Smittinidae (Bryozoa, Cheilostomata) from coastal habitats of Lebanon (Mediterranean sea), including new and non-indigenous species

Jean-Georges HARMELIN
Université de la Méditerranée, CNRS, UMR 6540 Dimar,
Centre d'Océanologie de Marseille, Station marine d'Endoume,
rue Batterie des Lions, F-13007 Marseille (France)
jean-georges.harmelin@univmed.fr

Ghazi BITAR
Lebanese University, Faculty of Sciences, Department of Natural Sciences,
Hadath (Lebanon)
ghbitar@ul.edu.lb

Helmut ZIBROWIUS
Station marine d'Endoume,
rue Batterie des Lions, F-13007 Marseille (France)

Harmelin J.-G., Bitar G. & Zibrowius H. 2009. — Smittinidae (Bryozoa, Cheilostomata) from coastal habitats of Lebanon (Mediterranean sea), including new and non-indigenous species. *Zoosystema* 31 (1): 163-187.

ABSTRACT

The still poorly-known marine benthos of the Levant (warmest area of the Mediterranean) continuously undergoes changes due to the immigration of exotic species arriving from the Red Sea via the Suez canal, and likely from other tropical and subtropical regions via ship transport. The study of a large collection of bryozoans from the coastal zone (3-35 m) of Lebanon revealed the presence of seven species of Smittinidae belonging to two genera, *Parasmittina* Osburn, 1952 and *Smittina* Norman, 1903, whose morphological features and habitat requirements are described here in detail. Only two of these (*P. raigii* (Audouin, 1826) and *P. rouvillei* (Calvet, 1902)) were previously known from other Mediterranean areas. *Parasmittina serruloides* n. sp. and *P. spondylicola* n. sp., together with *P. egyptiaca* (Waters, 1909), are presumed to be Red Sea immigrants. The geographic distribution of *P. protecta* (Thornely, 1905) and *S. nitidissima* (Hincks, 1880), as well as their habitat in Lebanon and their capacity as fouling species strongly suggest that they are not indigenous to the Levant and that their source populations may be either in the Red Sea or in west Africa. However, alternative hypotheses are also conceivable, such as their persistence in the Levant area as relicts from former warm periods of the Mediterranean, or their existence as groups of sibling species with a more restricted geographical range.

KEY WORDS
Bryozoa,
Parasmittina,
Smittina,
biogeography,
eastern Mediterranean,
Levant coasts,
Suez canal,
introduced species,
new species.

RÉSUMÉ

Smittinidae (Bryozoa, Cheilostomata) d'habitats côtiers au Liban (mer Méditerranée), dont des espèces nouvelles et des espèces exotiques.

Le benthos marin du Levant, la région la plus chaude de Méditerranée, est encore mal connu ; il est soumis à des changements constants dûs à l'immigration d'espèces exotiques venant de mer Rouge par le canal de Suez et probablement d'autres régions tropicales ou sub-tropicales, acheminées par la navigation. L'étude d'une vaste collection de bryozoaires de la zone côtière du Liban (3-35 m) a permis de distinguer sept espèces de Smittinidae appartenant à deux genres, *Parasmittina* Osburn, 1952 et *Smittina* Norman, 1903. Les caractéristiques morphologiques et l'habitat de ces espèces sont détaillés ici. Parmi celles-ci, seulement deux (*P. raigii* (Audouin, 1826) et *P. rouvillei* (Calvet, 1902)) sont aussi présentes dans d'autres zones de la Méditerranée. Deux nouvelles espèces, *Parasmittina serruloides* n. sp. et *P. spondylicola* n. sp., sont supposées être des immigrants de mer Rouge, comme *P. egyptiaca* (Waters, 1909). La distribution géographique des deux autres espèces, *P. protecta* (Thornely, 1905) et *S. nitidissima* (Hincks, 1880), ainsi que leur habitat au Liban et leur aptitude à être des espèces de fouling suggèrent fortement qu'elles ne sont pas indigènes au Levant et que leurs populations d'origine peuvent être soit en mer Rouge soit en Afrique de l'ouest. Toutefois, d'autres hypothèses sont envisageables, comme le maintien dans les eaux du Levant de relictes d'anciennes périodes chaudes de la Méditerranée, ou bien l'existence de groupes d'espèces jumelles avec des distributions géographiques plus restreintes.

MOTS CLÉS
Bryozoa,
Parasmittina,
Smittina,
biogéographie,
Méditerranée orientale,
côtes du Levant,
canal de Suez,
espèces introduites,
espèces nouvelles.

INTRODUCTION

The benthic fauna of the eastern Mediterranean has been for long less investigated than that of the western Mediterranean (Morri *et al.* 1999 and references herein) and the gap is still evident with respect to certain groups, including Bryozoa. However, some reliable assessments indicate that marine biodiversity is particularly reduced in the Levant area, by up to 30% according to Por (1989). Several major engineer species are obviously lacking in coastal communities, such as the sea-grass *Posidonia oceanica* Delile and the sea-fans *Paramuricea clavata* (Risso, 1826) and *Eunicella* spp., with probable consequences regarding their commonly associated fauna and flora. On the other hand, since the opening of the Suez canal in 1869 and subsequent to changes in the hydrographic conditions within the canal that have bettered the environment for marine biota (Pérès 1967), hundreds of species belonging to a large array of groups have immigrated from the Red Sea to the Mediterranean (e.g., Por 1990; Boudouresque 1999; Galil 2000; Zenetos *et al.* 2006). The distribution of these "Erythrean" or "Lessepsian" species in the Mediterranean is still restricted to the eastern and central Mediterranean, while reverse immigration from the Mediterranean to the Red Sea is limited to few taxa (Por 1978; Boudouresque 1999).

The Levant part of the eastern Mediterranean is particularly prone to colonisation by subtropical species because of its climate (Abboud-Abi Saad *et al.* 2004), being the "warmwater corner of the Mediterranean" according to Por (1989). The Red Sea is an obvious source of propagules, which can migrate stepwise through the canal to the Mediterranean, although ship transport by hull fouling and ballast waters may import species from any other tropical or subtropical region via the Suez canal or the Gibraltar strait. These alien species will settle first in places receiving a large shipping traffic, such as Cyprus, Iskenderun, Beirut, or Haifa. A significant example (but in the Aegean Sea, Turkey) is the recent record in Izmir Bay of an exotic bryozoan, *Celleporaria brunnea* (Hincks, 1884), which was known from California and other E Pacific localities (Koçak 2007), and has also been recorded in Lebanon (JGH unpubl. data).

Knowledge of the bryozoans of the Levant area is fragmentary. Available papers generally deal with small collections or provide species lists with few or no comment (Audouin 1826; Hastings 1927; O'Donoghue & de Watteville 1939; Gautier 1956; Powell 1969a; Ünsal 1975; Ünsal & d'Hondt 1978; d'Hondt 1988; Nicoletti *et al.* 1995; Chimenz *et al.* 1997; Bitar & Kouli-Bitar 2001; Koçak *et al.* 2002; Harmelin *et al.* 2007; Koçak 2007). Considering the taxonomic ambiguity that generally prevails among members of the biotic assemblages of this region, detailed revisions of taxa are recommended (Chimenz Gusso *et al.* 2004). The French-Lebanese programme of scientific cooperation, CEDRE, provided the opportunity to assemble a large collection of bryozoans from the coast of Lebanon (about 95 species). Characteristics of seven species of Smittinidae Levinsen, 1909 (Cheilostomata), including two new species of *Parasmittina* and putative exotic species, are presented here.

MATERIAL AND METHODS

The smittinid bryozoans described below were sorted from a large collection of benthos samples collected in the coastal waters of Lebanon, from Tripoli in the north to Sour (Tyre) in the south (Fig. 1). Samples were collected by SCUBA diving from 3 to 35 m depth mainly during several special field trips between 1999 and 2003, and also occasionally at an earlier date (GB).

The 31 sampling stations at 13 Lebanese localities (Fig. 1) where Smittinidae species were recorded are listed below (abbreviations: *Peg*, *Parasmittina egyptiaca*; *Ppr*, *P. protecta*; *Pra*, *P. raigii*; *Pro*, *P. rouvillei*; *Pse*, *P. serruloides* n. sp.; *Psp*, *P. spondylicola* n. sp.; *Sni*, *Smittina nitidissima*).

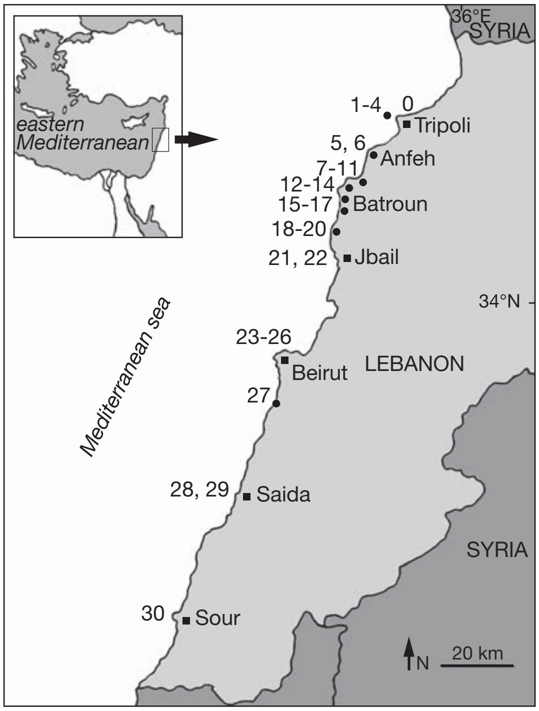

FIG. 1. — Location along the coast of Lebanon of the sampling stations (numbers 0 to 30) where Smittinidae were recorded.

0 Tripoli, harbour quay, 3 m, 19.IX.2002: *Peg*.
1 Tripoli, Ramkine Island, 13 m, on *Phyllangia mouchezii*, overhang formed by large boulder, 22.X.1999: *Peg*, *Sni*.
2 Tripoli, Ramkine Island, 14 m, overhang, 22.X.1999: *Peg*, *Pro*, *Pse*, *Sni*.
3 Tripoli, Ramkine Island, 5-7 m, cave porch, 14.VII.2003: *Peg*, *Sni*.
4 Tripoli, Ramkine Island, 12 m, on pottery debris and shells, 22.X.1999: *Pse*, *Sni*.
5 Anfeh, 20-22 m, on biogenic concretions, 26.X.1999: *Peg*, *Psp*, *Sni*.
6 Anfeh, 14 m, on biogenic concretions, 26.X.1999: *Sni*.
7 Ras El Chakaa, 5-6 m, cave, 4.VI.2000: *Sni*.
8 Ras El Chakaa, 13 m, 19.X.1999: *Sni*.
9 Chak El Hatab, 7 m, overhang, 4.VI.2000: *Pra*.
10 Chak El Hatab, 12 m, cave, 21.IX.2002: *Pse*.
11 Chak El Hatab, 14 m, cave, 5.VII.2003: *Peg*.
12 Selaata, 3-7 m, cave, 18.X.1999; *idem*, 22.X.1999: *Peg*, *Pse*, *Sni*.
13 Selaata, 6-7 m, overhangs, 6.VII.2003: *Peg*, *Sni*.
14 Selaata, 10 m, on *Spondylus* shell, V.2001: *Sni*.
15 Batroun, "Phenician wall", 9 m, 16.X.1999: *Pro*,

Pse, *Sni*.
16 Batroun, on shell, X.1999: *Pse*.
17 Batroun, *c.* 30 m, on biogenic concretion, X.1999: *Sni*.
18 Kafar Abida, 9 m, overhang, on *Phyllangia mouchezii*, 6.VIII.1995: *Peg*, *Pro*, *Pse*.
19 Kafar Abida, 7-8 m, tunnel, 30.V.2000: *Peg*, *Pra*.
20 Barbara, 28 m, on biogenic concretion, 8.VI.2000: *Sni*.
21 Jbail (Byblos), Tablieh shoal, on shell, 17 m, 17.X.1999: *Peg*, *Pse*, *Psp*, *Sni*.
22 Jbail (Byblos), Tablieh shoal, small cave, 16 m, 17.X.1999: *Peg*.
23 Beirut, harbour pier, outside, block overhang, 15 m, 9.VII.2003: *Peg*.
24 Beirut, airport pier, 3-11 m, 16.VII.2003: *Peg*, *Ppr*.
25 Beirut, harbour, wharf no. 60, 5-7 m, 16.IX.2002: *Ppr*.
26 Beirut, Harf El Kelb, 34 m, on rocks and shells, 21.X.1999: *Peg*, *Pro*, *Psp*, *Sni*.
27 Khalde, Marina Villamar pier, 3 m, 7.VI.2000: *Ppr*.
28 Saida (Sidon), Harf El Rijmeh, 11 m, on *Spondylus spinosus*, 5.VI.2000: *Peg*, *Sni*.
29 Saida (Sidon), island, 9 m, 27.VIII.1993: *Peg*.
30 Sour (Tyre), El Kasmieh, 36-42 m, on rock and *Phyllangia mouchezii*, 25.X.1999: *Sni*.

