Cosmopolitanism in Northern Hemisphere Cretaceous Charophyta (Clavatoroidae)

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ABSTRACT

Clavatoroidae were dominant charophytes in Early Cretaceous lakes and ponds of the Central Tethyan Archipelago and a significant contributor to the coeval non-marine floras of Asia and North America. From the 17 clavatoroidean evolutionary species reported, only four extended to reach a cosmopolitan or subcosmopolitan range. These species were originally limited in their biogeographic range to the islands of the Central Tethys, which were an active area of speciation for the whole family Clavatoraceae. In addition, most of them evolved from endemic Tethyan ancestors, suggesting that the ancestral biogeographic condition was one of range restriction rather than cosmopolitanism.

Three pulses of migration and biogeographic range expansion are recognized in Clavatoroidae. The first, late Berriasian to Early Valanginian pulse occurred in an Early period of the subfamily's evolution and involved one species, *Clavator grovesii grovesii*, which extended across Eurasia and North America, reaching full cosmopolitanism in a latitudinal belt. The second pulse, late Hauterivian to Barremian, involved the four species in Eurasia, i.e. *C. grovesii jiuquanensis*, *Clavator harrisii*, *Clavator calcitrapus* and *Hemiclavator neimongolensis*. The third migration pulse occurred in the Aptian and involved two species, *C. grovesii corrugatus* in Laurasia and *C. harrisii*, which reached full cosmopolitanism in the Northern hemisphere. These migration pulses lasted from 2.2 to 5 million years and are hypothesized to have been controlled by the paleogeographic connection of Early Cretaceous wetlands in Eurasia and by the adaptation of these species to a wide range of paleoenvironments. The influence of animal dispersal on the cosmopolitanism of species with a conjoint arrangement of gametangia, which is the rule in extant *Chara*, cannot be proposed as a testable hypothesis in Clavatoroidae, due to the lack of information about their male gametangia.

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1. Introduction

Cosmopolitanism in Cretaceous charophytes was first reported by Sirna (1963) and Palamarev (1971), and the subject became progressively more significant when particular cosmopolitan species, such as *Atopochara trivolvis* and *Clavator harrisii* (= *Flabellochara harrisii*), were observed in very distant areas of the planet and were consequently used for long-distance biostratigraphic correlation (e.g. Wang and Lu, 1982; Feist et al., 1995; Musacchio, 2000). However, the present understanding of the biogeographic dispersion and colonization processes in fossil charophytes, specifically Clavatoraceae, is far from complete. Analysis of the historical biogeography of the lineage *A. trivolvis* showed that cosmopolitanism only occurred during specific time spans of the species' evolution and was mainly controlled by paleogeographic connexions between continents and by paleoecological factors (Martín-Closas and Wang, 2008). Different species within this family show contrasting biogeographic patterns, which raises the question of

the origin of their cosmopolitanism and the reasons that determined the endemism of other closely related species (Martín-Closas and Wang, 2010). Gaining detailed knowledge of the historical biogeography of cosmopolitan Cretaceous charophytes could have far-reaching consequences that would spread beyond the study of this group. These charophytes are widely used for the aging of terrestrial floras and faunas in the Cretaceous and some paleontological sites of exceptional interest, such as the Jehol Biota, in Liaoning, China, or Las Hoyas Konservat-Lagerstätte in Spain, were mainly dated and correlated on the basis of such cosmopolitan charophytes (Wang et al., 2003a,b; Vicente and Martín-Closas, 2013).

With the aim of providing a better understanding of the historical biogeographic patterns of Cretaceous charophytes, and offering some guidelines for their use in long-distance biostratigraphic correlation, here the fossil record of cosmopolitan Clavatoroidae is documented and analyzed. This subfamily not only has an excellent fossil record due to the biocalcification of their fructifications, but it is also the only charophyte fossil group with a reasonably well-known phylogeny (Grambast, 1974; Martín-Closas, 1989, 1996; Schudack, 1993). Both these facts provide a unique opportunity to carry out the proposed study.

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2. Materials and methods

The dataset for this study results from reviewing the available bibliography regarding the occurrence of Clavatoroidae in the Northern hemisphere. A large amount of detailed information concerning the temporal and spatial distribution of this fossil subfamily is gathered in biostratigraphical studies from all the northern continents, providing a unique opportunity to perform biogeographical analysis with an excellent dataset. Reports of Southern hemisphere Clavatoroidae are only well-known from Argentina and Brazil (Musacchio, 1971, 1979, 1990, 2000) and there are no records from the other parts of Gondwana, probably due to a lack of specialized research about fossil charophytes in those areas. Hence only the data from the Northern hemisphere were used for the purposes of this study. Also, the time intervals considered for this biogeographic analysis correspond to one of the biozonations of the Northern hemisphere, i.e. the European charophyte biozones defined by Riveline et al. (1996). The database (Tables 1–8) includes studies with an appropriate illustration of the fossil material, which allowed the taxonomic attribution to be visually checked. Data from studies without illustrations were only included if they were provided by recognized authorities in charophyte taxonomy. The publication by Imam (2000) was excluded because he copied and misidentified the illustrations from a number of previous authors, specifically Soulié-Märsche (1994) for the clavatoraceans. Granier et al. (2009) considered this publication a case of scientific fraud.

The present study is based on the taxonomy proposed by Martín-Closas (1989, 1996) and Schudack (1993), which resulted from a cladistic analysis of the whole family Clavatoraceae and follows Simpson's (1961) and Wiley's (1978, 1981) concept of evolutionary species. As a consequence, a number of the traditional taxa of Clavatoroidae are included here within the same evolutionary species. This is of particular importance in the case of traditional taxa that belong to gradualistic lineages, i.e. uninterrupted successions of chronospecies, which are regarded here as a continuum of infraspecific forms (either varieties or subspecies), rather than as different species.

The contrasting points of view on this issue were debated in the past by Feist and Wang (1995) and Martín-Closas and Schudack (1997).

3. Morphology of the clavatoroidean fructification

The Clavatoroidae were characterized as a subfamily by Grambast (1969) on the basis of their fructification, which is a rather complex structure in comparison to that of other fossil and extant charophytes (Fig. 1A–L). The clavatoroidean gyrogonite has a regular ellipsoidal shape and a prominent apical neck that includes, on top, a large, rose-shaped apical pore. This gyrogonite is formed of five spiral cells, coiled clockwise from the base to the apex and calcified only at their periphery. The resulting empty tubes show that the clavatoroidean gyrogonite underwent a particular type of calcification, different from that of other Charales. Inside the base of the gyrogonite there is a unicellular, discoid, basal plate with a rounded, pentagonal outline (Fig. 1F), which is only rarely preserved (Martín-Closas, 1988). The gyrogonite is coated with two calcitic layers. The first is formed by semi-spherical micronodules showing a radial crystal growth and generally disposed along the spiral-cell sutures (Fig. 1H). These nodules probably function to strengthen the gyrogonite at its weakest points, represented by the sutures of the otherwise weakly calcified spiral cells. The second layer of the gyrogonite is formed by the utricle, which was a specialized vegetative coating of the clavatoracean fructification. The vegetative cells forming the utricle did not calcify. Instead, the area between these cells and the nodular layer calcified in microsparite to form a rigid oosporangial shell. Charologists use the term 'utricle' to refer to the calcitic shell, which is in fact the preserved fossil rather than the real biological structure. This shell shows on its external face the impression of the utricle cells (Fig. 1A–L), while the internal side is strongly cemented to the spiral cells and nodules of the gyrogonite. The clavatoroidean utricle always displays bilateral symmetry, in contrast to Atopocharoidae, the other large clavatoracean family, which has a triradial utricle structure. The bilateral symmetry of the clavatoroidean utricle is determined by an axial plane that contains the branchlet to

Table 1
Distribution dataset of *Clavator grovesii grovesii*.

Taxonomy	Age	Locality	Country	Reference
Clavator grovesi sp. nov.	Berriasian	Portesham, Dorsetshire (England)	United Kingdom	Harris (1939)
Flabellochara grovesi	Berriasian	Cala d'Inferno, Alghero (Sardinia)	Italy	Pecorini (1969)
F. grovesi	Berriasian	Pont de la Chaux, Jura	Switzerland	Grambast (1970)
		Dorset, England	United Kingdom	
F. grovesi	Berriasian	Tozo Borehole (Burgos)	Spain	Brenner (1976)
		Sopeña (Santander)		
Flabellochara xiangyunensis	Early Cretaceous	Yunnan	China	Wang et al. (1976)
F. xiangyunensis	Valanginian	Xiangyun, Chuxiong (Yunnan)	China	Wang and Lu (1982)
Flabellochara niwanensis sp. nov.	Early Cretaceous	Xining and Minhe Basins (Qinghai)	China	Hao et al. (1983)
Flabellochara aff. *grovesi*	Berriasian	Cala d'Inferno, Alghero, Sardinia	Italy	Colin et al. (1985)
F. grovesii	Berriasian	Coll de Querol, Castelló	Spain	Martín-Closas and
		El Mangraner, Castelló		Grambast-Fessard (1986)
F. grovesi	Early Berriasian	Bienne	Switzerland	Mojon and Strasser (1987)
F. grovesi	Berriasian	Quintanilla, Mambrillas, Hortezuelos (Bur.)	Spain	Schudack (1987a)
		Bijuesca (Zaragoza), Fitero (Rioja)		
	Early Valanginian	Hortezuelos (Burgos)		
	Late Kimmeridgian	Terroba		
Flabellochara longicollis sp. nov.	Valanginian	Waishan, Fanchang (Anhui)	China	Hu (1990)
F. grovesii	Berriasian	Fairlight Borehole, Weald	United Kingdom	Feist et al. (1995)
		Durdle Door, Dorset		
F. xiangyunensis	Valanginian	Wadhurst Park-3 Borehole, Weald	United Kingdom	Feist et al. (1995)
		Glynleigh Borehole, Weald		
		Kitchenham Borehole, Weald		
Clavator grovesii grovesii	Early Berriasian	Ammensen, Hils	Germany	Schudack (1996b)
C. grovesii grovesii	Berriasian	Coll de Querol (Castelló)	Spain	Martín-Closas (2000)
		Ladruñan (Teruel)		
		La Pleta de Garraf (Barcelona)		
		Portelárbol, Garray (Soria)		
		Hortezuelos, Quintanilla (Burgos)		
		Camesa, Dacabra (Palencia)		
C. grovesii grovesii	Late Berriasian–early Valanginian	Black Hills, S-Dakota and Wyoming	United States	Martín-Closas et al. (2013)

Table 2
Distribution dataset of *Clavator grovesii discordis*.

