Scorpiodinipora costulata (Canu & Bassler, 1929) (Bryozoa, Cheilostomata), a taxonomic and biogeographic dilemma: complex of cryptic species or human-mediated cosmopolitan colonizer?

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ABSTRACT

Despite implausible cosmopolitanism, the species *Scorpiodinipora costulata* (Canu & Bassler, 1929) has been attributed with reservations to small encrusting colonies with similar morphological features whose known distribution is scattered in tropical and subtropical seas: Pacific Ocean (Philippines), Indian Ocean (Oman), Red Sea, SE Mediterranean, SE Atlantic (Ghana) and SW Atlantic (Brazil). This material raised questions about its generic assignment. The genus *Scorpiodinipora* Balavoine, 1959 is redescribed with *Schizoporella costulata* Canu & Bassler, 1929, from the Philippines as the type species, as Balavoine misidentified the specimens to define the genus as *Cellepora bernardii* Audouin, 1826. Moreover, SEM examination of the cotypes of *S. costulata* showed that Canu & Bassler confused two genera among them. A lectotype and paralectotype were thus chosen from Canu & Bassler's syntypes corresponding with the present morphotype. *Hippodiplosia ottomuelleriana* var. *parva* Marcus, 1938, from Brazil, which presents the same morphotype, is provisionally considered as the junior synonym of *S. costulata*. Considering the broad allopatric distribution of this morphotype across the oceans and the low capacity of dispersal of species with short-lived larvae, it is likely that this material includes several sibling species. However, the role of man-mediated dispersal is not excluded, at least in regions with high shipping activity, such as that comprising the Suez Canal.

KEY WORDS
Bryozoans,
Hippoporidridae,
biogeography,
taxonomy,
sibling species,
dispersal,
introduced species.

RÉSUMÉ

Scorpiodinipora costulata *(Canu & Bassler, 1929) (Bryozoa, Cheilostomata), un dilemme taxonomique et biogéographique : complexe d'espèces cryptiques ou colonisateur cosmopolite par dispersion anthropique ?*

En dépit de l'improbabilité du statut de cosmopolite, l'espèce *Scorpiodinipora costulata* (Canu & Bassler, 1929) a été attribuée avec réserves à des petites colonies encroûtantes présentant les mêmes traits morphologiques dont la distribution est éparpillée dans les mers tropicales et subtropicales : Pacifique (Philippines), océan Indien (Oman), mer Rouge, Méditerranée SE, Atlantique SE (Ghana) et Atlantique SW (Brésil). L'attribution générique de ce matériel était problématique. Le genre *Scorpiodinipora* Balavoine, 1959 est redécrit avec pour espèce-type *Schizoporella costulata* Canu & Bassler, 1929, des Philippines, Balavoine ayant identifié de manière erronée les spécimens sur lesquels il avait défini le genre *Cellepora bernardii* Audouin, 1826. De plus, l'examen au MEB des cotypes de *S. costulata* a montré que Canu & Bassler avaient mélangé deux genres parmi eux. Un lectotype et un paralectotype ont donc été choisis parmi les cotypes de Canu & Bassler correspondant au morphotype présent. *Hippodiplosia ottomuelleriana* var. *parva* Marcus, 1938, du Brésil, qui présente le même morphotype, est considéré provisoirement comme un synonyme junior de *S. costulata*. Considérant la vaste distribution allopatrique de ce morphotype dans les océans et la faible capacité de dispersion de ce type d'espèces à larves à courte durée de vie, il est probable que ce matériel comprend plusieurs espèces jumelles. Toutefois, une dispersion d'origine humaine n'est pas exclue, au moins dans les régions avec une grande activité maritime, comme celle comprenant le canal de Suez.

MOTS CLÉS
Bryozoaires,
Hippoporidridae,
biogéographie,
taxonomie,
espèces jumelles,
dispersion,
espèce introduite.

INTRODUCTION

Cosmopolitanism attributed to marine species is, in many cases, a nebulous concept hiding the failure to detect subtle diagnostic differences between closely related or sibling species (e.g., Knowlton 1993; Klautau *et al.* 1999). This is even more obvious when considering sessile taxa whose dispersal depends essentially on short-lived free larval stages (Jackson 1986). On the other hand, intensification of the maritime traffic during the last centuries has considerably increased the chance of dispersal of species that are particularly prone to be transported upon ship hulls, in ballast tanks, or to travel with mariculture products (e.g., Carlton 1987; Gollasch 2002; Hewitt *et al.* 2009). As a result, there is a dramatic spread across all world oceans of introduced species displaying allopatric populations. In many cases, the exotic origin of those species is not recognised, or remains questionable (cryptogenic species: Carlton 1996). In certain cases, genetic differentiation may be rapid among presumed allochthonous populations. This was shown, for example, through chemical and genetic markers in different populations of *Bugula neritina* (Linnaeus, 1758) (Davison & Haygood 1999; McGovern & Hellberg 2003), one of the most famous bryozoan foulers (Gordon & Mawatari 1992).

In the phylum Bryozoa, the great majority of species brood short-lived larvae (Ryland 1981) resulting in a limited dispersal range and patchy distribution of local populations (Jackson 1986; McKinney & Jackson 1989; Watts *et al.* 1998). Rafting, i.e. colonisation of drifting natural (e.g., macrophytes) or artificial substrata (e.g., plastics), may explain at least part of the long-distance dispersal of bryozoan propagules (Arnaud *et al.* 1976; Winston 1982; Jackson 1986; Stevens *et al.* 1996; Winston *et al.* 1997; Barnes & Sanderson 2000; Barnes & Fraser 2003; Carter & Gregory 2005). Facultative epibiosis of fertile bryozoan colonies on mobile marine animals, either swimming offshore (e.g., turtles, sea snakes) or moving in benthic communities (arthropods, gastropod molluscs) may also play a role in the dispersal of species at different spatial scales (Landman *et al.* 1987; Taylor *et al.* 1989; Frazier *et al.* 1992; Key *et al.* 1995, 1996, 1999). On the other hand, as other invertebrates with short-lived larvae, many bryozoans could enhance their dispersal range and connectivity between distant populations when colonising small, discrete, benthic habitats acting as stepping stones (Harmelin 1986; Harmelin & Vacelet 1997).

Bryozoans show multiple examples of pseudo-cosmopolitanism, particularly among old taxa, such as *Microporella ciliata* (Pallas, 1766), *Celleporella hyalina* (Linnaeus, 1767) or *Cribrilaria radiata* (Moll, 1803), whose records all around the world often reflect the customary use of familiar species names combined with the difficulty of defining the species boundaries with the available tools. Scanning electron microscopy has changed the observation scale of the morphological features, allowing the use of new criteria for splitting old taxa (e.g., Harmelin 2006; Wright *et al.* 2007; Berning *et al.* 2008; Vieira *et al.* 2010). Still rarely used for resolving taxonomic problems in Bryozoa but extremely promising, molecular methods, such as DNA barcoding validated by mating trials, are efficient tools in clade discrimination within cosmopolitan species (Gómez *et al.* 2007; Nikulina *et al.* 2007; Hughes *et al.* 2008). However, the use of molecular tools is difficult to apply to taxa exhibiting only small and rare encrusting colonies. This is particularly evident when the studied material is provided by collections from old expeditions.