The specimens were examined and measured with a Wild stereomicroscope. SEM observations and photos were made with a Hitachi S-570 on specimens cleaned with sodium hypochlorite and gold-palladium coated.

Abbreviations

Measurements (abbreviations used in tables)

Av	avicularium;
AZ	autozooid;
L	length;
Ly	lyrula;
N	number of measurements;
Or	orifice;
Ov	ovicell;
sd	standard deviation;
W	width.

The type material and other specimens have been deposited in the following institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
BMNH	the Natural History Museum, London;
SMF	Senckenberg Museum, Frankfurt.

The remaining material is provisionally kept at the Centre d'Océanologie de Marseille (COM).

SYSTEMATICS

Genus *Parasmittina* Osburn, 1952

Parasmittina egyptiaca (Waters, 1909)
(Fig. 2; Tables 1; 2)

Smittia egyptiaca Waters, 1909: 157, pl. 15, figs 6, 9 (S Red Sea). — Hastings 1927: 342-345, figs 85-87.

?*Smittina egyptiaca* – Harmer 1957: 937, 938, pl. 64, figs 21, 22, 29-31.

Parasmittina egyptiaca – Powell 1967: 171, pls 3, 13. — Powell 1969b: 361, fig. 4.

Not *Smittina egyptiaca* – Balavoine 1959: 275, pl. 4, fig. 7.

Distribution. — *Parasmittina egyptiaca* was common at 17 stations (0-3, 5, 11-13, 18, 19, 21-24, 26, 28, 29) from nine Lebanese localities, distributed from Tripoli in the north to Saida in the south. The habitat types included caves and small cavities, overhangs, bioconcretions (bioherms) and shells, and ranged from 3 to 34 m depth.

Material examined. — **Lebanon.** Stn 0, 1 colony (BMNH 2008.4.21.1). — Stn 1, 1 colony (SMF). — Stn 2, several colonies on barnacles (MNHN). — Stn 5, 22 m, 1 large colony. — Stn 11, 1 large colony. — Stn 12, small colonies (MNHN). — Stn 13, several colonies on gastropod shell and *Cellepora* colony. — Stn 18, 1 small colony. — Stn 19, 1 colony (BMNH 2008.4.21.2). — Stn 21, 1 colony on shell. — Stn 22, several colonies (MNHN). — Stn 23, 1 colony (SMF). — Stn 24, several small colonies (MNHN). — Stn 26, several colonies on *Spondylus* shell. — Stn 28, 1 colony. — Stn 29, 1 colony (MNHN).

Description

Colony encrusting, generally small (< 1 cm²), unilaminar in most cases, occasionally multilaminar in small colony portions. Autozooids quadrangular to hexagonal, regularly arranged in files or in quincunx. Primary orifice square to rounded, slightly broader than long; distal rim of anter smooth; lyrula relatively broad, non alate, with distal edge straight and sides sloping at 45°; two condyles digitate or a little broader, slightly downcurved, with denticulate tip (4-6 teeth). Peristome interrupted distally, with two lateral, triangular lappets joined together by a low, proximal collar. Two orificial spines with

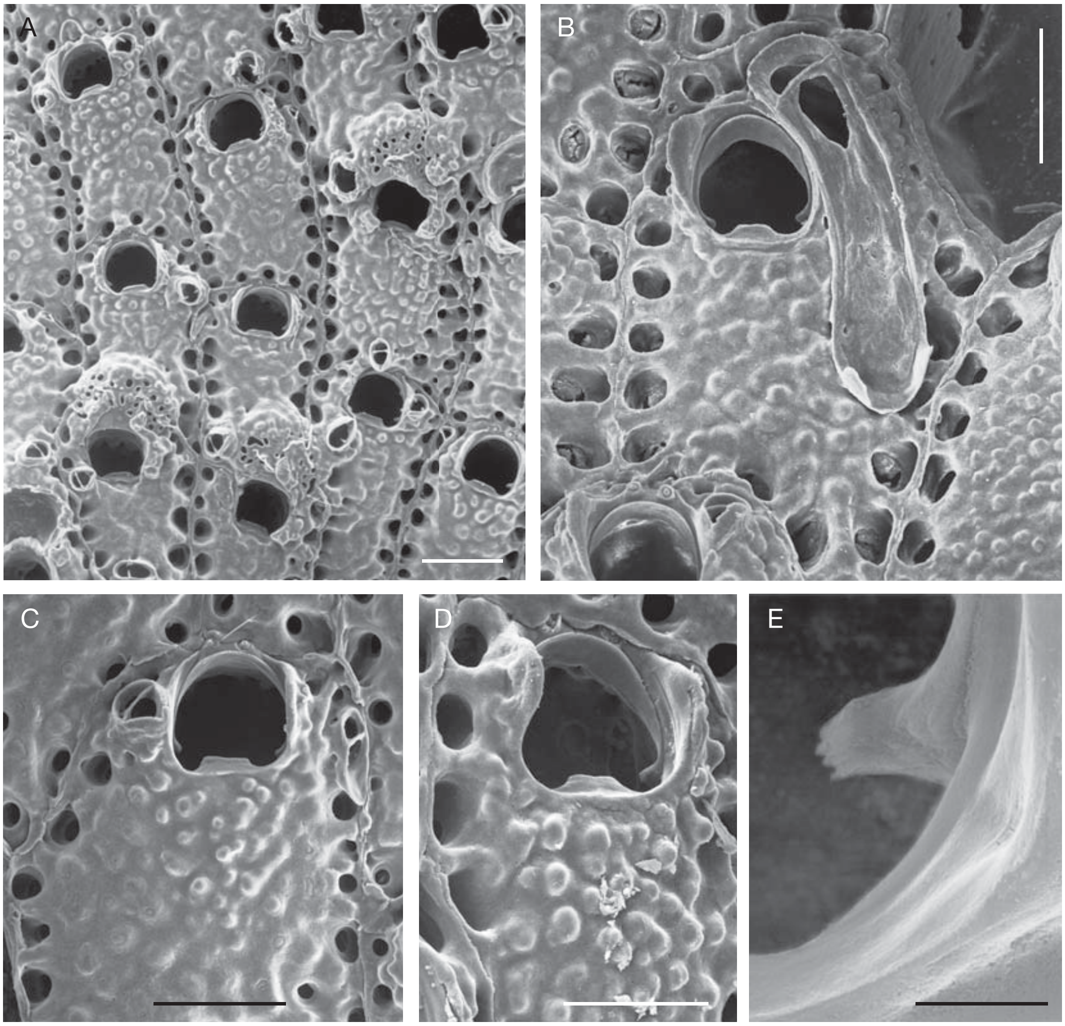

FIG. 2. — *Parasmittina egyptiaca* (Waters, 1909): **A**, part of colony with 3 ovicellate and 8 non-ovicellate autozooids; **B**, autozooid with a gigantic spatulate avicularium with distal lappets (morph 2); **C**, **D**, distal part of autozooids showing the lyrula and 2 types of small avicularia (morphs 1 and 3) (**C**) and the peristome (**D**); **E**, condyle; **A**, **C**-**E**, station 13; **B**, station 29 (see Fig. 1 and text for stations list). Scale bars: A, 200 µm; B, C, 150 µm; D, 100 µm; E, 15 µm.

small basal part, often indistinctly visible. Frontal shield moderately convex, markedly nodular, with a single series of 12-16 large marginal pores. Ovicell hyperstomial, broader than long, slightly convex, with 6-15 irregularly shaped and sized pores, often partially covered with a distal, nodular layer of secondary calcification. Avicularia adventitious, polymorphic, variously constant on autozooids according to colonies and localities (Table 1), of three main morphs with contrasting frequency: 1) most frequently, 1 or 2 small avicularia with triangular, pointed rostrum, extensive foramen, complete cross bar, leaning on peristomial lappets and generally directed towards aperture, or more rarely proximally, sometimes resting on the side of an ovicell; 2) less frequently, a single giant avicularium, budded from a disto-lateral areolar pore and directed proximally, resting against the peristome and along the lateral

Table 1. — Frequency (%) of different avicularia types in Lebanese specimens of *Parasmittina egyptiaca* (Waters, 1909). Localities: **1**, Tripoli, Ramkine, 14 m; **2**, Anfeh, 22 m; **3**, Chak El Hatab, 14 m; **4**, Selaata, 3-8 m, small caves; **5**, Beirut, airport pier, 3-11 m; **6**, Saida, Harf El Rijmeh, 11 m.

Localities	1	2	3	4	5	6
No avicularium	33.8	3.4	71.4	52.6	25.4	23.1
1 or 2 acute peristomial avicularia	58.5	96.6	19.6	40.4	73.3	73.1
1 giant avicularium	6.5	6.9	7.1	5.3	1.7	3.8
1 oval-tiped avicularium	1.3	0	1.8	1.8	0	0

Table 2. — Zooidal measurements of *Parasmittina egyptiaca* (Waters, 1909) (in µm), stations 1, 5, 11, 12, 28 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	492.4 ± 83.9	365-730	33
AZ W	338.1 ± 63.9	265-605	33
Or L	107.6 ± 12.4	85-130	28
Or W	113.8 ± 21.6	105-135	28
Ov L	205.2 ± 9.9	195-230	16
Ov W	236.3 ± 18.2	205-265	16
Giant Av L	371.5 ± 40.4	315-435	10
Giant Av W	108.3 ± 14.8	85-120	10

side of autozooids, sometimes slightly curved according to autozooid shape, rostrum moderately spatulate, with tip rounded and spoon-shaped, often bearing two lateral, triangular flaps, foramen occupying less than a third of the rostrum length, cross bar generally complete; and 3) very rarely, small to medium-sized avicularia, with parallel-sided, distally rounded mandible, located latero-distally and directed proximally or transversally near the proximal side of an autozooid.

Remarks

This species is characterised first by constant features of the orifice. The low, lateral flaps of the peristome which flank the two distal spines are typical, as is the primary orifice, which is entirely visible frontally, invariably with a square-rounded outline and a low, broad lyrula with straight distal edge and concave lateral sides. The shape of the condyles is also highly diagnostic. The frequency of autozooids without avicularia is very variable between colonies (3-71%, Table 1), but the present material does not allow determination of whether this variability is linked to individual traits, or depends upon local environmental factors. The giant avicularium displays diagnostic features, particularly the distal rim of the rostrum with paired, pointed blades. These flaps are sometimes lower, less pointed or even absent and, in the latter case, the distal end of the rostrum is spoon-shaped. The position of the giant avicularium, against the orifice and sometimes very distal, and the small size of its foramen are also characteristic. The conspicuous marginal pores and the nodular surface of the frontal shield are other traits typical of this species. The ovicells tend to be concentrated in certain parts of the colonies and their frequency also varies markedly between colonies. They further change in aspect with increasing secondary calcification, the variously-sized pores becoming hidden under a nodular layer.

