Biogeographia vol. XXV - 2004
(Printed December, 30th 2004)
Marine Biogeography of the Mediterranean Sea: patterns and dynamics of biodiversity

Importance of faunistic and taxonomical studies for a correct analysis of the zoogeography of Mediterranean Bryozoa

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Key words: Bryozoa, Mediterranean Sea, taxonomy, biogeography, species "complexes"

SUMMARY

Faunistic and biogeographical studies on Mediterranean Bryozoans are somewhat complicated by both taxonomical uncertainties and uneven sampling distribution. Many taxa, which are considered cosmopolitan, are actually "complexes" of species with different ecology and distribution; some others are less known owing to their cryptic habitus, or their preference for rarely sampled habitats. Examples are given of "complexes" of species of the genera *Watersipora*, "*Cleidochasma*" and *Monoporella*, species which have been probably uncorrectly identified (*Pherusella brevituba)* and, finally, some rare and cryptic species (*Cleidochasmidra çanakkalense* and *Arachnoidea protecta*, respectively).

INTRODUCTION

The analysis of the specific composition and biogeographic distribution of Mediterranean bryozoan assemblages presents some problems, which are also common to other taxa. Among the main difficulties we consider: incorrect identification; small size or cryptic habitus of some species, which are, consequently, little visible; sampling restricted to only a few habitats, or unevenly distributed in the Mediterranean Sea; the existence of "species complexes". In this article we illustrate and discuss some examples drawn from our own experience.

MATERIALS AND METHODS

The original description and iconography of each taxon were compared to our specimens. Some specimens, lent by the British Museum of Natural History (BMNH), were also studied. When using the Scanning Electron Microscope (SEM), photographs were taken with a Philips XL 30 microscope for *Watersipora subtorquata* (partly), *W. cucullata* and *Monoporella fimbriata carinifera*; with a Cambridge Stereoscan 360 for *Plesiocleidochasma mediterraneum*; and with a Cambridge Stereoscan 2000 for *Cleidochasmidra çanakkalense* and *W. subtorquata* (partly). When using transmitted light, photographs were taken with a Nikon Ortophot II for *Pherusella brevituba*, and with an Olympus SZX12 for *Arachnoidea protecta* and *W. subtorquata* (specimen from Naples).

RESULTS

Problems of identification: *Pherusella brevituba* Soule, 1951
Pherusella brevituba: Soule, 1951, p. 368, fig. 1 (1-2)
Pherusella brevituba: d'Hondt, 1983, p. 86, pl. VI, fig. 1
Pherusella brevituba: Chimenz Gusso and d'Hondt (in press), fig. 2 (A-E)
Ecology. This species was observed by Soule (1951) on a rocky bottom at a depth of 15-16 m, on algae and fanerogams. We collected it at a depth of 10-28m on *Posidonia oceanica.*
Distribution. General: California (Soule, 1951). Mediterranean (Fig. 1): Ustica (Sicily) (Chimenz Gusso and d'Hondt, in press)
Description. (Fig. 7). Zoaria are chitinous, transparent, light brown, small (no more than 8 individuals), unilaminar, encrusting the blades of *Posidonia oceanica.* At the beginning of the development, the zoarium shows two series of zooids opposing with their proximal part. Zooids are distinct, oval to hexagonal, lageniform, about 0.85 mm in length and 0.57 mm in width (n=12); the youngest are more oval. The interzooecial communication pores in the lateral walls have a chitinous ring pierced by two perforations. Distally the autozooids bear a short quadrangular peristomium (0.10 mm in length) (arrow in Fig. 7) which is consequently much shorter than in the congeneric *P. tubulosa*; the aperture, located at the extremity of the peristomium, is rectangular. No coenozoecia or spines. Polypide typically with 23 tentacles and a large digestive caecum, slightly longer than it is wide.
The genus *Pherusella* comprises other two taxa (d'Hondt, 1983): *P. tubulosa*, a cosmopolitan species found in warm and temperate waters, which differs from *brevituba* in the zooidal length (more than 1 mm), the tubular peristomial process 0.400-0.700 mm long, and the tentacle number (28); and *P.flabellaris*, from the China Sea, similar to *tubulosa*, except for the tentacle number (20).
Remarks. The general shape of the youngest zooids and the lack of kenozooids

make them close to some *Alcyonidium* species and could be the cause of some misidentifications; this species could also be mistaken for a young *P. tubulosa.*

Cryptic species: *Arachnoidea protecta* Harmer, 1915
Arachnoidea protecta: Harmer, 1915, p. 50, pl. I, figs. 7-11.
Arachnoidea (Arachnoidella) protecta: d'Hondt, 1983, p. 49, fig. 25 (I)
Arachnoidea (Arachnoidella) protecta: Chimenz Gusso et al., 1998, p. 235, figs. 1-5.
Ecology. Collected by Chimenz Gusso et al. (1998) on *Cystoseira* ind.
Distribution. General: Celebes (Harmer, 1915). Mediterranean (Fig. 1): Vulcano (Chimenz Gusso et al., 1998).
Description. (Figs. 3, 4). The zooids are discrete (Fig. 3); each consists of an erect part (peristome) and a basal encrusting part, comprising a broad plate and a long narrow filament. The irregularly shaped basal plate has a more or less ovate contour and bears the filament and three (or more) projections connecting it with an equal number of filaments of other zooids (Fig. 4). The origin of the filament is highly irregular, usually proximo-lateral, rarely disto-lateral or proximal. A variable number of irregular processes, about twenty, more or less long and digitate, project from the plate margin on a more basal level compared with the filament. In a retracted state, the peristome is quadrangular and the orifice is perfectly square. When protruded, the peristome shows a markedly chitinized proximal part, a less chitinized and corrugated intermediate portion and a distal collar supported by strong ribs, each of which ends distally with a tooth (Fig. 4). When retracted, the polypide lies in the basal plate. Dimensions:

