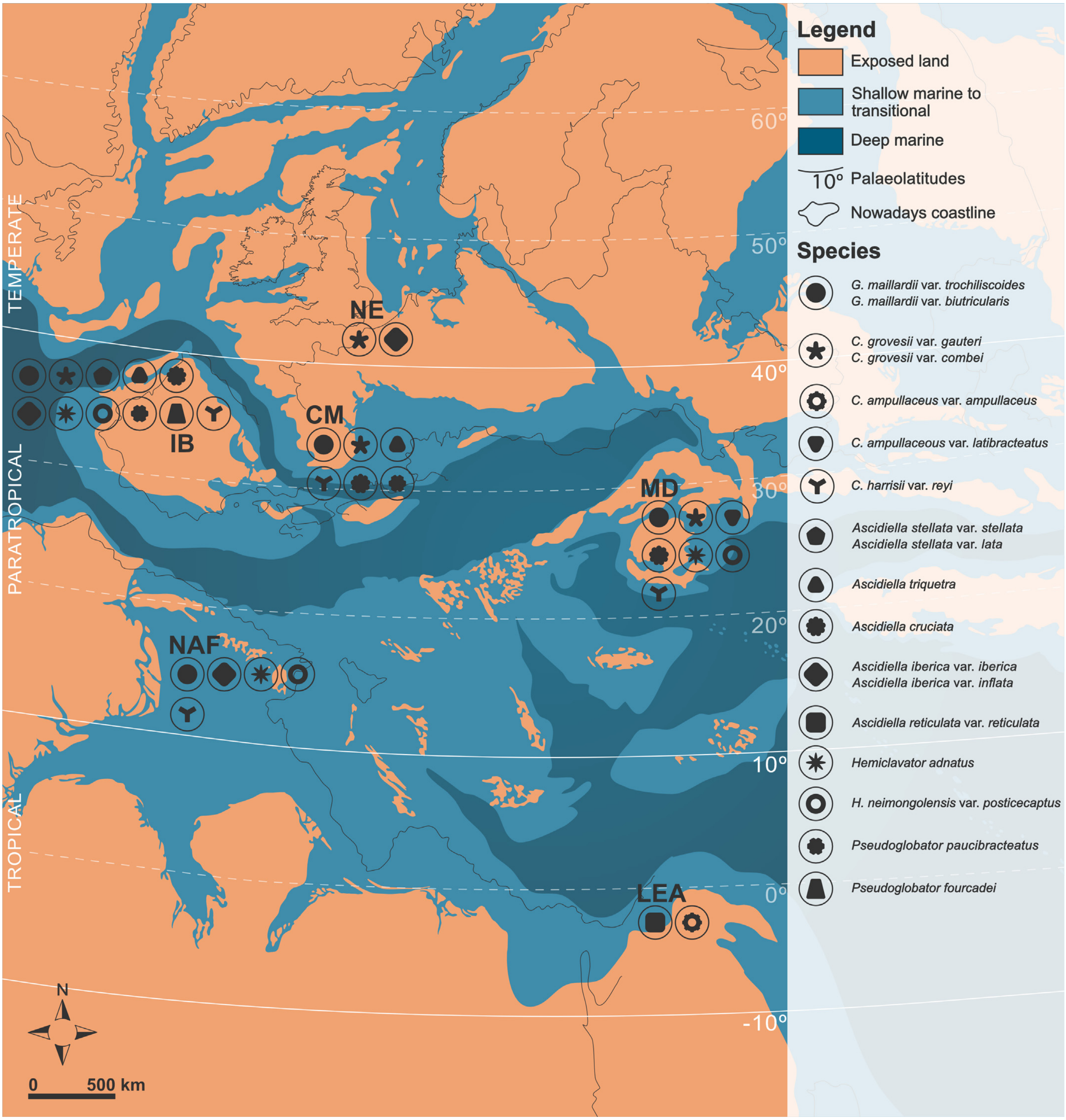

Fig. 3. Distribution of species characteristic of the Central Tethyan Archipelago during the Barremian and early Aptian. Palaeogeographic map modified from http://deeptimemaps.com (accessed November 2022) and Dercourt et al. (2000).

