

Some Miocene cheilostome bryozoan genera of Michel Vigneaux – systematic revision and scanning electron microscopic study

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ABSTRACT

In 1949 Michel Vigneaux published an important taxonomic work on fossil bryozoans that introduced numerous new taxa at family-, genus- and species-levels, the majority of which are still used today, in some cases for extant bryozoans. However, Vigneaux's material from the Miocene of the Aquitaine Basin in France has never been revised. Here we employ scanning electron microscopy (SEM) to study Vigneaux's type specimens of the type species of five of his genera: *Hemiphylactella*, *Pleuromucrum*, *Stephanollina*, *Schizosmittina* and *Hemicosciniopsis*. Based on this revision, *Pleuromucrum* is considered to be a subjective senior synonym of both *Lifuella* Gordon & d'Hondt, 1997 and *Allorhynchozoon* Liu in Liu, Yin & Ma, 2001.

RÉSUMÉ

Les genres de bryozoaires cheilostomes de Michel Vigneaux – révision systématique et étude au microscope électronique à balayage.

En 1949 Michel Vigneaux a publié un important travail sur les bryozoaires fossiles, introduisant de nombreux nouveaux taxons au niveau de la famille, du genre et de l'espèce. La majorité d'entre eux sont encore utilisés aujourd'hui, quelque fois pour des bryozoaires récents. Toutefois, le matériel de Vigneaux, provenant du Miocène du Bassin d'Aquitaine en France, n'a jamais été révisé. Dans ce travail nous avons utilisé la microscopie électronique à balayage (MEB) pour étudier les espèces-types de cinq genres : *Hemiphylactella*, *Pleuromucrum*, *Stephanollina*, *Schizosmittina* et *Hemicosciniopsis*. Sur la base de cette révision, *Pleuromucrum* est considéré comme synonyme de *Lifuella* Gordon & d'Hondt, 1997 et *Allorhynchozoon* Liu in Liu, Yin & Ma, 2001; étant le plus ancien il doit être utilisé en priorité.

KEY WORDS

Nomenclature,
fossil,
Miocene,
Neogene,
Aquitaine Basin,
lectotypification,
new combinations,
new synonyms.

MOTS CLÉS

Nomenclature,
fossile,
Miocène,
Néogène,
Bassin Aquitain,
lectotypification,
combinaisons nouvelles,
synonymes nouveaux.

INTRODUCTION

A major work on bryozoans by Michel Vigneaux, entitled ‘*Révision des Bryozoaires Néogènes du Bassin d’Aquitaine et essai de classification*’, was published in 1949. The author’s aim was to develop a new classification, mainly for fossil cheilostome bryozoans, based on skeletal characters significantly related to the biology and physiology of the zooid, though without any pretence of completeness. Vigneaux’s study was based on Neogene bryozoans from the Aquitaine Basin of southwest France, which are today housed in the collections of the University of Bordeaux, and those of J. Duvergier and F. Canu, as well as additional material collected by several researchers from the Faculty of Sciences at the University of Bordeaux. This work introduced 36 new family-rank and 18 new genus-rank taxa, and 60 new species. Of these, 14 families, 14 genera and 57 species are still considered as valid, although some of the new species have since been transferred to different genera.

Despite the importance of the material described by Vigneaux (1949), it has yet to be restudied. A recent visit to the micropalaeontological collections of the University of Bordeaux allowed study of the critical type specimens of the type species of some of the new Miocene genera introduced by Vigneaux. The aim of this paper is to illustrate these specimens, some for the first time, using scanning electron microscopy (SEM) and to give revised diagnoses for the genera. This research leads to a re-evaluation of Vigneaux’s little-known genera, some of which have been neglected because they were poorly illustrated when first published, as it is the case for *Pleuromucrum* Vigneaux, 1949, which is here considered as a subjective senior synonym of *Lifuella* Gordon & d’Hondt, 1997. In addition, this work will provide useful information for the revision of the cheilostome volume of the ‘*Treatise on Invertebrate Paleontology*’ currently in progress.

MATERIAL AND METHODS

The type specimens of the type species belonging to five cheilostome bryozoan genera introduced by Vigneaux (1949) were studied, namely *Hemiphylactella* (*H. pulchra*), *Pleuromucrum* (*P. saucatsense*), *Stephanollina* (*S. multidentata*), *Schizosmittina* (*S. planovicellata*) and *Hemicosciniopsis* (*H. incrustans*). Additionally, the type specimens of two other species of *Hemiphylactella* (*H.?* *crassovicellata* and *H.?* *latebrosa*) were studied. All of this material is housed in the micropalaeontological collection of the ‘Unité de Formation et Recherche Sciences de la Terre et de la Mer’ at the University of Bordeaux, France. Those genera introduced by Vigneaux (1949), but for which the descriptions were based on type species and specimens introduced by other authors (e.g., J. Duvergier, J. V. Audouin, F. Canu, and A. M. Norman), are not considered in this study. For comparison with *Pleuromucrum saucatsense*, the lectotype (NHMUK 1906.12.3.4) and syntype (NHMUK 1975.7.28.24) of the Recent species *Lifuella multidentata* (Thornely, 1905) from Ceylon, as well as two syntypes (NHMUK 1999. 3.9.7) of *Lifuella articulata* (Philipps, 1900) from Lifu, Loyalty Island, were studied.

Scanning electron microscopy (SEM) was conducted on uncoated specimens using a low-vacuum scanning electron microscope (LEO VP-1455) at the NHMUK. Zooidal measurements were taken from SEM images of the type specimens using the image-processing program ImageJ. Each measurement is given in the text as the mean value \pm the standard deviation, observed range, and total number of measurements made (the latter value enclosed in parentheses).

ABBREVIATIONS

Measurements

AvL	avicularium length;
AvW	avicularium width;
OL	orifice length;
OW	orifice width;
OvL	ovicell length;
OvW	ovicell width;
ZL	autozooid length;
ZW	autozooid width.

SYSTEMATIC PALAEOONTOLOGY

Family ROMANCHEINIDAE Jullien, 1888

Genus *Hemiphylactella* Vigneaux, 1949

TYPE SPECIES. — *Hemiphylactella pulchra* Vigneaux, 1949 by original designation.

EMENDED DIAGNOSIS. — Colony encrusting, multiserial, unilaminar, with zooids arranged quincuncially. Zooids with convex frontal shield, tubercular or smooth, imperforate apart from a single row of marginal areolar pores. Primary orifice with a straight, convex or concave proximal margin and small condyles, surrounded by a flared to tubular peristome; oral spines present or absent. Ovicells hyperstomial, small, globular. Avicularia absent. Pore-chamber windows present or absent.

REMARKS

In addition to the Burdigalian type species, *Hemiphylactella pulchra* (Fig. 1; see description below), two Serravallian species were included by Vigneaux (1949) in this genus: *H.?* *crassovicellata* (Fig. 2; see description below) and *H.?* *latebrosa* (Fig. 3; see description below), both from Salles, Gironde.

Hemiphylactella is similar to the smittinid *Phylactella* Hincks, 1879 in having a deep flaring peristome, but differs in having oral spines, an imperforate frontal shield and ovicell, and in lacking a lyrula. Among other genera included in Romancheinidae, *Escharella* Gray, 1848 is the most similar, differing from *Hemiphylactella* most conspicuously in having a large lyrula.

Hemiphylactella pulchra Vigneaux, 1949
(Fig. 1)

MATERIAL EXAMINED. — Figured syntype (Vigneaux 1949: 84, pl. 8, fig. 1), C.B.398. This specimen is here designated as the lectotype of the species.

TYPE LOCALITY. — Moulin de l’Eglise, Saucats, Gironde, Aquitaine, France.

AGE. — Burdigalian, early Miocene.