The finding of a cheilostomate species with a very simple and similar morphology in collections from the SE Mediterranean, the Red Sea and Oman raised questions about:

1) its generic assignment;

2) its taxonomic relationship with morphologically similar species from other tropical or sub-tropical regions (i.e. Brazil, W Africa and the Philippine Archipelago);

3) the status of these distant populations.

Do they represent a circumtropical cosmopolitan species, a cryptogenic, presumably introduced species, or a complex of sibling species? Examination of the specimen on which Balavoine (1959) founded the genus *Scorpiodinipora* revealed its conspecificity with our specimens from the same region and also that its species had been misidentified by Balavoine. The choice of another type-species was thus necessary for fixing the status of this valid genus.

MATERIAL AND METHODS

This study is based on material collected during diving field trips and on specimens kept in museums. Collections by SCUBA diving were performed:

1) in the SE Mediterranean, at six localities distributed from N to S Lebanon (JGH, Lebanese-French cooperation program CEDRE);

2) in the Red Sea, Egypt, one station at Ras Mohammed, S Sinai (JGH) and 13 stations in the Bay of Safaga (staff of the University of Vienna);

3) in the Indian Ocean, Arabian Sea, Oman, one station at Salalah, near Mirbat (ANO).

Specimens from the SW Atlantic, Brazil, were collected at São Sebastião, Sao Paulo state, using a small Van Veen grab sampler (LMV, BIOTA/FAPESP program). Museum specimens were examined at the MNHN, NHMUK, USNM, and MZUSP.

Colonies examined with a SEM were cleaned in a 7.5% solution of sodium hypochlorite, rinsed, air-dried and coated with gold or gold-palladium alloy, using a Hitachi S 570 (Marseille), Zeiss DSM 940 (São Paulo) and Jeol JSM-6400 (Vienna). Museum specimens were scanned using SEMs fitted with an environmental chamber at the NHMUK (LEO 1455VR) and USNM (Philips XL-30 ESEM + LaB6 electron source). Morphometric analysis was performed using a stereomicroscope with a micrometric eyepiece at the highest magnification possible, except for the material from Ghana (use of scale bars of SEM photos).

JGH's collection is deposited at the MNHN. All the specimens from the Bay of Safaga and Oman are currently kept at the DPUV. The final destination of this collection will be the Senckenberg Museum, Frankfurt am Main. Specimens from Brazil are kept at the MZUSP.

Abbreviations

Institutions where type specimens have been examined and other specimens deposited

DPUV	Department of Palaeontology, Geozentrum, University of Vienna;
MNHN	Muséum national d'Histoire naturelle, Paris;
MZUSP	Museu de Zoologia of Universidade de São Paulo, São Paulo;
NHMUK	Natural History Museum, London;
USNM	Smithsonian Institution, Washington.

SYSTEMATICS

The following description is based on specimens coming from distant localities and different seas. The authors are aware that this set of colonies sharing the same morphotype may include several distinct species. However, in the absence of clear morphological criteria allowing species splitting, all examined specimens have been considered as a whole and assigned to *Scorpiodinipora costulata* (Canu & Bassler, 1929). The case of *S. costulata* presents a remarkable combination of nomenclatural problems, which are addressed here. Two nominal species and subspecies display the same morphotype: *Schizoporella costulata* Canu & Bassler, 1929 and *Hippodiplosia ottomuelleriana* var. *parva* Marcus, 1938. Consequently, all specimens showing this morphotype have been assigned with *Schizoporella costulata*, provisionally considered as the senior synonym. However, in the description of this species, Canu & Bassler (1929) mixed specimens clearly belonging to two distinct genera. In order to clarify this confused situation, a lectotype and a paralectotype were chosen from Canu & Bassler's designated cotypes that conform to the morphotype described here. The assignment of the studied material to the genus *Scorpiodinipora* Balavoine, 1959 is confirmed by examining the original specimens of the Balavoine's collection. However, the status of this genus was puzzling as Balavoine misidentified these specimens with *Cellepora bernardii* Audouin, 1826, which clearly belongs to another genus. A new type species had thus to be designated in order to confirm the validity of the genus *Scorpiodinipora*, and *Schizoporella costulata* was selected.

Family Hippoporidridae Vigneaux, 1949

Genus *Scorpiodinipora* Balavoine, 1959

Type species. — Fixed here (under article 70.3 of the *International Code of Zoological Nomenclature* [ICZN 1999]) as *Schizoporella costulata* Canu & Bassler, 1929, misidentified as *Cellepora bernardii* Audouin, 1826 in the original designation by Balavoine (1959).

Diagnosis. — Colony encrusting, unilamellar. Autozooids hexagonal, medium-sized. Frontal shield non-pseudoporous, with marginal areolae and radiating ribs between them. Orifice not terminal, with anter and poster similarly sized and rounded, and lateral sides parallel, bearing distinct condyles a little lower than mid-height. No oral spines. No ovicells. No avicularia.

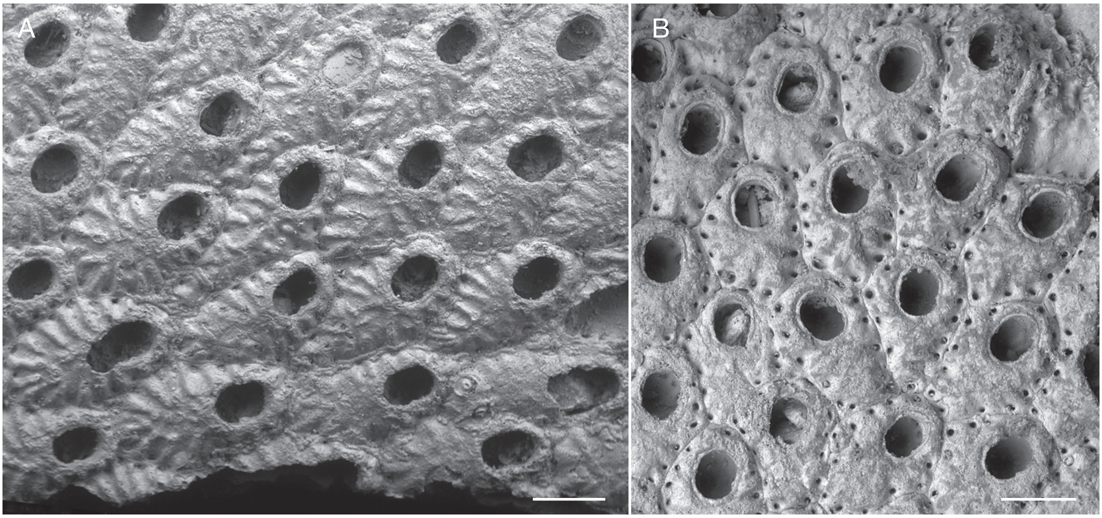

Fig. 1. — *Scorpiodinipora costulata* (Canu & Bassler, 1929), two specimens considered by Canu and Bassler in their description of *Schizoporella costulata*: **A**, specimen USNM 8080, chosen as lectotype, Philippines, Romblon Light; **B**, specimen USNM 8079, paralectotype, Philippines, Jolo Light. Scale bars: 200 µm.

