



Revision of the type species of some cheilostome bryozoan genera in the collection of the Swedish Museum of Natural History

EMANUELA DI MARTINO

Natural History Museum, University of Oslo, Norway.

e.d.martino@nhm.uio.no; <https://orcid.org/0000-0002-3892-4036>

Abstract

The zoological dry collection of the Swedish Museum of Natural History in Stockholm includes an important, historical bryozoan section that is rich in species and specimens and also diverse from a geographical point of view. This collection also contains the type specimens of the type species of some cheilostome bryozoan genera introduced by several naturalists and bryozoologists between the mid-1800s and 1900s. With a few exceptions, these have not been revised since the advent of scanning electron microscopy as a standard tool for bryozoan taxonomy. Here, the type specimen(s) of the type species of the following six cheilostome genera are described and illustrated using SEM micrographs for the first time: *Cheilopora* Levinsen, 1909; *Fedorella* Silén, 1947; *Floridina* Jullien, 1882; *Lepraliella* Levinsen, 1917; *Smittipora* Jullien, 1882; and *Stenopsella* Bassler, 1952. The type specimen(s) of the type species of the recently introduced *Terwasipora* Reverter-Gil & Souto, 2019 and the relatively recently revised *Doryporella* Norman, 1903 are also illustrated for the first time. This revision has identified some erroneous geographical records for some of the species/genera examined, and has led to the proposed synonymy of *Stenopsella* with *Gigantopora* Ridley, 1881. Lectotypes have also been selected. All of the images produced will also be publicly available through the SMNH online catalogue. The digitisation of natural history museum collections, with prioritisation of historical type specimens, is of paramount importance to facilitate access to the fundamental taxonomic units for scientists worldwide.

Key words: Taxonomy, Bryozoa, Cheilostomatida, scanning electron microscopy, historical museum collections

Introduction

In the last two decades, increasing efforts to digitise specimens in natural history museum collections has resulted in the creation of many formal digital collection projects. The benefits of digitising natural history collections are multiple and obvious for all to see. First, digitisation can guarantee the future preservation of the collections in the event of calamities, such as earthquakes and fires, reducing a potential incalculable loss of unique specimens. For instance, the great importance of a preventive digitisation was emphasized after a fire broke out in 2018 at the Museu Nacional do Rio de Janeiro in Brazil, and an estimated 20 millions of irreplaceable specimens/artifacts were destroyed. Unfortunately, in that case the crowdsource citizen campaign to compile photos from previous visits in order to build a digital archive could only be launched post-event. Second, digitisation can promote collection accessibility to scientists worldwide, including the younger generations, removing financial, sociological and institutional barriers (e.g. Hedrick *et al.* 2020) or, as we have witnessed in the last two years during the Covid-19 pandemic, overcoming travel limitations, allowing natural history museums to remain at the forefront of modern biodiversity research (e.g. Nelson & Ellis 2018).

However, natural history museum collections are extremely varied and digitisation methods should be optimized depending on the specimen/group studied. In the digitisation of zoological and palaeontological collections, type specimens should be prioritised as these are the fundamental taxonomic units, and the process should involve expert taxonomists of the target group in order to produce images that show all of the key morphological features and are usable for taxonomic revisions, which are a necessary baseline for meaningful ecological and biodiversity analyses.

A recent SYNTHESYS+-funded visit has allowed access to the zoological collection of the Swedish Museum of Natural History (SMNH) in Stockholm that contains an important, historical bryozoan section, which is rich in both species and specimens, and also highly diverse from a geographical point of view. This collection also contains type specimen(s) of the type species of some critical cheilostome bryozoan genera introduced between the mid-1800s and the mid-1900s by several authors, based on species described by Swedish bryozoologists such as F.A. Smitt and L. Silén. These specimens, with a few exceptions (e.g. Berning & Kuklinski 2008; Tilbrook 2012; Di Martino & Rosso 2015), have not been revised since the advent of scanning electron microscopy (SEM) as a standard tool for bryozoan taxonomy.

The broad aim of this paper is to contribute to the current increasing effort of digitisation of key specimens in natural history museums by illustrating type specimens, for the first time using SEM micrographs, which will also be in the near future publicly available through the online catalogue of the SMNH, and giving updated descriptions. This work also aims to offer bryozoan taxonomists either a starting point for more thorough reviews of genera known to be wastebasket for many onychocellid species (e.g. *Smittipora*), or a clarification of the definition of some little-known genera (e.g. *Cheilopora*, *Fedorella*, *Lepraliella*). Synonymy between *Stenopsella* and *Gigantopora* is proposed, and erroneous geographical records for some of the taxa investigated are identified. Lectotypes were also selected.

Material and methods

The type specimens of the type species of eight cheilostome bryozoan genera, housed in the zoological dry collection of the SMNH in Stockholm, were studied. For six genera, the type specimen(s) of the type species are illustrated for the first time using scanning electron microscopy (SEM), namely *Cheilopora* [*C. sincera* (Smitt, 1868)]; *Fedorella* (*F. minima* Silén, 1947); *Floridina* [*F. antiqua* (Smitt, 1873)]; *Lepraliella* [*L. contigua* (Smitt, 1868)]; *Smittipora* [*S. abyssicola* (Smitt, 1873)]; and *Stenopsella* [*S. fenestrata* (Smitt, 1873)]. For the two remaining genera, namely *Terwasipora* [*T. complanata* (Norman, 1864)] and *Doryporella* [*D. spathulifera* (Smitt, 1868)], the type species have been illustrated using SEM images in previous, recently published works that for the former introduced the genus as new (Reverter-Gil & Souto 2019), and for the latter revised all the species included in the genus (Grischenko *et al.* 2000). However, both studies are based on non-type material of the type species and do not illustrate the type specimens.

SEM examination was conducted on uncoated specimens using a FEI Quanta 650 FEG-SEM microscope operated at low-vacuum and back-scattered electron mode at SMNH. Macro photographs of the type specimen of *Smittipora abyssicola* and *Terwasipora complanata* were taken using an Olympus Tough TG-4 camera in microscope mode, equipped with a LED-light guide.

Morphometric measurements were taken from SEM images using the image processing program ImageJ (available at <https://imagej.nih.gov/>). Abbreviations for the measurements are: AvL, avicularium length; AvW, avicularium width; AvOpL, avicularium opesia length; AvOpW, avicularium opesia width; KzL, kenozooid length; KzW, kenozooid width; KzOpL, kenozooid opesia length; KzOpW, kenozooid opesia width; OpL, opesia length; OpW, opesia width; OpL*, opesia length in ovicellate zooid; OpW*, opesia width in ovicellate zooid; OrL, orifice length; OrW, orifice width; OrL*, orifice length in ovicellate zooid; OrW*, orifice width in ovicellate zooid; OvL, ovicell length; OvW, ovicell width; ZL, autozooid length; ZW, autozooid width.

Systematic account

Phylum Bryozoa Ehrenberg, 1831

Class Gymnolaemata Allman, 1856

Order Cheilostomata Busk, 1852

Superfamily Calloporoidea Norman, 1903

Family Doryporellidae Grischenko, Taylor & Mawatari, 2004

Genus *Doryporella* Norman, 1903

Type species *Lepralia spathulifera* Smitt, 1868

Doryporella spathulifera (Smitt, 1868)

(Fig. 1; Table 1)

Lepralia spathulifera Smitt, 1868: 20, 124, pl. 26, figs 94–98.