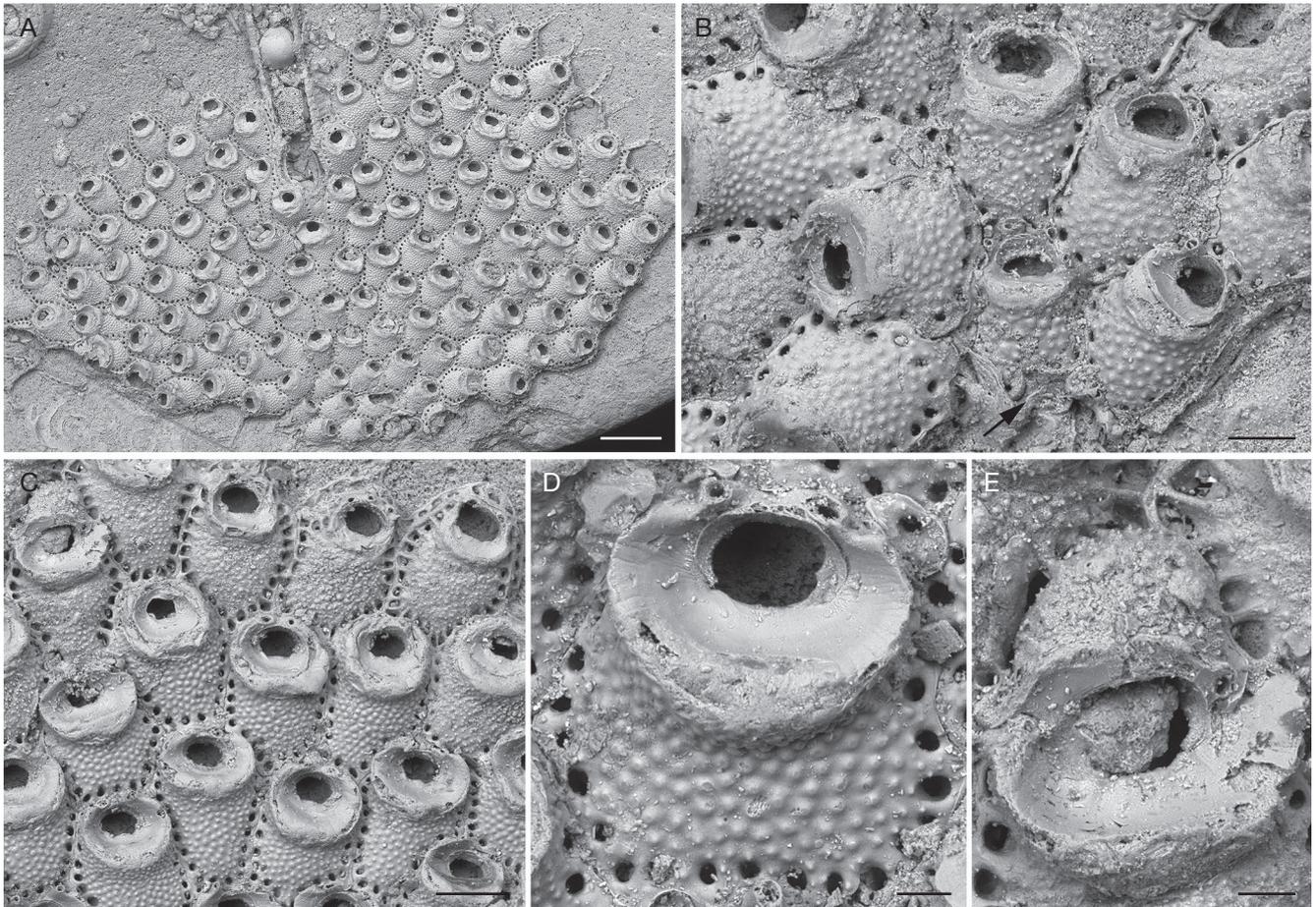


FIG. 1. — *Hemiphylactella pulchra* Vigneaux, 1949, figured syntype C.B.398, Burdigalian, early Miocene, Moulin de l'Église, Saucats, Gironde, Aquitaine, France: **A**, general view of the colony; **B**, ?first budded zooid (see arrow) and early astogeny; **C**, group of autozooids with a single ovicellate zooid; **D**, close-up of an autozooid; **E**, close-up of the oecium. Scale bars: A, 500 µm; B, 100 µm; C, 200 µm; D, E, 50 µm.

DESCRIPTION

Colony encrusting, multiserial, unilaminar (Fig. 1A). Ancestrula unknown; astogenetically oldest preserved zooid, probably the first budded autozooid (Fig. 1B, see arrow), similar to later autozooids but smaller, about 245 µm long by 180 µm wide, and bearing four oral spine bases. Zooids arranged quincuncially, distinct, boundaries marked by very narrow furrows, hexagonal, longer than wide (mean L/W = 1.24). Frontal shield slightly convex, tubercular, imperforate except for a single row of marginal areolar pores, on average 18 per zooid, oval to circular, 15–25 µm in diameter (Fig. 1C). Orifice placed distally, broader than long, the proximal rim slightly convex or straight and with two tiny condyles placed proximally to the mid-lateral position (Fig. 1D). A smooth, flared peristome, more developed proximally and laterally than distally, surrounds the orifice, embedding generally two, rarely three (Fig. 1C), distal, largely spaced oral spine bases, 25–35 µm in diameter. Ovicells hyperstomial. Oecium small, about 95 µm long by 165 µm wide, globular, cap-like, with a finer granulation than the frontal shield (Fig. 1E); the proximal rim of the oecium is covered by the smooth up-turned peristome. At least one oral spine base is still visible in ovicellate zooids (Fig. 1E). Avicularia absent. Numerous,

oval pore-chamber windows visible at colony growing edge along the distolateral zooidal margin, 25–40 µm long by 10–15 µm wide (Fig. 1C).

MEASUREMENTS

ZL 416 ± 25 , 365–470 (20); ZW 337 ± 26 , 277–389 (20); OL 64 ± 6 , 48–75 (20); OW 94 ± 4 , 87–103 (20).

REMARKS

Several differences occur between *Hemiphylactella pulchra* and the two congeneric species, such as the presence/absence of oral spine bases and pore-chamber windows (see below).

Hemiphylactella? crassovicellata Vigneaux, 1949 (Fig. 2)

MATERIAL EXAMINED. — Figured syntype (Vigneaux 1949: 85, pl. 8, fig. 2), C.B.450. This specimen is here designated as the lectotype of the species.

TYPE LOCALITY. — Salles, Gironde, Aquitaine, France.

AGE. — Serravallian, middle Miocene.

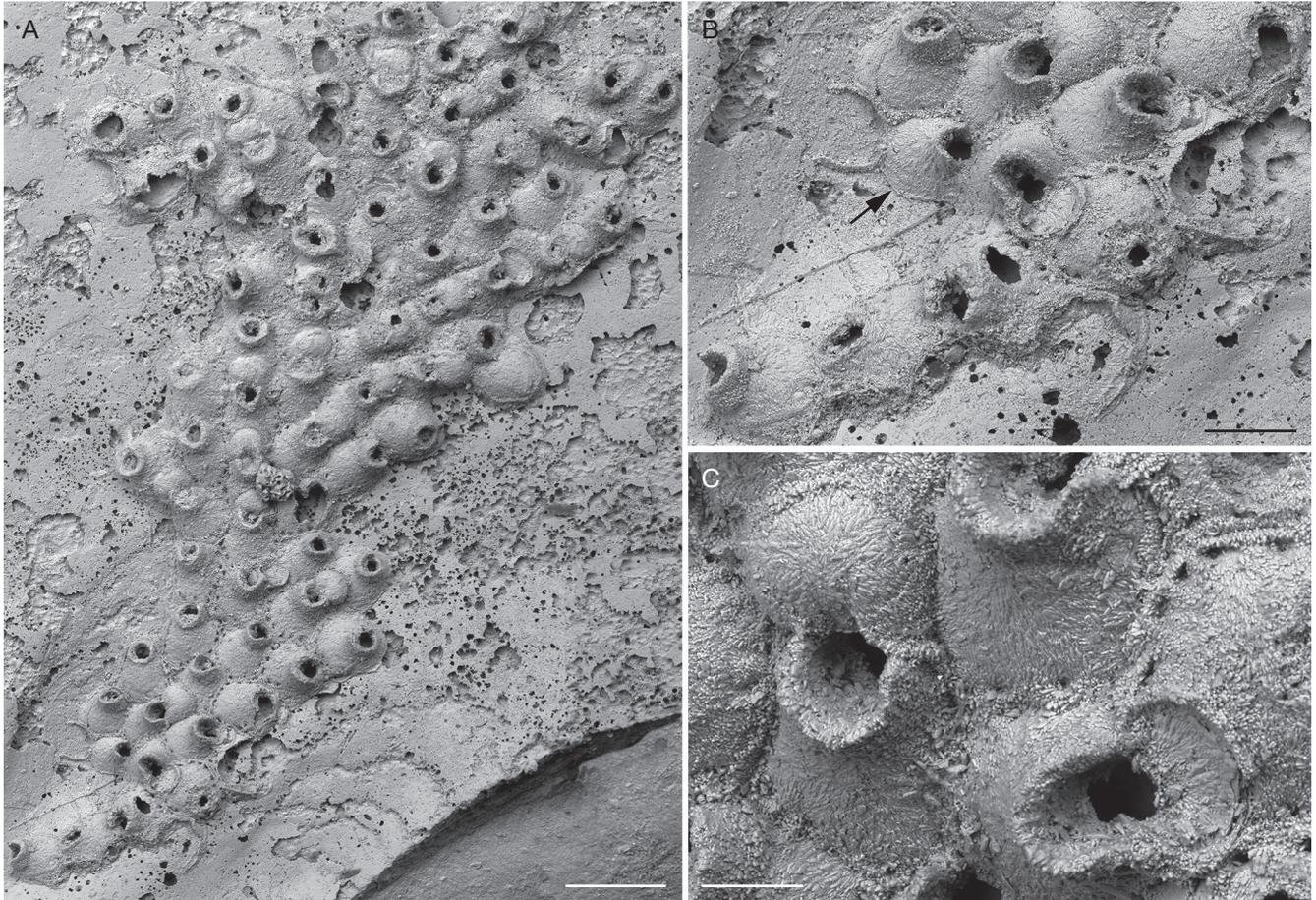


FIG. 2. — *Hemiphylactella? crassovicellata* Vigneaux, 1949, figured syntype C.B.450, Serravallian, middle Miocene, Salles, Gironde, Aquitaine, France: **A**, general view of the colony; **B**, ?ancestrula and early astogeny; **C**, close-up of an ovicellate zooid and autozooid showing the cleithridiate orifice. Scale bars: A, 500 µm; B, 200 µm; C, 100 µm.