The illustrations of *Smittia egyptiaca* given by Waters (1909) show regularly arranged autozooids, with a nodular frontal shield and clearly delimited marginal pores, sub-quadrate primary orifices are clearly visible in frontal view, with a wide, quadrate lyrula, and small, pointed avicularia lateral to the orifice. These characters are typical of the Lebanese specimens, and the main difference would be the lack of large spatulate avicularia in the material examined by Waters. However, giant avicularia are rare in the Lebanese material and may be entirely absent in some colonies (Table 1). A specimen from Port-Said (Egypt) illustrated by Hastings (1927) shows the same type of orifice, numerous small avicularia with pointed rostrum and a giant spatulate avicularium with the same lateral position as in the Lebanese specimens. Although of poor quality, the photograph of a specimen from Massawa, S Red Sea, ascribed to *P. egyptiaca* by Powell (1967: pl. 3, fig. 13) shows giant avicularia with a distal rim bearing paired triangular blades and autozooids with nodular frontal shield and large marginal pores. Another photograph of *P. egyptiaca* from Elat, Red Sea (Powell 1969b) shows autozooids very similar to the Lebanese ones. Conversely, examination of specimens from the Gulf of Suez (MNHN) attributed to *Smittina egyptiaca* by Balavoine (1959) proved that they belong to *Smittina nitidissima* (see below).

Parasmittina egyptiaca seems to be closely allied to a species from Mauritius attributed by Hayward (1988) to *P. ornata* (Thornely, 1912). That Mauritian form has similarly shaped secondary and primary orifices, and avicularia of same general types and position. However, the number of spines is different (1-3), the marginal pores are smaller, and the giant avicularia have a broader rostrum, without an alate tip. *Parasmittina betamorphaea* Winston, 2005, known for years as *P. nitida* morphotype B, also appears to be close to *P. egyptiaca*. This Caribbean-W Atlantic species has orifices of rounded outline, lyrula of similar shape and two orificial spines (e.g., Winston 1982: fig. 71). Giant avicularia with hooked tips occur in *P. uncinata* Soule & Soule, 1973 but the proximal part of these avicularia is triangular.

Parasmittina egyptiaca was recorded early in the Suez Canal by Hastings (1927), from Port Taufiq (Suez side entrance) to the Great Bitter Lake (Munro Fox 1927) but had not yet been recorded in the Mediterranean. Being common along the coast of Lebanon attests that it is now well established in the Levant.

Parasmittina protecta (Thornely, 1905)
(Fig. 3; Table 3)

Smittia trispinosa var. *protecta* Thornely, 1905: 123. — Waters 1909: 173, pl. 17, figs 5, 6. — Hastings 1927: 345.

Smittina protecta – Harmer 1957: 931, pl. 64, figs 12-17.

Parasmittina protecta – Cook 1968: 215. — Arístegui Ruiz 1984: 262-265, fig. 55a-d, pl. 15, figs 6-8. — Cook 1985: 188, pl. 23D. — d'Hondt 1988: 202, figs 5.4, 5.5.

Distribution. — *Parasmittina protecta* was collected at three stations (24, 25, 27), only on piers, in a small marina (Khaldé Villamar) and in a large harbour (Beirut).

Table 3. — Zooidal measurements of *Parasmittina protecta* (Thornely, 1905) (in µm), stations 24, 25, 27 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	402.6 ± 41.4	340-485	30
AZ W	302.5 ± 58.4	220-465	30
Or W	121.7 ± 5.2	115-130	6
Ov L	235.0 ± 10.6	220-250	9
Ov W	263.9 ± 24.8	220-295	9
Av L	120.7 ± 14.8	95-145	15
Ly W	61.4 ± 5.0	55-70	20

Material examined. — **Lebanon.** Stn 24, 1 small colony (MNHN). — Stn 25, 1 large colony (MNHN). — Stn 27, 1 fragmented colony (MNHN).

Description
Colony small, unilaminar or occasionally plurilaminar. Autozooids generally quadrangular and distributed in lines, sometimes more irregularly arranged on thicker colony parts, separated by salient borders; frontal wall granular, with 16-20 large, irregularly shaped, lateral pores. Orifice with 2, rarely 3, distal orificial spines; peristome interrupted distally, typically raised proximally with a mid-proximal notch, forming a thick collar sometimes considerably developed into a pointed, distally concave umbo or an oversize gutter-shaped umbo with thick lateral ribs. Primary orifice broader than high, often partially hidden by the proximal collar; lyrula broad, with a distinctly convex distal edge and concave sides; condyles narrow, pointed and downcurved. Avicularia infrequent (autozooids without avicularium: 93%, from 3 colonies and 3 sites), single or occasionally paired, with two differently shaped rostrum types: 1) short or medium-sized, spatulate with rounded termination, cross-bar generally interrupted, relatively small oval foramen leaving a broad calcified distal palate, proximo-lateral to the peristome and directed proximally or proximo-laterally; and 2) short, pointed, triangular, with slightly serrated edges, complete cross-bar, relatively large foramen leaving a small distal palate, disto-lateral, proximo-lateral or proximal to the orifice, directed laterally to proximally. Ovicell globular; frontal area (entooecium) perforated by 8-12 large, elongate, irregularly shaped pores; distal ectooecium occupying half or a third of the

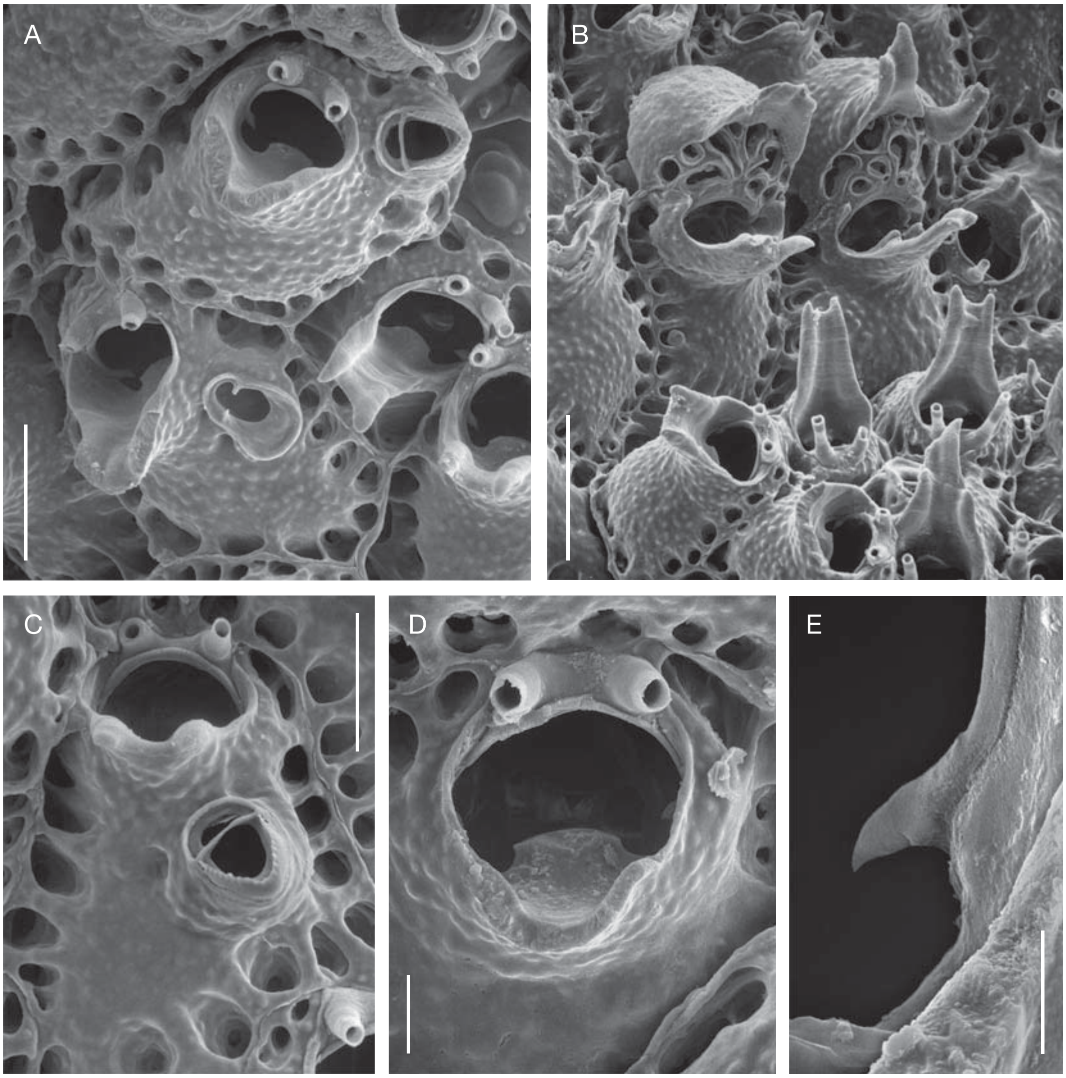

FIG. 3. — *Parasmittina protecta* (Thornely, 1905), station 25 (see Fig. 1 and text for stations list): **A**, non-ovicellate autozooids with 2 types of avicularia; **B**, ovicellate autozooids; **C**, non-ovicellate autozooid with pointed avicularium; **D**, orifice with bases of distal spines and lyrula; **E**, condyle. Scale bars: A, 150 µm; B, 250 µm; C, 100 µm; D, 50 µm; E, 15 µm.

surface of the ovicell, granular, with a proximal thickening which forms a vertically raised visor or a more prominent projection, sometimes with one or two pointed processes or concave blades.

REMARKS

Parasmittina protecta was first described and recorded from the Indian Ocean (Thornely 1905; Harmer 1957) and the Red Sea (Waters 1909; Hastings 1927; d'Hondt 1988) before being reported from the Atlantic Ocean (Guinea, Ghana, St Helena: Cook 1968, 1985; Canary Islands: Arístegui Ruiz 1984). According to the descriptions and illustrations, the specimens from these different regions share the following morphological traits, i.e. autozooids of simple geometric shape, regularly arranged in lines, frontal area nodular with large marginal pores, orifice with two spines in most cases, peristome raised proximally with a mid-proximal notch, ovicell globose, with a frontal area pierced by large, irregular pores and a well-developed ectooecium forming a more or less raised proximal ridge, avicularia oval or pointed, sometimes giant and spatulate. These features are also typical of the Lebanese specimens, except that the giant avicularia are missing. Absence of such avicularia, also noticed by d'Hondt (1988) in a specimen from the Gulf of Suez, may be a sampling bias due to insufficient material. The colonies from Lebanon and Grand Canary Island (Arístegui Ruiz 1984) conform very closely, particularly in the frontal shield with large peripheral areolae, the ovicell with a very peculiar, perforated frontal area and prominent visor, the raised peristome, and the position and shape of the non-giant avicularia. Arístegui Ruiz reported that some of these smaller avicularia are triangular, i.e. as now observed in the Lebanese colonies. SEM examination of the specimens from Levant showed that the primary orifice displays highly diagnostic characters with thin, sharply pointed and downcurved condyles and a low, broad lyrula, whose distal edge is always convex. These characters were previously not described nor figured, although Arístegui Ruiz (1984) simply mentioned a low and broad lyrula. Savigny (1816) figured an encrusting bryozoan, probably from the Red Sea (incrusting a "madrépore"), which was named *cellepora Jacotini* (*sic*) by Audouin (1826) and identified as *Parasmittina* sp. by d'Hondt (2006). Savigny's specimen comprises 19 autozooids and four ovicells, but no avicularia. The zooids are quadrangular and arranged in lines, their frontal shield is distinctly nodular and margined by large areolae, the orifices have a salient peristome, and the ovicells are globose. These features are shared with *P. protecta*. The lack of avicularia on Savigny's specimen can also support its identification with *P. protecta* as they are uncommon in the Lebanese specimens and also reported to be sometimes absent in Canarian colonies by Arístegui Ruiz (1984). The only apparent discrepancy with the Lebanese colonies is the ovicell, which lacks the coarsely porous area bordered by a prominent ridge typical of *P. protecta*. Considering that it is impossible to know if this difference is actual or is due to a misinterpretation by the illustrator, the name *Parasmittina jacotini* (Audouin & Savigny, 1826) is not adopted here.