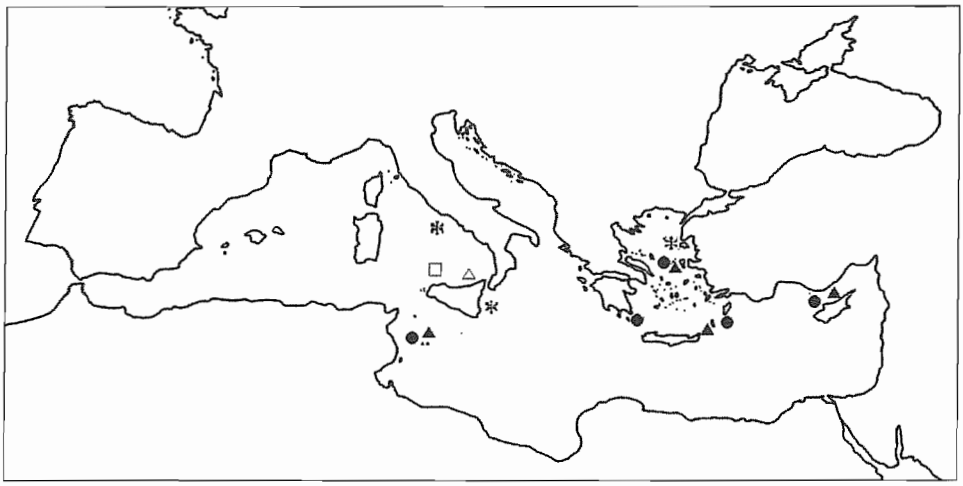


Fig. 1- Distribution in the Mediterranean Sea of: △: *Pherusella brevituba*; ▲: *Plesiocleidochasma mediterraneum*; ●: *Monoporella fimbriata carinifera*; □: *Arachnoidea protecta*; ✱: *Cleidochasmidra çanakkalense*

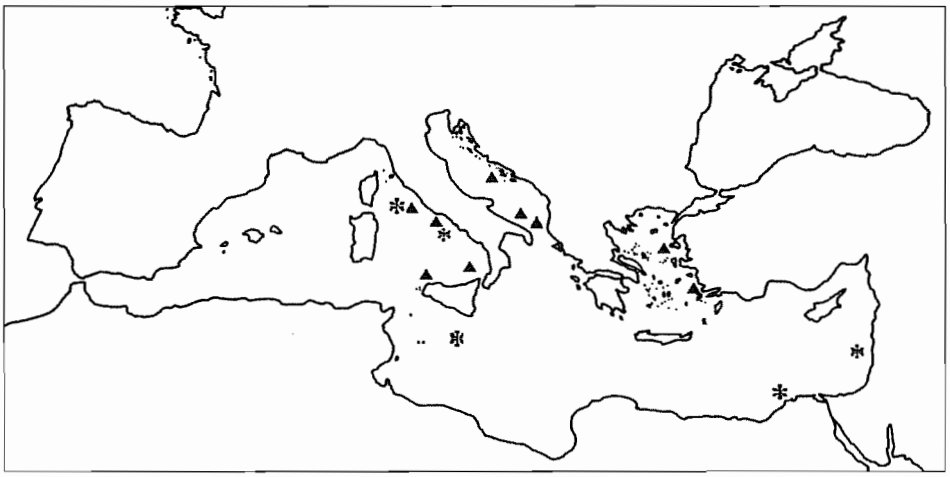
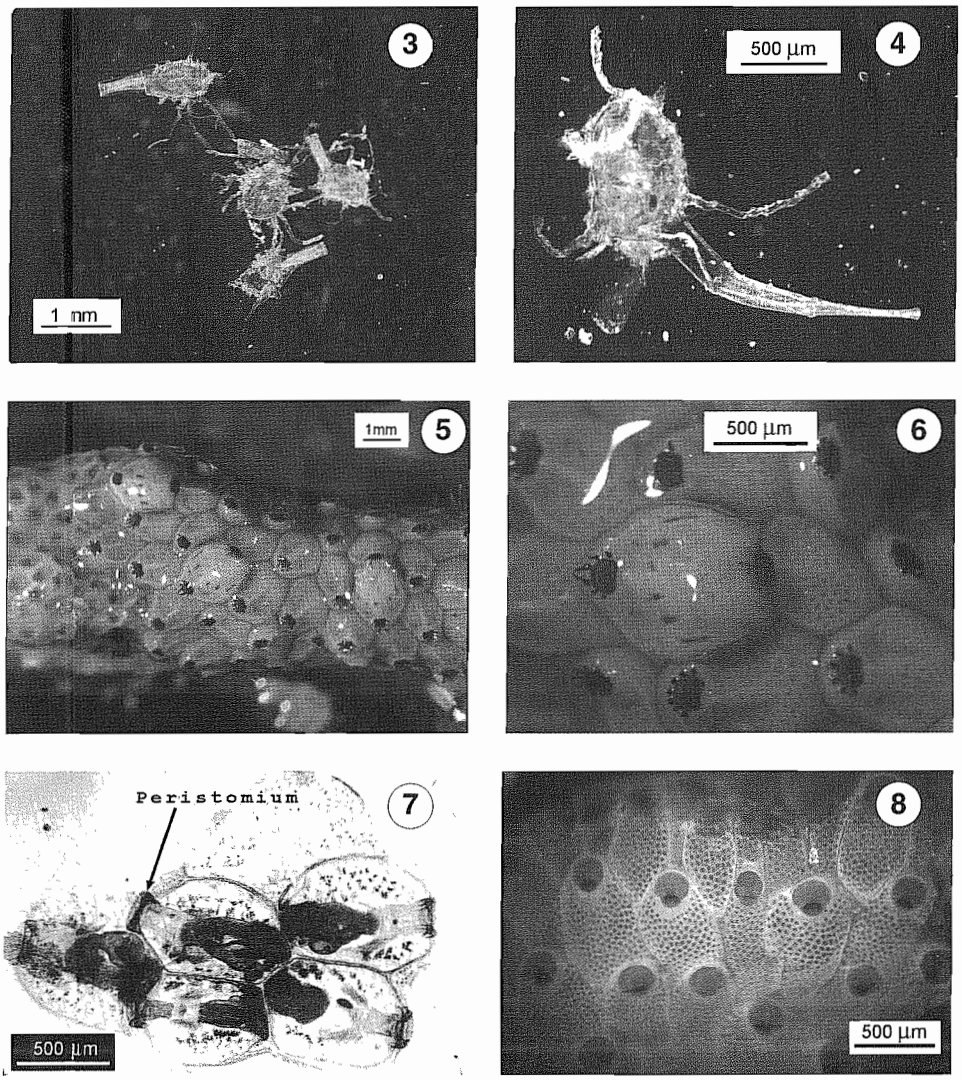