Basal pore-chambers small, numerous. Ancestrula similar to an autozooid but smaller; zone of astogenetic change including 2-4 zooids budded by the ancestrula and few others showing progressive increase of size and calcification.

Scorpiodinipora costulata
(Canu & Bassler, 1929)
(Figs 1-5; Table 1)

Schizoporella costulata Canu & Bassler, 1929: 317 (in part), pl. 36, fig. 10; not pl. 36, fig. 11.

Hippodiplosia otto-mülleriana var. *parva* Marcus, 1938: 39, pl. 9, fig. 22a, c; pl. 10, fig. 22b.

Scorpiodinipora bernardii – Balavoine 1959: 269, pl. 6, fig. 1.

Cyclocolposa ?*parva* – Banta & Carson 1977: 415, fig. 9d.

Hippopodinella parva – Cook 1985: 170, figs 19, 44.

?*Odontoporella* sp. – Gordon *et al.* 2007: 52, fig. 3d.

Not *Cellepora bernardii* Audouin, 1826: 238. — Savigny 1817: pl. 7, fig. 7 (unnamed drawing).

Not *Schizoporella bernardii* – Waters 1909: 169, pl. 17, figs 7-9.

Not *Stephanosella bernardii* – Harmer 1957: 1051, pl. 74, figs 21-23.

Not *Scorpiodinipora bernardii* – d'Hondt & Mascarell 2004: 464, fig. 1. — d'Hondt 2006: 24.

Type material. — USNM, Albatross collection, Philippine Archipelago, 2 specimens labelled *Schizoporella costulata* Canu & Bassler, 1929. Lectotype (designated here): USNM 8080, Romblon Light, 12°38'15"N, 122°12'30"E, 37 fms (figured by Canu & Bassler 1929: pl. 36, fig. 10). Paralectotype (designated here): USNM 8079, Jolo Light, 06°05'50"N, 121°02'15"E, 19 fms.

Other material examined. — Specimens referred to the present morphotype:
1) MZUSP 020, labelled "*Hippopodinella otto-mülleriana* var. *parva* (Marcus)", 1 colony with other bryozoans on shell of *Thais haemastoma* (Linnaeus, 1767) (gastropod), Brazil (no locality in label, but probably Santos, São Paulo, as described by Marcus [1938]) (E. Marcus identification);
2) NHMUK 1972.3.3.94, labelled "*Hippopodinella parva* (Marcus)", 2 colonies on *Drillia* sp. (gastropod), Ghana, south of Tema, 1970-72 (P. L. Cook identification);
3) MNHN, R. Ph. Dollfus collection (identifications by Balavoine [1959]), Red Sea, Gulf of Suez, specimen no. 7792, labelled "*Schismopora bernardii* (Aud. 1826)", Al Sayad, stn VI (29°11'N, 32°55'20"E, 35-69 m), 29/XI/1928, on gastropod; specimen no. 7816, labelled "*Schismopora bernardii*", G. de Suez, Al Sayad, stn X (29°N, 32° 39'E, 28-62 m), 8/XII/1928, on gastropod; specimen no. 7826, labelled "*Scorpiodinipora bernardii* Audouin. Figuré. Spécimen type de ce nouveau genre", Al Sayad, stn XI (28° 54'N, 32° 44'E, 31-25 m), 8/

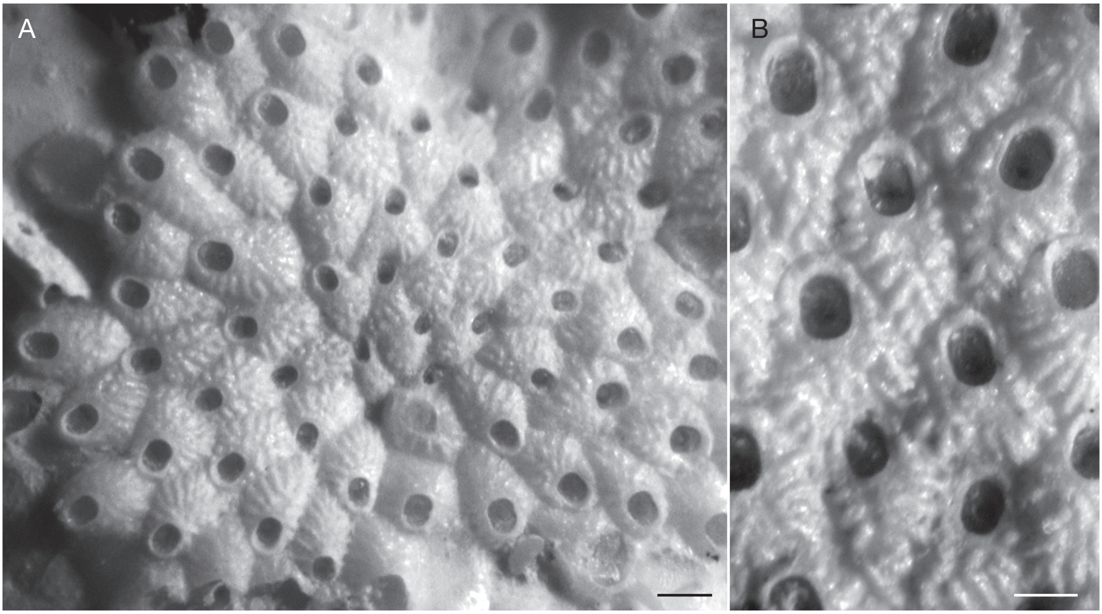

FIG. 2. — Specimen MNHN no. 7826 labelled "*Scorpiodinipora bernardii* Audouin" figured by Balavoine (1959 pl. 6, fig. 1), on which the genus *Scorpiodinipora* was established, Gulf of Suez, 31-25 m: **A**, general view of the colony; **B**, close up view of autozooids. Scale bars: A, 200 µm; B, 100 µm.