Doryporella spatulifera: Norman 1903: 106.

Doryporella spathulifera: Grischenko, Mawatari & Taylor 2000: 248, fig. 1.

Material examined. Lectotype (designated here) SMNH-Type-1729a (Fig. 1), and paralectotype SMNH-Type-1729b; two colonies encrusting the same bivalve shell; Hinlopen Strait, Waigatsöarna, Svalbard, Norway; 79°10'N 19°E; depth 55 m. Leg. Swedish Arctic Expedition 1861.

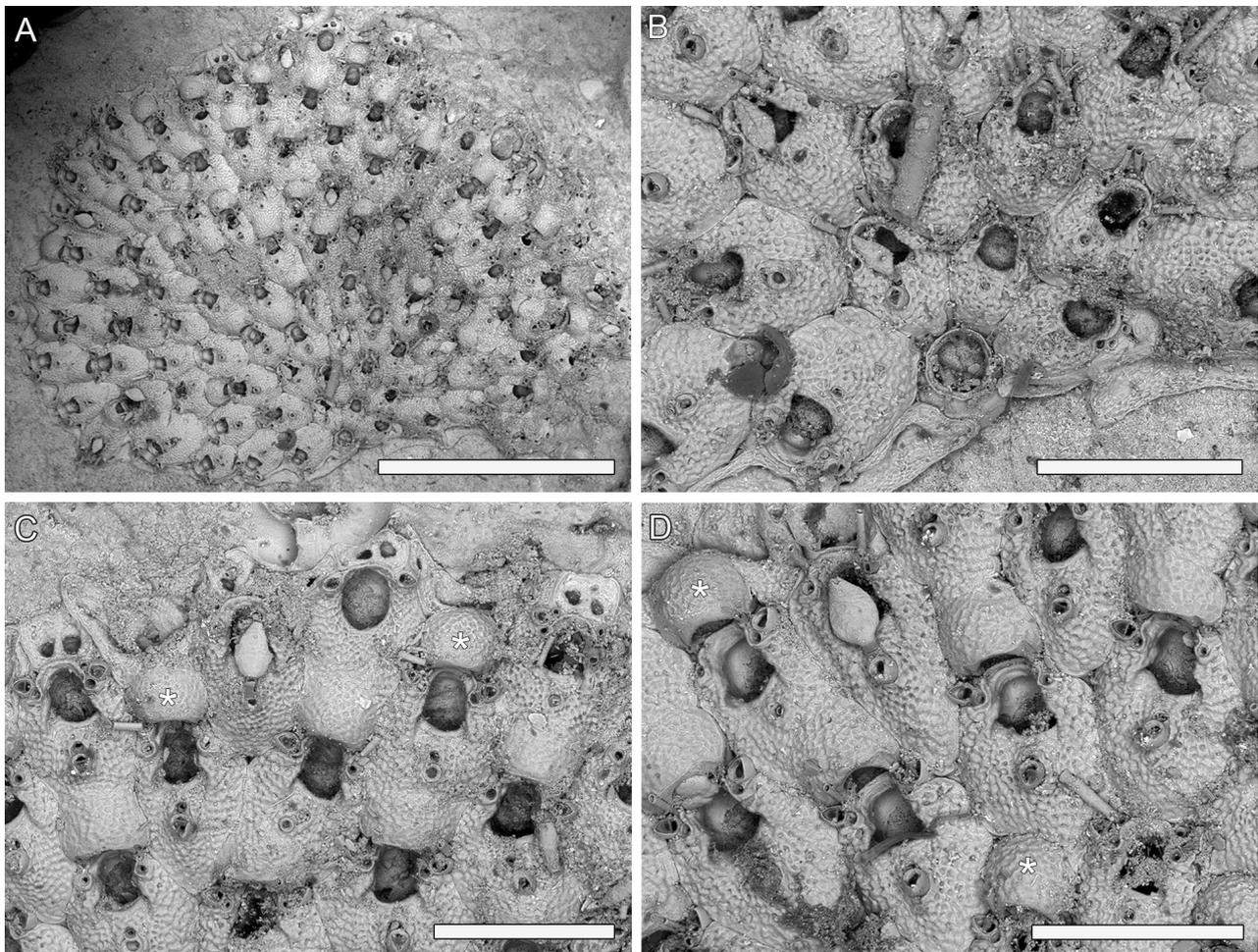


FIGURE 1. *Doryporella spathulifera* (Smitt, 1868), Lectotype (designated here) SMNH-Type-1729a, Hinlopen Strait, Svalbard, Norway. A. General view of the fan-shaped colony with subsequent generations of zooids budded only distally from the ancestrula. B. Close-up of the tatiform ancestrula and periancestrular zooids. C. View of colony growing edge showing paired distal pore chamber windows. Asterisks indicate kenozooidal ovicells. D. Group of ovicellate zooids showing ovicells produced either by a kenozooid (asterisks) or the distal autozooid, the suboral spatula-like spine and triangular avicularia mandibles. Scale bars: A = 2 mm; B–D = 500 µm.

Remarks. The four species of the genus *Doryporella* have been thoroughly described and illustrated in Grischenko *et al.* (2000, 2004). No type material of *D. spathulata*, the type species of the genus, was illustrated by these authors, although among the specimens examined (Grischenko *et al.* 2000, p. 248) some are from the Swedish Arctic Expedition and collected off Svalbard, as the type material illustrated here.

The two syntype colonies are both fan-shaped, 3.8 x 5.5 mm (lectotype) and 3.5 x 4.2 mm (paralectotype) in size respectively, with subsequent generations of autozooids budded only distally from the ancestrula (Fig. 1A).

The study of this material allows a better observation of the ancestrula confirming it to be tatiform (Fig. 1B), about 290 µm long by 220 µm wide; nine spines, about 70 µm long, are placed on the smooth gymnocyst and encircle the subcircular opesia, 175 µm long by 165 µm wide; the gymnocyst is well-developed proximally (90–100 µm); the opesia is outlined by a raised rim indented by the spines. An additional observation is related to the ovicell, which in the same colony can either be kenozooidal, occupying the space between autozooids and developed at the colony growing edge (Fig. 1D), or produced by the distal zooid and occupying most of its frontal surface. In this latter case, the distal zooid sometimes fails to bud the frontal, centrally placed, adventitious avicularium (Fig. 1C).

Compared to size measurements reported in Grischenko *et al.* (2000), the syntype colony shows slightly larger autozooids and ovicells, but narrower opesia (Table 1); frontal and latero-oral avicularia are similar in size.

TABLE 1. Measurements in µm of *Doryporella spathulifera* (Smitt, 1868), Svalbard, Norway; SMNH-Type-1729a.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	15, 1	515	57	434	630
ZW	15, 1	400	42	332	513
OpL	5, 1	170	14	146	183
OpW	5, 1	118	12	101	130
AvL	15, 1	64	7	54	76
AvW	15, 1	52	4	44	58
OvL	20, 1	205	24	179	252
OvW	20, 1	265	17	239	310

Superfamily Microporoidea Gray, 1848

Family Onychocellidae Jullien, 1882

Genus *Floridina* Jullien, 1882

Type species *Mollia antiqua* Smitt, 1873

Floridina antiqua (Smitt, 1873)

(Fig. 2; Table 2)

Mollia antiqua Smitt, 1873: 12, pl. II, fig. 73.