Fig. 2 - Distribution of the genus *Watersipora* in the Mediterranean Sea: ✱: *Watersipora subtorquata*; ▲: *Watersipora cucullata*

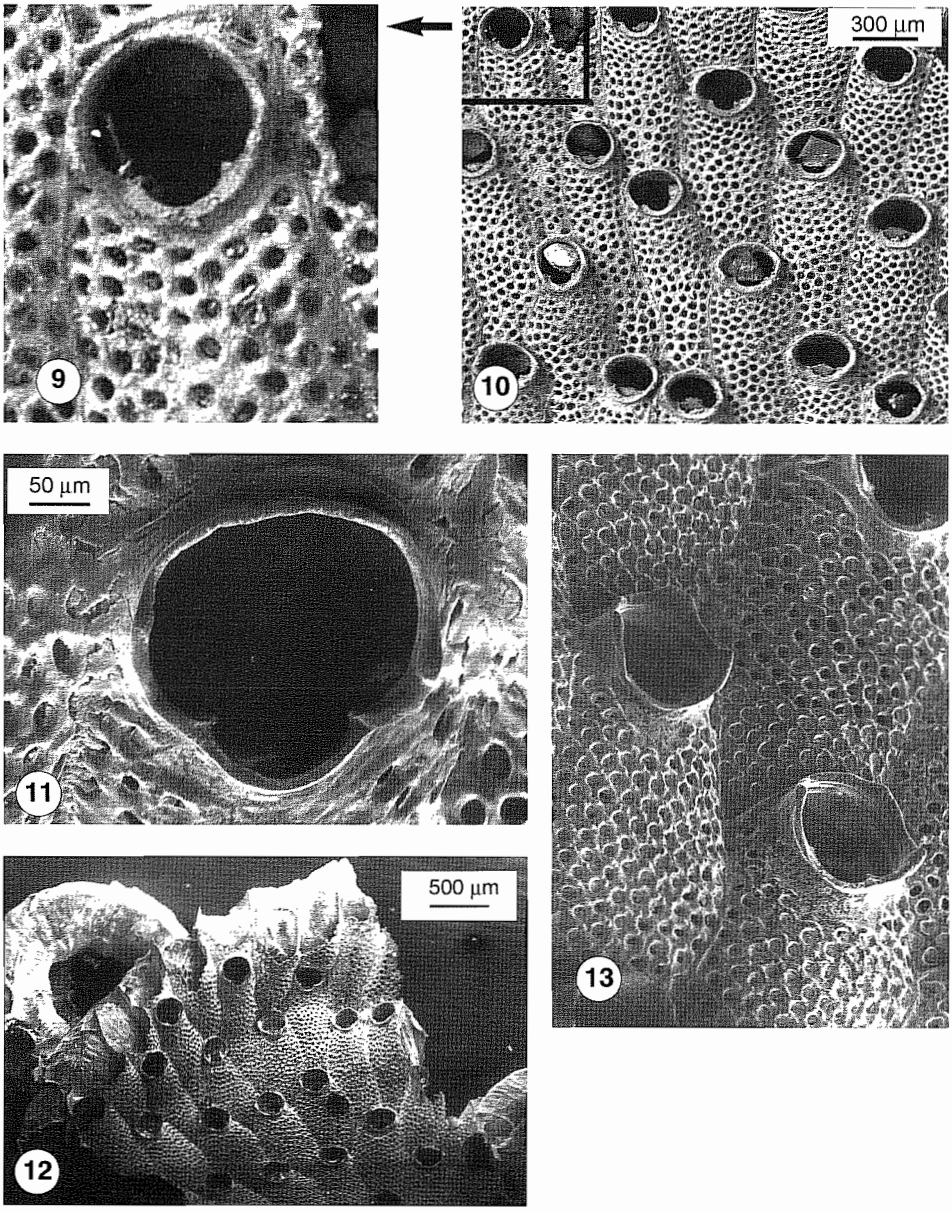
zooid length 0. 823 mm (n=6), width 0.524 mm (n=8); length of retracted peristome 0.516 (n=5), width 0.152 mm (n=12).
Remarks. This is a very inconspicuous and transparent species, difficult to see on the substratum, and it could easily go unobserved.

