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Geographic and stratigraphic distributions of the Caribbean species of *Cladocora* (Scleractinia, Faviidae)

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Abstract A complete account of the faviid genus *Cladocora* within the Caribbean is presented. In the Caribbean this genus represents an extant group that had its earliest occurrence during the Campanian-Maastrichtian of Jamaica. Recent forms have been reported throughout the Caribbean. The following forms were found (with stratigraphic ranges in the Caribbean): *C. arbuscula* (Pliocene-Recent), *C. debilis* (Pleistocene-Recent), *C. gracilis* (Middle-Upper Maastrichtian), *C. jamaicaensis* (Campanian-Maastrichtian and Eocene), *C. johnsoni* (Pliocene), and *C. recrescens* (Middle-Upper Oligocene). The occurrence of the genus *Cladocora* in the Caribbean is largely continuous from the Campanian to Recent, during the majority of the Caribbean species show affinities to European assemblages. For the time intervals Paleocene, Lower Oligocene, and Miocene the taxon has not been reported from the Caribbean.

Keywords Scleractinia · *Cladocora* · Cretaceous · Cenozoic · Caribbean · Paleobiogeography

Introduction

The genus *Cladocora* occurred fairly early in the Mesozoic history of scleractinian corals. The oldest record is the species *C. dendroidea* (Solomko 1888) from the Middle-Upper Jurassic of Crimea (Lathuilière 1989). During the Cretaceous about two dozen species of *Cladocora* occurred, almost evenly distributed between the Lower and Upper Cretaceous (Baron-Szabo 2002). The same pattern can be observed for the Cenozoic interval (this paper). About two dozen species have been reported from the Lower Paleocene to Recent (Tables 1 and 2), about one

dozen described from each of the time periods Paleocene-Oligocene and Miocene-Recent, respectively.

Caribbean species of *Cladocora* have been known for about one and a half centuries. The first form recorded of this genus was the recent species *C. arbuscula* (Lesueur 1821). Several decades later, the first fossil species *C. recrescens* was reported by Lonsdale (1845) from the Middle Oligocene of Antigua. Nearly half a century later, the earliest fossil species of the Caribbean (*C. jamaicaensis*) was described by Vaughan (1899) from the Blue Mountain Series (Campanian-Maastrichtian and Eocene) of Jamaica. Until now, the earliest record of *Cladocora* in the Caribbean is from the Campanian-Maastrichtian of Jamaica (Kiessling and Baron-Szabo 2004; Baron-Szabo 2005).

In contrast to a large number of works dealing with the revision and re-evaluation of Neogene to Recent species of the Caribbean (e.g., Weisbord 1974; Budd et al. 1994; Cairns 2000), Caribbean corals from the K/T-boundary to the Lower Tertiary were largely ignored until recently. The first detailed taxonomic work including Caribbean species of the suborders Astrocoeniina, Faviina, Rhipidogyrina, and Amphipora of the K/T-boundary is now in press (Baron-Szabo 2005). Caribbean corals of the Lower Tertiary, however, remain to be re-investigated.

The purpose of the present paper is to re-evaluate the Caribbean species of *Cladocora* and to put them into a global context.

Materials and methods

In evaluating the validity of described species, much weight was given to skeletal dimensions such as corallite diameter, number of septa, and arrangement of septal apparatus. To a minor extent other morphological features, such as branching angles of corallite tubes, were taken into consideration. Generally, type and original material was examined. Taxa that could not be studied are marked with 1–3 asterices in Table 1.

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Table 1 Geographic and stratigraphic distributions of species of *Cladocora* of the time period during which Caribbean forms have been recorded (Maastrichtian-Cenozoic)