Floridina antiqua: Jullien 1882: 284.

Material examined. Lectotype (designated here) SMNH-Type-1835a (Fig. 2), and paralectotypes SMNH-Type-1835b, c; three colony fragments encrusting bivalve shells; Florida, United States; depth 53 m. Leg. L.F. Pourtales 1868. Based on the original label, these are the specimens drawn in Smitt (1873, pl. 2, fig. 73).

Description. Colony encrusting, multiserial, uni- to multilaminar due to self-overgrowth, extensive, consisting of hundreds of zooids (Fig. 2A).

Autozooids arranged quincuncially, distinct with thin interzooidal furrows between slightly raised edges, hexagonal or pentagonal, distal edge rounded, proximal edge straight to slightly convex if the zooid is budded distally, or pointed acute if budded distolaterally, longer than wide (mean L/W 1.26) (Fig. 2B–D). Gymnocyst vestigial, visible along the zooidal margins only if slightly raised; cryptocyst extensive, occupying about half of zooidal frontal length, depressed and finely granular, outlined by a raised, striated rim, 35–60 µm wide.

Opesia occupying the remaining half of the zooidal length, bell-shaped with straight proximal margin (Fig. 2D), or trifoliate with more prominent lateral constrictions and opesiular indentations marked by slightly raised proximal margin, forming a trapezoidal process projecting into the opesia (Fig. 2E); an inner cryptocystal rim visible at the distal edge of the opesia in some non-ovicellate zooids (Fig. 2C); cryptocyst around the opesia with granules aligned in rows giving a striated appearance as along the zooidal margins.

Ovicellate zooids with distal edge formed either by the cryptocyst of the distal zooid (Fig. 2C), or sometimes cormidial and formed by the cryptocyst of the two distolateral, neighbouring autozooids (Fig. 2E), or an autozooid and a vicarious avicularium (Fig. 2B); opesia usually larger than in non-ovicellate zooids.

Vicarious avicularia infrequent (e.g. three avicularia out of 80 modules counted in a random portion of the colony; Fig. 2A) but occasionally clustered (Fig. 2B), pentagonal with raised, rounded, triangular rostrum showing the lateral, smooth gymnocyst (Fig. 2B); cryptocyst finely granular and striated along the margins as in autozooids; opesia elliptical, drop-shaped or ovoidal, centrally placed; an unusual rectangular rostrum observed in one avicularium (Fig. 2D), probably a teratology resulting from colony reparation.

Intramural budding observed in autozooids and vicarious avicularia, visible as a double rim of striated cryptocyst (Fig. 2E).

Putative kenozooids irregularly polygonal, with narrow cryptocyst having the same texture as autozooids and vicarious avicularia, and large elliptical to subcircular opesia (Fig. 2F), likely to be reduced and almost closed later in ontogeny (Fig. 2G).

Ancestrula not observed.

Remarks. When describing its specimens from Florida, Smitt (1873) refers to the Madeiran specimens of *Membranipora antiqua* of Busk (1858) as being very similar, differing only in the more pointed distal margin of some zooids. Busk's *Membranipora antiqua* was subsequently placed in *Onychocella* by Jullien (1882), and since then either considered as a distinct species or put in synonymy with *O. angulosa* and *O. marioni* (Taylor *et al.* 2018). Nonetheless, Jullien (1882) chose Smitt's *Mollia antiqua* as the type species of his new genus *Floridina*.

Floridina antiqua is considered a warm-water widespread species. Compared to the type material, the specimen from Ghana illustrated in Taylor *et al.* (2018, fig. 11a) has avicularia with more pointed rostra and deeper opesiular indentations owing to the more extensive tongue formed by the proximal margin of the orifice and more pronounced lateral constrictions; the specimens from the Florida *Oculina*-reef also show deeper opesiular indentations, and avicularia with more pointed, sometimes channelled, rostra (Winston 2016).

TABLE 2. Measurements in μm of *Floridina antiqua* (Smitt, 1873), Florida, United States; SMNH-Type-1835a.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	20, 1	502	40	406	580
ZW	20, 1	399	43	323	475
OpL	20, 1	214	12	192	235
OpW	20, 1	210	13	186	242
AvL	10, 1	479	38	417	532
AvW	10, 1	312	47	265	394
AvOpL	10, 1	206	25	151	246
AvOpW	10, 1	118	10	104	140
OpOvL	12, 1	249	19	221	282
OpOvW	12, 1	243	22	203	294
KzL	3, 1	471	40	424	496
KzW	3, 1	330	29	307	362
KzOpL	3, 1	232	10	224	243
KzOpW	3, 1	160	38	127	201