Little studied habitats: ***Cleidochasmidra çanakkalense*** Ünsal and d'Hondt, 1979.
Cleidochasmidra çanakkalense: Ünsal and d'Hondt, 1979, p. 620
Cleidochasmidra çanakkalense : Rosso, 1996, p. 63, pl. 1, fig. 6
Material: Ponza, st. 169, depth 45 m; st. 189, depth 49 m (Chimenz Gusso, unpublished data).
Ecology. Firstly described by Ünsal and d'Hondt (1979) at a depth of 60-70m; subsequently found in the Coastal Detritic biocoenosis (*sensu* Pérès and Picard, 1964) by Rosso (1996) at depth of 44 - 88 m, and on organogenic detritus and red ramified calcareous algae, at a depth of 45-49 m by Chimenz Gusso (unpublished data).
Distribution. Only Mediterranean (Fig. 1): Çanakkale (Aegean Sea); Gulf of Noto (Sicily); Pontine Islands (Latium).
Description (Fig. 20). Zoarium encrusting, small. Zooidal frontal wall bearing large granulations arranged in 4 or 5 rows more or less regularly concentric with the aperture. Orifice almost circular in shape, slightly elongated along the major autozooidal axis; provided with two proximal condyles, delineating a large shallow poster. Ovicell hyperstomial, globose (arrow in Fig. 20), not closed by the operculum, with large evenly arranged granulations like those of the frontal wall; with a distal depression linked by means of an axial linear suture with distal

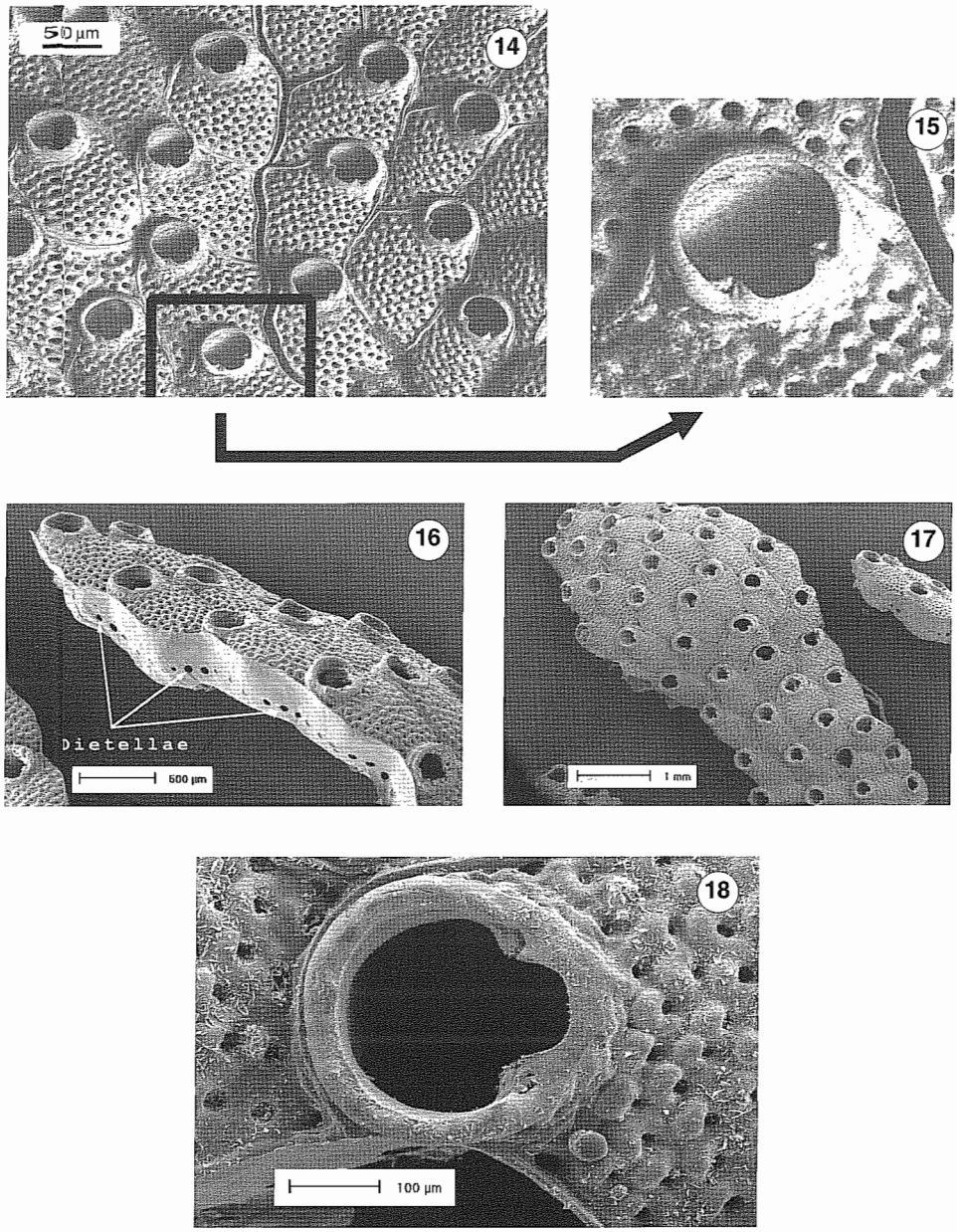


Figs. 3-8 - 3: *Arachnoidea protecta*, four zooids connected by filaments. 4: autozoid of the same species, with basal plate, filament and projections. 5: colony of *Monoporella fimbriata carinifera*. 6: same species; particular of some zooids with spines and median carina. 7: zooids of *Pherusella brevituba* with the short quadrangular peristomium (arrow). 8: *Watersipora subtorquata* (Naples, BMNH N° 1912.12.21.1019)). (Photographs 3, 4, 7, 8 under light transmission microscope)