Maastrichtian-Cenozoic species of <i>Cladocora</i>	Corallite diameter and (diameter of latest budding stage)	Number of septa in monocentric corallites	Additional features	Overall stratigraphic ranges (inside the Caribbean)	Geographic within the Caribbean	Distributions outside the Caribbean	Reference
<i>arbuscula</i> (Lesueur 1821)	2.8–4 (4.5)	30–36+s	S1 slightly larger, number of septa mainly 36	Plio-Rec (Plio-Rec)	Throughout, 0.5–27 m depth range	–	Weisbord (1974), Budd et al. (1994), Cairns (2000)
<i>barkii</i> ** (Duncan 1880)	7.5–12.5	Up to 48	Fourth septal cycle generally incomplete	Pal-?L. Eo (–)	–	Austria (Pal), Egypt (U. Pal), ?Somalia (U. Pal-L. Eo), Pakistan (Pal)	Baron-Szabo (2005)
<i>bosquensis</i> ** (Frost and Langenheim 1974)	10–12 (18)	22–24	Branching angles 40°–90°	M.-U. Eo (–)	–	Mexico	Frost and Langenheim (1974)
<i>cespitosa</i> (Linné 1767) [= pars <i>Lithodendron granulosum</i> (Goldfuss 1833); = <i>C. stellaria</i> (Milne Edwards and Haime 1849)]	3.5–5	28–40		Mio-Rec, 0–50 m depth range (–)	–	Italy (M. Mio-Rec.), Spain (Plio-Rec), Greece (Plio-Rec), Mediterranean (Rec)	Milne Edwards (1857), Felix (1927, 1929), Baron-Szabo (2002)
<i>contortilis</i> * (Tenison-Woods 1878)	2–5	(?) 24		Mio (–)	–	Australia (Aldinga)	Tenison-Woods (1878)
<i>crenaticosta</i> (Reuss 1869) [= <i>Dasyphyllia compressa</i> (d'Achiardi 1867)]	9–13	32–36	Bushy colony	Eo-Mio (–)	–	Egypt (Mio), Germany (L. Oligo), Italy (Oligo), Macedonia (Eo-Oligo)	Felix (1925, 1927), this paper
<i>debilis</i> (Milne Edwards and Haime 1849) [= <i>C. patriarca</i> (Pourtales 1874); = <i>C. paulmayeri</i> (Döderlein 1913)]	2.8–3.8	24–36	P1–P2 form discrete crown; septa sub-equal; juvenile corallites 1.5–2 mm	Pleisto/Hol-Rec (Pleisto./Hol.-Rec.)	Throughout, 32–480 m depth range	Gulf of Mexico (Pleisto/Hol) throughout Mediterranean (Rec.)	Cairns (2000)
<i>depauperata</i> (Reuss 1871)	Around 3	12 + s3		Mio (–)	–	?Austria (U. Mio), Czech Republic (Mio)	Kühn (1965)
<i>gaasensis</i> (Chevalier 1956)	5.5	48		L. Oligo (–)	–	France	Chevalier (1956)
<i>gracilis</i> (d'Orbigny 1850)	2.8–4.5 (6)	16–38		U. Cret.-Pal (M.-U. Maast)	Jamaica	Widespread in Europe (U. Cret), Argentina (Pal), Austria (Pal), Egypt (Pal), Mexico (Maast)	Baron-Szabo (2002, 2003, 2005)
<i>haimet</i> ** (Duncan 1864)	7.5–10	24+s4		L. Mio (–)	–	Pakistan	Duncan (1864, 1880)
<i>intricata</i> (Michelin 1842)	3	Up to 12		M.-U. Mio (–)	–	Italy	Milne Edwards (1857), Felix (1927)

Table 1 Continued

Maastrichtian-Cenozoic species of <i>Cladocora</i>	Corallite diameter and (diameter of latest budding stage)	Number of septa in monocentric corallites	Additional features	Overall stratigraphic ranges (inside the Caribbean)	Geographic within the Caribbean	Distributions outside the Caribbean	Reference
<i>jamaicensis</i> (Vaughan 1899)	3.5–7 (12)	28–50	Branching angles 20°–90°	Camp.-Eo (Camp-Maast. and Eo)	Jamaica	Antarctica (Pal), Egypt (Pal), Italy (Pal), Mexico (Maast)	Schafhauser et al. (2003), Kiessling and Baron-Szabo (2004), Baron-Szabo (2005), this paper
<i>johnsoni</i> (Gane 1895) [= <i>C. gamachotensis</i> (Chevalier 1961); = <i>C. vermiculata</i> (Chevalier 1961)]	2–2.8	24+s4	Few rudimentary septa of S4 occasionally present	L. Mio and Plio (M-U Plio)	South Florida	France (L. Mio), USA (Plio)	Gane (1895), Chevalier (1961), Weisbord (1974), Budd et al. (1994), this paper
<i>manipulata</i> (Michelin 1842) (non Reuss 1854) [= <i>C. reussi</i> (de Fromentel 1861); = <i>C. liburnensis</i> (Chevalier 1961)]	3–4 (5)	24–40	Generally three septal cycles developed; juvenile corallites around 2.5 mm	Oligo-Mio (–)	–	France (Oligo-Mio), Italy (Oligo-Mio); Austria (M. Mio), Czech Republic (M. Mio), Hungary (M. Mio), Italy (M.-U. Mio)	Milne Edwards (1857), Reuss (1871), Felix (1925, 1927), Chevalier (1961), this paper
<i>michelotti</i> *** (Milne Edwards and Haime 1851)	5	48+s5		U. Mio-Plio (–)	–	Italy	Milne Edwards (1857), Felix (1925, 1927)
<i>multicaulis</i> (Michelin 1847)	2.5–6	40–46	Endotheca sparsely developed	Oligo-Mio	–	France (Mio), Italy (Oligo-Mio)	Milne Edwards (1857), Felix (1925, 1927), Chevalier (1961)
<i>pacifica</i> (Cairns 1991)	2.2–5 (6)	24–62	Average corallite diameter 4–5 mm with 36 septa	Rec, 45–274 m depth range (–)	–	Pacific Ocean, off Galápagos and Cocos Is	Cairns (1991)
<i>prevostiana</i> *** (Milne Edwards and Haime 1849)	6	40		M. Mio and U. Plio (–)	–	Austria (M. Mio), Italy (U. Plio), Romania (M. Mio)	Milne Edwards (1857), Felix (1925, 1927)
<i>prolifera</i> (d'Achiardi 1866) [= <i>Aplophyllia paucicostata</i> (Reuss 1868); = <i>Rhabdophyllia intercostata</i> (Reuss 1868); = <i>Rhabdophyllia medunensis</i> (Dainelli 1915); = <i>Procladocora viai</i> (Reig Oriol 1990)]	2–5 (7)	24–48		Eo-Oligo (–)	–	Bosnia (Eo), Italy (Eo-Oligo), Spain (Eo)	Felix (1925), Pfister (1980), Alvarez Perez (1993)