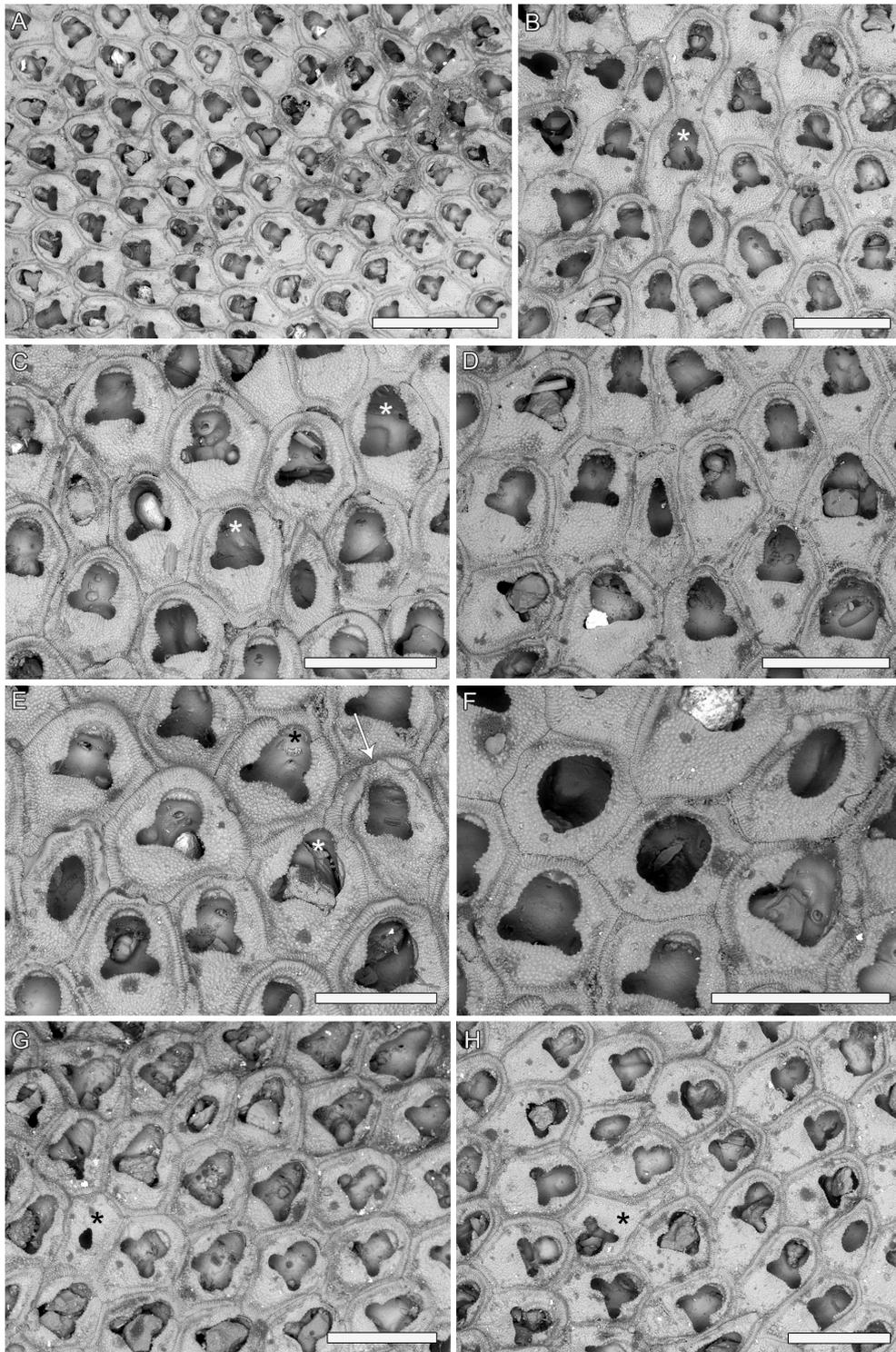


FIGURE 2. *Floridina antiqua* (Smitt, 1873), Lectotype (designated here) SMNH-Type-1835a, Florida, United States. A. Portion of the colony including about 80 zooids and three vicarious avicularia. B. Group of autozooids, ovicellate zooids (note the oecium formed by both the vicarious avicularium and the distal zooid, see asterisk), and vicarious avicularia with raised rostrum showing the smooth gymnocyst. C. Group of autozooids, ovicellate zooids (with oecium formed by the distal zooid, see asterisk), and vicarious avicularia. D. Group of autozooids and vicarious avicularium with an unusual rectangular rostrum. E. Close-up of zooids, those ovicellate with oecium formed by one (black asterisk) or two (white asterisk) distal zooids, avicularium with undulate, raised, triangular rostrum, and zooid showing signs of intramural budding (arrowed). F. Putative kenozooids. G. Group of zooids, vicarious avicularia and putative kenozooid with reduced opesia (asterisk). H. Group of zooids and vicarious avicularia, one zooid irregularly shaped and with reversed polarity (asterisk). Scale bars: A = 1 mm; B–D, F–H = 500 μ m; E = 400 μ m.

Di Martino *et al.* (2017) distinguished the Miocene *Floridina subantiqua* from the Chipola Formation of Florida based on two main characters: the lateral constrictions of the avicularium rostrum and the presence of a cryptocystal appendix projecting distally into the opesia. This latter feature was observed also in some zooids of the syntypes of *F. antiqua* (Fig. 2B), although it seems less developed and appears more arched, as a double, inner rim of the distal margin of the opesia.

Several teratologies have been observed in Smitt's syntypes, such as the vicarious avicularium with an unusual rectangular rostrum (Fig. 2D), autozooids and vicarious avicularia with calcification scars and concentric striated rims of cryptocyst (Fig. 2E), autozooids irregularly shaped and with reversed polarity (Fig. 2H), as well as unusual polymorphs, interpreted as kenozooids, with opesia variable in size from very large, occupying most of the frontal surface (Fig. 2F), to extremely reduced (Fig. 2G). All these structures seem to be related to colony repair after damage probably due to predation or growth on an irregular substrate, as also seen in other *Floridina* species (Di Martino *et al.* 2019). It is unlikely that the putative kenozooids, with reduced cryptocysts and extensive opesia, are incomplete autozooids given their position not at the growing edge, and with several rows of autozooids surrounding them both proximally and distally.

Floridina antiqua is not among the species re-described and illustrated by Winston (2005), which represents the most comprehensive revision of Smitt's Floridan bryozoans and is based on the material housed in the collection of the Museum of Comparative Zoology of Harvard University.

Genus *Smittipora* Jullien, 1882

Type species *Vincularia abyssicola* Smitt, 1873

Smittipora abyssicola (Smitt, 1873)

(Fig. 3; Table 3)

Vincularia abyssicola Smitt, 1873: 6, pl. I, figs 60, 61.

Smittipora abyssicola: Jullien 1882: 284.

Material examined. Lectotype [designated here; figured in Smitt (1873, fig. 61)] SMNH-Type-1815, North Atlantic Ocean, Florida, United States, depth 124 m, on a solitary coral. Leg. Gulf Stream Explorations 1868–69, coll. L.F. De Pourtales. Paralectotype SMNH-Type-9104, North Atlantic Ocean, off Cojima, Cuba, depth 824 m, on a phidoloporid bryozoan. Leg. Gulf Stream Explorations 1868–69, coll. L.F. De Pourtales.

Description. Colony starting with a more or less developed encrusting base (Fig. 3A, B), and later becoming erect, forming cylindrical branches, about 1 mm in diameter, comprised of 4–6 alternating longitudinal series of autozooids and vicarious avicularia (Fig. 3B, C, E), oligo- to multiserial (depending on the substrate available), unilaminar.

Ancestrula elliptical, similar to later autozooids but smaller (Fig. 3A, D), *c.* 500 µm long by 380 µm wide; cryptocyst extensive, finely granular, sloping inwards laterally, depressed and flat centrally; opesia rounded quadrangular, almost equidimensional, 176 µm long by 188 µm wide; three zooids budded directly from the ancestrula, one distally and two distolaterally, either exclusively autozooids (Fig. 3A), or both autozooids and vicarious avicularia (Fig. 3D), smaller than subsequent generations (first budded zooid: *c.* 525 µm long by 350 µm wide; first vicarious avicularium: *c.* 375 µm long by 295 µm wide); ancestrula later surrounded by six zooids.

Autozooids distinct with raised margins and shallow grooves, those of the encrusting base quincuncially or irregularly arranged, those forming the cylindrical branches arranged in alternating longitudinal series (Fig. 3C, E); semi-elliptical, elongate with V-shaped proximal edge, sometimes rounded hexagonal, longer than wide (mean L/W 1.56). Cryptocyst concave, finely granular, extensive (Fig. 3F). Opesia rounded quadrangular to rounded trapezoidal with proximal margin slightly concave (Fig. 3F) but slightly convex in periancestrular zooids (Fig. 3D).

Avicularia vicarious, smaller than autozooids, symmetrical, lozenge-shaped with acutely pointed proximal margin and rounded rostrum tip (Fig. 3D, F); mandible triangular (Fig. 3C), *c.* 600 µm long; cryptocyst concave and finely granular as in autozooids; opesia centrally located, oval to elliptical.

Fertile zooids not observed.