The discovery of some colonies of *P. protecta* in two harbours of Lebanon may suggest that its presence could be due to an introduction via hull fouling or ballast waters. In this case, the founder event may have occurred in the largest harbour (Beirut), which has a great merchant shipping activity, while the second, a small marina, may have been seeded afterwards by small boats. The report of this species from the entrance of the Suez canal by Hastings (1927) and from the Gulf of Suez by d'Hondt (1988) may point to a Red Sea origin of the Lebanese population. However, an import from the Atlantic via ships is also conceivable. Alternatively, these colonies from Lebanon could belong to an indigenous population that would be relictual from a larger one established during ancient warmer climate periods of the Mediterranean (Pérès 1985).

Parasmittina raigii (Audouin, 1826)
(Fig. 4; Table 4)

Unnamed drawings – Savigny 1816: pl. 7, figs 10.1, 10.2.

Cellepora raigii Audouin, 1826: 238.

Smittina raigii – Harmer 1957: 938-940 (in part).

Parasmittina raigii – Gautier 1962: 198, 199. — Arístegui Ruiz 1984: 265-267, fig. 55e-g, pl. 16, figs 1-5. — Zabala & Maluquer 1988: 119, fig. 252. — Hayward & Parker 1994: 71-73, figs 6F, 7A, B. — Koçak *et al.* 2002: 236 (list). — d'Hondt 2006: 27.

Smittina trispinosa – Gautier 1956: 556, figs 1, 2.

Distribution. — Few colonies collected at two stations (9, 19) in shallow water, shaded habitats (overhangs, small caves, 7-8 m).

Material examined. — **Lebanon.** Stn 9, 1 colony. — Stn 19, 3 colonies (MNHN).
France. Port-Cros, on *Posidonia*, 10 m, 17.VI.1969.

Description

Colony unilaminar with autozooids regularly arranged in files, or multilaminar. Autozooids

TABLE 4. — Zooidal measurements of *Parasmittina raigii* (Audouin, 1826) (in μm), stations 9, 19 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	479.0 ± 77.0	385-655	20
AZ W	316.0 ± 58.5	245-435	20
Or L	93.1 ± 5.3	85-100	10
Or W	112.2 ± 5.7	100-125	15
Ov L	213.8 ± 18.5	195-240	13
Ov W	251.9 ± 16.7	220-270	13
Av morph 1 L	113.6 ± 16.7	85-135	14
Av morph 2 L	295.5 ± 48.8	205-365	10
Av morph 3 L	233.3 ± 26.6	205-275	6
Ly W	43.7 ± 5.0	35-50	12

variable in size. Frontal shield glistening, nodular; marginal pores medium-sized. Orificial spines two in most cases (75%) or three (25%), with thick, prominent bases, present in almost all non-ovicellate zooids. Peristome raised with two lateral, triangular lappets and a mid-proximal notch, interrupted distally on non-ovicellate zooids, raised distally on ovicellate zooids, forming a prominent visor on the proximal part of the ovicell. Primary orifice broader than long; anter serrated with 5 or 6 small, low denticles; lyrula medium-sized (W orifice/W lyrula = 2.5 in average), with distal edge slightly convex and distinct pointed corners; condyles narrow, downcurved. Ovicell globular, broader than long, with 20-25 rounded pores evenly distributed on the whole surface except on a narrow, nodulous, distal rim formed by the calcified frontal wall of the distally adjacent zooid. Adventitious avicularia sporadic (20-50% of the autozooids), single or paired, polymorphic with three morphs: 1) small, oval-shaped avicularium, with complete cross-bar, rounded opesia and foramen, proximo-lateral to orifice and directed latero-proximally, or inserted proximally and directed distally; 2) large avicularium with broad opesial part, complete cross-bar, long rostrum with triangular foramen, tapered distally with tip narrow, rounded, sometimes denticulated, borne by swollen cystid proximo-lateral to orifice and directed latero-proximally; and 3) on some autozooids longer than average, large avicularium with very broad opesial part, relatively short, triangular, pointed rostrum (mandible shorter than opesia width), directed distally, inserted mid-proximally on large, swollen cystid.

REMARKS

In most features the specimens found in Lebanon closely resemble the neotype of *P. raigii* selected by Hayward & Parker (1994) among specimens of Harmer's collection from Hurghada (Red Sea, Egypt). In particular, the primary orifice also has a denticulate distal rim and lyrula and condyles of similar shape. The choice of this neotype appears judicious considering Savigny's illustration of *Cellepora raigii*. As pointed out by d'Hondt (2006), the original drawing is precise and illustrates well the shape of the secondary orifice, the 2 or 3 spines and the third type of avicularium, clearly characterised by its distal direction, its position on a proximal, swollen cystid, and its shape, with a broad opesial part and a large, pointed rostrum. These avicularia are numerous on the specimen illustrated by Savigny and apparently the only morph he observed. However, the small oval avicularia are often difficult to see, even with a modern microscope. Similar frequency of large distally-directed avicularia was observed on a limited part of a colony from Lebanon and also on a specimen from NW Mediterranean (Port-Cros Island, France, 10 m, on *Posidonia* rhizome, 17.VI.1969, JGH collection). This feature may thus vary within and between colonies. No indication is found in Audouin (1826) of the Mediterranean or Red Sea origin of the material examined by Savigny. Specimens from Syria first assigned to *Smittina trispinosa* by Gautier (1956) were afterwards placed in synonymy with *Parasmittina raigii* by Gautier (1962), who also recorded this species from Algeria, Corsica and the French Riviera. His descriptions and figures of the Syrian specimens (Gautier 1956) confirm the relevance of this attribution. Specimens from the Canary Islands well described and illustrated by Arístegui Ruiz (1984) are similar in every feature to the Lebanese colonies, including the primary orifice with 5 or 6 low, tiny denticles. The close resemblance of specimens from the Canary Islands, Port-Cros, Lebanon, and the Red Sea attests that *P. raigii* is not a recent intruder in the Mediterranean and that it is wide-spread in warm-temperate and tropical regions.

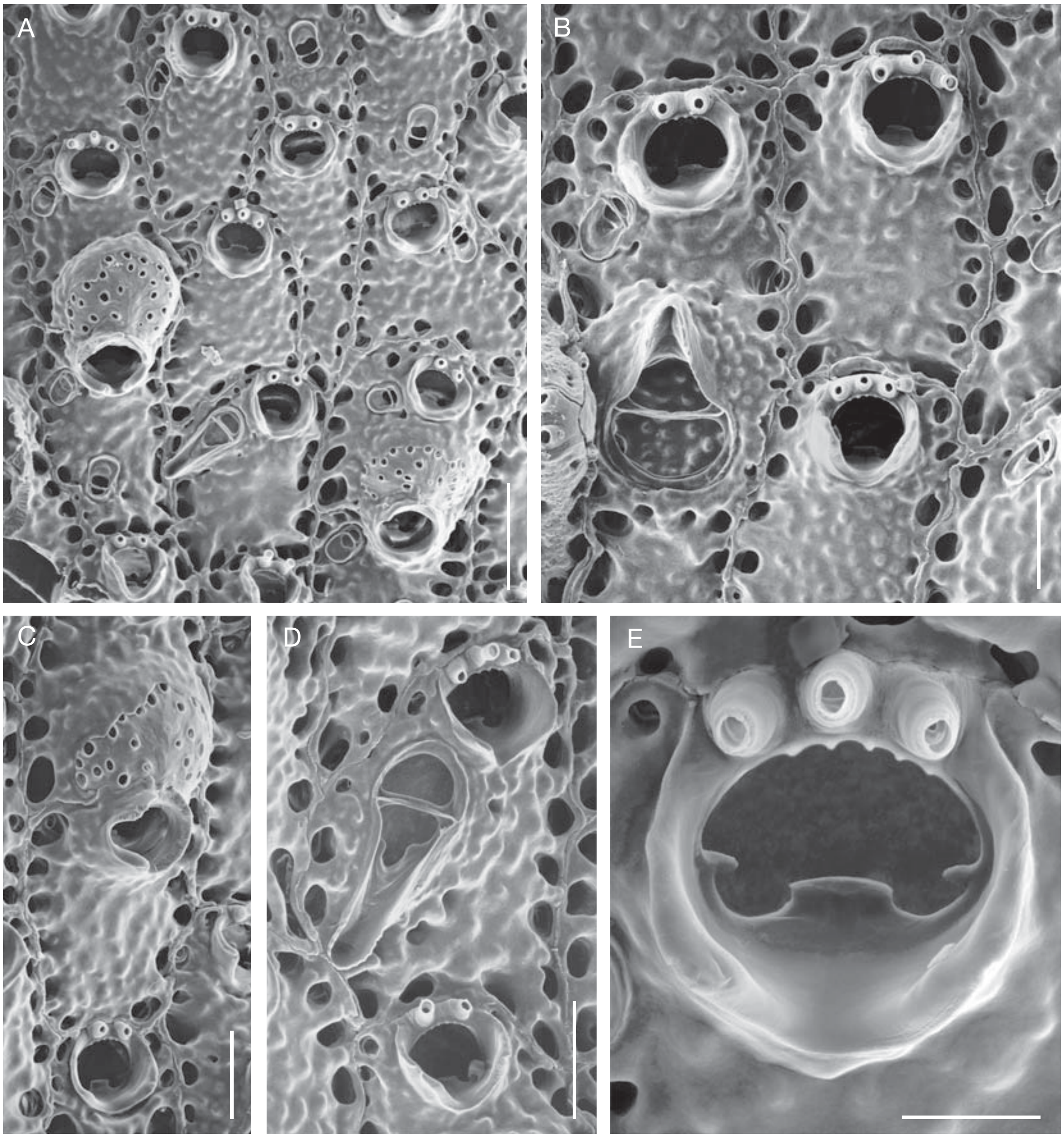

FIG. 4. — *Parasmittina raigii* (Audouin, 1826), station 9 (see Fig. 1 and text for stations list): **A**, part of colony with 2 ovicellate and 6 non-ovicellate autozooids; **B**, 3 autozooids, one bearing a typical proximal gigantic avicularium with triangular rostrum and a smaller avicularium with rounded rostrum; **C**, side view of an ovicellate autozooid; **D**, large avicularium with narrow rostrum directed proximally; **E**, orifice showing the denticulate distal edge, the lyrula and the condyles. Scale bars: A, 250 µm; B-D, 150 µm; E, 50 µm.

Parasmittina rouvillei (Calvet, 1902)
(Fig. 5; Table 5)

Smittia rouvillei Calvet, 1902: 57, 58, pl. 2, fig. 5; 1927: 26, 27, fig. 5.

Smittina rouvillei – Canu & Bassler 1930: 53, 54, pl. 6, figs 13-15.

Parasmittina rouvillei – Gautier 1962: 199, 200. — Ünsal & d'Hondt 1979: 623. — Hayward & McKinney 2002: 48, fig. 21D-G.

TABLE 5. — Zooidal measurements of *Parasmittina rouvillei* (Calvet, 1902) (in µm), station 2 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	617.0 ± 108.2	485-780	10
AZ W	400.5 ± 52.6	290-485	10
Ov L	–	220-245	3
Ov W	–	240-280	3
Av morph 1 L	307.0 ± 52.3	165-400	10
Av morph 2 L	–	100-120	2
Av morph 3 L	–	160-175	2
Ly W	–	32-37	3

Parasmittina tropica – Hayward 1974: 384, fig. 6 A, B. — Zabala i Limousin 1986: 416-421 (in part), fig. 137E, pl. 7A-F, pl. 9A-C. — Zabala & Maluquer 1988: 119 (in part).

?*Smittina porosa* Canu & Bassler, 1930: 52, 53, figs 16-21.

DISTRIBUTION. — *Parasmittina rouvillei* was uncommon in the studied collection. It was collected under overhangs at 9 and 34 m depth at stations 2, 15, 18 and 26.