Table 1 Continued

Maastrichtian-Cenozoic species of <i>Cladocora</i>	Corallite diameter and (diameter of latest budding stage)	Number of septa in monocentric corallites	Additional features	Overall stratigraphic ranges (inside the Caribbean)	Geographic within the Caribbean	Distributions outside the Caribbean	Reference
<i>recrescens</i> (Lonsdale 1845) [= <i>C. arborea</i> (d'Achiardi 1867)]	7.5–12 (14)	32–48	Branching angles 30°–60°; juvenile corallites around 6 mm	Eo-Oligo (M.-U. Oligo)	Antigua (M. Oligo), Puerto Rico (U. Oligo)	USA (Eo-Oligo), Italy (Eo-Oligo)	Vaughan (1900), this paper
<i>stipata</i> *** (d'Achiardi 1867)	5–7 (8)	32–48	Fourth septal cycle generally incomplete	Oligo (–)	–	Bulgaria (Oligo), Italy (U. Oligo)	Felix (1925)
<i>tenuis</i> (Reuss 1868) [ex <i>Rhabdophyllia tenuis</i> (Reuss 1868); = <i>C. oligocenica</i> (Quenstedt 1881)]	3.5–8	20–32		Eo-Oligo (–)	–	Bulgaria (Oligo), France (Eo), Italy (Eo-Oligo), Slovenia (Oligo)	Barta-Calmus (1973), Baron-Szabo (2005)

Note. Cret, Cretaceous; Camp, Campanian; Maast, Maastrichtian; Pal, Paleocene; Eo, Eocene; Oligo, Oligocene; Mio, Miocene; Plio, Pliocene; Pleisto, Pleistocene; Hol, Holocene; Rec, Recent; L, Lower; M, Middle; U, Upper; * host institution of specimen could not be tracked down yet; ** specimen reported to be lost; *** specimen could not be found at host institution

Original specimens and type material that were studied in the present work are housed at the following institutions.

BMNH	The Natural History Museum, London, UK
BSP	Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany
GBA	Geologische Bundesanstalt, Vienna, Austria
IPB	Geologisch-Paläontologisches Institut der Rheinischen Friedrich-Wilhelms-Universität, Bonn, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MNHN	Institut de Paléontologie du Muséum National d'Histoire Naturelle de Paris, France
MPUR	Museo di Paleontologia, Università di Roma, Italy
MSTN	Museo di Storia Naturale e del Territorio, Pisa, Italy
NHMW	Naturhistorisches Museum, Vienna, Austria
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, DC (formerly USNM)
NMHU	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
PMB	Natural History Museum Beograd, Serbia
PMU	Paleontologiska Museet, Uppsala, Sweden
SAZU	Slovenska akademija znanosti in umetnosti, Ljubljana, Slovenia
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
USNM	now NMNH

The following species were not included in this paper.

- *Cladocora articulata* (Abich 1859), from the Lower Miocene of Armenia (original material BMNH, R.10647), because the species belongs to the genus *Caulastrea*.
- *Cladocora ? bosniaca* (Oppenheim 1901), from the Eocene of Bosnia, because the original material could not be tracked down and the original description is insufficient.
- *Cladocora dubia* (Tenison-Woods 1880), which was transferred to the Bryozoa (Squires 1958: 93).
- *Cladocora subintricata* (d'Achiardi 1867), from the Oligocene of Italy, because the original material could not be found at MSTN and the original description is insufficient.
- *Cladocora ? unilaterialis* (d'Achiardi 1875), from the Oligocene of Italy, because the holotype (MSTN, specimen corresponding to the original illustration of d'Achiardi 1875, p. 9, Fig. 3) belongs to the genus *Caulastrea*.
- *Cladocora* sp. of Budd et al. (1994), from the Lower-Middle Miocene of Providencia, because its taxonomic and stratigraphic position are uncertain.

Results

The occurrence of the genus *Cladocora* in the Caribbean is largely continuous from the Campanian to Recent, except

Table 2 Stratigraphic distribution of *Cladocora* species occurring during the time interval Upper Cretaceous–Recent. *—* occurrence in the Caribbean. For references see text and Table 1