Taxonomy	Age	Locality	Country	Reference
Clypeator sp.	Berriasian	Stroit (Hils), Hannover	Germany	Grambast (1970)
Clypeator sp.	Berriasian	Escalada Bh., Ayoluengo Bh. (Burgos)	Spain	Brenner (1976)
Clypeator discordis sp. nov.	Hauterivian–Barremian	Predobrogean Basin	Moldavia-Ukraine	Shaikin (1976)
Clypeator zongjiangensis	Valanginian	Zhongjiang (Sichuan)	China	Wang and Lu (1982)
C. zongjiangensis	Valanginian	Bailong, Qiqusi, Gudian Fms. (Sichuan)	China	Huang (1985)
C. zongjiangensis	Berriasian	Ordejón, Quintanilla, Mambrillas (Burgos) Terroba, Bijuesca (Zaragoza)	Spain	Schudack (1987a)
	Late Kimmeridgian	Huerta del Rey (Burgos), Terroba		
C. discordis	Early Berriasian	Bienne	Switzerland	Mojon and Strasser (1987)
C. discordis	Berriasian	NW German Basin	Germany	Schudack (1990)
C. zongjiangensis	Early Cretaceous	Northern Tarim Basin (Xinjiang)	China	Lu and Luo (1990)
C. discordis	Berriasian	Lower Saxonian Basin	Germany	Feist and Schudack (1991)
Clypeator britannicus	Valanginian	Kingsclere Borehole, Hampshire	United Kingdom	Feist et al. (1995)
C. discordis	Late Tithonian	Swindon, Wiltshire	United Kingdom	Feist et al. (1995)
Clypeator grovesii discordis	Early Berriasian	Werle Borehole, South Mecklenburg	NW Germany	Schudack (1996a)
Clavator grovesii discordis	Early Berriasian	Ammensen (Hils)	NW Germany	Schudack (1996b)
C. grovesii discordis	Berriasian	Boleras, San Marcos Fms (Burgos) Garray (Soria) Camesa (Palencia)	Spain	Martín-Closas (2000)
Clypeator *discordis*	Late Tithonian	Murches (Lisboa), Brouco (Sintra)	Portugal	Pereira et al. (2010)

which the fructification was attached. A portion of this branchlet is usually calcified as a part of the utricle shell. On both sides of this axial plane the same vegetative structure is displayed. However, in some cases the preserved branchlet portion is small and the utricle may seem radial rather than bilateral in symmetry. The utricle is a species-specific structure on which the whole taxonomy and phylogeny of the Clavatoroidae are based.

4. Distribution of cosmopolitan and subcosmopolitan Clavatoroidae in time and space

In the Northern hemisphere, Cretaceous Clavatoroidae are recorded in four main regions: (1) North America; (2) the Central Tethyan Archipelago, including Western Europe and Northern Africa; (3) Eastern Europe and Western Asia, mainly from the Black Sea to Kazakhstan; and (4) Eastern Asia, including Mongolia, China and Korea. Taking into account the area where the subfamily is documented, it is understood that a species is cosmopolitan in the Northern hemisphere when it is represented in all these regions, while subcosmopolitanism is used here in the sense that the species is reported in least in two of the regions mentioned. The regions mentioned were all located along a latitudinal belt, roughly between 25° and 60°N, which was termed 'paratropical' by Saward (1992). Paleoclimatology is thought to exercise a general control over the distribution area of the group studied, limiting its expansion to the more tropical and temperate belts of the Cretaceous.

Of the seventeen evolutionary species of Clavatoroidae considered by Martín-Closas (1989, 1996) and Schudack (1993) only four reached a wide distribution across the Northern hemisphere in the Cretaceous: *Clavator grovesii*, *C. harrisii*, *Clavator calcitrapus* and *Hemiclavator neimongolensis*. In the following sections an account of the distribution data for these species in time and space is provided. *Nodosoclavator bradleyi*, regarded as the ancestral species of Clavatoroidae by Martín-Closas (1996), also had a wide distribution but has not been considered in this study since the fructification is completely plesiomorphic, i.e. devoid of distinct features, which sometimes makes its separation from other, closely related species difficult with only bibliographic data from some regions to hand.

4.1. Clavator grovesii Harris, 1939

The evolutionary species *C. grovesii* is one of the most basal species in the phylogeny of Clavatoroidae. It was first described by Grambast (1970, 1974) as a gradualistic succession of chronospecies called the *Flabellochara–Clypeator* lineage, which is especially useful in biostratigraphy (Riveline et al., 1996). Later, this succession was reinterpreted by Martín-Closas (1989, 1996) and Schudack (1993) as a single evolutionary species with a continuum of infraspecific forms, either subspecies or varieties (Fig. 2). The utricle characters of *C. grovesii* changed gradually from the late Tithonian to the Albian. At the origin of the lineage, the utricle is formed by a portion of the branchlet and two lateral fan systems, in turn formed of polygonal bract cells and embraced by larger bract cells at each side. The two fan systems are separated by

Table 3
Distribution dataset of *Clavator grovesii gautieri* and *C. grovesii combei*.

Taxonomy	Age	Locality	Country	Reference
Clypeator gautieri n. sp.	Hauterivian	Olba, Teruel	Spain	Grambast (1970)
Clypeator combei n. sp.	Early Barremian	El Mangraner-La Sènia, Castelló	Spain	Grambast (1970)
C. gautieri	Late Hauterivian–Early Barremian	Coll de Querol (Castelló)	Spain	Martín-Closas and Grambast-Fessard (1986)
C. combei	Hauterivian	Between rivers Pruth and Dniester	Moldavia, Ukraine	Shaikin et al. (1992)
C. combei	Late Hauterivian–Late Barremian	Warligham Borehole, Weald Ripe Borehole, Weald Hailsham Borehole Cowleaze Chine, Isle of Wight	United Kingdom	Feist et al. (1995)
Clavator grovesi var. *combei*	Early Barremian	Oliete and Aguilón basins (Teruel)	Spain	Soria et al. (1995)
C. grovesi var. *combei*	Valanginian–Barremian	Coll de Querol, El Mangraner (Castelló) Barranco Montoro, Olba, Mora (Teruel) Sucaina, Obón, Oliete, Aguilón (Teruel)	Spain	Martín-Closas (2000)
C. grovesii var. *combei*	Barremian	Berland	France	Martín-Closas et al. (2009)
C. grovesii var. *combei*	Late Barremian	La Huérguina (Cuenca)	Spain	Vicente and Martín-Closas (2013)

Table 4
Distribution dataset of *Clavator grovesii jiuquanensis*.

Taxonomy	Age	Locality	Country	Reference
Perimneste jiuquanensis	Late Jurassic–Early Cretaceous	Chijinbao, Gansu	China	Wang (1965)
P. aff. jiuquanensis	Albian	Babatag, Karakuz	Tadzhikistan	Kyansep-Romashkina (1967)
Clypeator corrugatus	Barremian–Aptian	Kalenik Borehole (Loveć)	Bulgaria	Palamarev (1971)
Clypeator europaeus	Barremian	Valea Akargea-Peştera (Dobrogea sud)	Romania	Neagu and Georgescu-Donos (1973)
Clypeator reyi	Aptian	Luz (Algarve)	Portugal	Rey and Ramalho (1974)
Clypeator jiuquanensis	Aptian–Albian	Ferghana North	Uzbekistan	Kyansep-Romashkina (1975)
Clypeator ovatus sp. nov.	Barremian	Predobrogean Basin	Moldavia-Ukraine	Shaikin (1976)
C. europaeus	Aptian	Luz, Algarve	Portugal	Grambast-Fessard (1980)
Clypeator jiuquansensis	Early Cretaceous	Gansu	China	Li (1981)
C. europaeus	Aptian	Nehden, Sauerland	Germany	Feist in Huckriede (1982)
C. jiuquansensis	Hauterivian–early Barremian	Chengxian-Liangdang, Jiuquan (Gansu)	China	Wang and Lu (1982)
C. jiuquanensis	Early Cretaceous	Gyeongsang basin	South Korea	Seo (1985)
C. jiuquanensis	Barremian	Seonsangun, Gyeongsangbukdo	South Korea	Choi (1989)
C. jiuquanensis	Barremian	Nehden (Sauerland)	Germany	Schudack (1987b)
C. jiuquanensis	Barremian	Between rivers Pruth and Dniester	Moldavia, Ukraine	Shaikin et al. (1992)
	Aptian	Volgograd (north Caspian Sea)	Russia	
Clypeator ovatus	Barremian	between rivers Pruth and Dniester	Moldavia, Ukraine	Shaikin et al. (1992)
C. jiuquanensis	Aptian–Albian	Chul	Kazakstan	Zhamangara (1998)
C. jiuquanensis	Barremian	Gaotai (Gansu)	China	Wang et al. (2003b)
C. jiuquanensis	Barremian	Inggen-Ejin Qi basin, Inner Mongolia	China	Peng et al. (2003)
C. jiuquanensis	Hauterivian–early Barremian	Shaojian, Shangxian Co. (Shaanxi)	China	Chen et al. (2006)
Clavator grovesii jiuquanensis	Early Barremian	Pas du Frou (Chartreuse)	France	Martín-Closas et al. (2009)

an abaxial bract cell, opposite the branchlet (Fig. 2). All utricle cells are closely packed together and completely cover the gyrogonite. This initial structure is characteristic of *C. grovesii* var. *grovesii* (including traditional *Flabellochara grovesii* and similar Chinese morphotypes, such as *Flabellochara xiangyunensis*). During the lower Cretaceous, the fan system progressively transformed into a radial shield (Grambast, 1970, 1974). Already in the late Tithonian, small new radial bract cells developed towards the base of the lateral fans in *C. grovesii* var. *discordis*, including traditional *Clypeator zongjiangensis*, *Clypeator britannicus* and *C. discordis*. These two morphotypes persisted into the early Valanginian, forming mixed populations with *C. grovesii* var. *grovesii*. The new radial bract cells became longer towards the base of the ancient fan, developing complete but asymmetrical radial shields during the Valanginian, Hauterivian and early Barremian, with *C. grovesii* var. *gautieri* (equivalent to traditional *Clypeator gautieri*) and *C. grovesii* *combei* (equivalent to traditional *Clypeator combei*), two forms which are only distinguished by their different size. A new, late Barremian and early Aptian morphotype, *C. grovesii* var. *jiuquanensis*, represented the further elongation of the lower radial bract cells, which resulted in completely symmetrical and prominent radial shields. Finally, the radial shield cells displayed some clockwise torsion around the tip of the bearing bract cells in *C. grovesii* var. *corrugatus* (equivalent to traditional *C. corrugatus* and *C. lusitanicus*) between the late Aptian and middle Albian. The last morphotype, *C. grovesii* var. *caperatus*, shows contorting radial cells in the lateral shields. The lineage underwent extinction probably by the end of the Albian.