35°N (Fig. 3). South of this area, the Levantine Island and the NE African region would have belonged to a tropical-equatorial belt ranging from ca. 10°N to about 10°S (Fig. 3). The separation between these three latitudinal belts suggests that the charophyte floras were climatically controlled. As a matter of fact, they correspond quite precisely with the temperate, paratropical, and tropical climatic belts defined for the Early Cretaceous by Scotese (2003). The islands in the temperate belt would have been influenced by wide temperature ranges and high seasonality. The paratropical belt would include lakes and wetlands with relatively high temperatures throughout the year but with high seasonal changes in precipitation (monsoonal climates), while the tropical belt would have been influenced by high temperatures and precipitation but with low seasonal changes (Scotese, 2003).

Besides the more evident latitudinal distribution of the CTA, there were also longitudinal relationships between them. This is observed in the occurrence of common taxa in the same longitudinal strip, i.e. separately in the eastern and the western islands of the archipelago. In the eastern part of the archipelago *Clavator ampullaceus* is shared between the Levantine-NE African area and the Moesian-Dacian area, i.e. across the paratropical and tropical belts (Fig. 3). However, this species developed two different varieties in each area, respectively; *Clavator ampullaceus* var. *ampullaceus* in the South (Sanjuan et al., 2021b and references therein) and *C. ampullaceus* var. *latibracteatus* in the North (Sanjuan et al., 2021a). In the two areas these varieties grew in euryhaline to freshwater wetlands. The same palaeogeographic pattern can be observed in the western islands, for instance in species such as *Ascidiella iberica*, which occurs only in the North African basins, Iberian basins, and British Island basins, i.e. across the paratropical and temperate belts and also in similar facies (mainly freshwater lakes). This north-south distribution pattern appears to be limited to a few species and might be related to specific dispersal mechanisms. Nowadays some charophytes are dispersed over long-distances in the digestive tract of migratory birds (Proctor, 1980), which may also have been the case in the early Aptian, by which time aquatic birds with well-developed sternums, capable of undertaking long-duration flights already existed (You et al., 2006).

4.3. Endemism within large islands

The Iberian Island was one of the largest islands in the Central Tethyan Archipelago and is probably the region for which most data are available on Early Cretaceous charophytes of the CTA. It appears that this island was sufficiently large and isolated to give rise to endemism (Figs. 1 and 3). Such is the case of *Pseudoglobator fourcadei* (Fig. 3), which is only known from the Prebetic Chain (Martín-Closas, 2000). Apart from this endemism, Iberia also had other possible Barremian endemic taxa, such as *Clavator calcitrapus* var. *calcitrapus* or *Ascidiella stellata* (Pérez-Cano et al., 2020). Endemic species may also have occurred in other large islands of the CTA. This is possibly the case of *Clavator ampullaceus* var. *latibracteatus* described from Romania, on the Moesian-Dacian Island, by Sanjuan et al. (2021a). However, in spite of these possible single-island endemisms, the homogeneity of the CTA bioprovince in terms of taxonomy was high throughout the entire time interval studied. Frequent sea-level changes during the Barremian and early Aptian probably helped to facilitate floral exchange between neighbouring islands and to maintain the biogeographic identity of the archipelago over a long period of time.

4.4. Comparisons with the biogeographic distribution of other non-marine fossil groups

Palaeobiogeographic zonation has a long tradition in palaeobotanical studies, mainly in palynology. The proposals available to date of a floristic zonation for the Early Cretaceous are based in sporomorphs and result in the definition of very large floristic provinces, which are approximately equivalent to latitudinal strips (e.g. Herngreen and Chlonova, 1981; Herngreen et al., 1996). This is possibly due to a mainly climatically controlled distribution of the sporomorph megaproducers used for biogeographic zonation, most of them from anemophilous (i.e. wind pollinated) plants. Wind-dispersal of sporomorphs facilitates their use in large-scale biostratigraphic correlation (e.g. Ied and Tahoun, 2019), but undermines any possible comparison with the results obtained here from charophytes. Other terrestrial groups, such as vertebrates and insects provide valuable biogeographic data for comparison (e.g. Peris et al., 2016), yet insufficient to undertake a biogeographic zonation. In order to test these results with other organisms that have fossil records and palaeoenvironmental conditions comparable with charophytes, we chosed non-marine ostracods. They are among the most common fossils in aquatic continental settings, at least since the Middle–Late Jurassic, being consequently one of the most useful groups in biostratigraphy, stratigraphic correlation, palaeoecology, and palaeobiogeography of the aquatic non-marine domain.