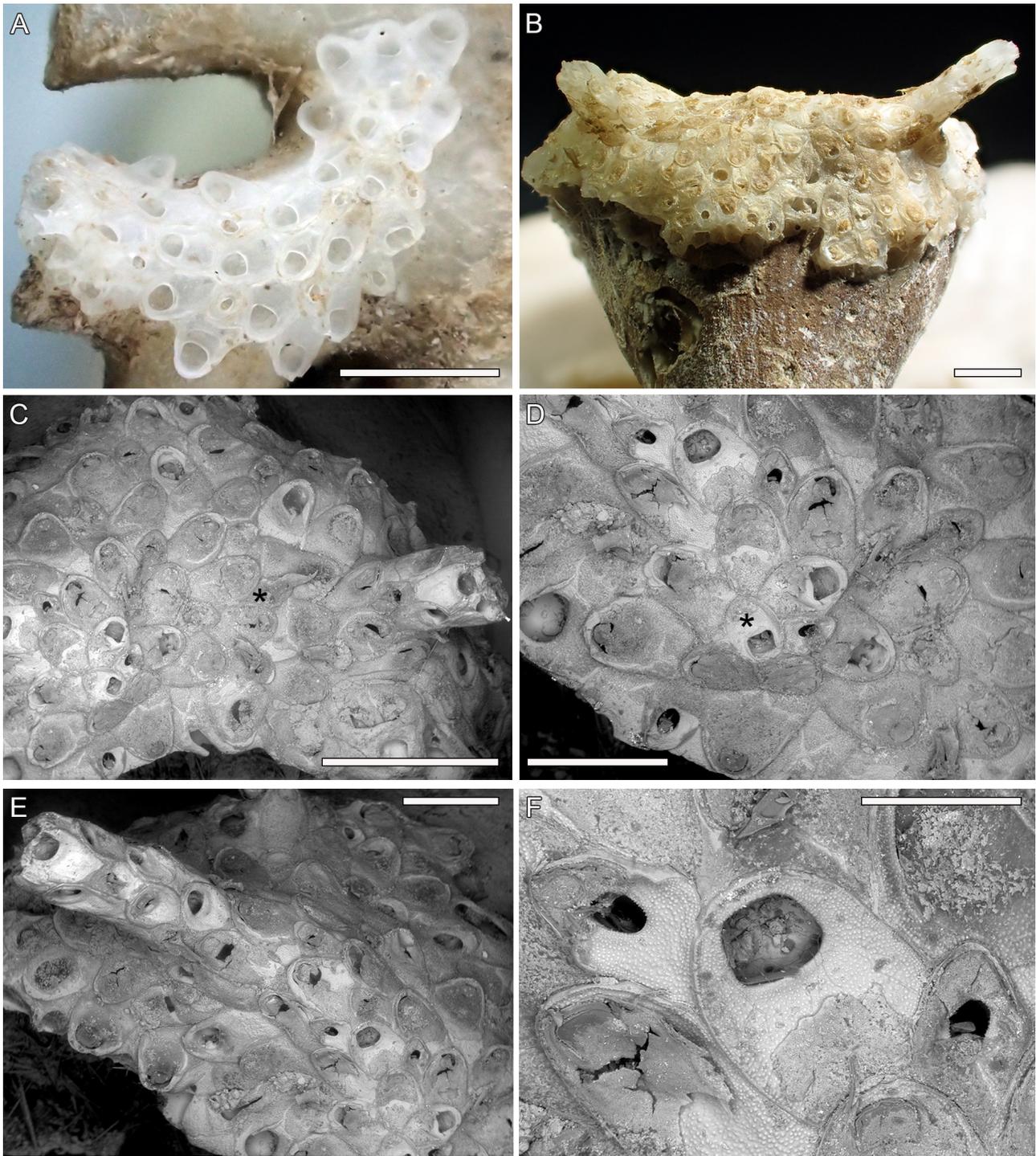


FIGURE 3. *Smittipora abyssicola* (Smitt, 1873). A. Paralectotype SMNH-Type-9104, off Cojima, Cuba. General view of the small colony encrusting a phidoloporida bryozoan. B–F. Lectotype (designated here) SMNH-Type-1815, Florida, United States. B. General view of the colony with encrusting base and two starting erect branches, encrusting a solitary coral. C. Group of zooids and vicarious avicularia (with triangular mandibles, see asterisk) at the encrusting base and at the start of an erect branch. D. Close-up of the ancestrula (asterisk) and periancestrular zooids and avicularia. E. Group of zooids and vicarious avicularia rising from the encrusting base to form an erect branch. F. Close-up of an autozooid and two vicarious avicularia. Scale bars: A–C = 2 mm; D, E = 1 mm; F = 400 μ m.

Remarks. In his description of *Vincularia abyssicola*, Smitt (1873) refers only to two specimens he obtained from Pourtales, one collected in deep waters off Cuba and encrusting a phidoloporida bryozoan (Fig. 3A), the other collected off Florida at a much lower depth and encrusting a coral (Fig. 3B). An additional specimen found in the

collection (Fig. 4; SMNH-Type-1786 North Atlantic Ocean, Florida, United States, depth 124 m, encrusting bivalve shell. Leg. Gulf Stream Explorations 1868–69, coll. L.F. De Pourtales) and catalogued as an additional syntype of *S. abyssicola* belongs instead to *S. americana* (Canu & Bassler, 1928). This species has leaf-shaped mandibles with long, pointed tips (Fig. 4A), and marked opesiular indentations (Fig. 4B).

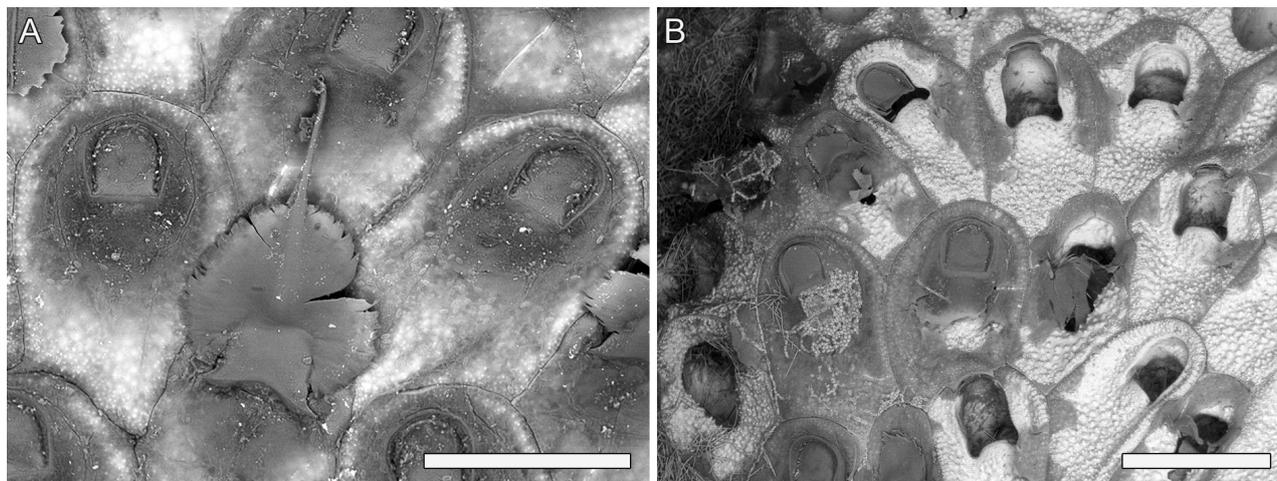


FIGURE 4. *Smittipora americana* (Canu & Bassler, 1928), catalogued as SMNH-Type-1786 of *S. abyssicola*, Florida, United States. A. Close-up of two zooids with opercula and vicarious avicularium with leaf-shaped, pointed mandible. B. Group of zooids, showing the opesia with indentations, vicarious avicularia and ovicells. Scale bars: A = 400 μm ; B = 500 μm .