The biogeographical distribution pattern of *C. grovesii* is rather complex as should be expected of a species with such a long evolutionary history. In the late Tithonian and early Berriasian, populations of *C. grovesii grovesii*, either homogenous or mixed with *C. grovesii discordis*, are restricted to the Tethyan Archipelago (Fig. 3, Tables 1–2). During the whole Berriasian, they were quite common in Portugal, Spain, Sardinia, France, England, Switzerland and Germany. The morphotype *C. grovesii grovesii* has also been reported from the upper Berriasian–lower Valanginian deposits of the North American Western Interior Basin (Martín-Closas et al., 2013) and from the Valanginian of China (Wang and Lu, 1982), meaning that the species underwent a first cosmopolitan expansion very early in its biogeographic history (Fig. 3). The morphotype *C. grovesii discordis* colonized localities as far east as the Predobrogean Basin of Ukraine and Moldavia (Shaikin, 1976) and the Yunnan, Sichuan, Xinjiang and Qinhai Provinces in China (Wang et al., 1976; Wang and Lu, 1982; Yang et al., 2008), but so far has not been reported from North America. Later in the Valanginian up to the early Barremian, *C. grovesii* appears to be limited to the Tethyan Archipelago with two morphotypes: *C. grovesii gautieri* and *C. grovesii combei* (Fig. 3, Table 3). They were especially abundant in the Iberian Chain, Spain (Grambast, 1970; Martín-Closas, 2000) but they have been reported from the Wealden facies of England (Feist et al., 1995) and in France (Martín-Closas et al., 2009), Ukraine and Moldavia (Shaikin, 1976) as well. Its absence from China or North America is highly significant. Especially in China, there is an excellent record of other charophytes from the same age; but *C. grovesii* is not

Table 5
Distribution dataset of *Clavator grovesii corrugatus* and *C. grovesii caperatus*.

Taxonomy	Age	Locality	Country	Reference
Perimneste corrugatus	Aptian	Terrell Co. (Texas)	United States	Peck (1941)
		Freedom (Idaho)		
Perimneste corrugata	Aptian	Freedom (Idaho)	United States	Peck (1957)
		Trinity (Texas)		
P. corrugata	Aptian	South Oklahoma	United States	Branson and Schmitz (1964)
Clypeator corrugatus	Aptian	Caribou County, Idaho	United States	Grambast (1970)
Clypeator cf. lusitanicus	Aptian	Luz (Algarve)	Portugal	Rey and Ramalho (1974)
C. lusitanicus n. sp.	Aptian	Luz, Algarve	Portugal	Grambast-Fessard (1980)
C. corrugatus	Aptian	Junction, Kimble County (Texas)	United States	Soulié-Märsche (1994)
Clavator grovesii corrugatus	Early–middle Albian	Foz Calanda (Teruel)	Spain	Martín-Closas (2000)
Clypeator caperatus	Albian?	Zavial (Algarve)	Portugal	Rey and Ramalho (1974)
C. caperatus n. sp.	Albian?	Zavial (Algarve)	Portugal	Grambast-Fessard (1980)

Table 6
Distribution dataset of *Clavator harrisii*.

Taxonomy	Age	Locality	Country	Reference
Clavator harrisi n. sp.	Aptian	Trinity (Texas)	United States	Peck (1941)
C. harrisi	Aptian	Drummond, Granite Co. (Montana)	United States	Peck (1957)
		Freemont Co (Wyoming)		
		Lincoln Co. (Wyoming)		
		Freedom School (Idaho)		
		Trinity (Oklahoma)		
C. harrisi	Aptian	Lepini, Ausoni, Aurunci Mts. (Latio)	Italy	Sirna (1963)
C. harrisii	Aptian	South Oklahoma	USA	Branson and Schmitz (1964)
Flabellochara harrisi	Aptian	Babatag, Karakuz	Tadzhikistan	Kyansep-Romashkina (1967)
		Kyzyl Pilyal, Ferghana	Uzbekistan	
Flabellochara asiatica sp. nov.	Albian?	Kyzyl Pilyal, Ferghana	Uzbekistan	Kyansep-Romashkina (1967)
F. harrisi	Barremian–Aptian	Kalenik Borehole (Loveć)	Bulgaria	Palamarev (1971)
		Serra del Montsec (Lleida)	Spain	
F. cf. *harrisi*	Aptian	Luz (Algarve)	Portugal	Rey and Ramalho (1974)
F. harrisi	Aptian–Albian	Ferghana North	Uzbekistan	Kyansep-Romashkina (1975)
F. cf. *harrisi*	Barremian–Aptian	Montoria (Alaba) Pino de Bureba (Burgos)	Spain	Brenner (1976)
F. aff. *harrisi*	Early Cretaceous		Argentina	Musacchio (1979)
Stenochara reyi n. sp.	Barremian–early Aptian	Nossa Sra. da Luz, Algarve.	Portugal	Grambast-Fessard (1980)
Stenochara zavialensis n. sp.	Albian?	Zavial, Algarve	Portugal	Grambast-Fessard (1980)
Flabellochara hangzhouensis n. sp.	Aptian	Zhejiang	China	Wang (1981)
Flabellochara hengyangensis n. sp.	Early Cretaceous	Hengyang (Hunan)	China	Hu and Zeng (1981)
Flabellochara dongjingensis n. sp.	Early Cretaceous	Hengyang (Hunan)	China	Hu and Zeng (1981)
F. harrisi	Early Cretaceous	Gansu	China	Li (1981)
Flabellochara liangdangensis	Early Cretaceous	Gansu	China	Li (1981)
Flabellochara irregularis sp. nov.	Early Cretaceous	Gansu	China	Li (1981)
Flabellochara huayaensis sp. nov.	Early Cretaceous	Gansu	China	Li (1981)
Flabellochara hebeiensis sp. nov.	Early Cretaceous	South Hebei	China	Zhang et al. (1981)
F. dongjingensis	Early Barremian	Hengyang (Hunan)	China	Wang and Lu (1982)
F. hengyangensis	Early Barremian	Hengyang (Hunan)	China	Wang and Lu (1982)
F. hebeiensis	Late Barremian	Qiuxian (Hebei)	China	Wang and Lu (1982)
F. harrisi	Late Barremian	Chengxian, Liangdang (Gansu)	China	Wang and Lu (1982)
F. hangzhouensis	Aptian	Taoyuan, Zhijiang (Hunan), Yiyang (Jiangxi), Hangzhou, Pinghu (Zhejiang) Qijiang (Sichuan)	China	Wang and Lu (1982)
F. liangdangensis	Aptian	Chengxian, Liangdang (Gansu)	China	Wang and Lu (1982)
Flabellochara jurongica	Aptian	Jurong (Jiangsu), Qinghai, Neimongol	China	Wang and Lu (1982)
F. jurongica	Early Cretaceous	Xining and Minhe basins (Qinghai)	China	Hao et al. (1983)
F. hangzhouensis	Early Cretaceous	Hetao (Inner Mongolia)	China	Shu and Zhang (1983)
Flabellochara sp.	Early Cretaceous	Junggar basin, Xinjiang prov.	China	Liu and Wu (1985)
F. hebeiensis	Late Barremian	Qijiahe Fm, Dongting basin (Hunan)	China	Hu and Zeng (1985)
F. hangzhouensis	Aptian–Albian	Jiangding Group (Sichuan)	China	Huang (1985)
F. hebeiensis	Early Barremian–Aptian	Qikeshu, Queshan (Henan)	China	Jiang et al. (1985)
F. harrisi	Barremian	Coll de Querol (Castelló)	Spain	Martín-Closas and Grambast-Fessard (1986)
		Les Rases d'Aiguaviva (Castelló)		
		Herbers-Barranc Escresola (Castelló)		
		El Parrissal, Beseit (Teruel)		
F. aff. *harrisi*	Earlymost Barremian	Rebenacq	France	Martín-Closas and Peybernés (1987)
F. harrisi	Barremian	Boulmane	Morocco	Andreu et al. (1988)
F. harrisi	Late Barremian	Uña (Cuenca)	Spain	Schudack (1989)
	Early Barremian	Galve (Teruel)		
F. harrisi	Aptian	Paso de Indios, Chubut	Argentina	Musacchio (1989)
F. harrisi	Aptian	San Jorge Basin	Argentina	Musacchio (1990)
F. hebeiensis	Late Barremian	Alxa Zuoqi, Neimongol prov.	China	Lu and Yuan (1991)
F. harrisi	Barremian	Between rivers Pruth and Dniester	Moldavia-Ukraine	Shaikin et al. (1992)
		Near Volgograd (North Caspian sea)	Russia	
F. harrisi	Aptian	Junction, Kimble County (Texas)	United States	Soulié-Märsche (1994)
Clavator *harrisii*	Valanginian	Sierra del Pozo, Jaén	Spain	García-Cortés et al. (1995)
C. harrisii var *dongjingensis*	Valanginian	Sierra del Pozo, Jaén	Spain	García-Cortés et al. (1995)
F. hangzhouensis	Aptian–Albian	Xinjiang basin (Jiangxi)	China	Wu (1995)
C. harrisii	Early Barremian	Oliete and Aguilón basins (Teruel)	Spain	Soria et al. (1995)
F. harrisi	Valanginian–Barremian	El Mangraner, Castelló	Spain	Mojon (1996)
	Early Barremian	Les Rases d'Aiguaviva, Castelló		
Flabellochara aff. *asiatica*	Aptian–Albian	Chul	Kazakhstan	Zhamangara (1998)
F. harrisi	Aptian	Aïn Mellouk, Anoual	Morocco	Feist et al. (1999)
Flabellochara neimongguensis	Early Barremian	Ordos Basin	China	Liu (1999)
F. jurongica	Aptian	Ordos basin	China	Liu (1999)
C. harrisii donjiangensis	Valanginian–Hauterivian	L'Avellà, El Mangraner (Castelló)	Spain	Martín-Closas (2000)
		La Pleta de Garraf (Barcelona)		
		Hortezuelos (Burgos)		
		Bonansa (Huesca)		
C. harrisii harrisii	Barremian–early Aptian	Coll de Querol, Herbers (Castelló)	Spain	Martín-Closas (2000)
		Villahermosa del Rio (Castelló)		
		Jaganta, Seno, Villores (Teruel)		
		Aliaga, Camarillas, Bco. Montoro (Teruel)		