XII/1928, on a small oyster shell (figured by Balavoine 1959: pl. 6, fig. 1);

4) SE Mediterranean, Lebanon, CEDRE collection (JGH), 17 colonies from 6 localities: Tripoli, Ramkine Island, overhang, 13 m, 3 colonies on gastropod shells, 22/X/1999; Anfey, 14 m, 1 colony on pebble, 26/X/1999; Selaata, 6-7 m, 3 colonies on gastropod shells and lichenoporid bryozoan skeleton, 18-22/X/1999; Batroun, 2-9 m, 7 colonies on gastropod shells and biogenic concretions, 26/VI/1997, 16/X/1999, 26/IX/2002; Jounieh Aquamarina, 20-30 m, 2 colonies on pebble, 10/VII/2003; Saida, Harf El Rijmeh, 11 m, 1 colony on *Spondylus spinosus* Schreibers, 1793, 5/VI/2000;

5) Red Sea, Egypt, South Sinai, JGH collection: Ras Mohammed, Yolanda wreck, 18 m, several small colonies on aluminium plates, 15/V/1983;

6) Red Sea, Egypt, Bay of Safaga, DPUV collection. 52 colonies from 13 stations: stn B3/12 (seagrass meadow), IV/1986, 6 m, 1 detached colony; stn A1/3 (muddy bottom + brown algae), 24-26/IV/1986, 18 m, 6 colonies on gastropod shells; stn A14/1, 24/II/1987, 35 m, 16 colonies on gastropod shells; stn A1-2/2 (sand), 27/IV/1986, 10 m, 2 colonies on gastropod shells; stn B3/2, 16/VII/1987, 4 m, 1 colony on gastropod shell; stn B17/1 (muddy sand), 11/VII/1087, 52 m, 1 detached colony; stn B5/0, 02/XI/1986, 6 m, 5 colonies on gastropod shells; stn B7/5 (muddy sand), 30/VII/1987, 48 m, 5 colonies on gastropod shells; stn B17/2 (muddy sand), 29/VII/1987, 50 m, 3 colonies on gastropod shells; stn B18/1 (muddy sand), 24/VII/1987, 32 m, 7 colonies on gastropod shells; stn C7/1, 20/II/1987, 14 m, 3 colonies on gastropod shells; unnamed station, Ras Abu Soma, IX/1992, 1-20 m, 1 colony on echinoid spine; unnamed station, 1 colony on gastropod shell;

7) Indian Ocean, Arabian Sea, Oman, DPUV collection: Salalah (near Mirbat), Kelp Bay, 9 m, 1 colony on bivalve shell, 16/I/2009;

8) SW Atlantic, Brazil, São Paulo state, São Sebastião, about 10 m, 2 colonies on fragments of shell and 1 colony on small gastropod shell, collected by A. E. Migotto & J. E. Winston.

Specimens referred to other species:

1) USNM, Albatross collection, Philippine Archipelago, USNM 8078: *Schizoporella costulata* Canu & Bassler, 1929, Jolo Light, 6°04'25"N, 120°58'30"E, 20 fms (figured by Canu & Bassler 1929: pl. 36, fig. 11);

2) MNHN (Jullien's collection), no. 3607: *Stephanosella bernardii*, Gambier Is.; no. 3888: *Stephanosella bernardii*, Gambier Is. (J. L. d'Hondt identification).

GEOGRAPHIC DISTRIBUTION. — SW Atlantic: SW Brazil (Marcus 1938 and present data); Caribbean Sea: Costa Rica (Banta & Carson 1977); E Atlantic: Ghana (Cook 1985); Pacific Ocean: Philippines (Canu & Bassler 1929);

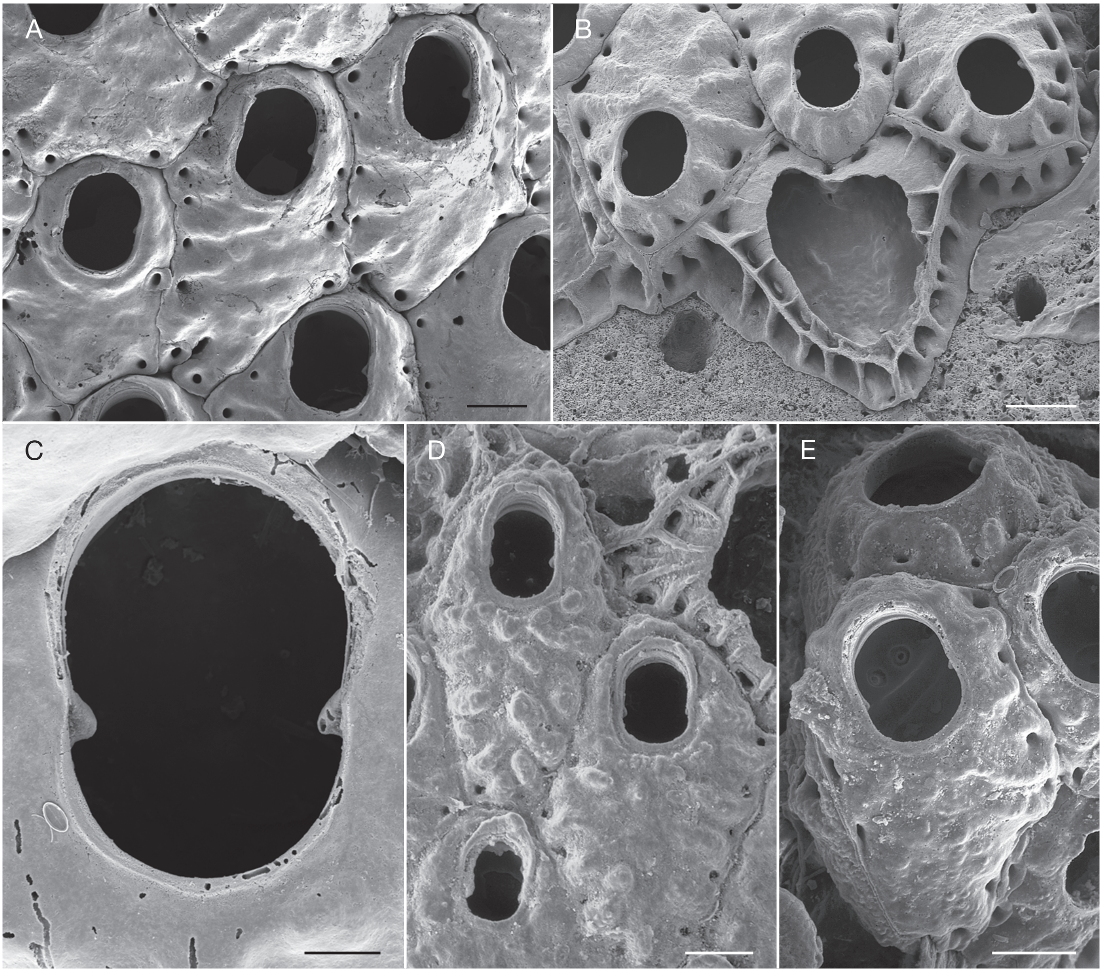

FIG. 3. — *Scorpiodinipora costulata* (Canu & Bassler, 1929): **A**, Red Sea, Egypt, Safaga; **B**, **C**, Arabian Sea, Oman; **D**, Red Sea, Egypt, Ras Mohammed; **E**, SE Mediterranean, Lebanon, Selaata. Scale bars: A, B, D, E, 100 µm; C, 20 µm.