MATERIAL EXAMINED. — **Lebanon.** Stn 2, 2 colonies (MNHN). — Stn 15, 1 colony. — Stn 18, 1 colony. — Stn 26, 1 small colony on *Spondylus* shell.

DESCRIPTION

Colony encrusting, uni- to plurilaminar, well calcified. Autozooids variously sized and shaped, irregularly arranged. Frontal shield convex, coarsely nodular, with 18-30 unevenly large marginal pores, the largest including sometimes 2 or 3 smaller pores; occasionally, some smaller additional pores variously placed on the frontal shield, sometimes close to the marginal ones. Primary orifice rounded, about as broad as long, hidden by a raised, complete peristome formed by a tall collar mid-proximally indented by a deep notch; no orificial spine visible in most autozooids; lyrula anvil-shaped, narrow, with distal edge straight or slightly convex, and pointed corners; condyles broad and rounded, down-curved, delicately serrated with several rows of minute denticles. Avicularia present on each autozooid, up to 6 on a single zooid, variously shaped and placed, conforming to three main morphotypes; 1) medium- to large-sized, proximo-lateral to the peristome, directed proximally, parallel-sided or moderately spatulate, tip rounded, cross-bar complete, extended calcified palate; 2) small-sized, similar in shape to morph 1, variously placed and directed on the frontal shield; and 3) small- to medium-sized, lateral to the peristome and directed towards the orifice or laterally, occasionally on the proximal third of the frontal shield, rostrum triangular with pointed tip, cross-bar complete, foramen large, leaving a small, distal, calcified palate. Ovicell globular, porous, the proximal third covered by a secondary non-porous layer, sometimes obscured by an avicularium.

REMARKS

The Lebanese material agrees in all respects with the available descriptions and illustrations (Calvet 1902, 1927; Gautier 1962; Hayward & McKinney 2002), and with the material from Provence coast, France (JGH collection). The orificial spines cannot be seen in the collected colonies because of the broken growing margin. The large autozooids are typically heterogeneous due to their variable shape and irregular arrangement, the abundance of pores and the great number of variously shaped and sized avicularia. As noticed by Hayward & McKinney (2002), the Mediterranean specimens ascribed to *P. tropica* by Hayward (1974) and Zabala & Maluquer (1988) in fact correspond to *P. rouvillei*. According to Gautier (1962), *P. rouvillei* is close to *Smittina porosa* Canu & Bassler, 1930, from Tunisia, which has two rows of marginal pores and long spatulate avicularia. These two features are commonly met on Lebanese specimens and were also noticed on colonies from Medes Islands (Spain) by Zabala i Limousin (1986) who considered *P. porosa* (Canu & Bassler 1930) as a variation of the morph *rouvillei* of *P. tropica*. *Parasmittina porosa* is thus most likely a junior synonym of *P. rouvillei*, which seems to be endemic to the Mediterranean.

Parasmittina serruloides n. sp.
(Fig. 6; Table 6)

?*Parasmittina tropica* – Harmer 1957: 934 (in part), pl. 64, fig. 23. — Menon 1972: 78, figs 20-23. — Zabala & Maluquer 1988: 119 (in part), figs 253, 255, pl. 10B.

?*Parasmittina serrula* – Gordon 1984: 96, pl. 35B, C. — Winston 1984: 23, fig. 45. — Scholz 1991: 325, pl. 20, figs 1, 2, 4. — Gordon & d'Hondt 1997: 21, fig. 27.

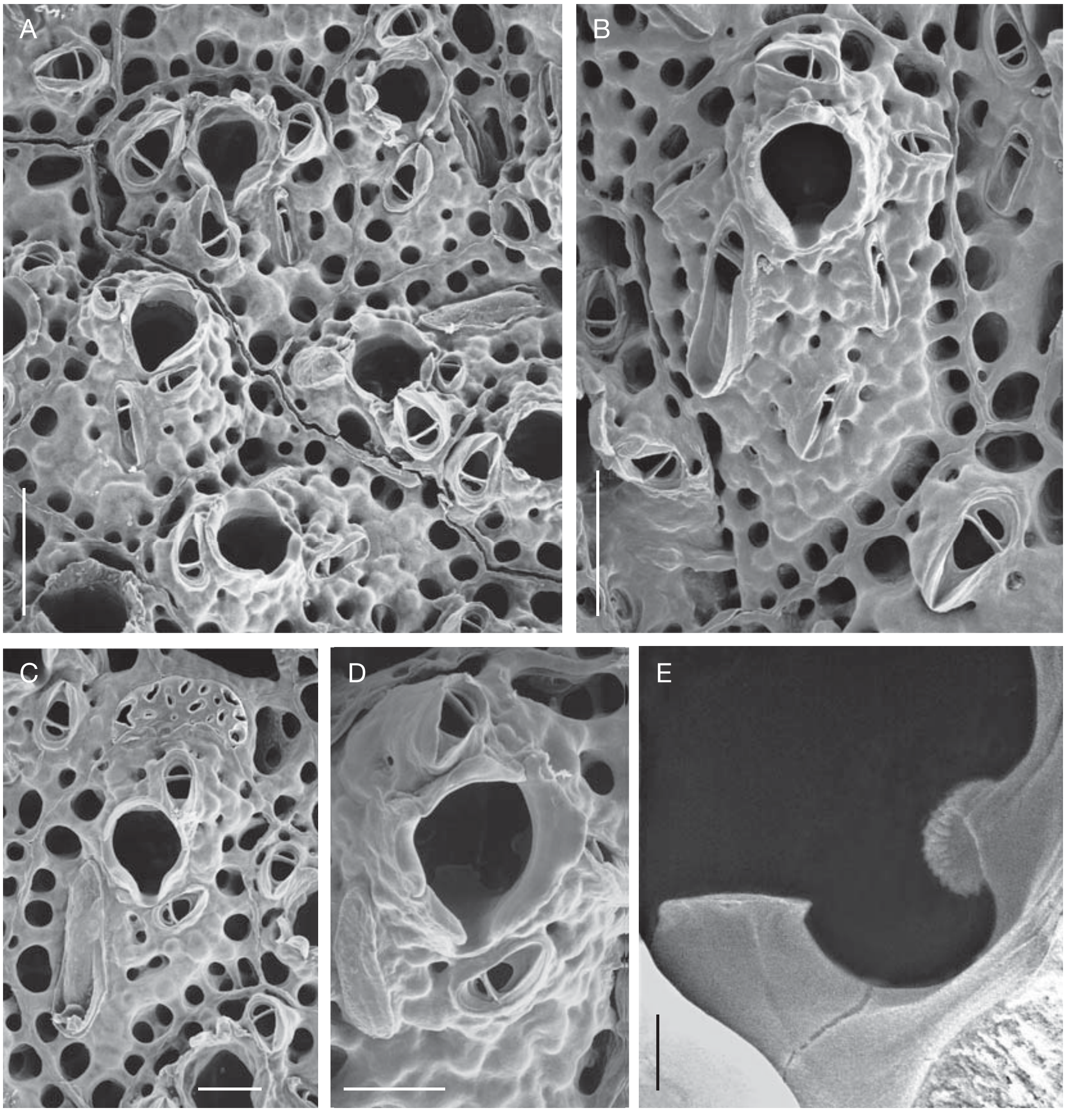

FIG. 5. — *Parasmittina rouvillei* (Calvet, 1902), station 2 (see Fig. 1 and text for stations list): **A**, part of colony with 5 non-ovicellate autozooids; **B**, autozooid with 6 variously shaped avicularia; **C**, ovicellate autozooid; **D**, secondary orifice with peristome and 2 avicularia; **E**, lyrula and 1 condyle. Scale bars: A, B, 200 µm; C, D, 100 µm; E, 50 µm.

Not *Parasmittina serrula* Soule & Soule, 1973: 386, fig. 3D-F. — Ryland & Hayward 1992: 272, figs 23e, f, 24a. — Tilbrook *et al.* 2001: 76, fig. 14E, F. — Tilbrook 2006: 154, 156, fig. 31A-C.

HOLOTYPE. — **Lebanon.** Stn 4, ovicellate colony on shell (MNHN: BRY-20265).

PARATYPES. — **Lebanon.** 1) Stn 12, small ovicellate colony, with *Cellepora* (MNHN: BRY-20266). — 2) Stn 2, small colony on cirripede (MNHN: BRY-20267). — 3) Stn 2, small colony (SMF). — 4) Stn 2, small colony (BMNH 2008.4.21.6). — 5) Stn 10, small colony (MNHN: BRY-20268). — 6) Stn 15, small colony on *Balanus* (MNHN: BRY-20269). — 7) Stn 21, 14 ovicellate colonies on *Spondylus* shell, with *P. spondylicola* n. sp. (1 colony: paratype), *P. egyptiaca* (1 colony), *Smittina nitidissima* (several colonies) and *Microporella* sp., etc. (MNHN: BRY-20270).

TABLE 6. — Zooidal measurements of *Parasmittina serruloides* n. sp. (in µm), stations 4, 12, 15, 18, 21 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	375.2 ± 48.2	270-460	29
AZ W	242.2 ± 31.9	180-300	29
Ov L	149.2 ± 11.7	125-160	23
Ov W	184.1 ± 12.3	160-205	23
Giant Av L	241.5 ± 29.5	195-330	26
Medium-sized Av L	115.0 ± 12.9	90-145	29

ETYMOLOGY. — From *serrula* and suffix *-oides*: similar to.

DISTRIBUTION. — *Parasmittina serruloides* n. sp. was found at 8 stations (2, 4, 10, 12, 15, 16, 18, 21) distributed from Ramkine Island (Tripoli) to Jbail (Byblos). All samples came from shaded habitats (overhangs, small caves, hidden side of shells) at shallow depth (3-17 m) where colonies were never abundant.

DESCRIPTION

Colony small, unilaminar. Autozooids glistening, irregularly shaped and sized, with coarsely nodular frontal shield and large marginal pores. Orificial spines 3 or 4 (rarely 2), with stout base, always visible on non-ovicellate zooids, forming a moderately curved arch over the whole anter, absent on ovicellate zooids. Primary orifice sub-rounded, as long as broad, with distal edge smooth; lyrula medium-sized (orifice/lyrula ratio for width = 3), anvil-shaped with straight distal edge, lateral corners poorly or not pointed; condyles relatively large, down-curved, tip coarsely denticulate with 2-5 teeth. Peristome raised with paired, more or less triangular, lateral flaps, separated by a mid-proximal, rounded notch; in addition, on ovicellate zooids, two distal arched wings extending from the distal corners of the orifice join to form a prominent visor over the proximal edge of the ovicell, sometimes with pointed, blade-like umbos. Ovicells frequent, globular, broader than long, frontal wall not covered by secondary calcification, with about 20 large pores; distal edge bordered with a low, nodular rim formed by the frontal wall of the distally adjacent autozooid. Adventitious avicularia single, including two morphs: 1) medium-sized, slim, parallel-sided, with rounded tip; and 2) large and narrow, with tip slightly pointed and down-curved and distal edges coarsely serrated; both morphs with complete cross-bar, latero-proximal to the orifice at the level of or just below the peristome notch, proximally or latero-proximally directed.