Table 6 (*continued*)

Taxonomy	Age	Locality	Country	Reference
C. harrisii harrisii		El Castellar, Mas Mina (Teruel)		
		Aguilón, Alacón, Blesa, Obón (Teruel)		
		Coll de Santa Cristina (Tarragona)		
		Hortezuelos, Quintanilla (Burgos)		
		Fm la Huérguina (Cuenca)		
		Dacabra (Palencia)		
C. harrisii reyi	Late Barremian–Aptian	Herbers (Castelló)	Spain	Martín-Closas (2000)
		Aliaga, Camarillas, Alacón (Teruel)		
		Blesa, Castel Cabra, Josa, Obón (Teruel)		
		Fm La Huérguina (Cuenca)		
C. harrisii zavialensis	Late Aptian–middle Albian	Foz Calanda (Teruel)	Spain	Martín-Closas (2000)
		Vilanova Meià (Lleida)		
F. hebeiensis	Barremian	Inggen-Ejin Qi basin, Inner Mongolia	China	Peng et al. (2003)
F. hebeiensis	Late Barremian	Kangping (Liaoning)	China	Wang et al. (2003b)
F. harrisi	Early Aptian	Rio de Mouro (Lisboa)	Portugal	Pereira and Cabral (2005)
Luzochara reyi nov. comb.				
F. harrisi	Early Cretaceous	Laohukou, Lanzhou (Gansu)	China	Chen et al. (2006)
F. cf. *jurongica*	Early Cretaceous	Laohukou, Lanzhou (Gansu)	China	Chen et al. (2006)
F. harrisi	Late Barremian–Early Aptian	Aïn Mellouk, Anoual	Morocco	Haddoumi et al. (2008)
F. harrisii	Early Barremian–Early Aptian	Central-High Atlas	Morocco	Mojon et al. (2009)
F. harrisi	Hauterivian?–Barremian	Iouaridene	Morocco	Haddoumi et al. (2010)
	Late Barremian–Aptian	Ait Imelloul		
C. harrisii zavialensis	Early Albian	Jebel Kebar	Tunisia	Trabelsi et al. (2010)
C. harrisii zavialensis	Early Albian	Jebel Koumine	Tunisia	Trabelsi and Martín-Closas (2012)
C. harrisii var. *reyi*	Late Barremian	La Huérguina and Las Hoyas (Cuenca)	Spain	Vicente and Martín-Closas (2013)

recorded. In the Barremian to early Aptian, *C. grovesii jiuquanensis*, showed a second significant widening of its distribution (Fig. 3, Table 4), since it has been recorded from a number of localities of Europe (e.g. Schudack, 1993; Martín-Closas et al., 2009), Central Asia (Kyansep-Romashkina, 1967, 1975), Kazakhstan (Zhamangara, 1998), China (e.g. Wang and Lu, 1982; Yang et al., 2008) and Korea (Seo, 1985). The next morphotype in the lineage, *C. grovesii corrugatus*, late Aptian to middle Albian in age, was not represented in Asia (Fig. 3, Table 4). It has however been recorded in the Iberian Peninsula (Rey and Ramalho, 1974; Grambast-Fessard, 1980; Martín-Closas, 2000) and in the southern part of the United States (Peck, 1957; Soulié-Märsche, 1994). The most derived and last morphotype, *C. grovesii caperatus* appears to be restricted to Portugal, where the species became extinct before the beginning of the Late Cretaceous (Fig. 3, Table 4).

In summary, *C. grovesii*, shows a first short endemic distribution in the Tethyan Tithonian to early Berriasian followed by a rapid expansion both to North America and to Asia, which resulted in a late Berriasian to early Valanginian cosmopolitan distribution in a latitudinal belt of the Northern hemisphere. Later the species retracted again to the Tethyan Archipelago during most of the Valanginian and Hauterivian. A second and short subcosmopolitan distribution peak occurred in the late Barremian and early Aptian, when the species was present in localities as far apart as the Tethyan Archipelago and Korea. However, before the end of the Aptian, *C. grovesii* disappeared from Eastern Asia. In the late Aptian it expanded westwards to North America, displaying a third subcosmopolitan pulse in Laurasia (North America and Europe). The final retreat of the species occurred at the end of the Albian, when it became restricted to the Iberian Peninsula before extinction.

This species colonized a wide range of environments during its evolution. From its very beginning, it has been found in non-marine limestone and marl representing both alkaline lakes (e.g. Purbeck facies in Mojon and Strasser, 1987) and alkaline brackish marshes (e.g. Wealden facies in England, Feist et al., 1995). Siliciclastic deposits related to fluvial systems were also among the oldest to be colonized, such as the localities from the Tera Formation in Spain (Martín-Closas and Alonso-Millán, 1998), the localities from the Black Hills margin in South Dakota and Wyoming, United States (Martín-Closas et al., 2013) and almost all the Chinese localities (e.g. Yang et al., 2008). A similar wide range of habitats was present during its whole evolution. Towards the end of its long history, this species was even capable of colonizing the relatively acidic water of peat ponds in the coal-bearing lower Albian of the Escucha Formation, in Spain (Martín-Closas, 1988, 2000).

Table 7
Distribution dataset of *Clavator calcitrapus*.

Taxonomy	Age	Locality	Country	Reference
Triclypella calcitrapa n. sp.	Barremian	Herbers (Castelló)	Spain	Grambast (1969)
Triclypella aff. *calcitrapa*	Barremian	China Muerta, Picún Leufú (Neuquén)	Argentina	Musacchio (1971)
T. calcitrapa	Barremian	Herbers (Castelló)	Spain	Martín-Closas and Grambast-Fessard (1986)
Triclypella jiangluoensis	Early Cretaceous	Gansu	China	Li (1981)
T. calcitrapa	Early Cretaceous	Hengyang (Hunan)	China	Hu and Zeng (1981)
T. calcitrapa	Early Barremian	Hengyang (Hunan)	China	Wang and Lu (1982)
Triclypella jiangluonensis	Hauterivian–early Barremian	Chengxian–Liangdang (Gansu)	China	Wang and Lu (1982)
T. calcitrapa	Hauterivian–early Barremian	Dongjing Fm, Hengyang basin (Hunan)	China	Hu and Zeng (1985)
T. calcitrapa	Early Barremian	Mambrillas (Burgos)	Spain	Schudack (1987a)
Triclypella patagonica nov. sp.	Late Hauterivian–early Barremian	China Muerta, Picún Leufú (Neuquén)	Argentina	Musacchio (1989)
T. calcitrapa	Hauterivian–early Barremian	Ripe Borehole (Weald)	United Kingdom	Feist et al. (1995)
		Hailsham Borehole (Weald)		
Clavator calcitrapus	Early Barremian	Herbers (Castelló)	Spain	Martín-Closas (2000)
		Galve (Teruel)		
		Ciria (Zaragoza)		

Table 8
Distribution dataset of *Hemiclavator neimongolensis*.