Indian Ocean: Oman (present data), Bangladesh (Gordon *et al.* 2007); Red Sea: Gulf of Suez(Balavoine 1959), S Sinai and Bay of Safaga (present data); SE Mediterranean: Lebanon (present data).

HABITAT. — *Scorpiodinipora costulata* is a shallow-water species showing a marked preference for calcareous organic substrates, especially gastropod shells (Table 2). However, this relationship is not strict as *S. costulata* was also observed on other substrates, either natural (pebbles) or artificial (aluminium plates). Colonies encrusting gastropod shells were generally smaller than those growing on flatter and smoother substrates such as the inner sides of bivalve shells. Cook (1985) noted that colonies from Ghana often encrusted gastropod shells inhabited by pagurids and were small: a single *Drilla* sp. shell could aggregate up to 10 colonies.

DESCRIPTION

Colony encrusting, unilamellar, often small (< 20 zooids), sometimes larger (> 200 zooids), frequently encrusting shells, especially of gastropods. Frontal shield convex, structured by radial ridges more or less prominent and mamillated, originating from vertical ridges between marginal pores (areolae); 15-20 areolar pores, widely open and elongated

TABLE 1. — Zooidal measurements (in µm); origin of data: autozooid: Lebanon (7 colonies, 4 sites), S Sinai (2 colonies, 1 site), Safaga (2 colonies, 1 site), Brazil (1 colony), Ghana (1 colony). Ancestrula: Lebanon (7 ancestrulae, 5 sites). Abbreviations: AN, ancestrula; A2, autozooid; L, length; N, number of measurements; OR, orifice; sd, standard deviation; W, width.

	Mean ± sd	**Range**	**N**
Autozooid			
Lebanon			
L AZ	434.0 ± 51.3	340-580	57
W AZ	300.4 ± 52.4	205-485	57
L OR	138.3 ± 8.6	120-158	54
W OR	110.0 ± 7.7	97-125	54
S Sinai			
L AZ	469.2 ± 25.6	425-510	13
W AZ	338.5 ± 41.7	270-410	13
L OR	141.4 ± 5.5	135-150	11
W OR	108.6 ± 7.4	95-120	11
Safaga			
L AZ	467.8 ± 55.05	340-610	71
W AZ	319.4 ± 44.1	230-400	71
L OR	150.7 ± 15.9	120-185	71
W OR	112.7 ± 10.6	90-140	71
Oman			
L AZ	373.0 ± 34.9	310-450	32
W AZ	286.6 ± 42.0	230-390	32
L OR	120.8 ± 17.0	90-160	32
W OR	90.5 ± 6.6	80-100	32
Ghana			
L AZ	318.0 ± 28.4	278-372	15
W AZ	221.0 ± 16.9	191-242	15
L OR	110.0 ± 7.3	96-118	15
W OR	79.0 ± 7.3	67-90	15
Brazil			
L AZ	360.0 ± 45.8	310-450	20
W AZ	250.0 ± 47.0	170-340	20
L OR	135.0 ± 14.5	100-160	20
W OR	90.0 ± 11.6	75-115	20
Ancestrula (Lebanon)			
L AN	282.1 ± 30.8	240-330	7
W AN	155.0 ± 19.4	135-185	7
L OR AN	101.2 ± 7.8	90-110	6
W OR AN	72.4 ± 6.3	60-80	7

in young zooids, becoming smaller and rounded, or totally hidden by calcification in older zooids. Orifice subterminal, with anter and poster similarly rounded and sized, lateral sides straight and parallel, down-curved condyles placed at mid-height or a little lower, a low visor occasionally raised perpendicularly over the anter. Small basal pore-chambers about as numerous as areolae. No ovicells. Infrequent occurrence (one case observed in a colony from Lebanon) of dwarfed zooids scattered among normal autozooids, with a costulate frontal shield and a small rounded orifice not terminal and bordered distally by ribs. Ancestrula similar to an autozooid but with cystid smaller and narrower (L/W = 1.8 vs 1.4 in material from Lebanon), orifice smaller and frontal shield smoother. Two to four autozooids budded by the ancestrula. Zone of astogenetic change extending over two or three generations of zooids, which increase progressively in size and frontal relief.

DISCUSSION

SIMILARITIES AND DIFFERENCES BETWEEN SPECIMENS

All examined specimens present the same general morphological features whatever their geographical origin (Pacific Ocean, Philippines: Fig. 1; Indian Ocean, Oman: Fig. 3B-C; Red Sea, Egypt: Figs 2, 3A, D; SE Mediterranean, Lebanon: Figs 3E, 5; SE Atlantic, Ghana: Fig. 4C, D; SW Atlantic, Brazil: Fig. 4A, B). The external aspect of the frontal wall may vary within and between colonies according to ontogeny and degree of calcification with more or less pronounced costae, but with the same range of variation among specimens from different localities. Similarly, the shape of autozooidal orifices and that of ancestrulae (see below) are invariable in the examined material. However, some differences observed among specimens are discussed below.

Our morphometric analyses suggest that the mean size of the autozooid and its orifice may vary regionally (Table 1). The lowest values were found in the colony from Ghana while the largest mean sizes were measured in colonies from both Red Sea localities (S Sinai, Safaga). These differences may be attributed to several causes, such as local environment including climatic conditions or specific traits of local populations (or clades). However, one must note that these data were obtained on a limited number of colonies in each region by different observers and two different methods of measurement (stereomicroscope vs