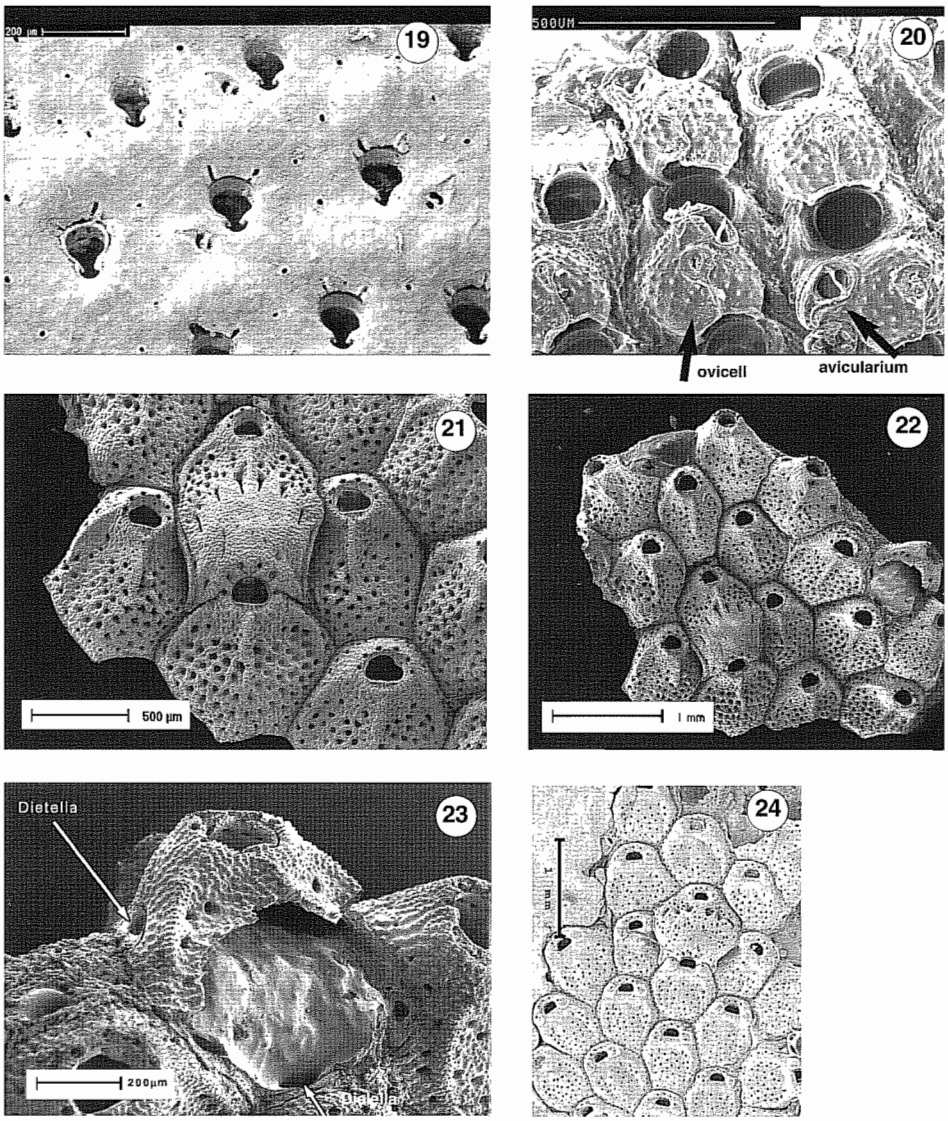
margin of the ovicell orifice; this suture resembles the junction between or the overlapping of the two flaps of a cloak. Oral adventitious avicularium proximal to the aperture, triangular, acuminate, placed either on the right or the left side of the aperture, either obliquely lateral or variously directed (arrow in Fig. 20). No spines. Measurements (after Ünsal and d'Hondt, 1979): zooid length 0.480-



Figs. 9-13 - 9-10: d'Orbigny type specimen of *Watersipora subtorquata* (9: orifice; 10: some zooids). 11-13: *Watersipora subtorquata* from Formia (11: orifice with pointed condyles; 12: some zooids; 13: zooids with "lappets"). (All SEM photographs)



Figs. 14-18: 14-15: type specimen of *Watersipora cucullata*. 16: group of zooids of *W. cucullata* from Vulcano showing dietellae. 17: whole colony of the same specimen. 18: a particular of the orifice of *W. cucullata* from Formia showing strong condyles. (All SEM photographs)



Figs. 19-24 - 19: Part of a colony of *Plesiocleidochasma mediterraneum*. 20: *Cleidochasmidra çanakkalense* with ovicells and oral adventitious avicularia (arrowed). 21: ovicell complex of *M. fimbriata carinifera*. 22: whole colony of *M. fimbriata carinifera*. 23: zooid of *M. fimbriata carinifera* perforated by dietellae. 24: group of zooids of *Monoporella nodulifera* from Australia. (All SEM Photographs)

0.520 mm, width about 0.300 mm; orifice length 0.125 mm, width 0.100 mm. Ovicell diameter 0.200 mm. Avicularium length 0.100, width 0.50 mm.