Mesozoic non-marine ostracods belong to the three superfamilies Cypridoidea Baird, Cytheroidea Baird, and Darwinuloidea Brady and Norman, among which the first has experienced a particular ‘explosive’ radiation during the Late Jurassic–Early Cretaceous worldwide (Whatley, 1990). Species of the two genera *Cypridea* (Cypridoidea) Bosquet and *Theriosynoecum* Branson (Cytheroidea) are the main tools used in biostratigraphy of the Purbeck-Wealden facies (Horne, 2009) and a large amount of distribution data are available about them during the Barremian–early Aptian interval studied here.

The Wealden Group, as defined in its English type locality, is chronostratigraphically calibrated to the Hauterivian–early Aptian time interval, assigned to the ostracod biozone Theriosynoecum fittoni of Horne (2009). The upper Wealden, Barremian–early Aptian in age, is assigned to the subzone Cypridea fasciata of Horne (2009), and mainly characterized by species of genus *Cypridea* such as *Cypridea tenuis* Anderson, *C. fasciata* Anderson, *C. clavata* Anderson, *C. comptonensis* Anderson, *C. bogdenensis* Anderson, *C. brendae* Anderson, *C. marina* Anderson, *C. pseudomarina* Anderson, *C. insulae* Anderson, *C. recta* Anderson, *C. hispida* Anderson, *C. pumila* Anderson, *C. dorsospinata* Anderson, *C. valdensis* Sowerby, and *C. tuberculata* Sowerby. They are usually associated to *Theriosynoecum fittoni* Mantell, *Rhinocypris jurassica* Martin, *Mantelliana mantelli* Jones, *Fabanella boloniensis* Jones, and *Alicenula leguminella* Forbes (Anderson, 1985; Horne, 1995, 2009). Such a species assemblage has also been described from Northwest Germany (Martin, 1940; Wolburg, 1959; Schudack, 1994; Elstner and Mutterlose, 1997) and Denmark (Christensen, 1963), within the North European landmass. Some Wealden ostracod species were also reported from southern European basins, mainly from the Iberian Island (IB), i.e. from Spain (Kneuper-Haack, 1966; Brenner, 1976; Swain, 1993; Schudack and Schudack, 2009) and Portugal (Damotte et al., 1990; Cabral, 1995), as well as from the North African domain, i.e. Tunisia (Trabelsi et al., 2015, 2021; Chnayna et al., 2021) and Morocco (Andreu, 1989, 1991; Andreu et al., 2003). Differences in the distribution of some Wealden ostracod assemblages highlights a north to south distribution pattern.

These data allow for a biogeographic comparison with the results presented here from charophytes. First the extension of the Clavatoracean Bioprovince coincides broadly with the distribution pattern of ostracods in the same time interval. The northern boundary of the Clavatoracean bioprovince is represented in the ostracod faunas by a latitudinal boundary between the northern Wealden assemblages (English, German, and Danish faunas) and those from the south (Iberia and North Africa), the latter corresponding to the Tethyan islands of the CTA. The southern boundary of the Clavatoracean Bioprovince, placed at 10°N latitude, is much better defined in ostracod faunas. Barremian–lower Aptian non-marine ostracod assemblages from the Levantine domain, mainly from Israel (Rosenfeld and Raab, 1984) and Lebanon (Bischoff, 1963) are formed by species completely different from the coeval Wealden fauna, hosting a significant proportion of endemic cypridean species, such as *Cypridea libanensis* Bischoff, *C. heliopolisensis* Bischoff, *C. aaleyensis* Bischoff, *C. baidarensis* Bischoff, *C. quadrangulata* Brenner, *C. orientalis* Bischoff, and *C. sidonensis* Bischoff. From these Levantine species, *C. heliopolisensis* has been recovered also from Brazil (Krömmelbein and Weber, 1971; Beurlen et al., 1994), and *C. aaleyensis* from North Somalia (Luger and Schudack, 2001). This suggests a southward extension and biogeographic connection of these faunas across the Gondwanan landmass. These differences between the biogeographic distribution of the Wealden ostracod species in the north and the Gondwanan faunas in the south highlights, also in ostracods, a climatic control during the late Early Cretaceous, as was already suggested by Anderson (1973).