Smittipora abyssicola, originally described from the western tropical Atlantic, was subsequently recorded pantropically, including the Pacific and Indian oceans. Some of these records were revised during the years, e.g. *S. abyssicola* sensu Harmer (1926) from Malaysia became the type species of *S. harmeriana* (Canu & Bassler, 1929), but some others await a revision. For instance, the specimen illustrated in Taylor *et al.* (2018, fig. 29) as *Smittipora abyssicola* from the west of East Channel, off Aldabra Island in the Indian Ocean, differs from the type specimens in having proportionally smaller opesia with distinct opesiular indentations, and avicularia with pointed rostra.

Onychocellid genera are all very similar and there is a limited number of characters to distinguish one genus from the other. The main features used to distinguish *Smittipora* from *Onychocella* are the relatively smaller opesia and the symmetrical avicularia in the former genus. In the type specimens of *Smittipora* studied here, the opesia are proportionally smaller but simply quadrangular/trapezoidal in shape, without proximal indentations or lateral constrictions. Nonetheless, a great number of species with proximal opesiular indentations are currently assigned to the genus.

As already highlighted by Taylor *et al.* (2018), a thorough revision is needed of the 42 Recent and fossil species currently assigned to *Smittipora* (Bock 2022), considering that some of these species have, in addition to the marked opesiular indentations, also asymmetrical vicarious avicularia.

TABLE 3. Measurements in μm of *Smittipora abyssicola* (Smitt, 1873), Florida, United States; SMNH-Type-1815.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	15, 1	908	109	777	1138
ZW	15, 1	581	78	388	718
OpL	5, 1	250	57	195	335
OpW	5, 1	251	11	239	265
AvL	13, 1	580	44	492	628
AvW	13, 1	394	50	304	473
AvOpL	6, 1	165	22	143	207
AvOpW	6, 1	109	25	91	159

Superfamily Celleporoidea Johnston, 1838

Family Phidoloporidae Gabb & Horn, 1862

Genus *Lepraliella* Levinsen, 1917

Type species *Cellepora ramulosa* forma *contigua* Smitt, 1868

Lepraliella contigua (Smitt, 1868)

(Fig. 5; Table 4)

Cellepora ramulosa forma *contigua* Smitt, 1868: 31, figs 198–201.

Lepraliella contigua: Levinsen 1917: 467.

Material examined. Lectotype (designated here) SMNH-Type-1695a (Fig. 5C–E), and paralectotypes SMNH-Type-1695b (Fig. 5A, B) and SMNH-Type-1695c (Fig. 5F); three colony fragments; North Atlantic Ocean, Hammerfest, Norway, depth 73–110 m. Leg. S. Lovén 1837.

Description. Colony encrusting, multiserial, uni- to multilaminar.

Autozooids quincuncially arranged (Fig. 5A, C) or irregularly arranged if in multilayered colonies (Fig. 5F); boundaries ill-defined, sometimes marked by marginal areolar pores and undulate grooves.

Frontal shield slightly convex centrally, nodular, imperforate apart from circular, marginal areolar pores, usually two per zooid, one located on the proximal corner and the other on the lateral corner (Fig. 5B, D) either side, 15–18 µm in diameter, from which secondary calcification obliterating the zooidal boundaries seems to spread.

Primary orifice semicircular, hidden proximally by the raised suboral avicularium, with two robust, rounded lateral condyles and smooth anter (Fig. 5D); secondary orifice reduced and eye-shaped (Fig. 5E); 3–5 oral spines (more commonly 4), equidistantly spaced, the base 25–45 µm in diameter, in both ovicellate and non-ovicellate zooids; all spines or only the most distal pair often obliterated because of the spreading of secondary calcification (Fig. 5D, E).

Adventitious avicularium suboral, placed on one side of the orifice, elliptical to slightly spatulate, raised distally, sloping proximally, directed proximo-laterally, seemingly with two triangular condyles often broken.

Ovicells subimmersed with a widely arched opening; oecium globular, resting on the next distal zooid, smooth, covered distally by secondary calcification (Fig. 5D).

Remarks. *Lepraliella contigua* is recorded from the Arctic, the northern Atlantic and the northern Pacific (Bock 2022). Smitt (1868) referred to the specimens from Hammerfest given to him by Prof. Lovén when first introducing this species, initially considering them as a variety of *Omalosecosa ramulosa* (Linnaeus, 1767) (previously *Cellepora*). Unfortunately, it is not possible to match the specimens with Smitt's drawings (1868, figs 198–201).

Levinsen (1917) when introducing the genus *Lepraliella* referred to two of Smitt's species, *L. contigua* and *L. hippopus*, without specifying a type, but with the latter subsequently used as the type species of the new genus *Hippoporella* by Canu (1917). Canu & Bassler (1920, p. 509) formally selected *Lepraliella contigua* as the type species of the genus *Lepraliella*. Levinsen's description and drawings of *L. contigua* were based on some specimens collected from rocks off north-east Greenland during the Denmark Expedition 1906–1908, at depths shallower (10–15 and 20–40 m) than those of the syntypes. Levinsen's drawings (1917, figs 2–14) agree with the features shown by the syntypes studied here (Fig. 5).

Levinsen (1917) placed his new genus in the family Reteporidae (now Phidoloporidae), based especially on the size and shape of the oecia. Canu & Bassler (1920), Bassler (1935), and Osburn (1952) followed Levinsen (1917), while Gordon (1993) placed *Lepraliella* in the family Lepraliellidae Vigneaux, 1949. Gordon (1993) based his decision on the observation in *Lepraliella* of some features typical of the family Celleporariidae Harmer, 1957. These features included the smooth frontal shield, asymmetrical suboral mucro equipped with avicularium, widely open ovicell, ancestrula encircled with small spines, but not the lepralioid frontal shield. In addition, *Lepraliella* lacked the typical beaded anter of phidoloporids. Celleporariids were then considered allied to lepraliellids and the family Celleporariidae substituted with Lepraliellidae, this latter family name having priority.