Species of <i>Cladocora</i>	Turonian-Santonian	Campanian	Maastrichtian	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene	Holocene
<i>gracilis</i> (d'Orbigny, 1850)			*—*							
<i>jamaicaensis</i> Vaughan, 1899		*—*			*—*					
<i>barkii</i> (Duncan, 1880)				?						
<i>bosquensis</i> Frost & Langenheim, 1974					—					
<i>prolifera</i> (d'Achiardi, 1866)					—	—				
<i>recrescens</i> Lonsdale, 1845						*—*				
<i>tenuis</i> (Reuss, 1868)					—	—				
<i>crenaticosta</i> (Reuss, 1869)					—	—				
<i>gaasensis</i> Chevalier, 1956					—	—				
<i>stipata</i> (d'Achiardi, 1867)					—	—				
<i>manipulata</i> (Michelin, 1842)					—	—				
<i>multicaulis</i> (Michelin, 1847)					—	—				
<i>haimei</i> Duncan, 1864					—	—				
<i>depauperata</i> Reuss, 1871					—	—				
<i>contortilis</i> Tenison-Woods, 1878					—	—				
<i>intricata</i> (Michelin, 1842)					—	—				
<i>johnsoni</i> Gane, 1895								*—*		
<i>prevostiana</i> Milne Edwards & Haime, 1849							—	—		
<i>micelotti</i> Milne Edwards & Haime, 1851							—	—		
<i>cespitosa</i> Linné, 1767							—	—		
<i>arbuscula</i> (Lesueur, 1821)						*—*	—	—	—	—
<i>debilis</i> Milne Edwards & Haime, 1849									*—*	—
<i>pacifica</i> Cairns, 1991										—

for the time intervals Paleocene, Lower Oligocene, and Miocene (Fig. 1; Table 2). While the absence of *Cladocora* during the Paleocene could be related to the K/T-boundary event, the absence of this genus in the Lower Oligocene and Miocene largely corresponds with the Neogene-Event (Flügel and Kiessling 2002), a major regional reef crises that is evident in the Caribbean region at the Oligocene–Miocene transition.

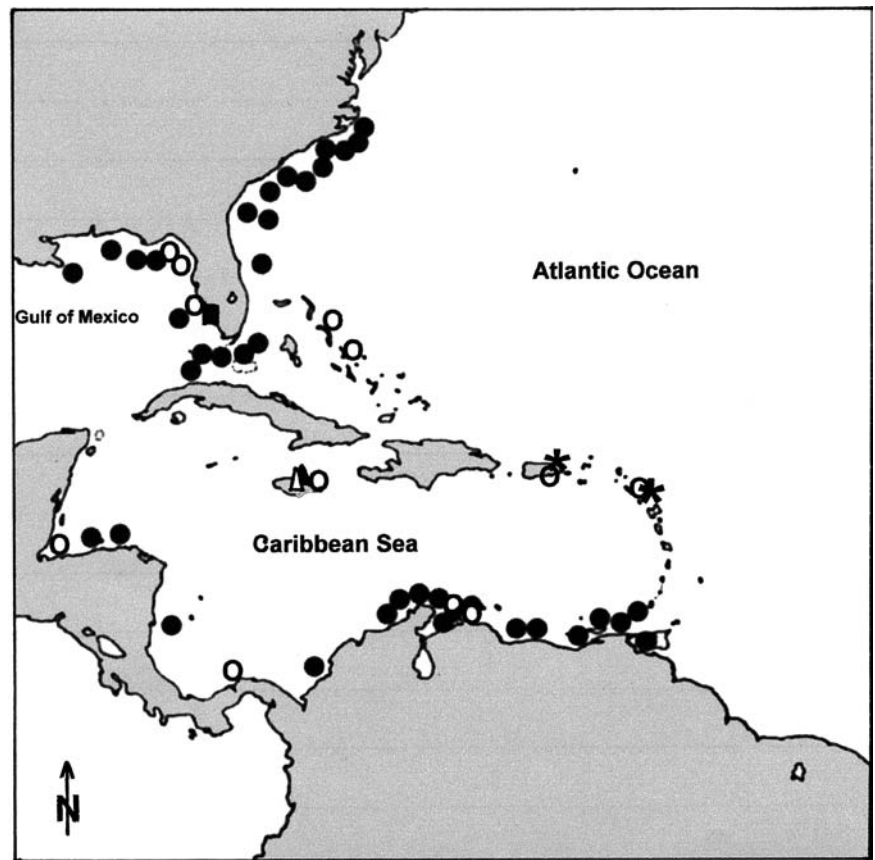
In addition to representing the earliest Caribbean species of *Cladocora*, *C. gracilis* (d'Orbigny 1850) and *C. jamaicaensis* Vaughan 1899, both show large and almost identical geographic and stratigraphic distributions that started right before the K/T-boundary event. Besides occurring in the Maastrichtian of the Caribbean, they appeared in the Maastrichtian of Mexico, and have been recorded from the Paleocene of central Europe, the Mediterranean, and the southern hemisphere (Argentina

and Antarctica, respectively). This suggests that after the K/T-boundary the Caribbean/northern Central America region served as a scleractinian source for other areas such as central Europe/Mediterranean and the southern hemisphere.

The majority of the Caribbean species of *Cladocora* show affinities to European assemblages, which are either older than their occurrence in the Caribbean (*C. gracilis* (d'Orbigny), *C. johnsoni* Gane 1895, and *C. recrescens* Lonsdale 1845) or younger than their Caribbean counterparts (*C. debilis* Milne Edwards and Haime 1849, and *C. jamaicaensis* Vaughan 1899). This indicates that a constant faunal exchange between the Caribbean and the European/Mediterranean region has existed since the Upper Cretaceous.