Remarks. The supposed rarity of this species could be ascribed to its ecology as it thrives on detritic bottoms, the bryozoan fauna of which is studied much less

than that on hard bottoms. The finding of *Cleidochasmidra* at Ponza (Tyrrhenian Sea) suggests a wider distribution than it was hitherto supposed (Rosso, 1996, stated that it was an endemic species of the Eastern Mediterranean).

Species complexes 1: *Watersipora "subovoidea".*

The genus *Watersipora* includes taxa with encrusting unilaminar or erect multilaminar zoaria, with autozooidal frontal shield regularly perforated, primary orifice bell shaped or sinuated with projecting cardelles. No spines, avicularia and ovicells are present.

Harmer (1957, p. 1022, pl. LXIX, figs. 11, 12, 14) renamed *Dakaria subovoidea* a highly variable taxon, with a cosmopolitan distribution (see the synonymy in Harmer, p. 1022 and the discussion in Soule and Soule, 1976). Following Harmer, this "species" was subsequently recorded worldwide by many authors. As it was firstly demostrated by Soule and Soule (1976) and lately confirmed by Gordon (1989), this taxon is actually a "complex" of several species, with different morphology, ecology and geographic distribution.

Based on the study of material both collected by us and lent by Museums, we recognized, in the Mediterranean Sea, the presence of two species, *W. cucullata* and *W. subtorquata.* The real distribution of these species should be checked out after a revision of the genus, which is beyond the scope of this article.

Watersipora subtorquata (d'Orbigny, 1852)
Cellepora subtorquata: d'Orbigny, 1852, p. 399
Watersipora subtorquata: Ryland, 1974, p. 345, fig. 3 (B)
Watersipora subtorquata: Soule and Soule, 1976, pl. 2, fig.3 ; pl. 3, fig. 3
Watersipora subtorquata: d'Hondt, 1988, p. 199, fig. 6 (1-2)
Watersipora subtorquata: Gordon, 1989, p. 40, pl. 20, fig. B-H
Watersipora subovoidea: Chimenz (1973), p. 72, pl. II, fig. 4; Chimenz et al. (1981), p. 193.
Material: Civitavecchia, harbour, st. 1, 3, 4, 5, 6, 7, 8, depth from 4 to 7.5 m (Chimenz, 1973)
Ischia, harbour, st. 2F1, 3F1 (Chimenz et al., 1981)
Formia, harbour (Chimenz Gusso, unpublished data)
BNMH:
N° 1911.10.1.1111 (Naples)
N° 1912.12.21.1019 (Naples)
N° 29.8.31.1 (Malta)
N° 1929.88.31.1 (Malta)
N° 1970.6.1.23 (Mikhmoret)
N° 1963.8.2.41 (Alexandria)
N° 99.7.1.5214 (Tangier)

Ecology. Collected at shallow depths in warm and temperate waters, on artificial substrata in harbours; also on algae and invertebrates.
Distribution. General: Atlantic Ocean (South Florida, West Indies, Brazil, Azores, Ghana, South Africa); Indo-Pacific Ocean (Japan, Australia, New Zealand, Red Sea, Arabian Sea). Mediterranean (Fig. 2): Naples, Formia, Civitavecchia, Ischia, Mikhmoret (Israel), Malta, Tangier, Alexandria .
Description (Figs. 8-13). Zoarium encrusting, unilaminar, centrally orange-brown with orange margins. Zooids elongated, rectangular, with frontal wall evenly perforated by numerous pseudopores (Figs. 10, 12). Aperture distal, wider than long, poster with a more or less shallow rounded sinus occupying less than half the width of the proximal edge (Figs. 9, 11). Orificial rim thin, often with two latero-proximal curling edges (lappets), distal margin sometimes with a narrow crest (Fig. 13). Condyles fine and pointed. Operculum has biconcave sclerite, which leaves a darker central area and two oval paler lateral areas. Dimensions: zooid length 0.900 mm (n=6), width 0.380 (n=7); orifice length 0.220 mm, width 0.250 mm (n=7); sinus length 0.04 mm, width 0.100 (n=10).

Watersipora cucullata (Busk, 1854)
Lepralia cucullata: Busk, 1854, p. 81, pl. XCVI, figs. 4-5
Schizoporella atrofusca: Hincks, 1886, pp. 269-270, pl. X, fig. 4
Watersipora subovoidea: Ryland, 1974, p. 345, fig. 3 (A)
Watersipora cucullata: Soule and Soule, 1976, pl. 2, fig. 2; pl. 3, fig. 1; pl. 4, fig. 3
Watersipora subovoidea: Nicoletti et al., 1996, p. 232
Watersipora cucullata: Chimenz et al., 1999, p. 260
Watersipora subovoidea: Hayward and McKinney, 2002, p. 63, fig. 29 (A-B)
Material: Pontine Islands, st. B85; Vulcano, st. Mastro Minico (10-21 m), st. Punte Nere (2-10 m), st. Punta Quadrara (5-15 m), st. molo Femmina (7-15 m), st. Capo Secco (10-15 m) ; Ustica, st. Punta Cavazzi, depth 10 m; South Turkey, st 92-04 (0.15 m), st. 92-02, depth 15 m.
BNMH:
N° 99.5.1.456 (Adriatic Sea)
N° 99.5.1.975 (Adriatic Sea)
N° 35.3.6.364 (Cape Verde)
N° 35.3.6.365 (Cape Verde)
N° 35.3.6.366 (Cape Verde)
N° 35.3.6.367 (Cape Verde)
N° 1973.1.10.1 (Cape Verde)
Ecology. Found in shallow clean waters on plants and invertebrates of rocky bottoms, and on detritic bottoms (Nicoletti et al., 1996; Chimenz et al., 1999; Chimenz, unpublished data)