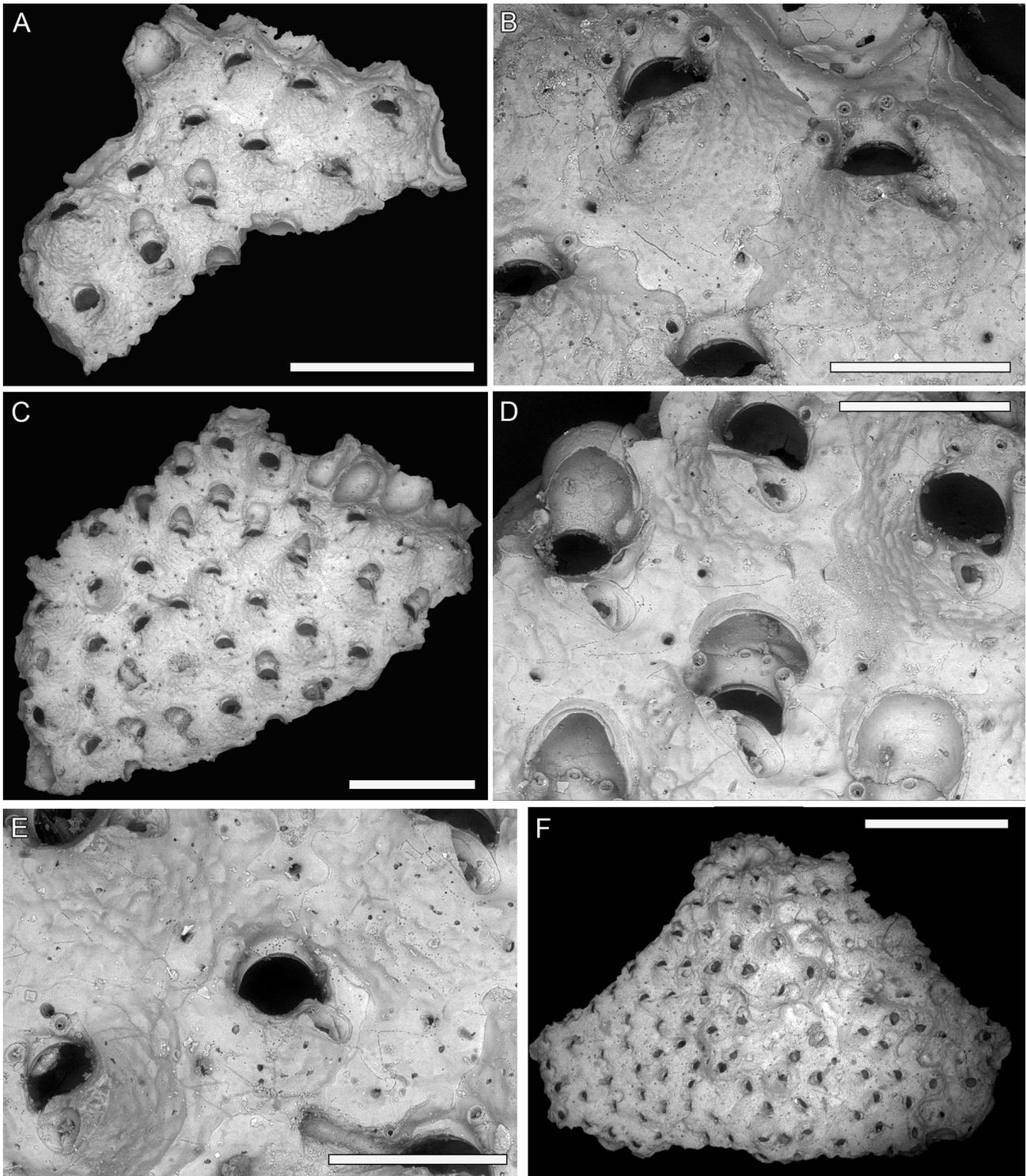


FIGURE 5. *Lepraliella contigua* (Smitt, 1868), Hammerfest, Norway. A, B. Paralectotype SMNH-Type-1695b. C–E. Lectotype (designated here) SMNH-Type-1695a. F. Paralectotype SMNH-Type-1695c. A, C, F. General view of the three colony fragments. B. Group of zooids, showing a variable number of oral spine bases, either due to spreading of calcification during ontogeny or to the development of ovicells. D. Close-up of zooids with suboral avicularium and developing oocyst. E. Close-up of a zooid showing the eye-shaped secondary orifice and the wrinkled to nodular surface of the frontal shield. Scale bars: A, C = 1 mm; B, D, E = 300 μ m; F = 2 mm.

Here, *Lepraliella* is returned to the Phidoloporidae based on the latest molecular phylogeny of cheilostome bryozoan available (Orr *et al.* in press), which shows *Lepraliella contigua* (specimen from the White Sea) well-nested within the monophyletic Phidoloporidae (Orr *et al.* 2021, in press), as sister clade to *Plesiocheilochasma*

Soule, Soule & Chaney, 1991, another phidoloporid genus having a smooth anter. *Lepraliella* shows also a close similarity in general appearance with other phidoloporid genera such as *Pleuromucrum* Vigneaux, 1949 and *Fodinella* Tilbrook, Hayward & Gordon, 2001. The main difference with *Pleuromucrum* is in ovicell formation: in *Lepraliella* the ovicells are formed solely by the distal zooid, in *Pleuromucrum* they are kenozooidal (Di Martino & Taylor 2017), while *Fodinella* has a denticulate anter (Tilbrook *et al.* 2001; Di Martino & Taylor 2017). Recent molecular phylogenies (Orr *et al.* 2021, in press) have shown that, with a few exceptions, cheilostome families are arbitrary and need to be rethought.

SEM images of *L. contigua* were first provided by Gordon (1993, figs 1–5), who figured a specimen from Svalbard, part of A.M. Norman's collection at the NHMUK, to illustrate the umbonuloid frontal shield.

Five additional species have been included in the genus *Lepraliella*, three fossil (Miocene of France and Pleistocene of Japan) and two Recent (Hawaii and Philippines). The unusual distribution of the genus in time and space was first noticed by Canu & Bassler (1929, p. 375) when describing a new species from the Philippines. Although originally recorded from the northern seas, these authors considered the discovery of the first fossil species of *Lepraliella* from the Aquitanian of France by Duvergier (1921) as a proof of a plausible much larger geographical distribution of the genus. However, *Lepraliella strophiae* Duvergier, 1921 is described and figured with a pseudoporous frontal shield that contrasts with the imperforate, umbonuloid frontal of the type species. Unfortunately, the low quality of the images provided in the original publications prevent to confirm or reject the generic attribution of the other species, calling for urging revision of the type specimens.

TABLE 4. Measurements in μm of *Lepraliella contigua* (Smitt, 1868), Hammerfest, Norway; SMNH-Type-1695a, b.

	N (zooids, fragments)	Mean	SD	Min	Max
ZL	10, 2	528	39	469	590
ZW	10, 2	347	35	302	417
AvL	14, 2	115	12	97	141
AvW	14, 2	66	10	47	86

Superfamily Mamilloporoidea Canu & Bassler, 1927

Family Cleidochasmatidae Cheetham & Sandberg, 1964

Genus *Fedorella* Silén, 1947

Type species *Fedorella minima* Silén, 1947

Fedorella minima Silén, 1947

(Figs 6, 7; Table 5)

Fedorella minima Silén, 1947: 55, text-figs 46–48, pl. 4, fig. 24.

Material examined. Lectotype (designated here) SMNH-128088a (Fig. 7A–C), tropical Atlantic Ocean, Anguilla, 18°N 62°W, depth 182–455. Leg. A.v. Goës 1869 (1861 in Silén 1947). Paralectotypes SMNH-128088b–h (seven colonies, two of which are figured here, Fig. 7D–F), same details as the lectotype. Paralectotypes SMNH-Type-8734, tropical Atlantic Ocean, Anguilla, 18°N 62°W, depth 364–546 m, ooze; 13 colonies (three of which figured here, Fig. 6). Leg. A.v. Goës 1869.

Description. Colony oval to pear-shaped (Figs 6A, C, 7A), 1.00–1.74 mm long by 0.88–1.37 mm wide (L/W 1.00–1.76, N 15), likely to be supported above the substrate by rhizoids.