In contrast to the other Caribbean species of *Cladocora*, the forms *C. arbuscula* (Lesueur) and *C. johnsoni* Gane

Fig. 1 Species of *Cladocora* and their geographic occurrence within the Caribbean. (▲) *jamaicensis*, Campanian-Maastrichtian and Eocene of Jamaica; (△) *gracilis*, Middle-Upper Maastrichtian of Jamaica; (*) *recrescens*, Middle Oligocene of Antigua, Upper Oligocene of Puerto Rico; (■) *johnsoni*, Middle-Upper Pliocene of south Florida; (○) *arbuscula*, Pliocene-Recent, throughout the Caribbean; (●) *debilis*, Pleistocene-Recent, throughout the Caribbean



are characterized by very restricted geographic distributions. Interestingly, both species form rather dense, bushy colonies and have been reported from exclusively carbonate/soft bottom environments (Budd et al. 1994; and this paper). All the other species have been reported from a greater variety of environments (this paper).

Systematics

Suborder: **Faviina** (Vaughan and Wells 1943).

Family: **Faviidae** (Gregory 1900).

Genus: **Cladocora** (Ehrenberg 1834).

Type species: *Madrepora flexuosa* (Pallas 1766) (= *Madrepora cespitosa* (Linné 1767); = *Caryophyllia caespitosa* (Lamarck 1816)); Recent, Mediterranean Sea.

Diagnosis

Colonial, variably branching, phaceloid-dendroid to subflabelloid or even subfasciculate. Gemmation intracalicular (polystomodaecal) and extracalicular. Costosepta compact, finely granulated laterally, dentate marginally. Paliform swellings can be present in front of S1 and S2. Pseudocolumella formed by trabecular extension of axial septal ends, irregularly parietal, spongy to papillose, sublamellar deeper in corallum. Wall septothecal and septoparathecal.

Endothecal dissepiments thin, vesicular. Epithecal wall often thin or reduced.

Cladocora arbuscula (Lesueur 1821)
(Fig. 2J–L)

v*1821 *Caryophyllia arbuscula* – Lesueur, p. 275, pl. 15, Fig. 2a–d [topotypes studied].

v1846 *Caryophyllia arbuscula* Lesueur – Dana, p. 281, Fig. 24 [original material studied].

v1849 *Cladocora arbuscula* (Lesueur) – Milne Edwards and Haime, p. 307 [original material studied].

v1919 *Cladocora arbuscula* (Lesueur) – Vaughan, pp. 225, 228, 362 [original material studied].

v1974 *Cladocora arbuscula* (Lesueur) – Weisbord, p. 372, pl. 40, Figs. 1 and 2 [older synonyms cited therein, topotypes and original material of Weisbord studied].

v1982 *Cladocora arbuscula* (Lesueur 1821) – Cairns, p. 287, Fig. 128a [original material studied].

v1994 *Cladocora arbuscula* (Lesueur 1821) – Budd et al., pp. 957, 965, 975 [original material studied].

Dimensions

Corallite diameter (monocentric): 2.8–4 mm, up to 4.5 mm in late budding stages; number of septa (in monocentric corallite): 30–36+s.

Characteristics

Bushy, dense dendroid-subfasciculate colony; costosepta subequal, arranged in three complete and a beginning fourth cycle in six systems; number of septa generally 36 or larger; axial ends of S1–S2 bear a series of small paliform teeth, not formed in a crown; costae strongly developed; wall often septothecal, thick.

Type locality of species

Recent, West Indies.

Distribution

Pliocene-Pleistocene of Florida (South Bay), Pleistocene of Panama (Mt. Hope and Colon; Canal Zone), Recent throughout the Caribbean.

Distribution within the Caribbean

Pliocene-Recent, throughout.

Ecology

Carbonate/soft bottom, at 0.5–23 m depth range.

Cladocora debilis (Milne Edwards and Haime 1849) (Fig. 2F, I)

v*1849 *Cladocora debilis* – Milne Edwards and Haime, p. 308 [type material studied].

v2000 *Cladocora debilis* (Milne Edwards and Haime 1849) – Cairns, pp. 88–92, Figs. 18, 102–107 [older synonyms cited therein, original material of Cairns and material housed at the Smithsonian Institution studied].

Dimensions

Corallite diameter (monocentric): 2.8–3.8 mm; number of septa (in monocentric corallite): 24–36.

Characteristics

Corallites branch off at right angle from main corallite; branching not crowded; costosepta arranged in three complete cycles; larger corallites with additional pairs of S4; 12 paliform lobes well-formed and discrete, forming a single crown around columella; columella made of up to eight papillose elements.

Remarks

Due to rather similar dimensions of skeletal elements, some authors have synonymised *C. debilis* with *C. arbuscula*.

However, according to Cairns (2000: 90) the two species differ in a number of features. *C. debilis* is characterized by well-formed and discrete paliform lobes (P1–P2) that are arranged in a crown; a small, sparsely branched colony that is irregular in shape; and usually 36 or fewer septa in *C. debilis*. In *C. arbuscula* the axial ends of S1–S2 bear a series of small paliform teeth, not formed in a crown, the number of septa is often 36 or more; and the colony shape is rather robust, densely branched.