Taxonomy	Age	Locality	Country	Reference
Clavator thorali	Barremian	Valea Akargea-Peştera (Dobrogea sud)	Romania	Neagu and Georgescu-Donos (1973)
Hemiclavator neimongolensis	Late Barremian	Guide (Neimongol)	China	Wang and Lu (1982)
Pseudoglobator posticecaptus	Early Barremian	Coll de Querol, Herbers (Castelló)	Spain	Martín-Closas and Grambast-Fessard (1986)
H. neimongolensis	Early Barremian	Galve (Teruel)	Spain	Schudack (1989)
Pseudoglobator neimongolensis	Early Barremian	Oliete and Aguilón basins (Teruel)	Spain	Soria et al. (1995)
H. neimongolensis	Barremian	Volgograd (North Caspian Sea)	Russia	Shaikin et al. (1992)
P. neimongolensis	Barremian	El Mangraner, Castelló	Spain	Martín-Closas and Salas (1994)
P. neimongolensis var. *posticecaptus*	Late Hauterivian–early Barremian	Coll de Querol, Morella, Castelló	Spain	Martín-Closas and Salas (1994)
H. neimongolensis	Hauterivian–early Barremian	El Mangraner (Castelló)	Spain	Mojon (1996)
H. neimongolensis var. *posticecaptus*	Hauterivian–early Barremian	Coll de Querol, Herbers (Castelló) Jaganta, Seno, Villores (Teruel) El Castellar, Galve, Castelvispal (Teruel)	Spain	Martín-Closas (2000)
H. neimongolensis var. *neimongolensis*	Barremian	Herbers (Castelló) Alacón (Teruel) Terradets (Lleida)	Spain	Martín-Closas (2000)
H. neimongolensis	Late Barremian	Pas du Frou (Chartreuse)	France	Martín-Closas et al. (2009)
H. neimongolensis var. *posticecaptus*	Early Barremian	Pas du Frou (Chartreuse)	France	Martín-Closas et al. (2009)
H. neimongolensis posticecaptus	Hauterivian–early Barremian	Aït Attab	Morocco	Mojon et al. (2009)

4.2. Clavator harrisii Peck, 1941

The evolutionary species *C. harrisii* is a Clavatoroidae derived from the most plesiomorphic morphotype of *C. grovesii*, i.e. *C. grovesii grovesii*, with which it shows strong similarity. *C. harrisii* displays a utricle formed of two opposite lateral fans made of about 6–10 digitated bract cells borne on a central pedicel, which is embraced at each side by long basal bract cells (Fig. 2). These two fan systems are separated from each other by a large, abaxial bract cell, opposite the bearing branchlet portion. In contrast to *C. grovesii grovesii*, the utricle of *C. harrisii* has quite a loose appearance, leaving parts of the nodules of the gyrogonite visible between the utricle cells and giving the utricle cells a lanceolate rather than polygonal shape.

According to Martín-Closas (1989, 1996) the evolutionary species *C. harrisii* includes a number of traditional taxa, assigned to the genus *Flabellochara*, i.e. *F. harrisii*, *Flabellochara jurongica*, *Flabellochara hebeiensis* among others. These taxa, which are very useful for biostratigraphic purposes, are distinguished from each other by minor differences in the utricle structure, such as the relative length or width of the fan-cells. Also in the Tethyan domain, the last representatives of the evolutionary species exhibit slight calcification of the utricle and are distinguished as two different subspecies or varieties, i.e. *C. harrisii reyi* and *C. harrisii zavialensis*. This slight calcification has led to some confusing taxonomical attributions. They were initially assigned to the genus *Stenochara*, belonging to the family Porocharaceae by Grambast-Fessard (1980); and later transferred into the new genus *Luzochara* within this family by Pereira and Cabral (2005).

C. harrisii was already reported from Valanginian and Hauterivian formations of the Iberian Chain, Spain (Martín-Closas and Salas, 1988; Martín-Closas, 2000), where it appears to display an endemic initial distribution (Fig. 4 and Table 6). From the late Hauterivian to the Aptian, the species was widely distributed in the Central Tethyan Archipelago, in many localities of Portugal, Spain, France, England, Germany, Central Italy, Sardinia, Lebanon and Northern Africa. During the same period, *C. harrisii* expanded eastwards and also occurred on the Eurasian mainland, from Moldavia and Ukraine to Central Asia, Kazakhstan, and China, where it was conspicuous (Fig. 4, Table 6). Thus, it has been reported from the Chinese provinces of Sichuan, Hunan, Jiangxi, Zhejiang, Jiangsu, Shandong, Hebei, Neimongol, Gansu and Qinghai (Wang and Lu, 1982). In these Chinese localities, the species developed slightly different morphotypes (the traditional species *F. jurongica* and *F. hebeiensis* were especially abundant), probably indicating some type of regional specialization. Later in the Aptian this species appears to colonize North America as well, where it occurred across a wide range of localities in the North American Interior Foreland Basin, from the present day Gulf Coast to the Rocky Mountains (Peck, 1941, 1957; Soulié-Märsche, 1994). Consequently, after a first pulse of Eurasian late Hauterivian to Barremian subcosmopolitanism, it was during the Aptian when this species finally reached full cosmopolitanism in a Northern hemisphere latitudinal belt (Fig. 4, Table 6). In addition, *C. harrisii* was also reported from the early Barremian of Argentina and the Aptian of Brazil (Musacchio, 2000). Finally, in the middle Albian, *C. harrisii* had disappeared from China; and, as far as reported, from the whole of Asia but was still well present in the Central Tethyan Archipelago, particularly in the Iberian, Tunisian and Levantine Islands, i.e. present day Lebanon (Fig. 4, Table 6). The species probably became extinct before the beginning of the Cenomanian.

From the point of view of paleoecology, the first occurrence of the species in the Iberian Valanginian was in alkaline lakes represented by non-marine limestone and marl. From the late Hauterivian to the early Aptian, *C. harrisii* broadened its initial paleoecological requirements since it is found both in Tethyan freshwater and brackish limestones and in Chinese fluviatile red beds and shallow siliciclastic lakes. During the last period of its evolution, in the late Aptian to Albian, the main habitats of this species were siliciclastic floodplains in Laurasia and North Africa (e.g. the Tunisian Kebar Formation described by Trabelsi et al., 2010) and even coal-bearing facies in Spain (Martín-Closas, 1988).

4.3. Clavator calcitrapus (Grambast, 1969) nov. comb. Martín-Closas ex Schudack, 1993

The species *C. calcitrapus* (= *Triclypella calcitrapa*) is a Clavatoroidae derived from *C. grovesii* var. *gautieri*, an endemic morphotype of the European Valanginian and Hauterivian (Martín-Closas, 1996). Thus, a Tethyan origin was also probably the case for this species. *C. calcitrapus* is defined on the basis of its utricle structure, formed of three bract cells supporting at their top a whorl of polygonal bracteoles, closely packed together, and completely covering the gyrogonite (Fig. 2). A basal scar corresponding to the bearing branchlet may be present as well.

The evolution and distribution pattern of this species is relatively short in comparison to other widely distributed clavatoracean species (Fig. 5, Table 7). During the late Hauterivian and early Barremian it occurred in the Central Tethyan Archipelago, especially in England and Spain (Grambast, 1969; Schudack, 1993; Feist et al., 1995; Martín-Closas, 2000), and in China, where it has been reported in the Hunan and Gansu provinces (Wang and Lu, 1982). Thus, *C. calcitrapus* reached a subcosmopolitan distribution in Eurasia shortly after its appearance. In addition, it has been reported in lower Barremian deposits
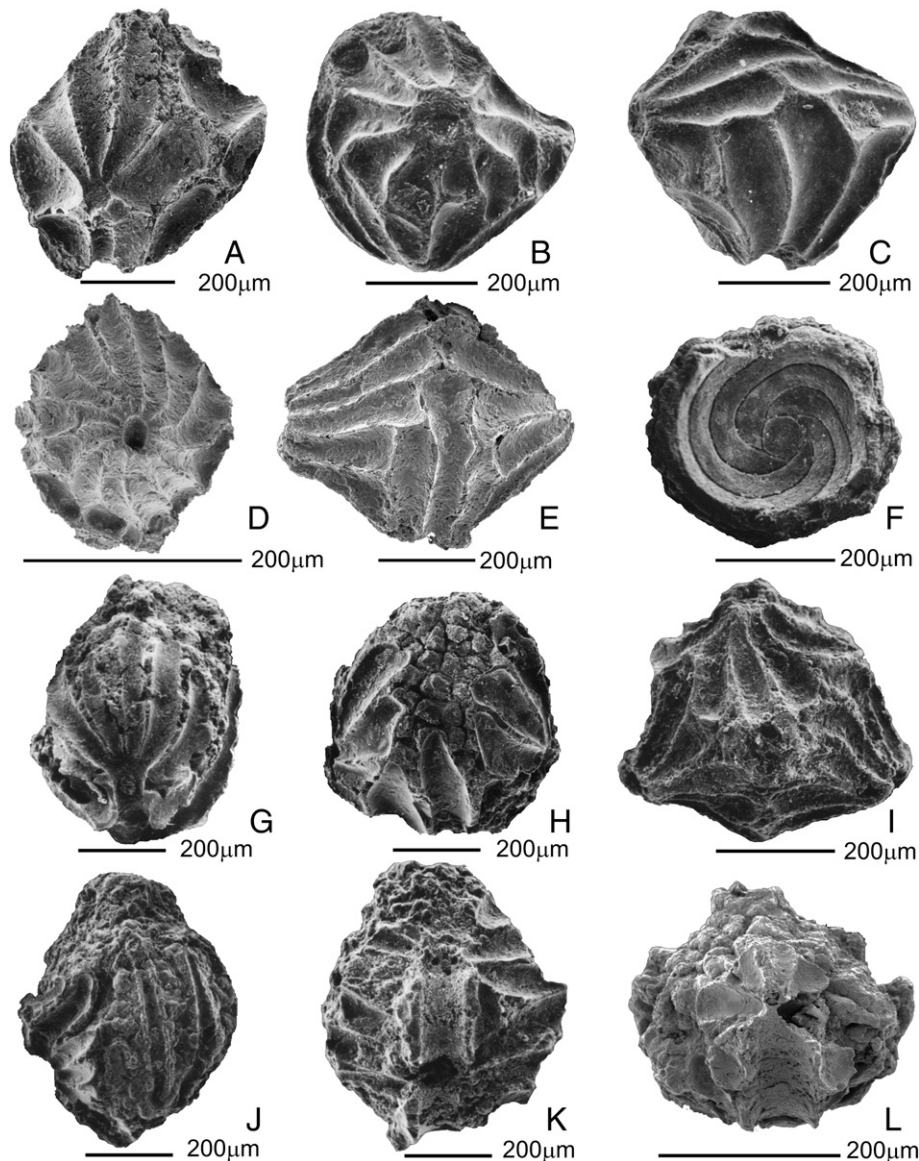
Fig. 1. Main features of utricles of cosmopolitan clavatoroidae. A. *Clavator grovesii grovesii* (lateral view), B. *C. grovesii gautieri* (lateral view), C. *C. grovesii gautieri* (abaxial view), D. *C. grovesii jiuquanensis* (lateral view), E. *C. grovesii jiuquanensis* (abaxial view), F. *Clavator harrisii* (inside of gyrogonite showing unicellular basal plate), G. *C. harrisii* (lateral view), H. *C. harrisii* (abaxial view showing the nodular layer), I. *Clavator calcitrapus* (apical view), J. *Hemiclavator neimongolensis posticecaptus* (lateral view), K. *Clavator neimongolensis posticecaptus* (adaxial view), L. *Clavator neimongolensis neimongolensis* (adaxial view). A–C and F–K from the Early Cretaceous of the Iberian Chain, Spain (modified from Martín-Closas, 2000). D–E and L from the Early Cretaceous of the Subalpine Chains, France (modified from Martín-Closas et al., 2009).

from the Neuquén Basin, Argentina (Musacchio, 1971). Its extinction occurred before the late Barremian.