REMARKS

This species resembles *P. serrula* Soule & Soule, 1973 in having large avicularia similarly arranged laterally to the orifice and with serrated rostrum edges, the same type of ovicell, 3 or 4 orificial spines, and similarly shaped peristome. However, according to the descriptions by Soule & Soule (1973), Ryland & Hayward (1992), Tilbrook *et al.* (2001) and in particular Tilbrook (2006) who examined a paratype from Hawaii, *P. serrula* is characterised by a primary orifice with a distinctive denticulate anter and giant avicularia exhibiting a marked distal flare and edges with a wavy serration. Thus, *P. serruloides* n. sp. is readily distinguished from *P. serrula* in having orifices with a straight anter and narrower giant avicularia with a thinner serration limited to the distal third or quarter of the rostrum. *Parasmittina serruloides* n. sp. closely resembles the specimen from the Philippines illustrated by Gordon & d'Hondt (1997) as *P. serrula*, which apparently differs from the Lebanese specimens only in having smaller marginal pores and avicularia that can be paired. The specimens ascribed to *Parasmittina serrula* from Cebu Island, Philippines (Scholz 1991) and from Kermadec Ridge (Gordon 1984) resemble *P. serruloides* n. sp. in many features, including the peristome, the spines, the frontal shield and the avicularium. All these forms may correspond to the present species although Gordon (1984) reports the occasional occurrence of an avicularium "much larger and swollen at its proximal end". The description and figures of specimens from India identified with *P. tropica* (Waters, 1909) by Menon (1972) strongly suggest that these, too, belong to *P. serruloides* n. sp., considering the type and position of serration of the rostrum, the shape and position of the avicularium and the orifice with 3 or 4 spines and a notched peristome. Soule & Soule (1973) considered that the specimen from India illustrated by Harmer (1957: pl. 64, fig. 23) as *Smittina tropica* was close to *P. serrula*, but in fact it may also correspond to *P. serruloides* n. sp.

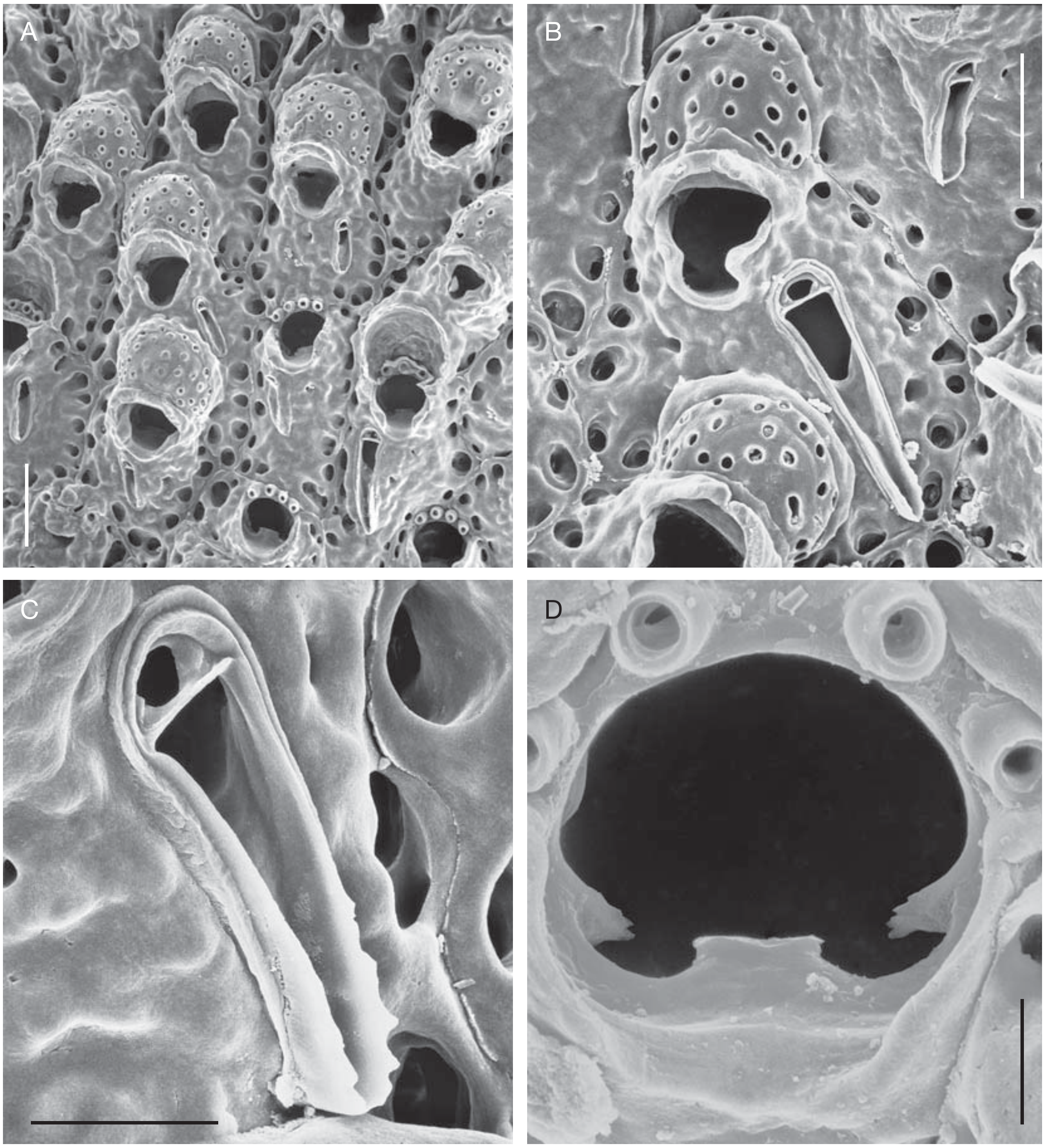

FIG. 6. — *Parasmittina serruloides* n. sp.: **A**, part of colony with 6 ovicellate and 1 non-ovicellate autozooids; **B**, ovicellate autozooid with typical peristome and large avicularium with narrow rostrum and serrated tip; **C**, close-up of a long avicularium with serrated tip; **D**, orifice with lyrula and 2 condyles; **A**, station 18; **B**, **C**, station 15; **D** station 4 (see Fig. 1 and text for stations list). Scale bars: A, B, 150 µm; C, 50 µm; D, 25 µm.

Specimens from Jamaica and Belize recorded by Winston (1984) as *P. serrula* show several features similar to *P. serruloides* n. sp.: long, narrow, arched avicularia with serrated edges, peristome with a proximal notch, 4 spines, frontal shield nodular. However, the SEM picture of specimen USNM 377797 (housed at the National Museum of Natural History, Washington, DC) shows a lyrula taller and narrower than in the Lebanese colonies and coarser condyles. Several illustrations of Mediterranean specimens ascribed to *P. tropica* by Zabala & Maluquer (1988) might depict *P. serruloides* n. sp. However, those drawings are difficult to interpret: autozooids bear long avicularia with serrated edges near the tip whereas other features are not in accordance with *P. serruloides* n. sp. such as non-ovicellate autozooid without spine and ovicell resembling that of *P. rouvillei* (Zabala & Maluquer 1988: fig. 253), or non-ovicellate autozooid with 5 spines and presence of a small, pointed avicularium on the proximal edge of the ovicell (Zabala & Maluquer 1988: fig. 255).

Parasmittina spondylicola n. sp.
(Fig. 7; Table 7)

Parasmittina sp. 2 – Sternhell *et al.* 2002: 226, fig. 3e, f.

?*Parasmittina tropica* – Scholz 1991: 327, pl. 19, figs 5-7.

?*Parasmittina* aff. *tropica* – Ristedt & Hillmer 1985: 138, pl. 4, fig. 8.

Holotype. — **Lebanon.** Stn 5, 1 colony on dead reteporid (MNHN: BRY-20271).

Paratypes. — 1) Stn 5, 1 colony on dead reteporid (MNHN: BRY-20272). — 2) Stn 21, 1 colony on *Spondylus* shell with paratype series of *P. serruloides* n. sp. (MNHN: BRY-20273). — 3) Stn 26, 2 colonies on *Spondylus* shell with *P. egyptiaca* (SMF). — 4) Stn 26, 1 colony on *Spondylus* shell with *P. egyptiaca* (BMNH 2008.4.21.5).

Etymology. — From *Spondylus*, occasional substrate of *P. spondylicola* n. sp.

Distribution. — *Parasmittina spondylicola* n. sp. was found on mineralised biotic substrata between 17 and 35 m depth at three Lebanese localities (stations 5, 21, 26). In two cases (stations 21 and 26), colonies occupied the inner side of empty shells of *Spondylus spinosus*, a lessepsian bivalve very abundant on rocky grounds in Lebanon. It was also found on an old colony of *Reteporella* (station 5).

Description

Colony unilaminar, small, delicate. Autozooids longer than wide, arranged in quincunx or in lines, separated by prominent ridges; frontal shield irregularly nodular with large, marginal pores. Primary orifice broader than long, poorly visible in frontal view except on young autozooids with lower peristome; lyrula broad, with straight distal edge and laterally salient corners; condyles low, relatively long. Secondary orifice consisting of a high, tubular peristome, incomplete distally, with nodular, relatively thick base, wavy-edged tip and proximal inner side indented by a mid-proximal notch; distal fenestra lyre-shaped, recumbent on ovicell or surrounding a single orificial spine with robust base on non-ovicellate autozooids. Ovicells frequent, rounded, wider than long, with 15-20 pores distributed on the whole frontal area. Avicularia of two types: 1) the more common, located proximally to the peristome and directed proximally, inserted medially or more frequently laterally to the median line; rostrum long, narrow, moderately spatulate (nearly parallel-sided) with round tip, foramen elongate, often with a median digitation, cross-bar complete; and 2) the less common, located laterally to the orifice and directed proximally, replacing a lateral half of the peristome, with curved, pointed rostrum.

Remarks

This small and delicate species is easy to identify thanks to the combination of distinctive features. Those obvious diagnostic characters include a single orificial spine, a particularly high tubular peristome interrupted distally, and a club-shaped adventitious avicularium with relatively narrow, slightly spatulate rostrum and round tip, sometimes replaced by a peristomial avicularium with acute rostrum. The particular frequency of ovicells, which are clearly prominent and not obscured by secondary calcification, is also typical of this species and may indicate a reproductive strategy adapted to opportunistic colonisation of free spaces and short life duration.

Few other *Parasmittina* species have constantly a single orificial spine and they differ significantly from *P. spondylicola* n. sp. in other morphological features. Plurilaminar colonies are developed by *Parasmittina tubula* Ryland & Hayward, 1992, from the Great Barrier Reef, which has a complete peristome obliterating the distal spine in older