DESCRIPTION

Colony encrusting, oligoseriate to multiserial, fan-shaped, unilaminar (Fig. 2A). Putative ancestrula similar to later autozooids but smaller, about 215 µm long by 190 µm wide, budding four zooids arranged in a semicircle (Fig. 2B). Later zooids arranged quincuncially, distinct, boundaries marked by raised ridges, rounded polygonal, slightly longer than broad (mean $L/W = 1.18$). Frontal shield slightly convex, apparently finely granular, imperforate except for a sometime visible single row of marginal areolar pores, on average 10 per zooid, oval to circular, 10–25 µm in diameter (Fig. 2B, C). Orifice placed distally, almost equidimensional, about 65 µm long by 60 µm wide, key-hole shaped (cleithridiate), with the proximal rim straight and two tiny condyles placed proximally to the mid-lateral position (Fig. 2C). A smooth, tubular peristome, more developed and slightly flared proximally, surrounds the orifice (Fig. 2C); oral spine bases absent. Ovicells hyperstomial. Ooecium broader than long, globular to elliptical, apparently finely granular like the frontal shield (Fig. 2B, C). Avicularia absent. Oval pore-chamber windows not observed.

MEASUREMENTS

ZL 364 ± 38 , 308–432 (20); ZW 309 ± 38 , 229–386 (20); OvL 148 ± 12 , 132–183 (16); OvW 205 ± 8 , 190–219 (16).

REMARKS

The figured syntype specimen of *Hemiphylactella? crassovicellata* is a small colony encrusting a shell fragment. The specimen is poorly preserved. Severe recrystallization prevents the observation of the marginal areolar pores in the majority of the zooids, the orifice is often obliterated by cement or sediment, while pore-chamber windows seem genuinely absent. The epitaxial calcite cement on the surfaces of the zooids hinders clear observation of the texture of the frontal shield, which is interpreted here as finely granular. *Hemiphylactella? crassovicellata* differs from *H. pulchra* in the lack of oral spine bases and pore-chamber windows, in having a much larger ooecium, which is not cap-like, a smaller key-hole shaped orifice surrounded by a less flared peristome, and an apparently finer granulation of the frontal shield. If our interpretation of the ancestrula is correct, this would imply very early sexual maturity in the colony as ovicells are present in the first generation of budded zooids.

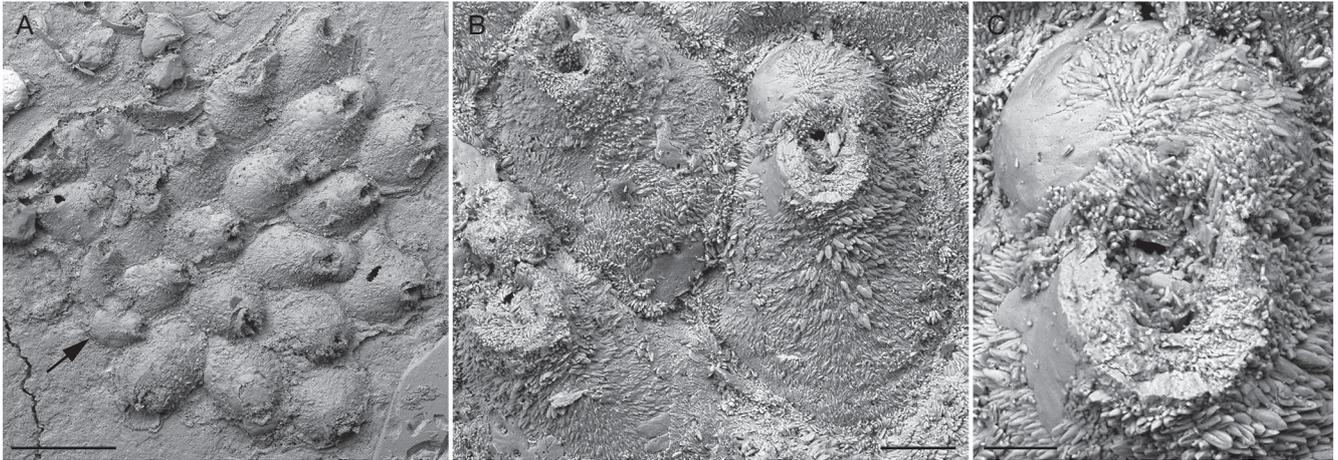


FIG. 3. — *Hemiphylactella? latebrosa* Vigneaux, 1949, figured syntype C.B.451, Serravallian, middle Miocene, Salles, Gironde, Aquitaine, France: **A**, general view of the colony with ?ancestrula (see arrow) and early astogeny; **B**, close-up of an ovicellate zooid and autozooid; note the smooth frontal shield and frontal surface of the oecium where not affected by recrystallization. Marginal areolar pores are visible in the bottom left corner; **C**, close-up of the oecium and ?cleithridiate orifice. Scale bars: A, 500 µm; B, 100 µm; C, 50 µm.

Hemiphylactella? latebrosa Vigneaux, 1949
(Fig. 3)

MATERIAL EXAMINED. — Figured syntype (Vigneaux 1949: 85, pl. 8, fig. 3), C.B.451. This specimen is here designated as the lectotype of the species.

TYPE LOCALITY. — Salles, Gironde, Aquitaine, France.

AGE. — Serravallian, middle Miocene.

DESCRIPTION

Colony encrusting, multiserial, unilaminar (Fig. 3A). Putative ancestrula similar to later autozooids but smaller, about 280 µm long by 180 µm wide, budding two zooids laterally (Fig. 3A). Later zooids arranged quincuncially, distinct, boundaries marked by narrow furrows, rounded polygonal, longer than broad (mean L/W = 1.26). Frontal shield slightly convex, smooth, imperforate except for an occasionally visible single row of marginal areolar pores, transversely oval to circular, 15–20 µm long (Fig. 3A, B). Orifice placed distally, longer than broad, about 120 µm long by 95 µm wide, seemingly key-hole shaped (cleithridiate) with a concave proximal edge (Fig. 3C). A slightly raised, tubular peristome surrounds the orifice proximally and laterally (Fig. 3C); oral spine bases absent. Ovicells hyperstomial. Oecium broader than long, globular, cap-like, smooth like the frontal shield (Fig. 3B, C). Avicularia absent. Pore-chamber windows not observed.

MEASUREMENTS

ZL 453 ± 33, 412–504 (10); ZW 360 ± 24, 306–399 (10); OvL 73 ± 10, 65–84 (3); OvW 189 ± 10, 178–198 (3).

REMARKS

Hemiphylactella? latebrosa differs from *H. pulchra*, the type species of the genus, in lacking oral spine bases and pore-chamber windows, for which reason we assign this species only tentatively to *Hemiphylactella*. Furthermore, *H.? latebrosa*

has a smooth frontal shield while in *H. pulchra* the frontal shield is coarsely granular. The two species possess ovicells of similar shape and size, whereas the ovicell in *H.? crassovicellata* is much larger than in the other two species. *Hemiphylactella? crassovicellata* also has a finely granular frontal shield

Family SFENIELLIDAE Gordon, 2006

EMENDED DIAGNOSIS. — Colony encrusting, planar. Autozooids with marginal areolar pores, with or without sparse pseudopores penetrating the frontal shield. Secondary orifice cormidial, defined by surrounding frontal shields. Oral spines present. Avicularia and zooidal polymorphs present or absent. Ovicells prominent.

Genus *Stephanollina* Vigneaux, 1949

TYPE SPECIES. — *Stephanollina (Stephanollina) dentata* Vigneaux, 1949 by original designation.

EMENDED DIAGNOSIS. — Colony encrusting. Zooids with ill-defined boundaries. Frontal shield nodular, imperforate apart from sparse marginal areolar pores. Primary orifice with a shallow sinus; secondary orifice cormidial with lobes and cusps. Oral spines present. Avicularia adventitious, budded from marginal areolar pores. Ovicell globular.

REMARKS

Stephanollina was introduced by Vigneaux (1949) as a subgenus of *Stephanollona* Duvergier. Gordon (2006) ruled out any relationship between *Stephanollina* and *Stephanollona*, suggesting elevation of *Stephanollina* to genus rank and tentatively including it in the family Sfeniellidae. However, the diagnosis of the family Sfeniellidae is based solely on *Sfeniella* and must be modified to include *Stephanollina* (see above). The latter genus lacks the sparse pseudopores penetrating the frontal shield and the polymorphs resembling autozooids but with reduced orifices that are typical of *Sfeniella*, while avicularia are present. *Stephanollina* shares with *Sfeniella* a cormidial secondary orifice

and the presence of oral spine bases. The diagnostic features of *Stephanollina* were observed also in '*Gemelliporella vorax* Canu & Bassler, 1923 *sensu* Gordon (2006: pl. 2, figs 3, 4), which is here considered as congeneric, although limited to the specimens re-examined by Gordon (2006) from the Miocene of North Carolina. Other specimens figured in Canu & Bassler (1923: pl. 19, figs 1-9) seem to belong to different genera.