Little is known of the paleoecology of *C. calcitrapus*, since it is not a common species. In the Iberian Peninsula it was found forming monospecific populations in siliciclastic swamp facies from the Iberian Chain along with a larger number of localities represented by non-marine carbonate facies, where it is less abundant. In China the species occurred in siliciclastic gray siltstone representing shallow lakes in a fluviatile context (Q.F. Wang, pers. oral comm., 2009). These data indicate an affinity of this species for siliciclastic depositional settings.

4.4. Hemiclavator neimongolensis *Wang and Lu, 1982*

This clavatoroidean species is derived from *Hemiclavator adnatus*, an endemic species of the Iberian Peninsula (Martín-Closas, 1996). *H. neimongolensis* is characterized on the basis of a utricle formed of a number of abaxial long and digitated bract cells and an adaxial structure

formed initially of a portion of the branchlet and a number of lateral fans made of small triangular cells (Fig. 2). This adaxial structure is displayed by the oldest morphotype, *H. neimongolensis posticecaptus*, and passed gradually to a more derived morphotype, *H. neimongolensis* s.s. with a single adaxial hand-shaped fan (Martín-Closas and Grambast-Fessard, 1986; Martín-Closas, 1996).

The distribution of this species was originally restricted to the Iberian Island, where the morphotype *H. neimongolensis posticecaptus* is already reported in lower Valanginian formations of the Iberian Chain (Martín-Closas and Salas, 1988) and it continues until the earliest Barremian (Martín-Closas and Grambast-Fessard, 1986) (Fig. 6, Table 8). Intermediary forms between *H. neimongolensis posticecaptus* and *H. neimongolensis* s.s. occur in the lower Barremian deposits of Spain. The latest morphotype, *H. neimongolensis neimongolensis*, in contrast, displays a much larger distribution. In addition to the Barremian of the European localities belonging to the Central Tethyan Archipelago, it also occurred near the present-day Caspian Sea (Shaikin
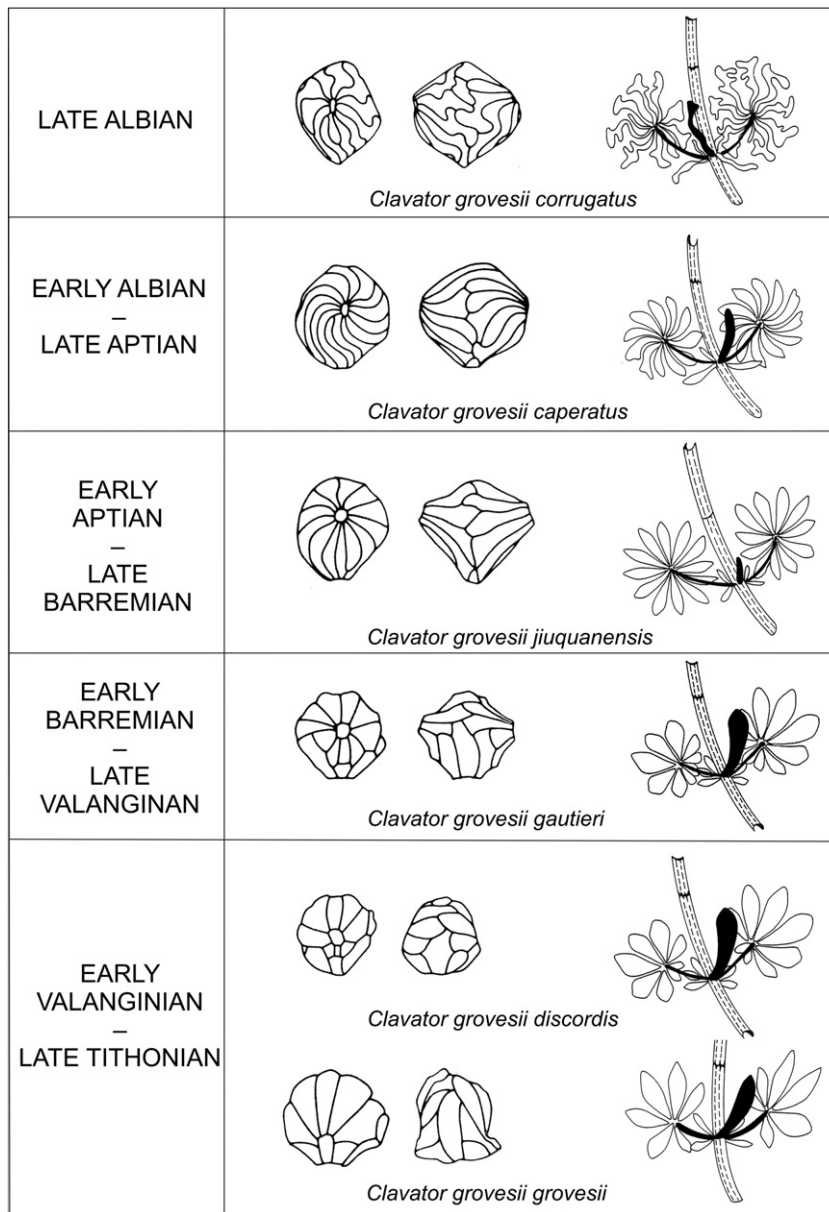
Fig. 2. Gradual evolution of the utricle structure in *Clavator grovesii* (modified from Grambast, 1974, and Martín-Closas, 1996). Left column shows lateral and abaxial views of utricles, right column shows reconstruction of the vegetative structure of utricles.

et al., 1992) and in the Neimongol Province of China, where it was first described by Wang and Lu (1982). *H. neimongolensis neimongolensis* was probably extinct before the Aptian.

The paleoecology of this species appears to include an initial preference for non-marine carbonatic environments by *H. neimongolensis posticecaptus*, and it later colonizes a wider range of habitats, especially represented by the occurrence of *H. neimongolensis* s.s. in siliciclastic shallow lakes in a fluviatile context from the Neimongol Province in China.

5. Discussion of the historical biogeography of widely distributed Clavatoroidae

The Late Jurassic and Cretaceous subfamily Clavatoroidae is mainly composed of species limited to the Central Tethyan Archipelago: only four out of 17 species enlarged their distribution area to become subcosmopolitan or cosmopolitan in the Northern hemisphere during the Early Cretaceous. These species share some common patterns in their biogeographic history, which sheds light on the origin and of factors controlling cosmopolitanism in these Cretaceous charophytes.

5.1. Biogeographic origin and phylogenetic ancestry of widely distributed Clavatoroidae

The oldest occurrence of all the subcosmopolitan or cosmopolitan species in the subfamily Clavatoroidae appears to be in the Central Tethyan Archipelago. This region also contains a high number of endemic clavatoroideans, which suggests that it was the main source of speciation for this subfamily. Also, the Early Cretaceous Tethyan paleogeography, composed of a number of islands, suggests that clavatoracean speciation in this archipelago was probably allopatric. Accepting the phylogenetic hypotheses of Schudack (1993) and Martín-Closas (1989, 1996) as a basis for interpretation, a second interesting point is that most clavatoroidean species with a wide biogeographic range had an ancestor which was, in the time of speciation, endemic to that region. In the case of *C. grovesii*, the ancestor was *C. reidii*, which occurs in the Tithonian and early Berriasian of Western
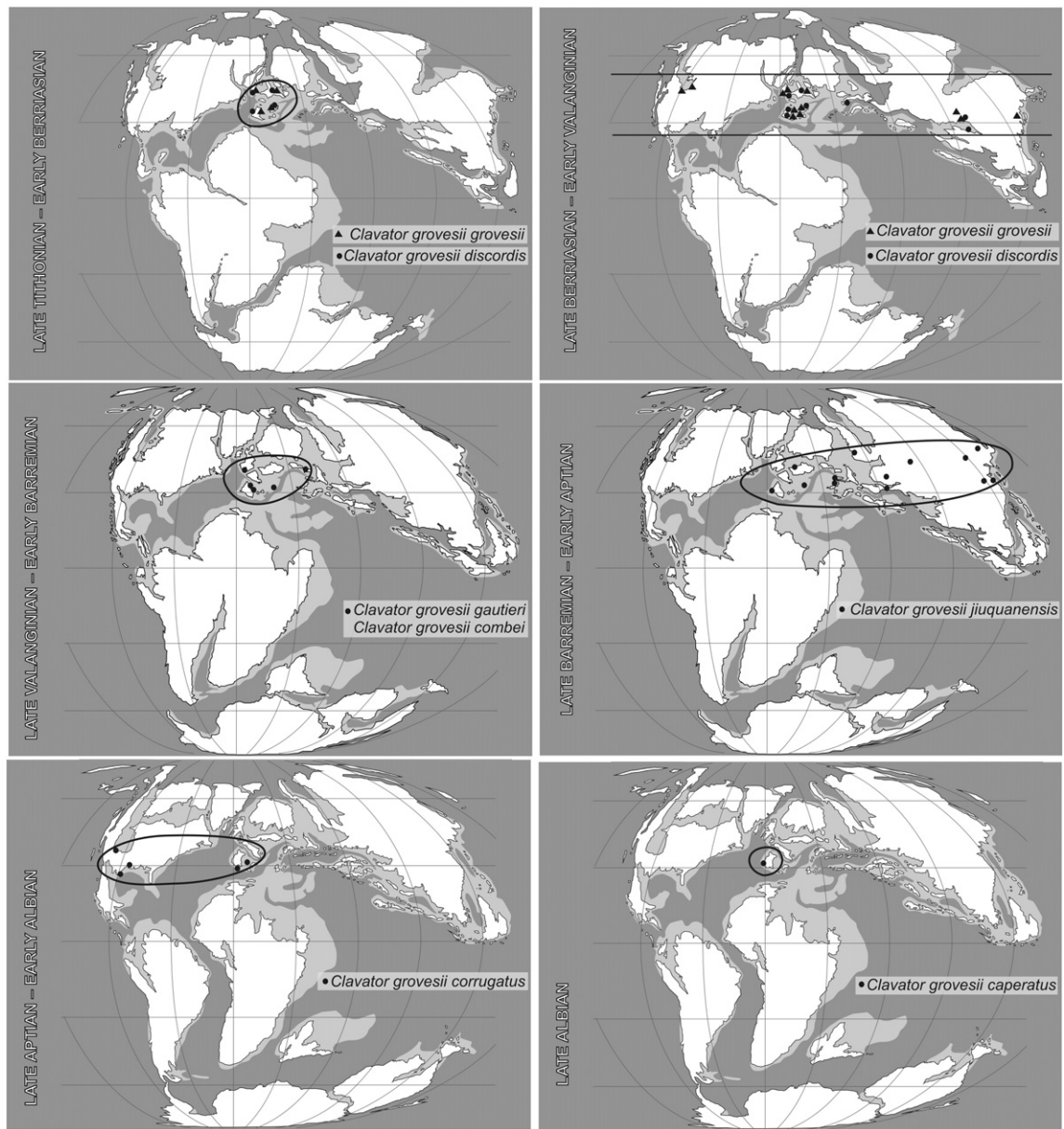
Fig. 3. Distribution maps of *Clavator grovesii*. Paleogeography modified from Blakey (2006). Late Tithonian to late Valanginian data plotted on a paleogeographic map at 150 Ma. Late Valanginian to Late Barremian data plotted on a paleogeographic map at 120 Ma. Late Aptian to Late Albian data plotted on a paleogeographic map at 105 Ma.