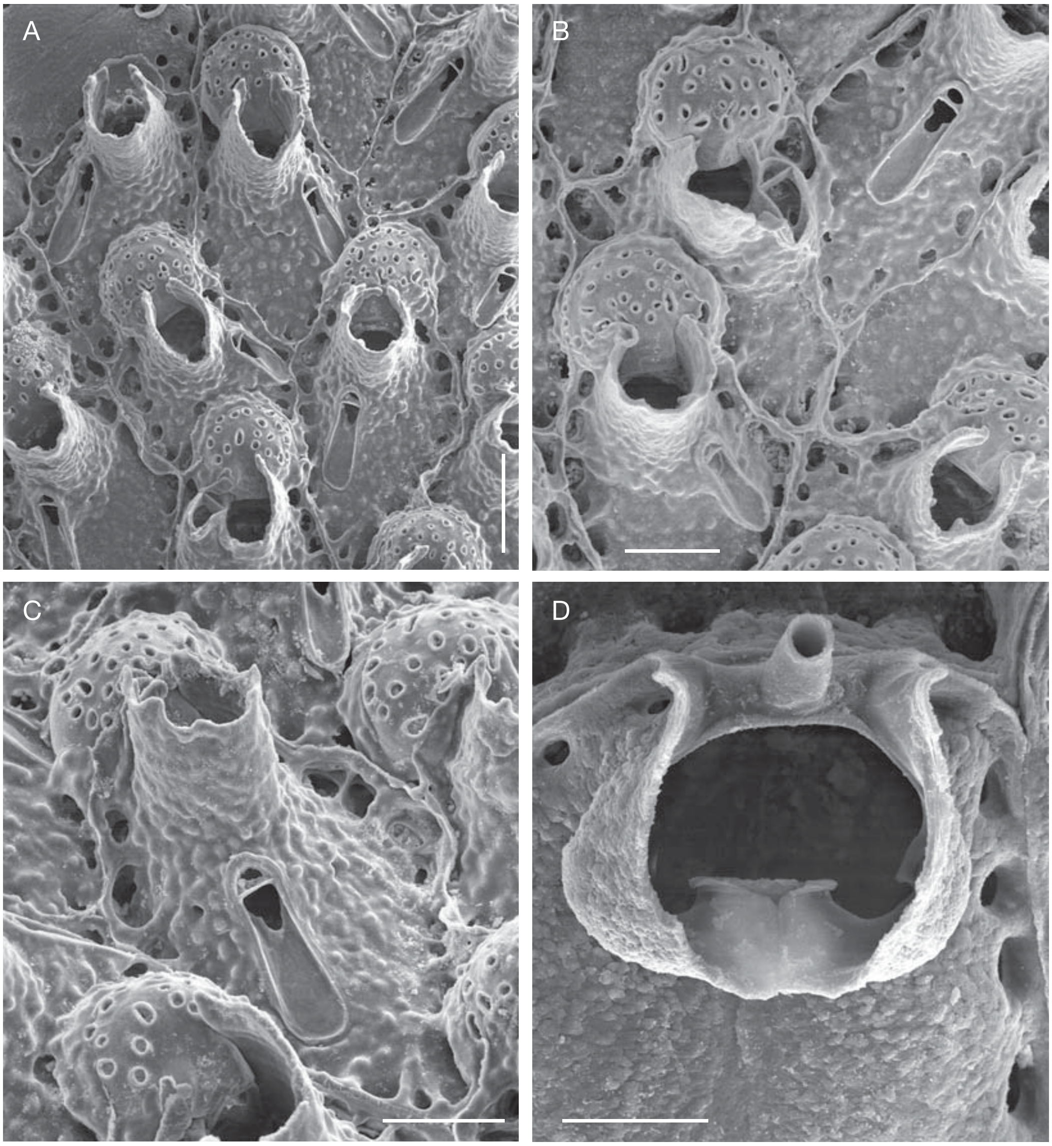

FIG. 7. — *Parasmittina spondylicola* n. sp., station 21 (see Fig. 1 and text for stations list): **A**, part of colony with 4 ovicellate and 1 non-ovicellate autozooids; **B**, ovicellate autozooids with spatulate and pointed avicularia; **C**, ovicellate autozooid with tubular peristome and spatulate avicularium; **D**, orifice with single spine, lyrula and 1 condyle. Scale bars: A, 150 µm; B, C, 100 µm; D, 50 µm.

zooids, and numerous polymorphic avicularia, in particular several around the peristome with pointed rostrum directed medially. *Parasmittina parsloeparsloei* Hayward & Parker, 1994 from South Australia grows as erect, thick, anastomosing sheets and is characterised by autozooids bearing a robust, distal orificial spine, a primary orifice with a denticulate distal edge, a peristome formed by proximo-lateral flaps and large avicularia with a broad opesial part. In other species, such as *P. delicatula* (Busk, 1884) (cf. Hayward & Parker 1994), *P. collifera* (Robertson, 1908) (cf. Soule & Soule 2002a), *P. aviculifera*

TABLE 7. — Zooidal measurements of *Parasmittina spondylicola* n. sp. (in µm), stations 5, 21, 26 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	433.8 ± 64.8	280-510	16
AZ W	230.6 ± 20.7	190-265	16
Ov L	172.2 ± 8.0	160-185	17
Ov W	193.8 ± 8.2	180-215	17
Av L	198.7 ± 29.2	160-265	19
Av W	–	50-60	4
Ly W	71.0 ± 4.2	65-75	5

Soule & Soule, 2002, the number of orificial spines is more variable (1-2 or 1-3) and they also differ from *P. spondylicola* n. sp. in several features. *Parasmittina cautela* Hayward, 1988, a small species from Mauritius, also has a tall, tubular peristome with a medioproximal notch, but it differs from *P. spondylicola* n. sp. in the lack of orificial spine and the occurrence of avicularia with acute rostrum and frontally flattened ovicells.

The specimen from Elat (Aqaba Gulf, Israel) named *Parasmittina* sp. 2 by Sternhell *et al.* (2002) most likely belongs to *P. spondylicola* n. sp. It shows typical characters of this species: tubular peristome with waved edge and distal fenestra harbouring a single orificial spine, primary orifice with a broad lyrula and low condyles, and a long avicularium with sub-parallel sides, inserted proximally to the peristome. The specimen from Cebu illustrated and identified as *P. tropica* by Scholz (1991) presents characters close to *P. spondylicola* n. sp., in particular a single mediodistal orificial spine and a tall, tubular peristome with a distal fenestra and denticulated tip.

The types of substratum occupied by *P. spondylicola* n. sp. in Lebanon (shells, old bryozoan colony) and at Elat, Red Sea (metallic panels: aluminium-based galvanic couples, Sternhell *et al.* 2002), together with the early and abundant production of ovicells suggest that *P. spondylicola* n. sp. is an opportunistic fouling species in shaded environments.

The record of this species from both Lebanon and the Gulf of Aqaba, and probably also from the Philippines Islands, argues for the status of an introduced species in the Mediterranean.

Genus *Smittina* Norman, 1903

Smittina nitidissima (Hincks, 1880) (Fig. 8; Table 8)

Porella nitidissima Hincks, 1880: 78, pl. 10, fig. 2 (Madeira).

Smittina nitidissima – Cook 1968: 213; 1985: 187, pl. 23, fig. C. — Dumont 1981: 636 (list). — Arístegui Ruiz 1984: 258, pl. 14, fig. 8, pl. 15, figs 1-3. — Hayward 1988: 297.

Smittina malleolus – Powell 1967: 170, pl. 3, 12. — d'Hondt 1988: 194.

Smittina egyptiaca – Balavoine 1959: 275, pl. 4, fig. 7.

?*Smittina smittiella* – Marcus 1953: 302, figs 63-65.

Not *Porella malleolus* Hincks, 1884: 361, pl. 13, fig. 5.

Not *Smittina malleolus* – Harmer 1957: 921, pl. 63, figs 7-10.

Not *Smittia egyptiaca* Waters, 1909: 157, pl. 15, figs 6-9.

DISTRIBUTION. — *Smittina nitidissima* was collected at various depths (3-42 m) at 18 stations (1-8, 12-15, 17, 20, 21, 26, 28, 30) from 10 localities between Ramkine Island (off Tripoli) in the north and El Kasmieh (off Sour) in the south of Lebanon. It was frequent on small, rocky or biogenic substrates such as shells or large bryozoan skeletons (e.g., *Margaretta cereoides*).

MATERIAL EXAMINED. — **Lebanon.** Stn 1, 1 small colony. — Stn 2, several small colonies on *Margaretta cereoides* (MNHN; BMNH 2008.4.21.3). — Stn 3, 1 colony. — Stn 4, several small colonies. — Stn 5, 1 colony. — Stn 6, 1 colony. — Stn 7, 1 colony. — Stn 8, several colonies on shells and rock (MNHN; BMNH 2008.4.21.4). — Stn 12, small colonies. — Stn 13, 1 colony on gastropod shell. — Stn 14, several small colonies. — Stn 15, several small colonies on barnacles, coralline algae and *Margaretta cereoides* (MNHN; SMF). — Stn 17, 1 colony. — Stn 20, 1 colony. — Stn 21, 1 colony on *Spondylus* shell. — Stn 26, several colonies on *Spondylus* shell. — Stn 28, 1 colony. — Stn 30, several colonies on rock and *Phyllangia mouchezii*.

OTHER MATERIAL EXAMINED. — Balavoine's collection, MNHN-7824 and MNHN-7833: *Mucronella egyptiaca*; Al Sayad stn XI, 9.XII.1928, Gulf of Suez, 25-31 m.

DESCRIPTION

Colonies small, encrusting, unilaminar. Autozooids sub-quadrangular, longer than wide (× 1.5 in aver-

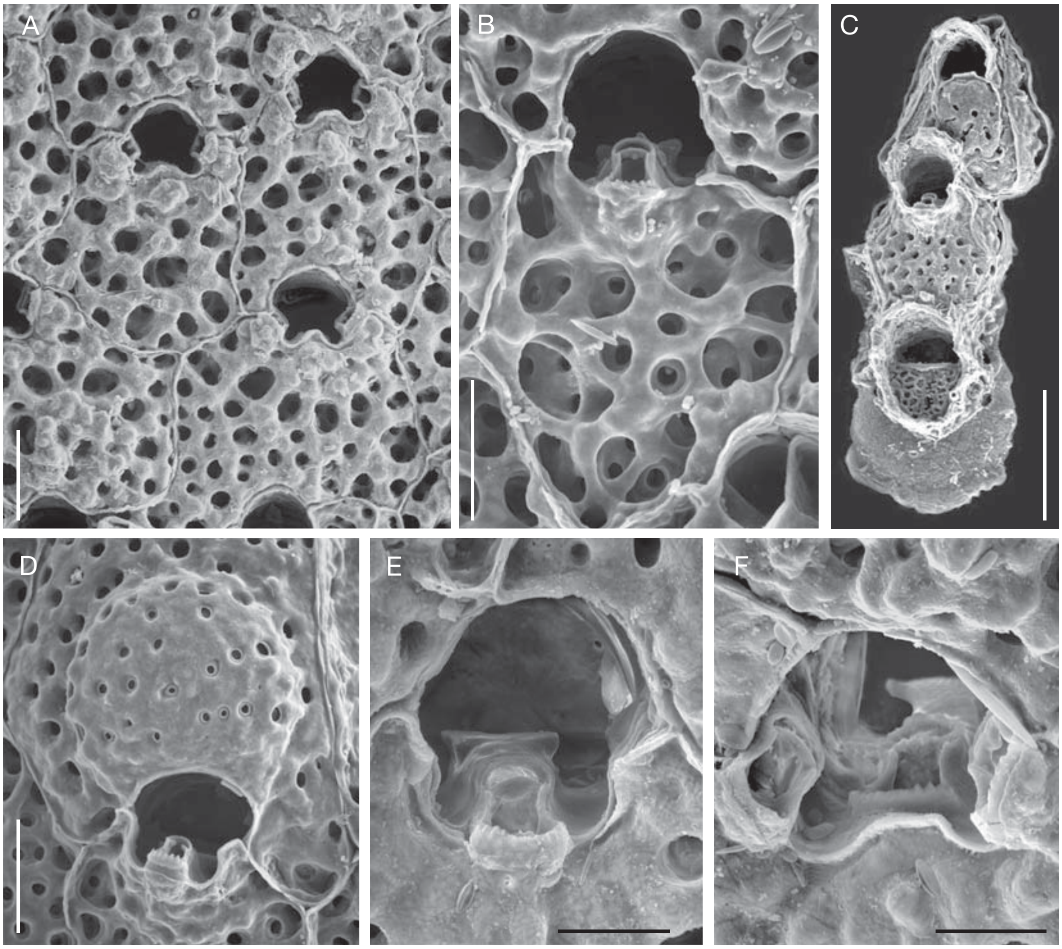

FIG. 8. — *Smittina nitidissima* (Hincks, 1880): **A**, part of colony with 3 non-ovicellate autozooids; **B**, non-ovicellate autozooid showing the particular structure of the frontal shield; **C**, ancestrula with 2 successive zooids; **D**, ovicell and orifice with a single avicularium; **E**, orifice with a single avicularium in front of lyrula; **F**, orifice with lyrula and 3 avicularia; **A**, **C**, **E**, **F**, station 4; **B**, **D**, station 13 (see Fig. 1 and text for stations list). Scale bars: A, C, 200 μm; B, D, 100 μm; E, F, 50 μm.

age) separated by salient rims. Frontal shield thick, porous, with many small pores evenly distributed throughout the whole frontal area in early astogenetic stages, while in older autozooids those pores are obscured by secondary calcification consisting of a meshwork of trabeculae defining large, irregular spaces including 2 or 3 primary pores. Orifice clearly distal, delimited by a thin, distal wall occasionally forming a low rim above the proximal side of the succeeding autozooid. Primary orifice orbicular, with a broad, straight lyrula (width = 80-85 μm), slightly or more distinctly alate, condyles short, slightly prominent. Secondary orifice as broad as long, slightly broader in ovicellate autozooids, more or less trifoliate due to the occurrence of avicularia inside the peristome; peristome not salient. Avicularia associated to the orifice, 1-5 in number, directed outwards, elongate, mandible spatulate with rostrum tip rounded and serrated with 8-12 robust, triangular teeth, cross-bar entire with a median bulge; one constant avicularium immediately proximal to the lyrula in both non-ovicellate and

TABLE 8. — Measurements of non-ovicellate autozooids of *Smittina nitidissima* (Hincks, 1880) (in µm), stations 1, 8, 15 (see Fig. 1 and text for stations list and abbreviations).