Type locality of species

Recent, off Madeira.

Distribution

Pleistocene-Holocene boundary of the Gulf of Mexico, Recent throughout the Atlantic and Mediterranean, 32–480 m depth range.

Distribution within the Caribbean

Pleistocene-Recent, throughout.

Ecology

Siliciclastic and carbonate/soft bottom, 32–480 m depth range.

Cladocora gracilis (d'Orbigny 1850) (Fig. 2C, G)

v*1850 *Calamophyllia gracilis* – d'Orbigny, p. 204 [topotype studied].

v1854 *Cladocora tenuis* m. – Reuss, p. 112, pl. 6, Figs. 24 and 25 [topotypes studied].

v1930 *Cladocora libidinum* n. sp. – Oppenheim, p. 362, pl. 38, Fig. 14 [topotypes studied].

v1982 *Procladocora tenuis* (Reuss) 1854 – Beauvais, vol. 1, p. 103, pl. 7, Fig. 2, pl. 8, Fig. 1 [type material studied].

v2002 *Cladocora gracilis* (d'Orbigny 1850) – Baron-Szabo, p. 34, pl. 17, Fig. 1.

v2003 *Cladocora gracilis* (d'Orbigny 1850) – Baron-Szabo, p. 122, pl. 5, Fig. 9, pl. 9, Figs. 3–5.

v2003 *Cladocora gracilis* (d'Orbigny 1850) – Schafhauser, Götz, Baron-Szabo and Stinnesbeck, p. 190ff [original material studied].

v2004 *Cladocora* cf. *C. gracilis* (d'Orbigny 1850) – Baron-Szabo, Casadio and Parras, p. 79R.

v2005 *Cladocora gracilis* (d'Orbigny 1850) – Baron-Szabo, p. 36, pl. 4, Figs. 4 and 6.

Dimensions

Corallite diameter (monocentric): 2.8–4.5 mm, up to 6 mm in late budding stages; number of septa: 16–40, in late budding stages number of septa is larger.