Second, the dispersal of ostracods between islands of the CTA appears to have been also common fact, like in charophytes. For instance, cypridean species such as *Cypridea cyrtorostralis* Brenner and *C. ventriosa* Brenner, though to be endemic from Iberia, were recently reported from the Central Tunisian Atlas (Trabelsi et al., 2015, 2021; Chnayna et al., 2021). Dispersal of Wealden ostracod species within CTA is also confirmed by the occurrence of the traditionally West-European species *Theriosynoecum fittoni*, *Cypridea recta,* and *C. fasciata* in Romania, i.e. in the Moesian-Dacian domain (Antoniade, 2016).

Another important similitude in the biogeography of Barremian–early Aptian charophytes and non-marine ostracods is that some of them, notably genera *Cypridea*, *Harbinia* Tsao, *Theriosynoecum*, and *Alicenula* Rossetti et Martens, achieved cosmopolitan range during this time interval. They have been described from Europe and North America (Sames, 2011a, b and references therein), North Africa (Andreu, 1991; Trabelsi et al., 2015; Chnayna et al., 2021), South America and West Africa (Grekoff and Krömmelbein, 1967; Poropat and Colin, 2012 and references therein), East Africa (Luger and Schudack, 2001; Sames, 2008), Asia (Hou et al., 2002; Hayashi, 2006), Middle East (Rosenfeld and Raab, 1984; Sanjuan et al., 2021b). Accordingly, Trabelsi et al. (2015), and Sames and Trabelsi (2018) suggested that peri-Tethyan islands could have worked as effective bridges for non-marine ostracods dispersal by 'island-hopping' of larger animals.

5. Conclusions

Charophyte bioprovincialism is first explored in the charophyte fossil record. Previous attempts to study the biogeographic distribution of fossil charophytes were limited to describing the composition of charophyte floras in the different continents along geological time, without providing a biogeographic analysis of bioprovincialism.

The Central Tethyan Archipelago (CTA) is proposed here to host a particular subtropical bioprovince at least during the Barremian–early Aptian interval. The new bioprovince is characterized by up to 2 genera and 8 species belonging to the family Clavatoraceae, which are unique to this area, i.e. most of the Tethyan Europe and North Africa. The Middle East and north-east Africa had evident relationships with the CTA charophyte bioprovince, especially because their charophyte floras were also dominated by the same family, but with a different taxonomic composition at the species level. Although the data about this latter area are insufficient yet, a future definition of a different, properly equatorial bioprovince for Early Cretaceous charophytes in this southern domain of the Tethys would seem justified, and is already clear for other aquatic groups, such as ostracods.

Outside the Central Tethyan Archipelago charophyte bioprovincialism during the Early Cretaceous remains undefined. However, bioprovinces in these areas will be possibly based in charophyte families different than the Clavatoraceae, since only a few species of this family migrated from the CTA to the neighbouring continents to reach a sub-cosmopolitan or cosmopolitan distribution. The Characeae and the paraphyletic group of the Porocharaceae are the two charophyte families dominating outside the Central Tethyan Archipelago.

The CTA clavatoracean bioprovince shows a latitudinal pattern which is certainly related to climatic constraints. However longitudinal strips of regions within the bioprovince and the neighbouring areas suggest that other factors may have impinged the distribution of charophyte floras within the bioprovince. In the east of the CTA this is the case of the links between Moesia-Dacia and the putative equatorial bioprovince, while to the west of the archipelago, North Africa and Iberia shared some species with the North European landmass. These longitudinal affinities may be linked to the dispersal vectors of particular species that migrated in a north to south axis. Other possible variables in the biogeographic distribution of clavatoraceans include the palaeoecological constraints of the different species. They are of difficult evaluation at the present state of the art, since only a few palaeoecological studies have been carried out to date with clavatoraceans, and most of them were devoted to the Iberian floras.

In spite of all these superposed climatic and biogeographic controls, the homogeneity of the CTA charophyte bioprovince remained high during the time interval studied, i.e. several millions of years, as attested by the low number of endemic species and the restriction of regional differences to the infraspecific rank. Similar biogeographic patterns are found for non-marine ostracods suggesting that the CTA charophyte bioprovince can be extrapolated at least to other aquatic non-marine benthic groups, while data available from terrestrial groups are either too limited (e.g. vertebrates and arthropods) or provide a very different biogeographic signal (sporomorphs) due to very distinct dispersal vectors.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2023.105752.