Distribution. General: found by Ryland (1974) on the Great Barrier Reef (North Australia); Cape Verde Islands. Mediterranean (Fig. 2): Pontine Islands, Naples, Vulcano, Ustica, North and South Adriatic Sea, Aegean Sea, South Turkey.
Description. (Figs. 14-18). Zoarium encrusting, unilaminar, more strongly calcified than in *W. subtorquata*, almost black along the margins as well. Zooids less elongated than in *W. subtorquata* (Figs. 14, 17); zooid orifice either as wide as long or slightly wider than long, with thickened rims and distal rim often projecting like a hood; poster with a distinct U-shaped or squared sinus, occupying half width of proximal edge (Figs. 15, 18). Condyles strong, blunt. Operculum dark, with opercular sclerite parallel-sided, leaving two lateral paler rectangular areas. Dimensions: zooid length 0.742 mm (n=5), width 0. 475 mm (n=5); orifice length 0.240 mm, width 0.260 mm (n=7); sinus length 0.075 mm, width 0.107 mm (n=4).
Remarks. The following specimens may belong to this species, but require further study: tiny fragments, lacking opercula, from detritic bottoms off Noto (Sicily); specimens from a cave near Lecce (Apulian coast) slightly different from typical *cucullata* in the wider sinus. *W. subovoidea* from off Rovinji (Hayward and McKinney, 2002) is identical, in our opinion, to Hincks's *Schizoporella atrofusca* from the Adriatic Sea (BMNH specimens n. 99.5.1.456 and 99.5.1.975) and is actually *cucullata.* Soule and Soule (1976) published some photographs of *W. cucullata* from Naples (collected by Osburn in 1910). We studied *Watersipora* specimens BMNH n. 1912.12.21.1019 and n. 1911.10.1.1111 from Naples, which resulted to be *subtorquata.*

Species complexes 2: *"Cleidochasma porcellanum"*
Also this taxon is considered cosmopolitan, but probably comprises several entities. Chimenz Gusso and Soule (2003) described a new species, *Plesiocleidochasma mediterraneum*, which corresponds to Harmelin's (1969) *Cleidochasma* sp. and – probably – to Hayward's (1974) *Cleidochasma porcellanum*, both from the Aegean Sea.

Plesiocleidochasma mediterraneum Chimenz Gusso and Soule (2003)
Plesiocleidochasma mediterraneum n. sp.: Chimenz Gusso and Soule (2003): fig 2 (A-F)
Cleidochasma sp.: Harmelin, 1969, p. 202, fig. 3 (6-7)
? *Cleidochasma porcellanum*: Hayward, 1974, p. 379
Ecology. Found on hard and detritic bottoms (Harmelin, 1969) from 28 to about 80 m; on leaves and rhizomes of *Posidonia oceanica*, at 28 m depth, and on photophilic algae, at 16 m depth (Chimenz Gusso and Soule, 2003)
Distribution. (Fig. 1). Aegean Sea, South Turkey, Lampedusa Island (Sicily); Tunisia? Madeira?

Description. (Fig. 19). Main diagnostic characters: aperture distally rounded, deeply rimmed without beading, with 3-4 spines (visible in young zooids), strong condyles directed proximally, proximal margin below condyles with a strongly arcuate sinus; avicularium acute, beside or proximal to aperture, directed outward either distally or disto-laterally, with complete hinge bar with thick columella and relatively large acute palate; ovicell with pronounced bilateral incisions and a median notch (becoming a pore and successively closed in older ovicells).
Remarks. *Hippoporina simplex* Canu and Bassler, 1930 from Tunisia (p. 49, pl. VI, figs. 3-6) and *Lepralia porcellana* Busk from Madeira (p. 283, pl. XXXI, fig. 3) may be of this species, although the types have not been found so far.

Species complexes 3: *Monoporella "nodulifera"*
Hincks (1881, p. 135, pl. 1, fig. 4) described a species of *Monoporella* found in the Bass Straits, characterized by one nodule on each side of the aperture, 2-4 apertural spines and two lateral carinas; no figures of ovicell were included. Harmer (1926) ascribed to this taxon specimens from various Pacific localities, with a spine number from 2 to 8, with or without median carina, and ovicell either smooth or with 4 grooves (Harmer, 1926, p. 310, pl. XX, figs. 21-23). In his pl. XX, one can see one zooid (fig. 22) with two apertural nodules, and two zooids with a little marked median carina, and a smooth ovicell (fig. 21). Canu and Bassler (1929) described *Monoporella fimbriata* in two varieties, both of which with 5-8 apertural spines: *M. fimbriata carinifera* (pl. 17, fig. 11), with a constant median carina and zooids wider than in *M. fimbriata crassa*, which lacks the median carina (pl. 17, fig. 10). According to Canu and Bassler, *M. fimbriata* differs from *M. nodulifera* in the larger number of spines and in the "fringed" ovicell. Harmelin (1969) identified as *M. fimbriata carinifera* Canu and Bassler 1929 a species found in the Aegean Sea, with 6-7 apertural spines, one median and two lateral carinae, ovicell with 5-6 grooves (detailed figures are provided). Hayward (1974) considered *M. fimbriata carinifera* and *M. nodulifera* as conspecific, and ascribed the variations in the number of spines and of ovicell grooves to the age dependent degree of calcification (see discussion, pp. 375-377, Hayward, 1974). Gordon (1989) agreed with Hayward; his specimens from the Kermadec Islands bear 3-5 apertural spines, a median carina, ovicell with fine longitudinal grooves and several basal indentations distally. Our material displays the same characteristics as the Aegean specimens. Although descriptions and figures made by earlier Authors (such as Hincks, Harmer, Canu and Bassler) lack details at the comparative level, it may be claimed that *M. nodulifera* Hincks, 1881 and *M. fimbriata* Canu and Bassler, 1927 are not conspecific, as additionally confirmed also by a photograph of the specimen of *M. nodulifera* from South Australia (Fig. 24). Our specimens seem to agree closely with that described and figured by Harmelin (1969) from the Aegean Sea. Canu and