Measurements	Mean ± sd	Range	N
AZ L	418.4 ± 42.9	325-485	19
AZ W	275.8 ± 47.4	220-390	19
Or L	102.6 ± 7.2	90-120	19
Or W	103.8 ± 5.9	90-110	19

ovicellate zooids; additional avicularia in most ovicellate zooids (> 95%), including generally (> 70%) two lateral avicularia inserted just below the latero-proximal corners of the ovicell, less frequently a fourth avicularium (< 25%) borne by the inner proximal border of the ovicell (upper side of orifice), and occasionally a fifth avicularium in front of the mid-proximal one. Ovicell frequent (> 50% of autozooids), prominent in young stages with 20-25 scattered, round pores but rapidly subimmersed and indistinct due to secondary calcification from the distally adjacent autozooid. Ancestrula 0.3-0.4 mm long, oval with gymnocyst expanded proximally (25-40% of total ancestrula length), tatiform with few, indistinct spines rapidly embedded in the peripheral mural rim; cryptocyst extensive, longer than the remaining uncalcified area (opesia), covered by a mesh-shaped secondary calcification leaving a median, longitudinal, zigzag scar.

REMARKS

The Lebanese specimens attributed to *S. nitidissima* display evident diagnostic characters such as a coarsely porous frontal shield comprising two stages of pores and trifoliate ovicellate orifices bearing up to 4 or 5 avicularia. These characters are visible in the illustration of a specimen from the southern Red Sea (Migiunia Reef, off Massawa) identified as *Smittina malleolus* (Hincks, 1884) by Powell (1967). This species was also recorded in the Mediterranean from Haifa, Israel by d'Hondt (1988), unfortunately without description. When studying bryozoans from West Africa, Cook (1968) considered that *Smittina malleolus* and *S. smittiella* Osburn, 1947 were junior synonyms of *Porella nitidissima* Hincks, 1880, originally described from Madeira. However, it is clear from the descriptions and figures by Hincks (1884) and Harmer (1957) that *S. malleolus* differs from both the Mediterranean and Red Sea specimens. It is also obvious from good SEM illustrations by Arístegui Ruiz (1984) that the Canarian specimens of *S. nitidissima* do not differ from the Lebanese material. The orificial avicularium is always single in *S. malleolus* while orifices in the present species commonly bear 3 and sometimes 4 or 5 avicularia when ovicellate. Moreover, *S. malleolus* presents a frontal adventitious avicularium with a long, pointed rostrum directed towards the orifice, a detail observed neither in the Lebanese specimens nor in the Red Sea material as stated by Powell (1967), who also pointed out the occurrence of lateral sub-oral avicularia. *Smittina nitidissima* was listed without comments from the Sudanese Red Sea by Dumont (1981). Balavoine (1959) recorded and figured *Smittina egyptiaca* (Waters, 1909) from the Gulf of Suez (Al Sayad stn XI, 9.XII.1928). Examination of those specimens at the MNHN proved that they belong to the same species as the present Lebanese material. *Smittina smittiella*, originally described from the Caribbean (Aruba Island and Florida) and later recorded from the eastern Pacific (Osburn 1952), also presents a frontal wall with secondary reticulation and a similarly shaped sub-oral avicularium with serrated rostrum tip. However, in both Caribbean and Pacific specimens, ovicellate autozooids apparently bear only a single sub-oral avicularium. Marcus (1953) ascribed to *S. smittiella* a specimen from Espirito Santo, Brazil, which strikingly resembles Lebanese colonies in having the same reticulate structure of the frontal wall and ovicellate zooids with a similar trifoliate peristome bearing three avicularia with a serrated, rounded tip. According to Soule & Soule (1973), the species illustrated by Marcus is neither *S. smittiella* nor *S. malleolus*. The close agreement between the Brazilian, W African, Lebanese and Red Sea specimens in those particular characters can be a sufficient reason for placing them provisionally in the same species, *S. nitidissima*. This hypothesis is supported by the probably high ability of this species to be transported in ship fouling. The small size of colonies and great abundance of ovicells seem to indicate that this species is able rapidly to occupy vacant spaces and to disperse opportunistically. Alternatively, these geographically scattered populations could represent sibling species, one of them being the true *S. nitidissima*. Cook (1985) considered *S. nitidissima* as part of a species complex distributed world-wide in warm waters. The group of *Smittina* species that share the same reticulate type of frontal shield and sub-oral avicularia with spatulate mandible and rounded, serrate rostrum tip might also be considered as a new genus. The group in question includes at least *S. nitidissima*, *S. malleolus*, *S. smittiella*, *S. kukuiula* Soule & Soule, 1973, and *S. torques* Powell, 1967 (*sensu* Gordon 1984).

DISCUSSION

Diagnostic characters

The genus *Parasmittina* is particularly speciose as attested by the continuous additions of new species descriptions (e.g., Tilbrook 2006) and taxonomic revisions (e.g., Hayward & Parker 1994; Soule & Soule 2002a, b; Reverter-Gil & Fernández-Pulpeiro 2007). The routine use of scanning electron microscope allows taking into account minute morphological characters as reliable diagnostic criteria and to estimate more precisely the morphological variability of species. That variability can be great indeed, but sometimes has been overestimated (e.g., Zabala i Limousin 1986 for *P. tropica*). Priority diagnostic characters to be looked for are the orificial part of autozooids (to be observed at various stages of ontogenetic development): number and persistence of spines, morphological features of the peristome, characters of the primary orifice, especially the distal edge, serrate or smooth, and the shape and relative size of the lyrula and condyles, which appear to be particularly reliable. The avicularia also offer obvious species specific characters, such as the number of morphological types, their shape, placement and frequency. However, in some species, the frequency of the different avicularian morphs is highly variable between colonies and habitats. This implies that specimens from various localities need to be examined, preferably at different ontogenetic stages. Features of the ovicell and the frontal shield (e.g., wall calcification, number and size of pores) also provide valuable criteria.

Regional diversity of the Smittinidae

The extensive sampling along the coasts of Lebanon allowed the regional diversity of Smittinidae in the coastal zone to be assessed and evidenced the importance of introduced species. While total richness is relatively low at both genus (two taxa) and species (seven taxa) levels, that of *Parasmittina*, a genus particularly well represented in tropical and subtropical regions, is surprisingly high in Lebanon with six species. In a recent evaluation of species diversity of the Mediterranean Bryozoa, Rosso (2003) recorded 17 species of Smittinidae belonging to five genera. The genera missing (not yet recorded) in Lebanon are *Prenantia* Gautier, 1962, *Smittoidea* Osburn, 1952 and *Phylactella* Hincks, 1879. However, there was no possibility of finding *Phylactella* since deep sandy bottoms usually inhabited by *P. mediterranea* Rosso, 2004 (Rosso 2004) were not sampled during this study. It is more remarkable that *Smittoidea reticulata* (MacGillivray, 1842) and *Smittina cervicornis* (Pallas, 1766), common in coastal hard bottom communities of other parts of the Mediterranean, have not been found. Conversely, *Smittina nitidissima*, recorded only once in the Mediterranean from Israel (d'Hondt 1988), proved to be very common along the Lebanese coast. Although the actual diversity of *Parasmittina* in the whole Mediterranean needs to be re-appraised using reliable criteria, the number of *Parasmittina* species recorded in Lebanon contrasts with that found in the rest of the Mediterranean. For instance, only four species were listed by Rosso (2003), a number that could be reduced to three after synonymic adjustment concerning the Mediterranean records of *P. tropica* (Hayward & McKinney 2002). This geographic discrepancy can be explained at least in part by the inputs of exotic species to the Levant fauna.

Biogeography

The marine environment of Lebanon is on the border between warm-temperate and subtropical climates (Abboud-Abi Saab *et al.* 2004). The Levant region is thus open to the settlement of organisms

TABLE 9. — Geographic distribution of the seven smittinid species found in Lebanon according to published records and critical examination herein. •, attested occurrence; (•), more doubtful occurrence. Abbreviations: ***Peg***, *Parasmittina egyptiaca* (Waters, 1909); ***Ppr***, *P. protecta* (Thornely, 1905); ***Pra***, *P. raigii* (Audouin, 1826); ***Pro***, *P. rouvillei* (Calvet, 1902); ***Pse***, *P. serruloides* n. sp.; ***Psp***, *P. spondylicola* n. sp.; ***Sni***, *Smittina nitidissima* (Hincks, 1880).

	Peg	*Ppr*	*Pra*	*Pro*	*Pse*	*Psp*	*Sni*
Mediterranean: western basin			•	•			
Mediterranean: eastern basin			•	•			
Mediterranean: Levant coasts	•	•	•	•	•	•	•
E Atlantic: Mediterranean approaches		•	•				•
E Atlantic: W Africa		•					•
W Atlantic: Caribbean and south America					(•)		•
Red Sea	•	•	•			•	•
Indian Ocean		•			(•)		(•)
Pacific Ocean					(•)	(•)	

arriving from warm seas worldwide (Por 1989), but in particular via the Suez canal. Considering the difficulties in identifying species of Smittinidae, especially of the genus *Parasmittina*, and the probable occurrence of widespread species complexes, the biogeographic distribution of species remains uncertain in most cases. Nevertheless, an attempt is made to outline the distribution of the seven species found in Lebanon (Table 9). Among the six species of *Parasmittina*, only two, *P. rouvillei* and *P. raigii*, are present in both western and eastern basins. At the present state of knowledge, the former can be considered as a Mediterranean endemic whereas *P. raigii* also occurs in the Canary Islands and in the Red Sea (the latter being the origin of the neotype chosen by Hayward & Parker 1994). Three species out of the four other *Parasmittina* recorded for the first time in the Mediterranean (*P. egyptiaca*, *P. serruloides* n. sp. and *P. spondylicola* n. sp.), are likely to have arrived in the Mediterranean through the Suez canal ("lessepsian species") as can be argued on the basis of morphological similarities with Red Sea and Indian Ocean material. The occurrence in Lebanon of *P. protecta*, presently known only from ports, may be due to a recent introduction in the Mediterranean by shipping. Morphological similarities with previously recorded material indicate that the geographical source could be as well the Red Sea (Waters 1909; Hastings 1927; d'Hondt 1988) as the African East Atlantic (Cook 1968, 1985; Arístegui Ruiz 1984). The alternative hypothesis would be that it is indigenous with a relictual distribution. The wide distribution and abundance of *Smittina nitidissima* in Lebanon (and probably Israel; d'Hondt 1988) show that it is well established in the Levant area while its general features suggest the ability to proliferate and to travel as a fouling species. The possibility cannot be excluded that the occurrence of *S. nitidissima* in the extreme SE of the Mediterranean and also in the Red Sea may result from ship-transport from the eastern Atlantic where the species had originally been described (Madeira). However, the present distribution may also be relictual, resulting from fragmentation of an ancient distribution during warmer periods (Pleistocene or older) when the Mediterranean was colonised by "Senegalian" biota (Pérès 1967, 1985). This hypothesis does not exclude the existence of an as yet unrecognised species complex.

Acknowledgements
This study was supported by the French-Lebanese Cooperation CEDRE. Thanks are expressed to the staff of the Centre CNRS of Batroun, Lebanon, particularly Dr G. Khalaf, director, and to the persons who helped us during field trips. JGH is grateful to J.-L. d'Hondt for his hospitality and help at the MNHN during examination of collections, to P. J. Hayward and P. Kuklinski for providing useful comments and corrections, and to C. Bézac, Centre d'Océanologie de Marseille, for help with SEM work.

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Submitted on 7 December 2007;
accepted on 17 June 2008.