Europe. *C. grovesii* itself was the ancestor for two widely distributed species, *C. harrisii* and *C. calcitrapus*; however, while the former originated during the first cosmopolitan stage of the ancestor (*C. grovesii grovesii*), the latter derived from an infraspecific morphotype endemic to the Tethyan area, which was *C. grovesii gautieri*. The fourth cosmopolitan species, *H. neimongolensis*, derived directly from the ancestral line of Clavatoroidae (Martín-Closas, 1996) is represented, as said, by a plesiomorphic fructification with insufficient characters to be considered in biogeographic analysis. In short, endemism in the Tethyan archipelago rather than cosmopolitanism appears to be the biogeographic condition for most ancestors of cosmopolitan and subcosmopolitan clavatoroidean species.

5.2. Migration pulses in Early Cretaceous Clavatoroidae

The migration of Clavatoroidae appears to be multi-episodic, either within one species or among species (Fig. 7). The first case is clear for *C. grovesii*, which displays three pulses. The first, late Berriasian–early Valanginian, allowed the species to expand into North America and

Asia. The second pulse, late Hauterivian–early Barremian represented Eurasiatic subcosmopolitanism; while the third, in the late Aptian, represented a migration into North America. Between the first and the second migration pulses there was a period of endemism in the Tethyan Archipelago. *C. harrisii* displays two pulses of migration, the first (late Hauterivian to early Barremian) into Asia and the second into North America during the late Aptian. Finally, two more species have only one short episode of migration from the Tethyan domain into Asia. This is the case of *C. calcitrapus* in the late Hauterivian and early Barremian and *H. neimongolensis* in the late Barremian.

These patterns show that, even if there were multiple episodes of migration, only one interval, late Hauterivian–Barremian, led to the cosmopolitanism or subcosmopolitanism of all the species studied. A continuum in the paleogeographic distribution of wetlands within the paratropical belt of Saward (1992) would explain this optimum of charophyte migration. Meanwhile, the first cosmopolitan episode of *C. grovesii* (late Berriasian to early Valanginian) was not shared by other species because it occurred at an early stage of development of the subfamily, when it had yet to diversify.
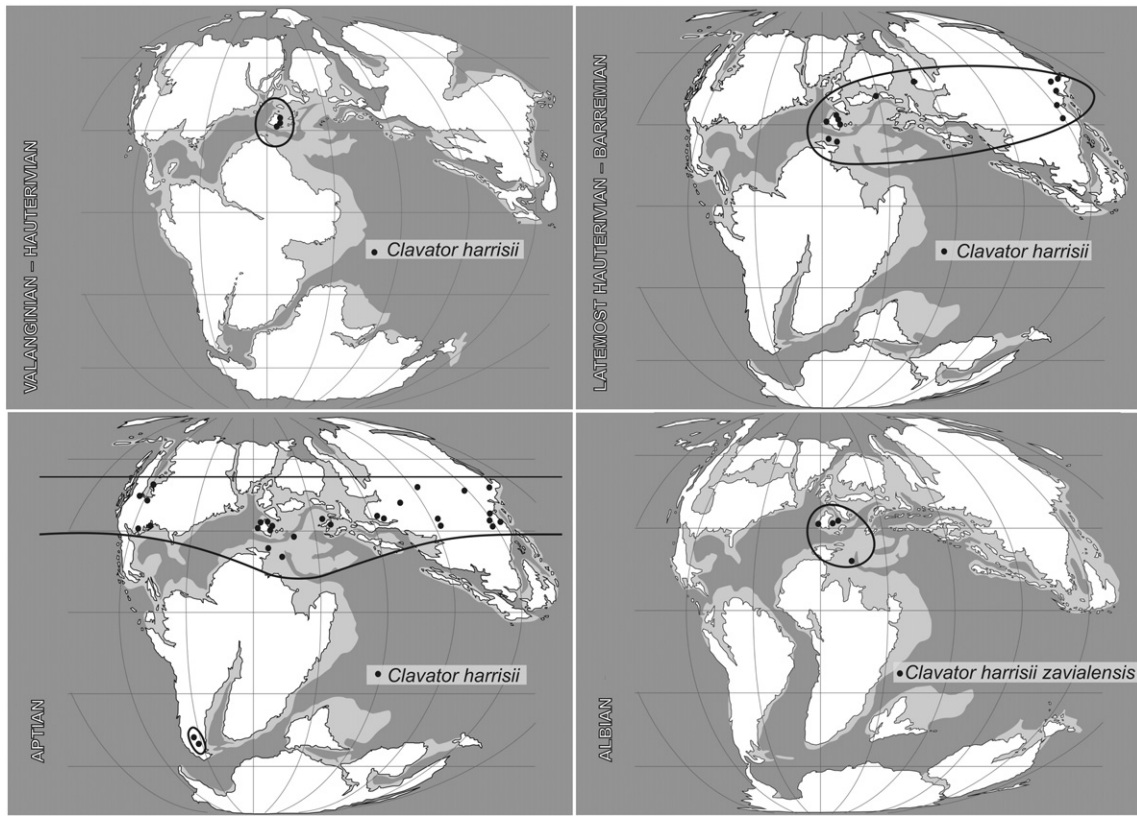
Fig. 4. Distribution maps of *Clavator harrisii*. Paleogeography modified from Blakey (2006). See legend of Fig. 3 for more detail.

5.3. Time needed by a clavatoroidean charophyte to reach a wide distribution

The fossil record of charophytes is mainly known from biostratigraphic studies, which provide significant data for the dating of the biogeographic events described above. The time needed for a clavatoroidean species to extend to a number of continental areas varies widely. *C. calcitrapus* displays one of the shortest time spans. The species extended to Eurasia (and South America) during the early Barremian, i.e. within a maximum time span of ca 2.2 million years; probably much less, taking into account that this time interval represents the total duration of its subcosmopolitan distribution. *C. neimongolensis*

needed a similar time (the late Barremian) to expand across Eurasia. *C. harrisii* expanded during the whole Barremian, first in Eurasia and then into North America, prior to reaching full cosmopolitanism in the Aptian. This results in a maximum time span of ca 5 million years. Finally, the migration pulse of *C. grovesii grovesii* to reach a cosmopolitan distribution occurred within the late Berriasian and early Valanginian, i.e. in a maximum time span of ca 5 million years as well. This duration is similar to what is known of another clavatoracean (*A. trivolvis*), according to Martín-Closas and Wang (2008), of Paleogene characeans (Sanjuan and Martín-Closas, 2015), and of extant charophytes (family Characeae). Among the latter, *Lychnothamnus barbatus* reached Eurasiatic distribution during the Pliocene and Quaternary in a time span of about 6 million years (Bhatia, 2006).