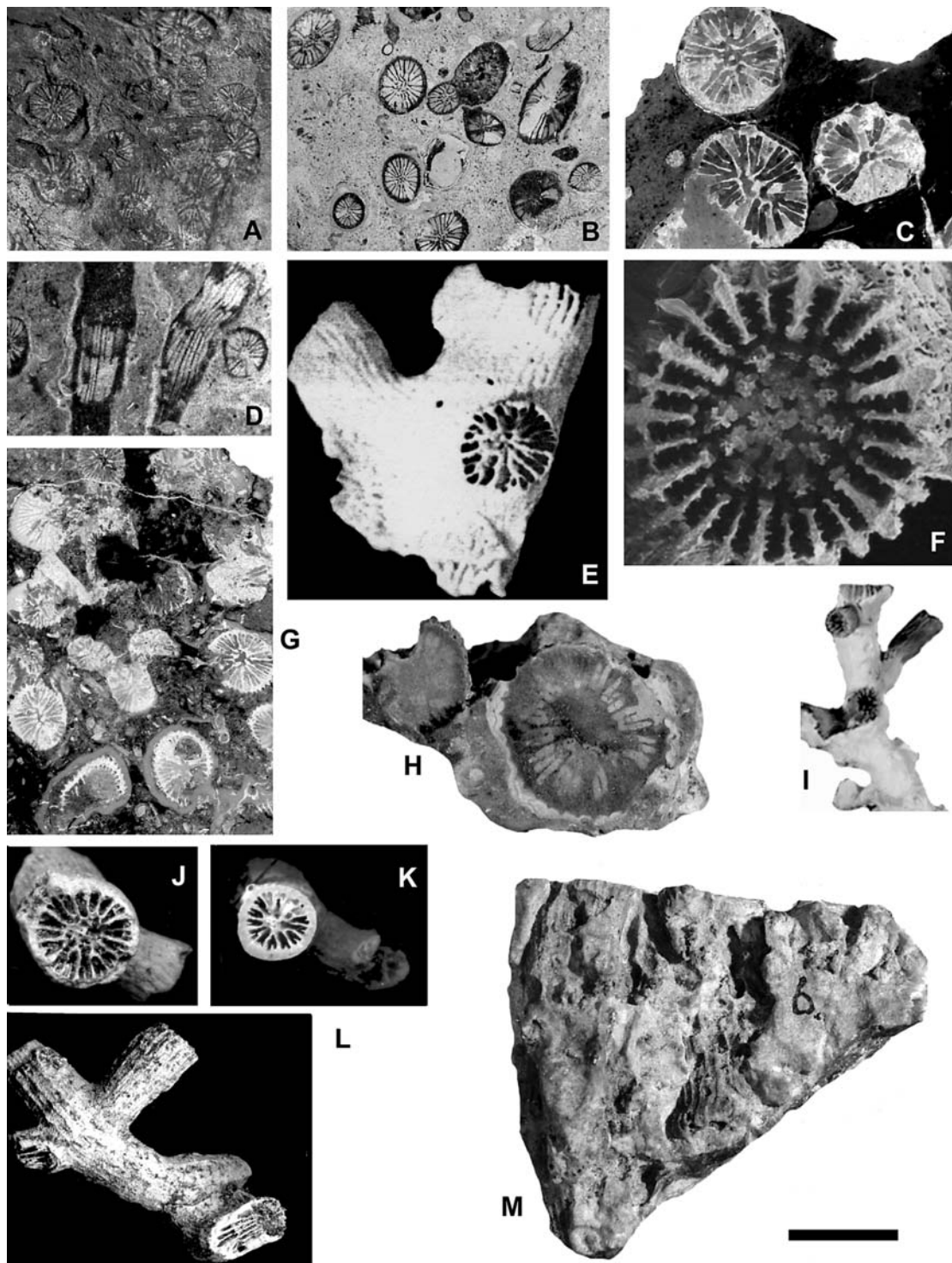


Fig. 2 Caribbean species of *Cladocora* spanning the time range Campanian-Recent. **A, B, D** *Cladocora jamaicaensis* (Vaughan 1899), holotype MCZ 114203, Campanian-Maastrichtian and Eocene of Jamaica (Blue Mountain Series). **A** Upper surface, scale bar: 10 mm. **B** Cross view, polished surface, scale bar: 15 mm. **D** Longitudinal view, slightly oblique, scale bar: 10 mm. **C, G** *Cladocora gracilis* (d'Orbigny 1850), Middle-Upper Maastrichtian of Jamaica. **C** cross thin section, NMNH, Coates collection, no. 553, Rio Minho, scale bar: 4 mm. **G** NMNH, Coates collection, no. 424b-II, scale bar: 6 mm. **E** *Cladocora johnsoni* (Gane 1895), Middle-Upper Pliocene of south Florida (Caloosahatchee Marl), NMNH, USNM 3300-b, upper surface, scale bar: 2.5 mm. **F, I** *Cladocora debilis* (Milne

Edwards and Haime 1849), Recent of the Atlantic. **F** upper surface, cross view, NMNH, USNM 10452, Silver Bay (north off Cuba), photograph courtesy Steve Cairns, scale bar: 1 mm. **I** syntype, BMNH 1974.6.15.2, upper surface, longitudinal view of colony, off Madeira, scale bar: 7.5 mm. **H, M** *Cladocora recrescens* (Lonsdale 1845), holotype, BMNH, R.34340., Middle Oligocene of Antigua (Seaforth Formation). **H** cross view, polished surface, scale bar: 7 mm. **M** longitudinal view, scale bar: 10 mm. **J–L** *Cladocora arbuscula* (Lesueur 1820), Recent, western Caribbean (Mt. Hope, Panama, Canal Zone), NMNH, USNM 75214. **J** cross view, upper surface, scale bar: 4 mm. **K** cross view, upper surface, scale bar: 5 mm. **L** upper surface, longitudinal view, scale bar: 5 mm

Characteristics

Phaceloid to subdendroid; costosepta arranged radially and bilaterally in three complete cycles in six systems in older corallites; S1 reach the center of the corallite, their axial ends sometimes fuse with the columella; S2 subequal or alternate in length and thickness; youngest septa distinctly thinner and shorter, regularly alternating with septa of the preceding cycle; columella trabecular or formed by elongated segments.

Type locality of species

Upper Coniacian of France (Soulatgé, Marno-calcaires à Gauthiericeras).

Distribution

Upper Turonian of Bulgaria, Turonian and Upper Santonian of France, Upper Turonian-Santonian of Austria (Gosau Group), ?Upper Santonian of Spain, Santonian-Campanian of Slovenia and Croatia, Santonian-Maastrichtian of ?Italy (Sicily), Middle-Upper Maastrichtian of Jamaica, Maastrichtian of Mexico (Cardenas Formation), Danian of Argentina, Paleocene of Austria, Upper Paleocene of Egypt.

Distribution within the Caribbean

Middle-Upper Maastrichtian of Jamaica.

Ecology

Various siliciclastic, carbonate, and mixed environments, coarse grained to soft bottom, at depth ranging from 0 m to outer shelf.

Cladocora jamaicaensis (Vaughan 1899)
(Fig. 2A, B, D)

v*1899 *Cladocora jamaicaensis* – Vaughan, p. 234, pl. 36, Figs. 5–7 [type material studied].

v1994 ? *Cladocora antarctica* n. sp. – Filkorn, p. 77, Figs. 29 and 30 [type material studied].

1996 *Cladocora* cf. *prolifera* (d'Achiardi 1866) – Schuster, p. 77, pl. 16, Fig. 5a, b [not seen].

v1997 *Cladocora* sp. – Vecsei and Moussavian, p. 131, pl. 36, Fig. 5 [original material studied].

2003 *Cladocora jamaicaensis* (Vaughan 1899) – Filkorn, p. 1 [not seen].

v2003 *Cladocora jamaicaensis* (Vaughan 1899) – Schafhauser, Götz, Baron-Szabo and Stinnesbeck, p. 190ff [original material studied].

v2005 *Cladocora jamaicaensis* (Vaughan 1899) – Baron-Szabo, p. 34, pl. 5; Fig. 1.