Stephanollina dentata Vigneaux, 1949
(Fig. 4)

MATERIAL EXAMINED. — Figured syntype (Vigneaux 1949: 80, pl. 7, fig. 13), C.B.429-1. This specimen is here designated as the lectotype of the species.

TYPE LOCALITY. — Manciet, Gers, Aquitaine, France.

AGE. — Langhian, middle Miocene.

DESCRIPTION

Colony encrusting, multiserial, unilaminar (Fig. 4A). Zooids quincuncially arranged with ill-defined boundaries, sometimes marked by marginal areolar pores or narrow, shallow furrows (Fig. 4A, B). Frontal shield slightly convex or flat, nodular, imperforate apart from sparse, circular to elliptical, marginal areolar pores, 15-30 µm long (Fig. 4B). Primary orifice somewhat rounded, almost equidimensional, with two small condyles proximally placed separating an arched anter from a very shallow, slightly narrower sinus with a faintly concave proximal margin (Fig. 4C, D). Secondary orifice cormidial, formed by the frontal shield of the three surrounding distal zooids, forming a crenulated margin of lobes and cusps, the latter in the position of the oral spines (Fig. 4C, D). A suboral mucro rarely developed (Fig. 4A, see arrow). Five distal oral spine bases, the proximalmost pair generally larger, about 20 µm in diameter, while the others are about 10 µm in diameter (Fig. 4C, D). Adventitious avicularia budded from marginal areolar pores, often latero-oral, elliptical, without condyles or pivotal bar (Fig. 4B, C). No complete ovicells observed; incomplete ovicells with oecium longer than broad, resting on the frontal shield of the next distal zooid or pair of zooids (Fig. 4A, B).

MEASUREMENTS

ZL 275 ± 20, 247-329 (15); ZW 223 ± 26, 186-276 (15); OL 76 ± 4, 71-82 (10); OW 86 ± 1, 84-88 (10); OvL 103 ± 6, 96-113 (5); OvW 150 ± 14, 127-162 (5); AvL 63 ± 6, 53-71 (10); AvW 49 ± 6, 40-57 (10).

REMARKS

Stephanollina dentata is very similar in appearance to the specimen of *Stephanollina vorax* (Canu & Bassler, 1923) n. comb. figured by Gordon (2006: pl. 2, figs 3, 4), the two species differing mainly in the number of oral spine bases (five in *S. dentata*, four in *S. vorax* n. comb.), and in the shape of the official sinus, which is deeper and more markedly concave in *S. vorax* n. comb. Ovicells and avicularian chambers are generally broken or incomplete in both species.

Family BITECTIPORIDAE MacGillivray, 1895

Genus *Schizosmittina* Vigneaux, 1949

TYPE SPECIES. — *Schizosmittina planovicellata* Vigneaux, 1949 by original designation.

EMENDED DIAGNOSIS. — Colony encrusting with zooids arranged in alternating parallel rows or bilamellar. Frontal shield evenly pseudoporous with distinct marginal areolar pores. Orifice sinuate with distinct condyles, often corrugated; lyrula absent; oral spines evanescent, present on marginal zooids only. Avicularia present or absent, adventitious or vicarious, when adventitious often suboral and associated with the peristome. Ovicells with a peripheral band of rugose calcification and a broad, flat, pseudoporous frontal area. Basal pore-chamber windows or mural septula present.

REMARKS

The genus *Schizosmittina* was resurrected by Gordon (1984) and subsequently recorded in both fossil and Recent material from a wide geographical area. Gordon (1994) noted that he had examined Vigneaux's type material of *S. planovicellata*, scanning a few isolated zooids and using this information to rediagnose the genus. The earliest occurrence is *Schizosmittina ovicellata* Zágorský & Kázmér, 2001 from the Priabonian (late Eocene) of Hungary, followed by the Rupelian (early Oligocene) *S. bathydonta* (Brown, 1952) from New Zealand. Among extant species, four (*S. bicornis*, *S. cinctipora*, *S. conjuncta*, *S. melanobater*) are currently known from New Zealand waters (Gordon 1984, 1989), two (*S. maplestonei* and *S. vitrea*) from Australia (MacGillivray 1879), one (*S. lizzya*) from South Africa (Florence *et al.* 2007), and one (*S. pedicellata*) from the eastern Pacific off USA coast (Soule *et al.* 1995).

Schizosmittina planovicellata Vigneaux, 1949
(Fig. 5)

MATERIAL EXAMINED. — Figured syntype (Vigneaux 1949: 104, pl. 10, fig. 5), C.B.510-1. This specimen is here designated as the lectotype of the species.

TYPE LOCALITY. — Salles, Gironde, Aquitaine, France.

AGE. — Serravallian, middle Miocene.

DESCRIPTION

Colony encrusting, multiserial, unilaminar (Fig. 5A). Zooids arranged in parallel rows, distinct by deep furrows, subrectangular, twice as long as wide (mean L/W = 2.05). Frontal shield slightly convex, nodular, evenly pseudoporous; pseudopores circular, large, about 20 µm in diameter (Fig. 5A, B). Marginal areolar pores distinct, larger than pseudopores, about 35 µm in diameter (Fig. 5A, B, D). Orifice longer than wide, about 100 µm long by 70 µm wide, with a narrow, deep U-shaped sinus and two, rectangular, corrugated condyles (Fig. 5C); oral spines absent. A raised peristome, more developed proximally and laterally, hides the primary orifice, and encloses a small, oval

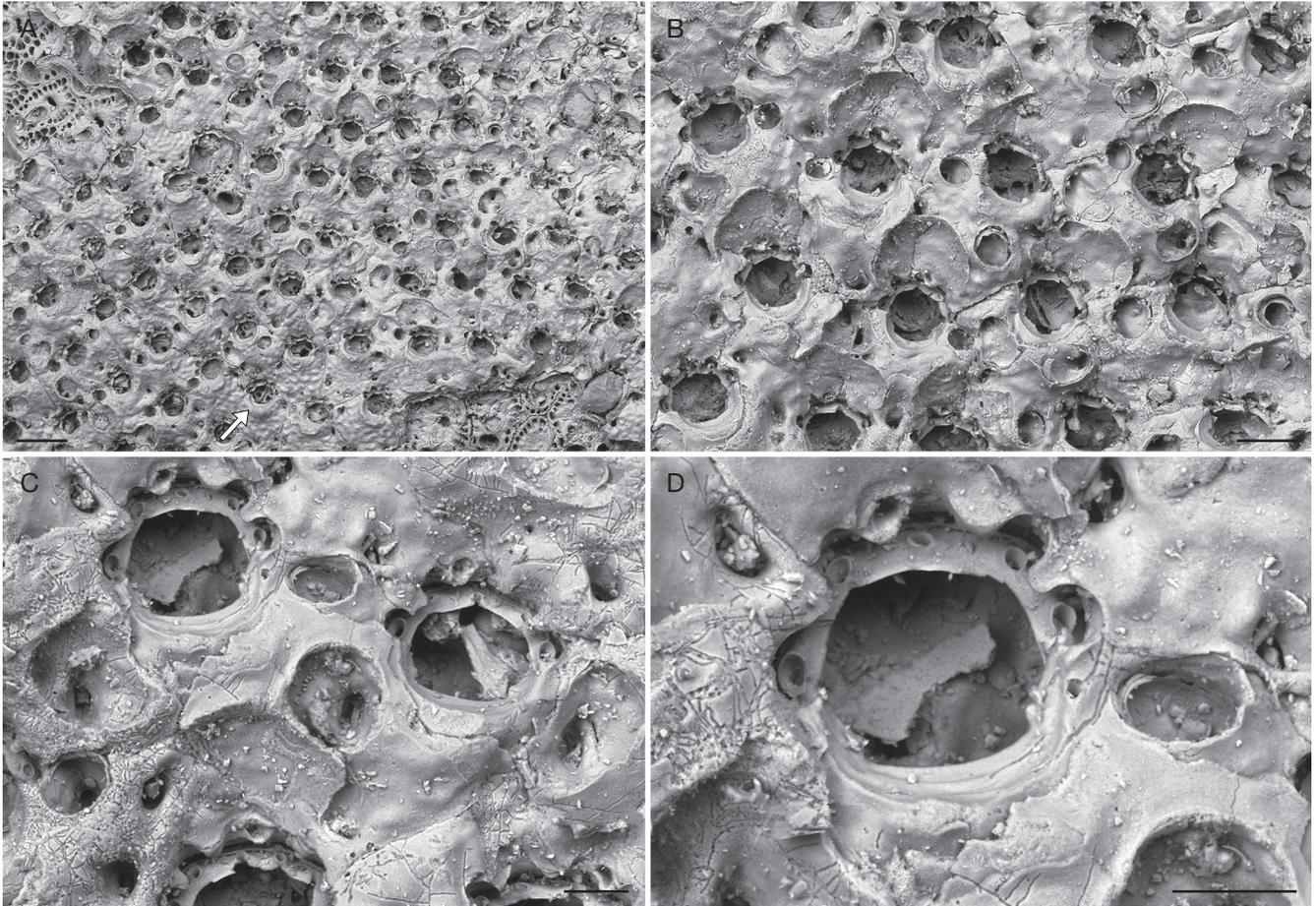


FIG. 4. — *Stephanollina dentata* Vigneaux, 1949, figured syntype C.B.429-1, Langhian, middle Miocene, Manciet, Gers, Aquitaine, France: **A**, general view of the colony; the arrow shows an autozoid with developed suboral mucro; **B**, group of zooids with incomplete ovicells and broken avicularian chambers; **C**, close-up of two autozooids with elliptical avicularia; **D**, close-up of the primary orifice showing five oral spine bases and the cornidial secondary orifice with alternating lobes and cusps. Scale bars: A, 200 μ m; B, 100 μ m; C, D, 50 μ m.

suboral avicularium sloping inwardly, proximally directed and with a complete crossbar (Fig. 5D). Vicarious avicularia absent. Ovicells large, globular, pseudoporous covered by a band of rugose calcification continuous with the frontal shield of the next distal zooid (Fig. 5A, B, D). Basal pore-chamber windows visible along distolateral zooidal margins at the colony growing edge, elliptical, about 15 μ m long by 10 μ m wide (Fig. 5E).