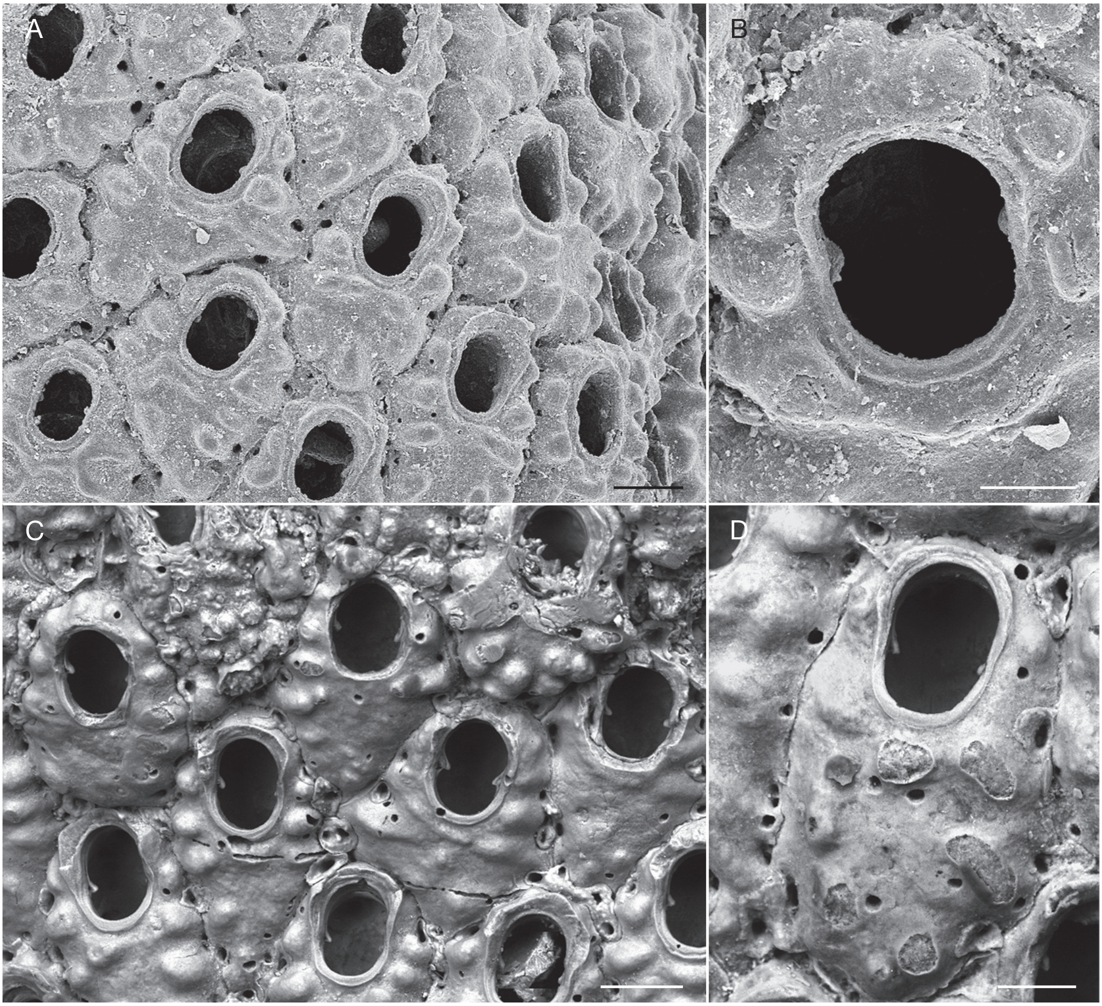

FIG. 4. — *Scorpiodinipora costulata* (Canu & Bassler, 1929): **A**, **B**, SW Atlantic, Brazil, São Sebastião, specimen MZUSP 545; **C**, **D**, SW Atlantic, Ghana, specimen NHMUK 1972.3.3.94, labelled "*Hippopodinella parva* (Marcus)", P. L. Cook identification. Scale bars: A, C, 100 µm; B, D, 50 µm.

SEM photos) were used. Therefore, several possible sources of biases forbid a sound interpretation of these apparent regional differences.

The exceptional occurrence of three dwarfed zooids (Fig. 5) in a single colony from Lebanon is rather enigmatic considering that 17 colonies from this region and many other ones from other regions were examined. This colony with dwarfed zooids is similar in all other features to the rest of our material, including colonies from the same sample. These dimorphic zooids might be male zooids as suggested by the occurrence of sexually dimorphic zooids in the Hippoporidridae (Gordon 1989; Ryland 2001), the family in which we propose to place *Scorpiodinipora* (see also below). However, considering their rarity and the variable size of their rounded orifice and cystid, these heterozooids are rather interpreted as zooids stunted by an external agent. Dwarfism as a result of repair after a predator attack should be considered.

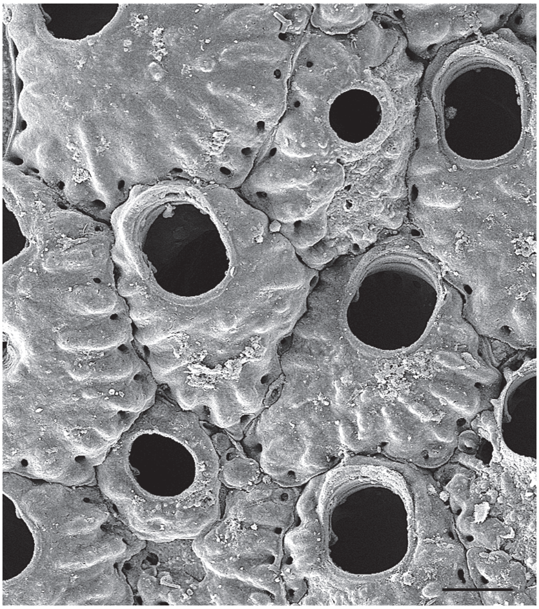

Fig. 5. — *Scorpiodinipora costulata* (Canu & Bassler, 1929): two dwarfed zooids inserted among normal autozooids. Lebanon, Batroun, 9 m. Scale bar: 100 µm.

The available material supplied reliable information on the periancestrular zone. Drawings of an ancestrula and adjacent autozooids are given by Marcus (1938: pl. 10, fig. 22b) and Cook (1985: fig. 19), and one ancestrula is visible on the photo of the specimen chosen by Balavoine for typifying *Scorpiodinipora* (Balavoine 1959: pl. 6, fig. 1 and herein Fig. 2A). In our material, ancestrulae were observed in colonies from Lebanon (nine ancestrulae from five localities), Red Sea, S Sinai (one ancestrula), and Brazil (two ancestrulae). In every case, the shape of the ancestrula and that of its orifice are similar to those of an autozooid but with smaller dimensions and a smoother frontal wall. Also, the material from Lebanon indicates that the ratio length/width of the cystid is greater in the ancestrulae than in the autozooids (1.8 vs 1.4; Table 1). No difference was observed between ancestrulae from different localities, but the number of daughter autozooids budded by the ancestrula appeared variable though often difficult to interpret due to colony growth. The drawing given by Marcus (1938) shows a group of six zooids including two equally-sized smaller ones with a smooth frontal wall, which are adjacent proximally and grow in opposite directions. Although only the right one is labelled “a” for ancestrula, both look similar and are symmetrically bordered by four older autozooids seemingly budded from their lateral sides. This picture may be interpreted as an ancestrula budding three or four autozooids or, alternatively, as an accidental meeting of two ancestrulae each budding two autozooids. The drawing by Cook (1985) depicts an ancestrula with three daughter autozooids, one budded proximally and two proximolaterally. In the large specimen from *Scorpiodinipora* of Balavoine’s collection, the ancestrula is encircled by six autozooids among which four may have been budded distally and distolaterally. The material from Lebanon provided confirmation that the daughter zooids can be equally budded from both proximal and distal halves of the ancestrula and that their number can vary from two to four (Fig. 6).