Dimensions

Corallite diameter (monocentric): 3.5–7 mm, up to 12 mm in late budding stages; number of septa: 28–50.

Characteristics

Corallum phaceloid to subdendroid; calices circular or elongated in outline; costosepta compact, developed in four complete cycles in adult corallites, irregularly alternating in length and thickness; 6–12 septa reach the center of the calice, their inner ends may fuse, terminate into claviform thickenings, or produce trabecular prolongations, forming a pseudo-columella; S3 distinctly thinner, reaching about half the length of the oldest ones; youngest septa somewhat smaller, or nearly equal with S3; columella reduced, trabecular, or absent; wall septothecal; epithecal wall present occasionally; endothecal dissepiments short and slightly arched in central region of the corallite, long and vesicular in peripheral area.

Remarks

The taxa *Cladocora antarctica* Filkorn, *Cladocora* sp. of Vecsei and Moussavian (1997), *Cladocora* cf. *prolifera* of Schuster (1996), and *Cladocora jamaicaensis* (Vaughan 1899), closely correspond to each other in having a calicinal diameter of generally 4–7 mm that can reach up to 9–12 mm in latest budding stages and be around 3 mm in earliest ones. In addition, in all the taxa the number of septa corresponds to three complete cycles in six systems and the beginning of a fourth cycle. The fourth cycle is always incomplete. Moreover, the type of budding (not visible in *Cladocora* sp. of Vecsei and Moussavian 1997) is identical in the specimens in that the new corallites spring off at angles ranging between 20° to nearly 90°.

Type locality of species

Campanian (-Maastrichtian) and Eocene of Jamaica (Blue Mountain Series).

Distribution

Campanian-Maastrichtian and Eocene of Jamaica (Blue Mountain Series and new material, this paper), Maastrichtian of Mexico (Ocozocuahtla and Cardenas Formations), Paleocene of Antarctica (Seymour Island) and Egypt, Upper Thanetian of Italy (Maiella Platform).

Distribution within the Caribbean

Campanian-Maastrichtian and Eocene of Jamaica.

Ecology

Various siliciclastic, carbonate, and mixed environments, coarse grained to soft bottom, at depth ranging from shallow water to around 120 m.

Cladocora johnsoni (Gane 1895) (Fig. 2E)

v*1895 *Cladocora johnsoni* n. sp. – Gane, p. 10 [type material studied].

v1919 *Cladocora johnsoni* Gane – Vaughan, p. 222 [original material studied].

v1961 *Cladocora vermiculata* Matheron in coll. – Chevalier, p. 227, pl. 17, Figs. 5–8, text-fig. 79a [type material studied].

v1961 *Cladocora gamachotensis* nov. sp. – Chevalier, p. 228, pl. 5, Figs. 5–7, text-fig. 79b [type material studied].

v1974 *Cladocora johnsoni* Gane – Weisbord, p. 375, pl. 40, Figs. 3 and 4 [original material studied].

v1994 *Cladocora johnsoni* (Gane 1895) – Budd, Stemmann and Johnson, pp. 957, 965, 975 [listed, original material studied].

Dimensions

Corallite diameter (monocentric): 2–2.8 mm; number of septa: 24 + s4.

Characteristics

Bushy-dendroid colony; corallites only around 2 cm long, giving the colony a very dense appearance; costosepta thin, subequal, developed in three cycles in six systems; few rudimentary septa of S4 occasionally present; wall septoparathecal, thin.

Type locality of species

Pliocene of South Carolina (Waccamaw River).

Distribution

Lower Miocene of France, Pliocene of South Carolina (Waccamaw River), Middle-Upper Pliocene of south Florida (Caloosahatchee Marl).

Distribution within the Caribbean

Middle-Upper Pliocene of south Florida.

Ecology

Carbonate/soft bottom.

Cladocora recrescens (Lonsdale 1845) (Fig. 2H, M)

v*1845 *Cladocora* (?) *recrescens* – Lonsdale, p. 517, Fig. a [type material studied].

v1867 *Cladocora arborea* – d'Achiardi, p. 8 [original material studied].

v1900 *Cladocora recrescens* Lonsdale – Vaughan, p. 138, pl. 15, Figs. 1–3 [original material studied].

1979 *Cladocora recrescens* – Frost and Weiss, 113ff, Fig. 8 [not seen].

Dimensions

Corallite diameter (monocentric): 7.5–12 mm, in late adult stages up to 14 mm; s: 32–48.

Description

Corallum phacelo-dendroid; corallites circular or elliptical in outline; costosepta thin, arranged in four complete cycles in six systems in older corallites; S1 reach the center of the corallite, remaining septa alternate in length and thickness; columella irregularly trabecular; wall septoparathecal, thin.

Type locality of species

Middle Oligocene of Antigua (Seaforth Formation).

Distribution

Eocene-Oligocene of Italy (Ronca, Castelgomberto) and the USA (Georgia and South Carolina), Middle Oligocene of Antigua, Upper Oligocene of Puerto Rico.

Distribution within the Caribbean

Middle Oligocene of Antigua.

Ecology

Carbonate/clastic, shallow water.

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