MEASUREMENTS

ZL 478 ± 25 , 452-519 (10); ZW 234 ± 22 , 204-271 (10); OvL 149 ± 10 , 136-167 (10); OvW 186 ± 13 , 167-203 (10).

REMARKS

Schizosmittina planovicellata differs from the fossil congeneric species, *S. ovicellata* and *S. bathydonta*, in having an encrusting rather than an erect colony-form. Recent species also differ: *S. maplestonei* (MacGillivray, 1879) has a pair of frontal tubercles proximal to the orifice; *S. vitrea* (MacGillivray, 1879), *S. conjuncta* (Uttley & Bullivant, 1972) and *S. melanobater* Gordon, 1989 have a much broader, widely rounded sinus; *S. cinctipora* (Hincks, 1883) has large

adventitious avicularia on the frontal shield; *S. bicornis* Gordon, 1989 is distinguished by a pair of prominences present on either side of the orifice; *S. lizzya* Florence, Hayward & Gibbons, 2007 has a subimmersed tripartite ovicell with a single, almost medial foramen. The five, stout oral spines present in *S. pedicellata* Soule, Soule & Chaney, 1995 link this species more with *Schizomavella* rather than *Schizosmittina*.

Family GIGANTOPORIDAE Bassler, 1935

Genus *Hemicosciniopsis* Vigneaux, 1949

TYPE SPECIES. — *Hemicosciniopsis incrustans* Vigneaux, 1949 by original designation.

EMENDED DIAGNOSIS. — Colony encrusting with zooids irregularly arranged. Frontal shield evenly pseudoporous. Orifice dimorphic: cleithriate in non-ovicellate autozooids, bell-shaped with a broader sinus in ovicellate zooids. Oral spines absent. Avicularia suboral with complete crossbar. Ovicells bulbous with pseudopores and calcification resembling the frontal shield.

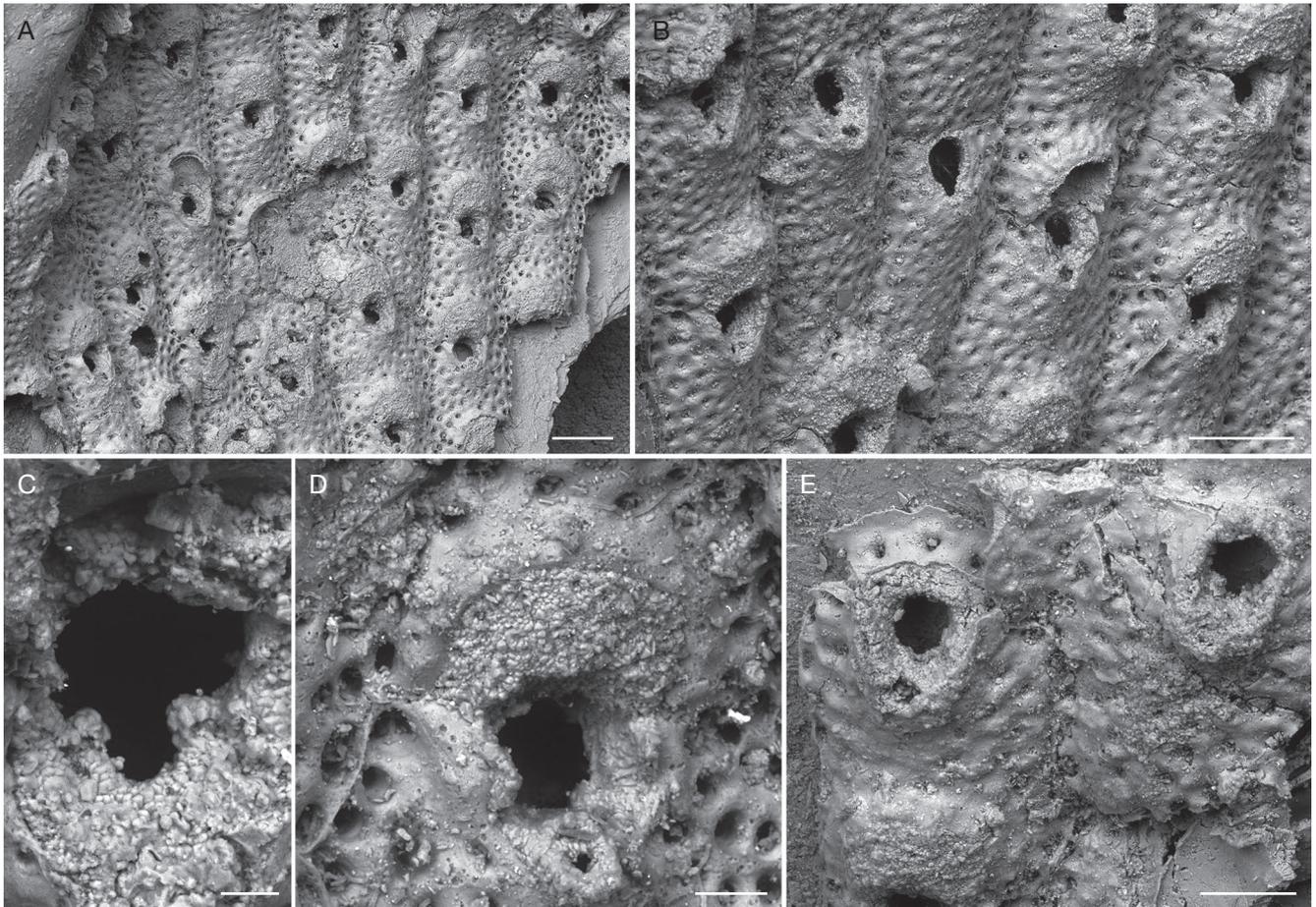


FIG. 5. — *Schizosmittina planovicellata* Vigneaux, 1949, figured syntype C.B.510-1, Serravallian, middle Miocene, Salles, Gironde, Aquitaine, France. **A**, group of ovicellate autozooids; **B**, close-up of autozooids and ovicellate zooids; **C**, close-up of the orifice showing the deep, narrow sinus and the corrugated condyles; **D**, close-up of an ovicell and suboral avicularium with complete crossbar; **E**, close-up of two autozooids at the colony growing edge showing basal pore-chamber windows. Scale bars: A, B, 200 μ m; C, 20 μ m; D, 50 μ m; E, 100 μ m.

REMARKS

Vigneaux (1949) introduced the genus *Hemicosciniopsis* for *Cosciniopsis*-like species with differently shaped orifice in non-ovicellate and ovicellate (maternal) autozooids. Based on Tilbrook's (2006: 236) revised diagnosis of *Cosciniopsis*, *Hemicosciniopsis* differs also in having avicularia. However, although the type species of *Cosciniopsis*, *C. coelatus* Canu & Bassler, 1927, lacks avicularia, other species assigned to the genus, such as the well-known *C. lonchaea* (Busk, 1884), have latero-oral avicularia.

Hemicosciniopsis incrustans Vigneaux, 1949
(Fig. 6)

MATERIAL EXAMINED. — Figured syntype (Vigneaux 1949: 76, pl. 7, fig. 6), C.B.97-1. This specimen is here designated as the lectotype of the species.

TYPE LOCALITY. — Pessac, Lorient, Gironde, Aquitaine, France.

AGE. — Aquitanian, early Miocene.

DESCRIPTION

Colony encrusting, uniserial, multilaminar (Fig. 6A). Zooids irregularly arranged, separated by more or less marked furrows,

irregularly polygonal, longer than wide (mean L/W = 1.25). Frontal shield convex, nodular and evenly pseudoporous (Fig. 6B, C); pseudopores circular, large, 15-25 μ m in diameter, arranged quincuncially, on average 30 per zooid. Orifice dimorphic: cleithriate in non-ovicellate autozooids with two small, rounded condyles medially directed, separating an arched anter from a smaller bowl-shaped sinus, about 150 μ m long by 130 μ m wide (Fig. 6D); bell-shaped and slightly larger in ovicellate zooids, about 180 μ m long by 150 μ m wide, with two robust condyles downwards directed separating an arched anter from a larger, shallow poster (Fig. 6E). Depending on the degree of calcification, in some zooids the orifice may be completely or partially obliterated (Fig. 6B, F). Sometimes a smooth, imperforate, peristomial ridge surrounds the orifice proximally, enclosing a small, elliptical, adventitious avicularium, proximolaterally directed and with complete crossbar (Fig. 6F). Ovicells bulbous resting on the frontal shield of the next distal zooid, calcification pseudoporous and resembling a frontal shield (Fig. 6B, C, E).