Choice of species name

All examined specimens show evident morphological similarities with two specific and subspecific taxa: *Schizoporella costulata*, from the Philippines, and *Hippodiplosia ottomuelleriana* var. *parva*, from Brazil.

Only part of the material cited by Canu & Bassler (1929) in their description of *S. costulata* corresponds to the present morphotype. Examination by SEM of specimens USNM 8080 figured by Canu & Bassler (1929: pl. 36, fig. 10; D. 5179: Romblon Light, Romblon) and USNM 8079 (D. 5144: Jolo Light, Jolo) kept at the USNM confirmed that they are morphologically similar (Fig. 1) to all other specimens we have examined (Figs 2-5). In contrast, another specimen figured by Canu & Bassler (1929: pl. 36, fig. 11; D. 5137 / USNM 8078: Jolo Light) is totally different and belongs to another genus. This obvious disparity was noted by the authors: “We found two forms, one recalling *Schizopodrella unicornis* Johnston, 1847, and the other *Schizopodrella nivea* Busk, 1884.” (Canu & Bassler 1929: 318.) However, curiously, they left them under the same species name and designated both morphotypes as cotypes of the new species *Schizoporella costulata*. To clarify this situation,

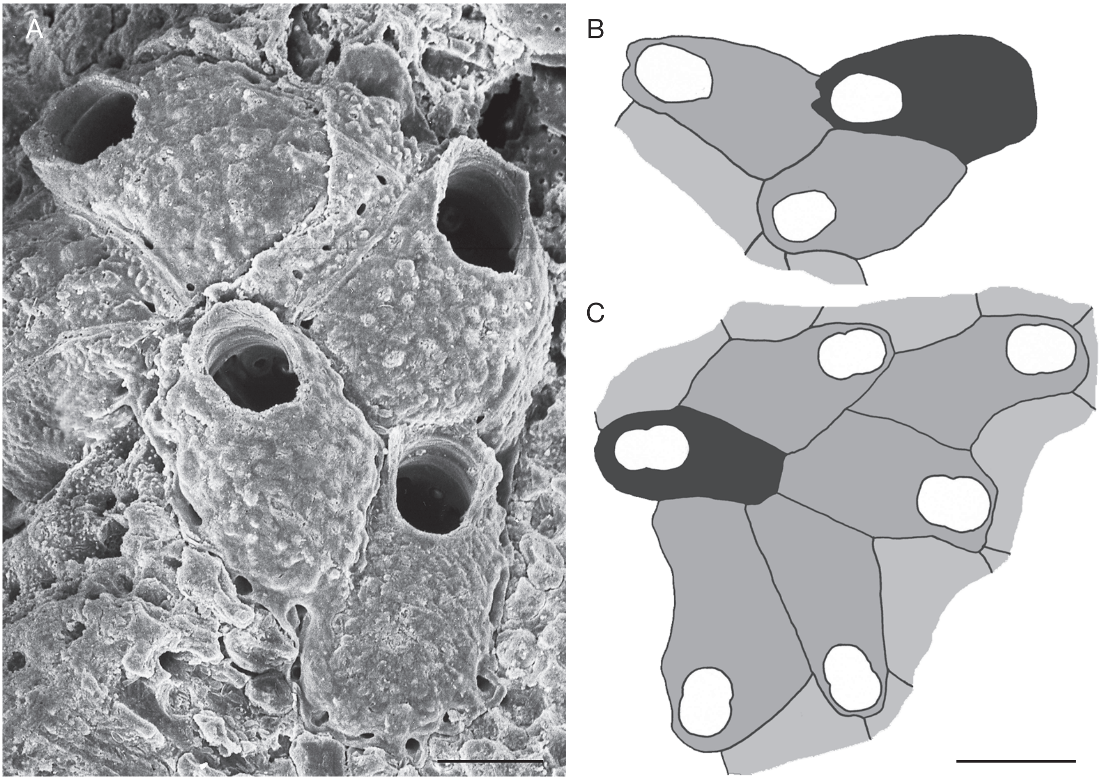

Fig. 6. — *Scorpiodinipora costulata* (Canu & Bassler, 1929), ancestrula and periancestrular budding: **A**, proximal part with ancestrula of a very small colony, Lebanon, Batroun, 9 m; **B**, **C**, schematic representation of two ancestrulae with different periancestrular budding pattern; **B**, distal budding of two zooids, same colony as A; **C**, proximal budding of four zooids, Lebanon, Tripoli, 13 m. Scale bars: 200 µm.

the specimen USNM 8080 is designated here as lectotype of this species, with specimen USNM 8079 as paralectotype (Fig. 1A, B).

The figures of Marcus (1938) of *H. ottomuelleriana* var. *parva* as well as those of *Cyclocolposa parva* from Costa Rica (Banta & Carson 1977) and of *Hippopodinella parva* from Ghana (Cook 1985) depict the morphotype studied here. This was confirmed by examining the holotype specimen of *H. ottomuelleriana* var. *parva* (MZUSP 020), other Brazilian specimens collected near the type locality of this holotype (Fig. 4A, B) and one Ghanaian specimen (NHMUK 1972.3.3.94) from Cook's collection (Fig. 4C, D) at the NHMUK.

Assignment of specimens with the morphotype *costulata* from the Gulf of Suez (MNHN n°7792, 7816, 7826) to *Cellepora bernardii* Audouin, 1826 by Balavoine (1959) was erroneous but the new genus he erected for them, *Scorpiodinipora*, is valid (see below). However, the report of *Scorpiodinipora bernardii* from the south Red Sea by Powell (1967) and Dumont (1981) cannot be interpreted in the absence of descriptions or figures. *Schizoporella bernardii* (Audouin, 1826) reported from Red Sea by Waters (1909) differs from the morphotype *costulata* in having small sinuate orifices and two types of avicularia.

In conclusion to the problem of species attribution, we consider that there are presently no substantial arguments for distinguishing separate species among all examined specimens presenting the same morphotype. Consequently, *S. costulata* is provisionally considered as the senior synonym of *H. ottomuelleriana* var. *parva*.

TABLE 2. — Number of colonies recorded in four habitat types: **A**, gastropod shells; **B**, other biogenic substrates; **C**, lower face of pebbles; **D**, artificial substrates.