5.4. Origin of cosmopolitanism and subcosmopolitanism in Clavatoroidae

The origin of cosmopolitanism in extant *Chara* has been related to the high dispersal capabilities of monoecious species (i.e. species displaying a conjoint arrangement of male and female gametangia) by animal vectors, such as migratory birds, mainly ducks (Proctor, 1980). An analogous situation could provide the origin of the cosmopolitanism of the Cretaceous monoecious species *A. trivolvis*, as discussed by Martín-Closas and Wang (2008). Unfortunately, the fossil record of Clavatoroidae does not provide similar evidence regarding the features and arrangement of male gametangia, which hinders testing any hypothesis about its influence in paleobiogeography. Meanwhile, the biogeographic patterns observed in Clavatoroidae are very similar to the patterns described by Martín-Closas and Wang (2008) for *A. trivolvis*: the paleogeographic continuity of wetlands during the main migration periods and the adaptation of these species to colonize new biotopes are also of prime significance in Clavatoroidae. Moreover, the multiepisodic migration of some species and the coincidence of the migration of different species in time and towards similar regions suggest that the conjoint arrangement of gametangia is not solely sufficient to
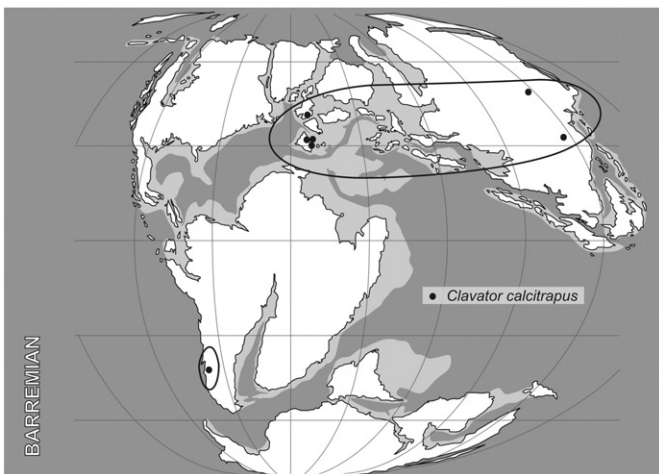

Fig. 5. Distribution map of *Clavator calcitrapus*. Paleogeography modified from Blakey (2006). See legend of Fig. 3 for more detail.
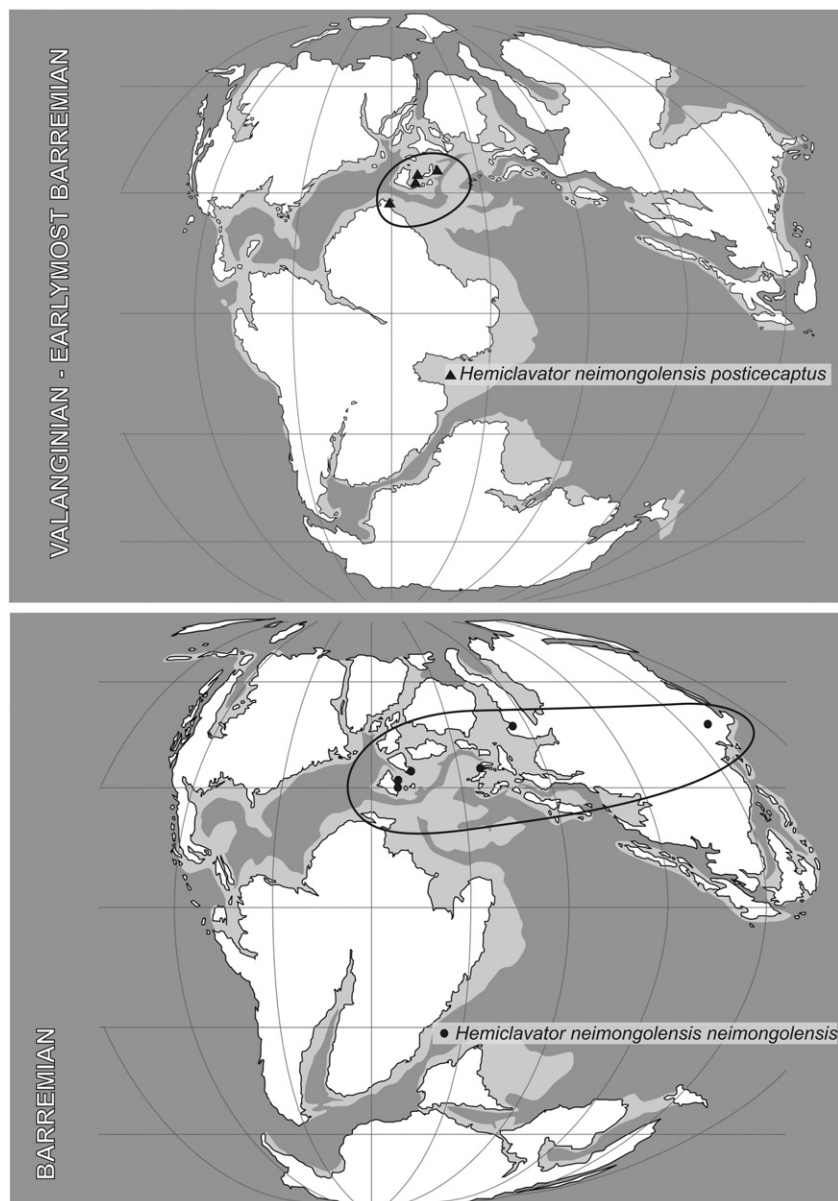
Fig. 6. Distribution maps of *Hemiclavator neimongolensis posticecaptus* and *H. neimongolensis neimongolensis*. Paleogeography modified from Blakey (2006). See legend of Fig. 3 for more detail.

produce a worldwide expansion of a particular species. It is improbable that the multiple migration pulses of one species were produced by repeated changes in the arrangement of the gametangia. Instead, these pulses may rather indicate strong paleogeographic, paleoclimatic or paleoecological control of the migrating process. The same factors would determine during which periods different species were prone to migrate, e.g. late Hauterivian–Barremian for Clavatoroidean charophytes.

6. Conclusions

Four out of 17 evolutionary species of the Cretaceous charophyte subfamily Clavatoroidae, in the sense of Martín-Closas (1996), displayed a subcosmopolitan to cosmopolitan distribution: *C. grovesii*, *C. harrisii*, *C. calcitrapus* and *H. neimongolensis*. Three of these species derived from ancestors endemic to the Tethyan Archipelago and three of them passed through an initial period of endemism in that area before reaching a larger distribution. Three main pulses of biogeographic expansion are recognized. The first was late Berriasian–early Valanginian, which occurred at an early period of the subfamily's evolution, prior to

its diversification, and affected only *C grovesii*. The second was late Hauterivian–Barremian and affected the four species mentioned, though in slightly different stages: late Hauterivian to early Barremian for *C. grovesii jiuquanensis*, *C. harrisii* and *C. calcitrapus* in Eurasia; late Barremian for the Eurasiatic *H. neimongolensis*. This pulse coincides also with the cosmopolitan episode documented by Martín-Closas and Wang (2008) in a species of the Atopocharoidae, the other important subfamily of clavatoracean charophytes. The third pulse occurred in the late Aptian and represented the colonization of North America by two species, *C. grovesii corrugatus* and *C. harrisii*, the latter thereby reaching full cosmopolitanism in the Northern hemisphere. The time needed for these species to reach a subcosmopolitan to cosmopolitan distribution ranged from 2.2 to 5 million years. The fossil record of Clavatoroidae does not provide evidence of whether or not their dispersal capacity could be related to the conjoint arrangement of gametangia, as is the case in extant *Chara* and perhaps in the Cretaceous *A. trivolvis* lineage. However, it appears that two significant controlling factors were the paleogeographic connection of wetlands and the adaptive capacity of each species to colonize new biotopes.
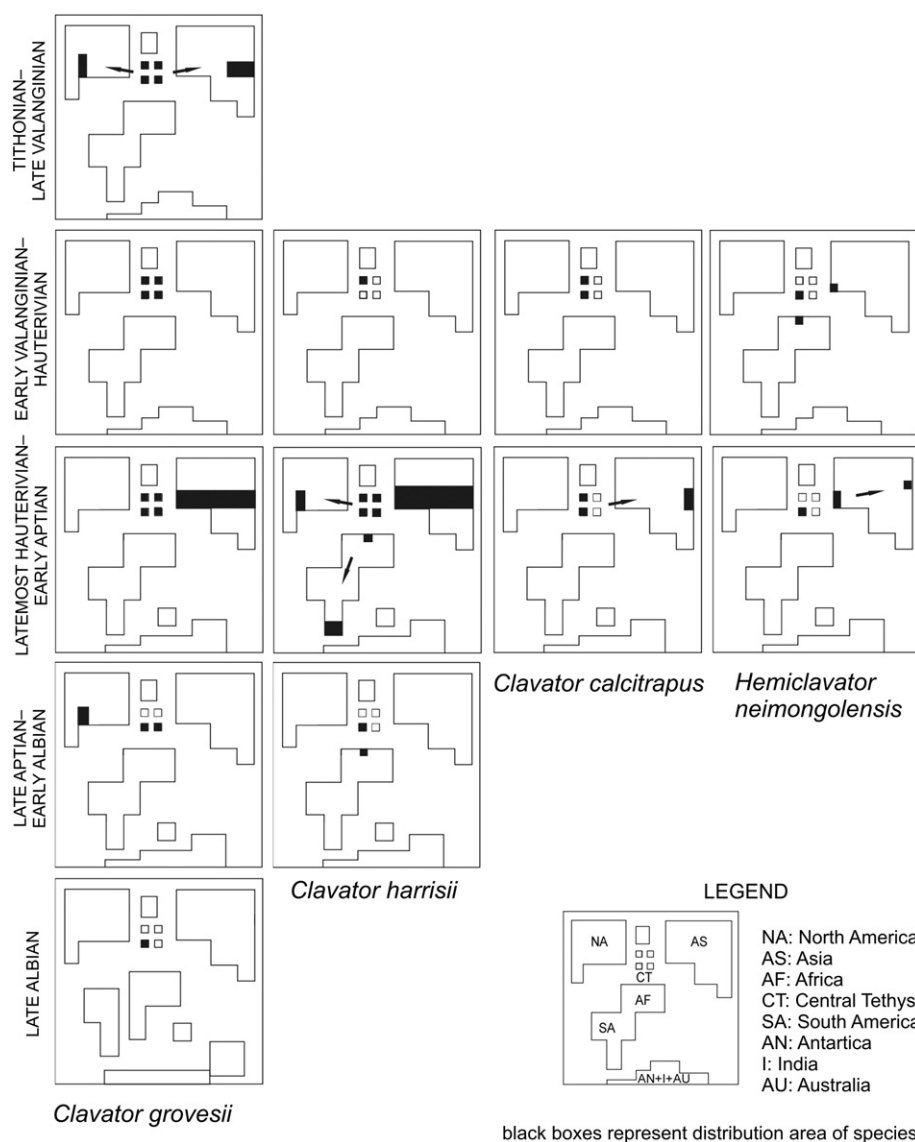
Fig. 7. Cartoon summary of the main Clavatoroideae biogeographic events through time.

Acknowledgments

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