MEASUREMENTS

ZL 512 \pm 46, 457-593 (12); ZW 408 \pm 37, 330-451 (12); OvL 208 \pm 6, 200-215 (5); OvW 279 \pm 18, 265-303 (5); AvL 65 \pm 9, 53-74 (5); AvW 43 \pm 5, 34-47 (5).

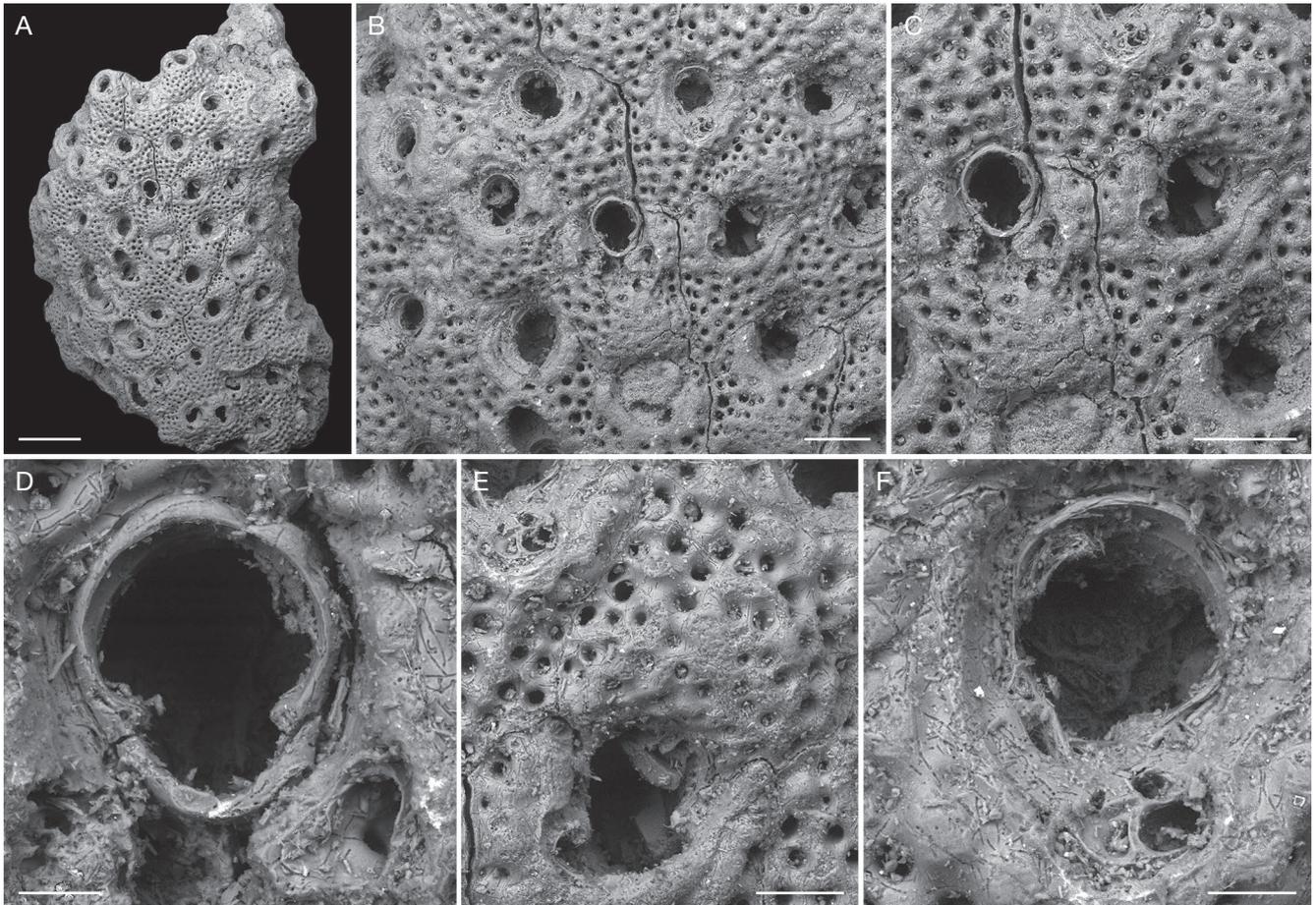


FIG. 6. — *Hemicosciniopsis incrustans* Vigneaux, 1949, figured syntype C.B.97-1, Aquitanian, early Miocene, Pessac, Lorient, Gironde, Aquitaine, France. **A**, general view of the colony; **B**, group of ovicellate and non-ovicellate zooids; **C**, close-up of an autozooid and ovicellate zooid showing dimorphic orifices; **D**, close-up of an autozooid orifice with suboral avicularium; **E**, close-up of the ovicell and orifice of a maternal zooid; **F**, close-up of a suboral avicularium showing complete crossbar. Scale bars: A, 500 μ m; B, C, 200 μ m; D, F, 50 μ m; E, 100 μ m.

REMARKS

The two small fragments of *Hemicosciniopsis incrustans* available for study are likely to have encrusted an ephemeral substrate, such as an alga or seagrass, based on the hollow, cylindrical colony-form.

Family PHIDOLOPORIDAE Gabb & Horn, 1862

Genus *Pleuromucrum* Vigneaux, 1949

Lifuella Gordon & d'Hondt, 1997: 21, n. syn.

Allorhynchozoon Liu in Liu, Yin & Ma, 2001: 821, n. syn.

TYPE SPECIES. — *Pleuromucrum saucatsense* Vigneaux, 1949 by original designation.

EMENDED DIAGNOSIS. — Colony encrusting. Zooids with convex frontal shield, nodular, imperforate apart from occasionally sparse marginal areolar pores. Primary orifice bell-shaped, with a broadly arcuate, smooth-rimmed anter and more or less developed condyles. Oral spines present in both fertile and infertile zooids. A suboral mucro often developed. Adventitious avicularia, when present, triangular and latero-oral or sparse on the frontal shield, budded from marginal areolar pores. Ovicells subimmersed, globular, with a widely arched opening.

REMARKS

Since its introduction by Vigneaux (1949) the genus *Pleuromucrum* has been largely overlooked, although Cheetham (1963: 73) placed it in synonymy with *Pleurolyrula* Vigneaux, 1949. However, *Pleurolyrula* as the name suggests possesses a lyrula which is absent in *Pleuromucrum*. Examination of the type species of *Lifuella* Gordon & d'Hondt, 1997, *Lepralia multidentata* Thornely, 1905 (Fig. 7), and the type species of *Pleuromucrum*, *P. saucatsense* Vigneaux, 1949 (Fig. 9), allowed us to ascertain the close similarity between these two genera, and consequently *Lifuella* is here considered as a junior subjective synonym of *Pleuromucrum*.

Gordon & d'Hondt (1997: 58) introduced *Lifuella* for *Lepralia calyciformis* Philipps, 1900, as well as all of the tropical and warm-temperate species previously attributed to *Hippoporella* Canu, 1917, which seemingly had little in common with the boreal-arctic type species of *Hippoporella*, *H. hippopus* (Smitt, 1868), including the type species of *Lifuella*, *L. multidentata* (Thornely, 1905). Subsequently, Tilbrook *et al.* (2001: 95) assigned *Lifuella calyciformis* to the new genus, *Fodinella* Tilbrook, Hayward & Gordon, 2001, which differs from *Lifuella* in having a beaded anter.