Locations	**A**	**B**	**C**	**D**
SE Mediterranean	9	5	3	–
Red Sea	52	1	–	several
Oman	–	1	–	–
Ghana	several	–	–	–
Brazil	2	2	–	–

CHOICE OF GENUS AND FAMILY

The morphotype *costulata* as it is characterized here appears in the literature under various generic names: *Schizoporella* Hincks by Canu & Bassler (1929), *Hippodiplosia* Canu by Marcus (1938), *Cyclocolposa* Canu & Bassler by Banta and Carson (1977), *Hippopodinella* Barroso by Cook (1985), *Odontoporella* Héjjas by Gordon *et al.* (2007) and *Scorpiodinipora* by Balavoine (1959). The latter was erected by Balavoine (1959) for a large colony from the Gulf of Suez (MNHN no. 7826) labelled "*Scorpiodinipora bernardii* (Aud. 1826), Spécimen type de ce nouveau genre" (Fig. 2A, B). The similarity of this specimen and others from the same collection with the morphotype studied here was apparent on the published photo (Balavoine 1959: pl. 6, fig. 1) and was confirmed by examination of the collection at the MNHN. Unfortunately, Balavoine erroneously ascribed it to *Cellepora bernardii*, a species which has only the presence of radiating ribs on the frontal shield in common with the present morphotype. The original figure of *C. bernardii* by Savigny (1817) is very precise and clearly shows numerous, large, hyperstomial ovicells ornamented with tubercles, orifices surrounded by a well raised peristome with a proximal indentation apparently corresponding to a sinus, and an elongate or nodular bulge proximolateral to the orifice, which may correspond to an avicularium. Examination of the specimens from Gambier Islands (Jullien's collection at the MNHN) illustrated by d'Hondt and Mascarell (2004: fig. 1) and reported as *Scorpiodinipora bernardii* confirmed that they agree quite well with the original figure of Savigny (1817) and the redescription of *Cellepora bernardii* by Harmer (1957). These specimens have a sinuate primary orifice, avicularia latero-proximal to the orifice, and hyperstomial ovicells bearing prominent pores. Therefore, as there is no doubt that the specimens on which Balavoine founded the genus *Scorpiodinipora* are not congeneric with *Cellepora bernardii* but are conspecific with the specimens found by us in Lebanon, Red Sea and Oman, we consider that *Scorpiodinipora* is a valid genus. The replacement of its type-species is thus necessary (ICZN: art. 70.3) and we propose to change it for *Schizoporella costulata* Canu & Bassler, 1929. We also propose to place *Scorpiodinipora* in the family Hippoporidridae Vigneaux, 1949. The placement of *Scorpiodinipora* in this family, as defined by Gordon (1989), is supported by most characters including encrusting growth-form, structure of the frontal shield with small marginal areolar pores, occurrence of small pore-chambers, shape of the orifice with a broad rounded poster and lateral condyles, lack of orificial spines, and frequent colonisation of gastropod shells inhabited by pagurids (Table 2). According to Gordon (1989), members of this family may or may not have an ovicell but possess avicularia. However, we consider that the lack of avicularia in *Scorpiodinipora* is not a sufficient argument for rejecting its placement in the Hippoporidridae. *Scorpiodinipora* seems to be close to *Odontoporella* in having autozooids with similar wall structure and no ovicell, but the latter has adventitious avicularia and an ancestrula without frontal shield (Carter & Gordon 2007).

CONCLUSIONS

The decision to assign all examined specimens to a single nominal species, *S. costulata*, is not truly satisfactory despite their evident morphological likeness. This statement is questionable as: 1) the characterization of the morphotype *costulata* relies only upon few taxonomic characters, a constraint that can generate identification biases; and 2) its geographic distribution is worldwide in tropical and sub-tropical seas with allopatric populations.

The central questions raised by this material are: does it represent a single species or consist of a complex of cryptic (sibling) species? If it is a single species, is its apparent cosmopolitanism a natural feature or an effect of man-mediated dispersal?

The intrinsic dispersal abilities of *S. costulata* can be assessed considering the criteria analyzed by Watts *et al.* (1998). As in all ascophorans, *S. costulata* is inferred to produce coronate larvae whose short free life precludes long-range dispersal (Jackson 1986; Watts *et al.* 1998). Transoceanic migration by direct larval transit is obviously impossible as well as step-to-step transit using available substrata across bathyal and abyssal bottoms because of ecological barriers. On the other hand, coastal dispersal thanks to colonization of various discrete microhabitats acting as relays can be an effective process allowing the spreading of populations along a continuous coastline and/or across a moderate depth cline (Harmelin 1986; Harmelin & Vacelet 1997). Not being epiphytic, *S. costulata* is likely incapable of dispersal by rafting on macrophytes, which is assumed to be a common means of long-range species dispersal (Highsmith 1985; Jackson 1986). The rising abundance of marine debris increases the chance of dispersal for bryozoans that are able to colonize them (Winston 1982; Stevens *et al.* 1996; Barnes & Sanderson 2000; Gregory 2009). However, it seems unlikely that the very broad geographic range of *S. costulata* could solely result from this mode of colony transit.

Shipping and artificial connection between ocean basins are responsible for most of the man-mediated species introductions (Carlton 1987; Zibrowius 1991; Gollasch 2002; Hewitt *et al.* 2009). The propensity of *S. costulata* to foul ship hulls and ballast structures is unknown but expected to be moderate as suggested by habitat preferences identified in the examined material and features of fouling species analysed by Gordon & Mawatari (1992).

This species presents a marked preference for living on shells and other organic mineralized parts but not exclusively: it was also found on lower faces of pebbles and artificial substrata (aluminium sheets from a wreck, S Sinai). However, *S. costulata* has never been identified as a fouler despite its wide present geographic range, which would imply a long-standing invasive process. Its common occurrence along the Lebanon coast indicates that it is well established there and suggests that its occurrence in the SE Mediterranean is strongly related with its distribution in the Red Sea, including the Gulf of Suez. This pattern may result from an old Lessepsian migration from the Red Sea, but also from introduction events occurring on both sides of Suez Canal caused by vessels arriving from remote ocean basins. The maritime traffic through the canal and across the Mediterranean is intense (Abdulla & Linden 2008) and its influence on the geographic range of apparently non-indigenous bryozoan species is suspected (Harmelin *et al.* 2009). The growing importance of exotic bryozoan species in marine communities should be more thoroughly assessed, particularly in the Mediterranean. As stressed by Carlton & Geller (1993: 81): "The discovery of previously unrecognized species in regions impacted by ballast water release (almost all coastal zones of the world) must now be viewed critically as potential invasions."

Nominal species displaying both few diagnostic features and allopatric populations are suspected not to be biological species (Mayr 1963) but to denote cryptic species or species complexes (Knowlton 1993; Bickford *et al.* 2006). With discrete records across a very broad geographic range the morphotype *costulata* may represent a typical example of cryptic (sibling) species. Unfortunately, many features of this morphotype, such as its encrusting growth form, small colony size and relative rarity, will not permit easy use of molecular tools for testing genetic distinctiveness.

In conclusion, one must stress that the hypothesis of cryptic species does not exclude the hypothesis of man-mediated introduction events, at least in some regions, such as the SE Mediterranean.

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