Bassler's variety named *carinifera* is probably a true species; however, we prefer to retain the name *M. fimbriata carinifera*, until more Mediterranean and extra-Mediterranean material will be studied.

Monoporella fimbriata carinifera Canu and Bassler, 1929
Monoporella fimbriata carinifera: Canu and Bassler, 1929, pp. 156-158, pl. 17, fig. 11
? *Monoporella nodulifera*: O'Donoghue and de Watteville, 1939, p. 35
Monoporella fimbriata carinifera: Harmelin, 1969, p. 1189, fig. 1, 6-8
Monoporella nodulifera: Hayward, 1974, pp. 374-377, fig. 3, a-b
Monoporella fimbriata carinifera : Chimenz Gusso and Tomassetti, 2004, p. 413
? *Monoporella nodulifera*: Bitar and Kouli-Bitar, 2001, p. 72
Material: Yenikas (South Turkey), st. AKD 92/ 19, depth 18-28 m; Lampedusa (Strait of Sicily), st. Capo Grecale, 42 m.
Ecology. Found on photophilic algae and *Posidonia oceanica* rhyzomes (Nicoletti et al., 1995; Chimenz Gusso and Tomassetti, 2004); on various substrates in detritic organogenic bottoms, between 28 and 66 m in depth (Harmelin, 1969; Hayward, 1974).
Distribution. General: Philippines. Mediterranean (Fig. 1): Aegean Sea (Scarpanto, Cerigo, Chios), South Turkey, Lampedusa (Sicily Strait).
Description. (Figs. 5, 6, 21-24). Colonies encrusting, unilaminar. Ectocyst rose coloured. Zooids approximately hexagonal (Fig. 22), separated by shallow grooves dark coloured (Fig. 5). Cryptocyst strongly calcified, finely granular, punctured by numerous pores, with three carinae (two lateral and one median frontal). Peristome more or less thickened. Aperture semicircular with 6-7 black spines (Fig. 6); operculum light brown, with a peripheric sclerite . Two opesiules either as large or little larger than the cryptocyst pores, situated in each angle and delimited by median and lateral carinae. Zooidal walls perforated by six large dietellae (one proximal, one distal and four lateral) (Fig. 23). Ovicell hyperstomial, large, buried in the distal zooid, with six distal longitudinal grooves (Fig. 21). Orifice of the maternal zooid larger than in sterile zooids.
The species differs from *M. nodulifera* Hincks, 1881 mainly for the number of spines (6-7 instead of 2-4), the constant presence of a median carina, the absence of nodules and the shape of zooids.
Remarks. Other specimens cited as *M. nodulifera* must be examined again: from Alexandria (mentioned, but not illustrated by O'Donoghue and de Watteville, 1939); from Lebanon (Bitar and Kouli-Bitar, 2001); from Capo Verde Islands (Cook, unpublished data, specimen lost). The distribution of this species in the Mediterranean Sea seems limited to the Eastern basin. Its presence at Cape Verde needs to be confirmed.

CONCLUSIONS

- Examples given suggest that more exhaustive samplings and a reliable taxonomic knowledge are needed in the study of both ecology and biogeography of Bryozoans.
- The iconography produced here indicates the importance of recent techniques of observation and documentation in the study of diagnostic characters. In particular, Scanning Electron Microscopy (SEM), at much higher magnifications, reveals details that are not visible using light microscopy. Thanks to SEM, the knowledge of Bryozoa biodiversity has been increased considerably in recent years (see for example the large number of species of *Schizoporella*, *Schizomavella* and of Cribrilinidae recently described by European authors).
- The assessment of biodiversity can be enhanced by sampling campaigns carried out in comparatively unstudied habitats or geographic areas.
- Zones which are subject to accidental introduction of alien species can also provide interesting information (see for example Chimenz Gusso and d'Hondt, in press)

ACKNOWLEDGEMENTS

Studies partially funded by M.U.R.S.T. 60%

We warmly thank Mary Spencer Jones (British Museum of Natural History, London) for sending us specimens of *Watersipora* sspp. and SEM photographs of the type specimen of *Watersipora cucullata*; and P. Taylor for the SEM photographs of the type specimen of *W. subtorquata.*

For SEM photographs we thank: Pr. M. Bologna and Dr. A. Di Giulio (University Roma 3) (*W. cucullata, W. subtorquata, Monoporella fimbriata carinifera*); Dr. N. Tagliaventi (University of Rome "La Sapienza") (*Cleidochasmidra çanakkalense);* Pr. D. Soule (Allan Hancock Foundation, University of Southern California, U.S.A.) (*Plesiocleidochasma mediterraneum).* For light transmission photographs of *Arachnoidea protecta* and *Pherusella brevituba* we thank Pr. R. Argano and Dr. A. Campanaro (University of Rome "La Sapienza").

We are grateful to Dr M. Oliverio and Dr L. Nicoletti for useful suggestions.

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