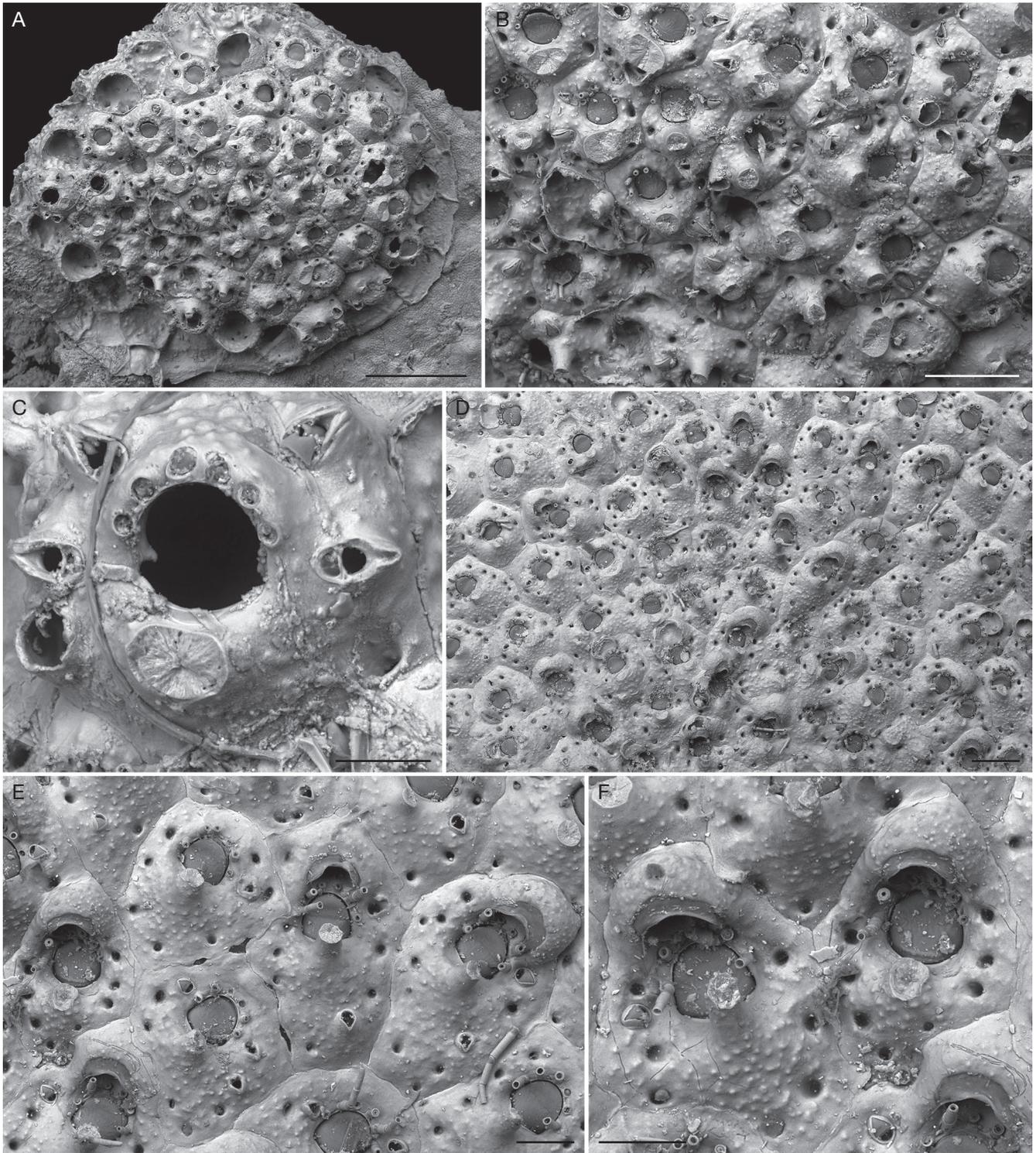


FIG. 7. — *Pleuromucrum multidentatum* (Thornery, 1905) n. comb. **A–C**, lectotype NHMUK 1906.12.3.4, Recent, Ceylon. **A**, general view of the colony; **B**, group of zooids; **C**, close-up of an autozooid showing six oral spine bases, orificial condyles, stout broken-off suboral mucro and multiple adventitious avicularia budded from marginal areolar pores. **D–F**, syntype, NHMUK 1975.7.28.24, Recent, Ceylon. **D**, general view of the colony; **E**, group of autozooids and ovicellate zooids; **F**, close-up of two ovicellate zooids. Scale bars: A, 500 µm; B, C, D, 200 µm; E, F, 100 µm.

Allorhynchozoon Liu in Liu, Yin & Ma, 2001 is a junior subjective synonym of *Lifuella* (<http://bryozoa.net> by P. Bock, accessed 10.I.2017) and therefore also of *Pleuromucrum*. The type species of *Hippoporella*, *H. hippopus*, dif-

fers from the type species of *Pleuromucrum*, *P. saucatsense*, in the ovicell originating from the distal zooid and in the presence of distinct basal pore-chambers (not obvious in *Pleuromucrum*).

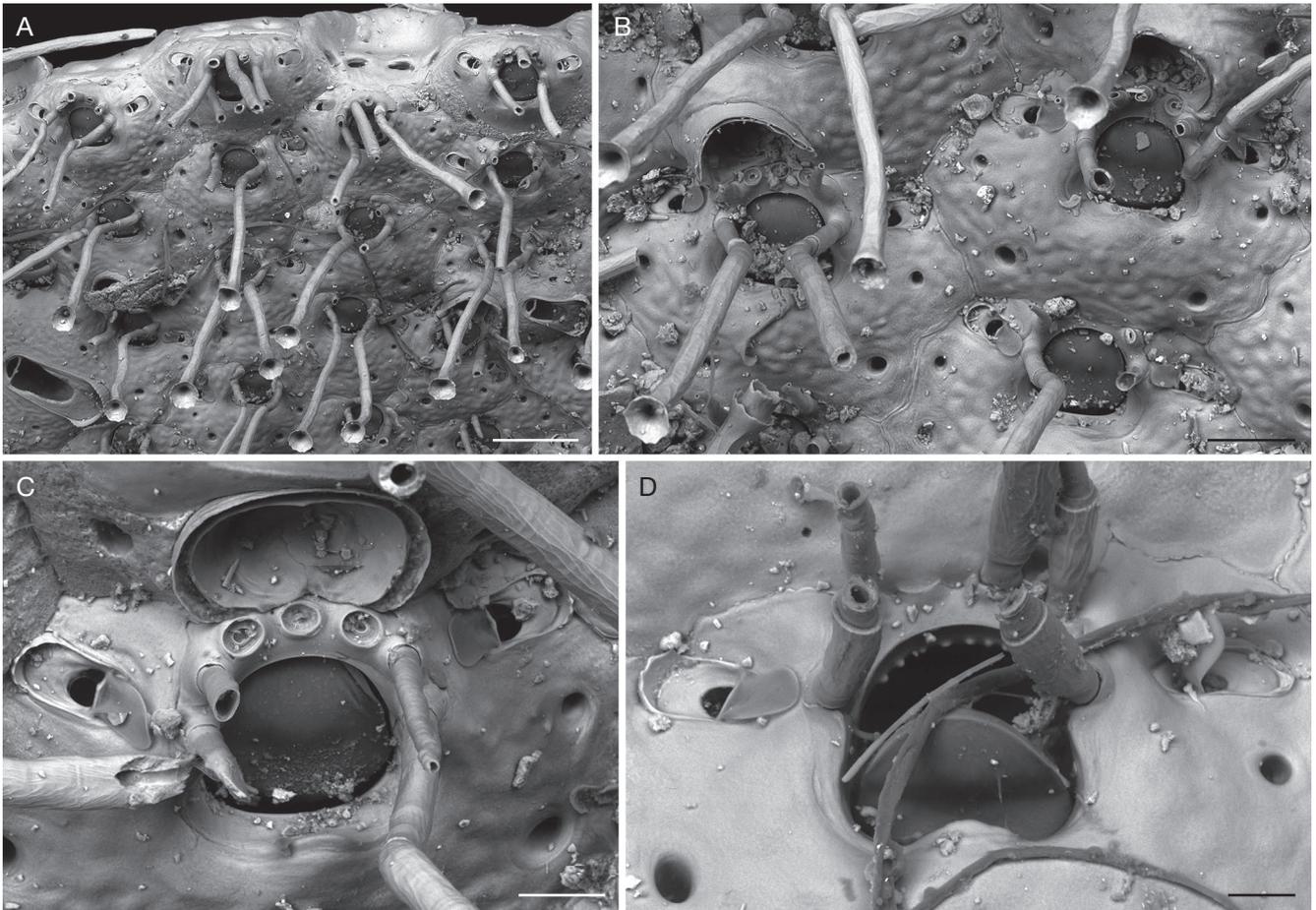


FIG. 8. — *Fodinella articulata* (Philippis, 1900) n. comb., syntypes NHMUK 1999.3.9.7a, b, Recent, Lifu, Loyalty Island, Sandal Bay. **A**, group of zooids; **B**, two ovicellate zooids; **C**, close-up of the distal part of a zooid showing the ovicell in formation, seven spine bases and the distolateral avicularia with serrated rostrum tips; **D**, close-up of an orifice showing the beaded anter and proximal mucro. Scale bars: A, 200 µm; B, 100 µm; C, 50 µm; D, 30 µm.

Of the seven species currently included in *Lifuella*, we are able to reassign two – *L. multidentata* (Thornely, 1905) and *L. gorgonensis* (Hastings, 1930) (see Di Martino *et al.* 2017) – to *Pleuromucrum* based on the re-examination of the type material, while a further three can be transferred to *Pleuromucrum* based on SEM images published in the literature: *L. porelliformis* (Kirkpatrick, 1888) *sensu* Tilbrook *et al.* (2001: 96, fig. 20C), *L. lepralielloida* (*Pleuromucrum lepralielloidum* n. comb.; Liu *in* Liu *et al.* 2001: pl. 80, figs 1-3) and *L. granulata* (*Pleuromucrum granulatum* n. comb.; Liu *in* Liu *et al.* 2001: pl. 80, figs 4-6). Re-examination of the type material of *Lifuella articulata* (*Fodinella articulata* n. comb.; Philippis 1900) revealed a beaded anter (Fig. 8) typical of *Fodinella*, to which it is here reassigned. *Lepraliella moorabolensis* (MacGillivray, 1895) *sensu* Gordon (1984) was tentatively placed in *Lifuella* by Tilbrook *et al.* (2001). Based on Gordon's (1984: 123) description the anter of this species as “smoothly rounded distally with no beading”, this species fits within the diagnosis of *Pleuromucrum*. However, the specimen figured by (Gordon 1984: pl. 50, fig. D) shows small oval adventitious avicularia with serrated rostrum tips more typical of species of *Fodinella*. Restudy of the type material of *L. moorabolensis* is needed to ascertain whether this fossil Australian species is

conspecific with the Recent New Zealand species, and into which genus it should be referred.

Two further fossil species of *Pleuromucrum* were found in the early Miocene Chipola Formation of Florida (Di Martino *et al.* 2017).

Pleuromucrum saucatsense Vigneaux, 1949 (Fig. 9)

MATERIAL EXAMINED. — Figured syntypes (Vigneaux 1949: 105, pl. 10, figs 6, 7), C.B.317-1 and C.B.318-2. C.B.318-2 is here designated as the lectotype of the species.

TYPE LOCALITY. — Saucats, Pont-Pourquey, Gironde, Aquitaine, France.

AGE. — Burdigalian, early Miocene.

DESCRIPTION

Colony encrusting, multiserial, unilaminar (Fig. 9A). Autozooids distinct, delineated by narrow interzooidal furrows, quincuncially arranged, hexagonal, longer than wide (mean L/W 1.45). Frontal shield convex, granular, imperforate except for a single row of subcircular to elliptical, marginal areolar

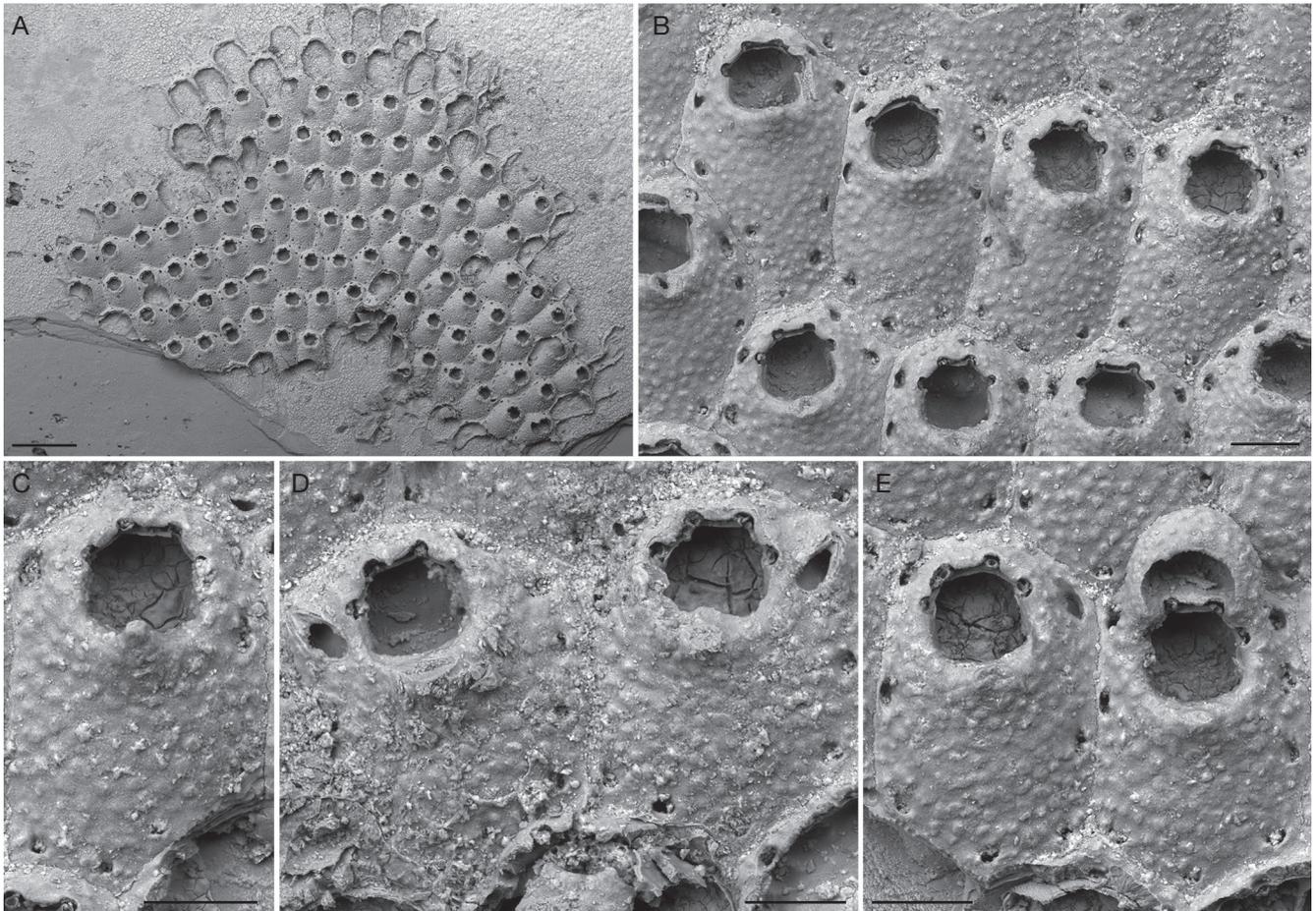


FIG. 9. — *Pleuromucrum saucatsense* Vigneaux, 1949, figured syntype C.B.318-2, Burdigalian, early Miocene, Saucats, Pont-Pourquey, Gironde, Aquitaine, France. A, general view of the colony; B, group of autozooids; C, close-up of an autozooid showing the suboral mucro; D, two autozooids with adventitious avicularia; E, close-up of an autozooid and an ovicellate zooid. Scale bars: A, 500 μ m; B, C, D, E, 100 μ m.

pores, 15–25 μ m long (Fig. 9B). Orifice bell-shaped, almost equidimensional (Fig. 9C, D); four distal oral spine bases in both ovicellate and non-ovicellate zooids, about 10 μ m in diameter (Fig. 9C, D). Suboral mucro conical with a rounded tip (Fig. 9C). Adventitious avicularia single or absent, latero-oral, rounded triangular, distolaterally directed (Fig. 9D); crossbar not observed. Ovicells subimmersed, with the same granular appearance as the frontal shield, imperforate, with a widely arched opening (Fig. 9E).

MEASUREMENTS

ZL 368 ± 34 , 308–435 (20); ZW 254 ± 29 , 211–319 (20); OL 85 ± 4 , 79–82 (20); OW 105 ± 4 , 103–108 (20); OvL 105 ± 4 , 103–108 (2); OvW 133 ± 11 , 126–141 (2); AvL 72 ± 8 , 66–78 (2); AvW 37 ± 2 , 36–39 (2).

REMARKS

In the two type specimens available for study we observed only two avicularia, both lacking a pivotal bar, which may be a preservational artifact rather than a genuine absence. As the presence of a single latero-oral avicularium may be related to the age of the colony, we cannot exclude the possibility that older colonies of this species could develop paired latero-oral

avicularia, as well as other avicularia sparse on the frontal shield and budded from marginal areolar pores, as observed for other species of the genus. *Pleuromucrum saucatsense* differs from *P. multidentatum* (Thornely, 1905) n. comb. in having four oral spine bases instead of six, a bell-shaped orifice without well defined condyles, and a slender and shorter suboral mucro. Furthermore, zooids in *P. multidentatum* n. comb. are generally smaller (ZL 298 ± 50 , 209–389 [20]; ZW 274 ± 41 , 202–341 [20]), although highly variable in size, and with a lower mean ratio L/W (1.09 vs 1.45) than those of *P. saucatsense*. Among other species here assigned to *Pleuromucrum*, *P. gorgonensis* (Hastings, 1930) n. comb. and *P. porelliformis* (Kirkpatrick, 1888) n. comb. differ in having two and eight oral spine bases respectively. *P. gorgonensis* n. comb. also differs in having a trifid suboral mucro and elongate adventitious avicularia. *Pleuromucrum porelliformis* n. comb. is characterised by a finely serrated lip on the distal edge of the suboral mucro.

DISCUSSION

Restudy of the long-neglected bryozoans described by Vigneaux (1949) from the Miocene of Aquitaine, France, has focused on

type specimens of the type species of five cheilostome genera introduced in this work. Application of SEM has allowed the identities of *Hemiphylactella*, *Pleuromucrum*, *Stephanollina*, *Schizosmittina* and *Hemicosciniopsis* to be clarified for the first time. Whereas *Schizosmittina* has been used as a repository for several Eocene–Recent bryozoan species, the other genera have been largely forgotten, to some extent because their identities could not be clearly understood from Vigneaux’s descriptions and figures. None of Vigneaux’s genera can be considered as junior synonyms of earlier genera and all have taxonomic utility. One genus – *Pleuromucrum* – is interpreted as an objective senior synonym of *Lifuella* Gordon & d’Hondt, 1997 and *Allorhynchozoon* Liu in Liu, Yin & Ma, 2001.

Further studies are required of the Vigneaux and other collections from the Miocene of Aquitaine to elucidate the taxonomy and stratigraphical distributions of bryozoans from a region containing the historical stratotypes of two Miocene stages, the Aquitanian and the Burdigalian.

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