Autozooids arranged in 5–6 whorls of up to 10–12 zooids each (the highest number of zooids usually at colony mid-length), distinct with deep grooves and a thin rim of smooth calcification, irregularly polygonal, pentagonal, hexagonal or rectangular, with undulate margins, almost equidimensional (mean L/W 1.01).

Frontal shield imperforate and coarsely tubercular; tuberculation seemingly increasing with ontogeny (Fig. 7A); tubercles in the first two generations of zooids concentrated along the proximal and lateral margins of the

zooid leaving the centre completely smooth (Figs 6D, 7E, F); in some zooids two pairs of circular marginal areolar pores visible laterally, one pair proximally and the other pair distally, at about the same level as orifice mid-length (Fig. 6D).

Primary orifice cleithriate, slightly longer than wide (mean L/W 1.1), a horseshoe-shaped anter separated from a widely arcuate sinus by two small pointed triangular condyles proximomedially directed (Figs 6B, 7B). Paired oral spine bases present distolaterally only on the first two generations of autozooids (Figs 6D arrowed, 7F). Smooth closure plates observed sealing the orifice of the zooids in the first whorls (Fig. 7F)

Adventitious avicularia of two types, present on the majority of autozooids, single or paired, placed lateral to the orifice; type 1 avicularia drop-shaped, small, with slightly raised, triangular rostrum directed laterally (Figs 6D, 7E, F) or slightly distolaterally (Figs 6B, D, 7B), with complete crossbar, placed at level with the distal third of orifice length; type 2 avicularia spatulate, large, with raised, spoon-shaped, serrated rostrum (Figs 6B, 7B, C) directed distally or slightly distolaterally, with complete crossbar, placed at level with the orifice proximal margin. When paired, three combinations of avicularia types were observed: (i) two small drop-shaped (Figs 6D, 7B); (ii) one small drop-shaped and one large spatulate (Fig. 6B); (iii) two large spatulate (Fig. 7B, C). When single, either types of avicularia observed (e.g. only type 1 see Figs 6D, 7E, F; only type 2 see Fig. 6C).

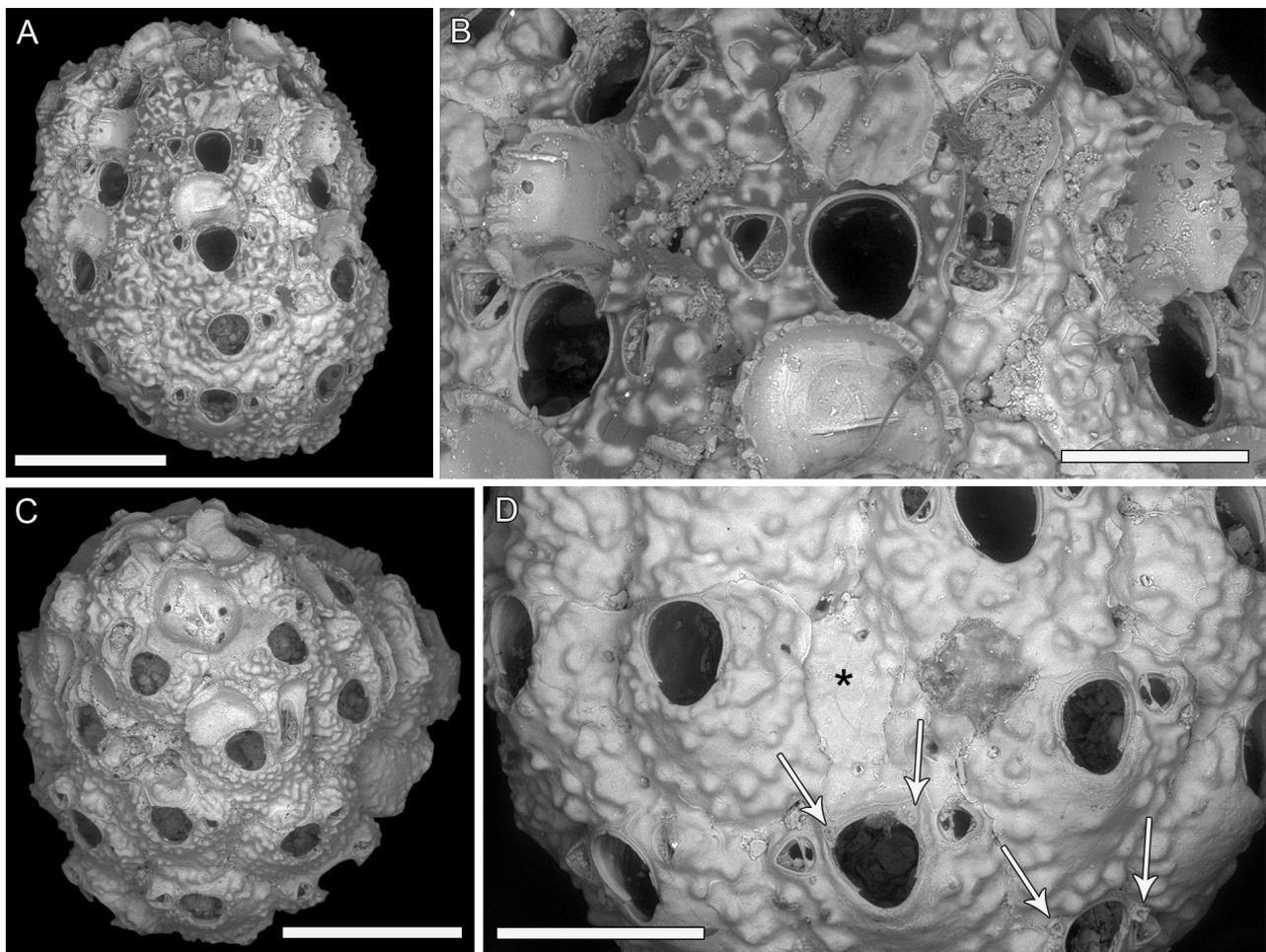


FIGURE 6. *Fedorella minima* Silén, 1947, Anguilla. A, B. Paralectotype SMNH-Type-8734a. A. General view of the colony. B. Close-up of a zooid with paired avicularia, one small and triangular, the other one giant and spatulate. C. Paralectotype SMNH-Type-8734b, general view of the colony with zooids having single avicularium. D. Paralectotype SMNH-Type-8734c, group of zooids, some with paired distolateral, oral spine bases (arrowed) and a kenozooid (asterisk). Scale bars: A, C = 500 μ m; B = 200 μ m; D = 300 μ m.

Ovicells prominent, globular, occupying the entire length of the frontal shield of the next distal zooid; oecium coarsely tubercular as zooidal frontal shield but evenly and densely pseudoporous; pseudopores circular, about 10 μ m in diameter, placed at the centre of subcircular pits, about 25 μ m in diameter (Fig. 7C, D); oecial aperture large, about 85 x 105–125 μ m, rounded triangular (Fig. 7D), not closed by the zooidal operculum.

Kenozooids rare, rectangular, as long as autozooids but narrower, without openings but with two marginal areolae at opposite corners as seen also in autozooids (Fig. 6D asterisk), seemingly space-fillers owing to colony reparation.

Intramural budding observed in autozooids, visible as a series of concentric orificial rims (Fig. 7E).

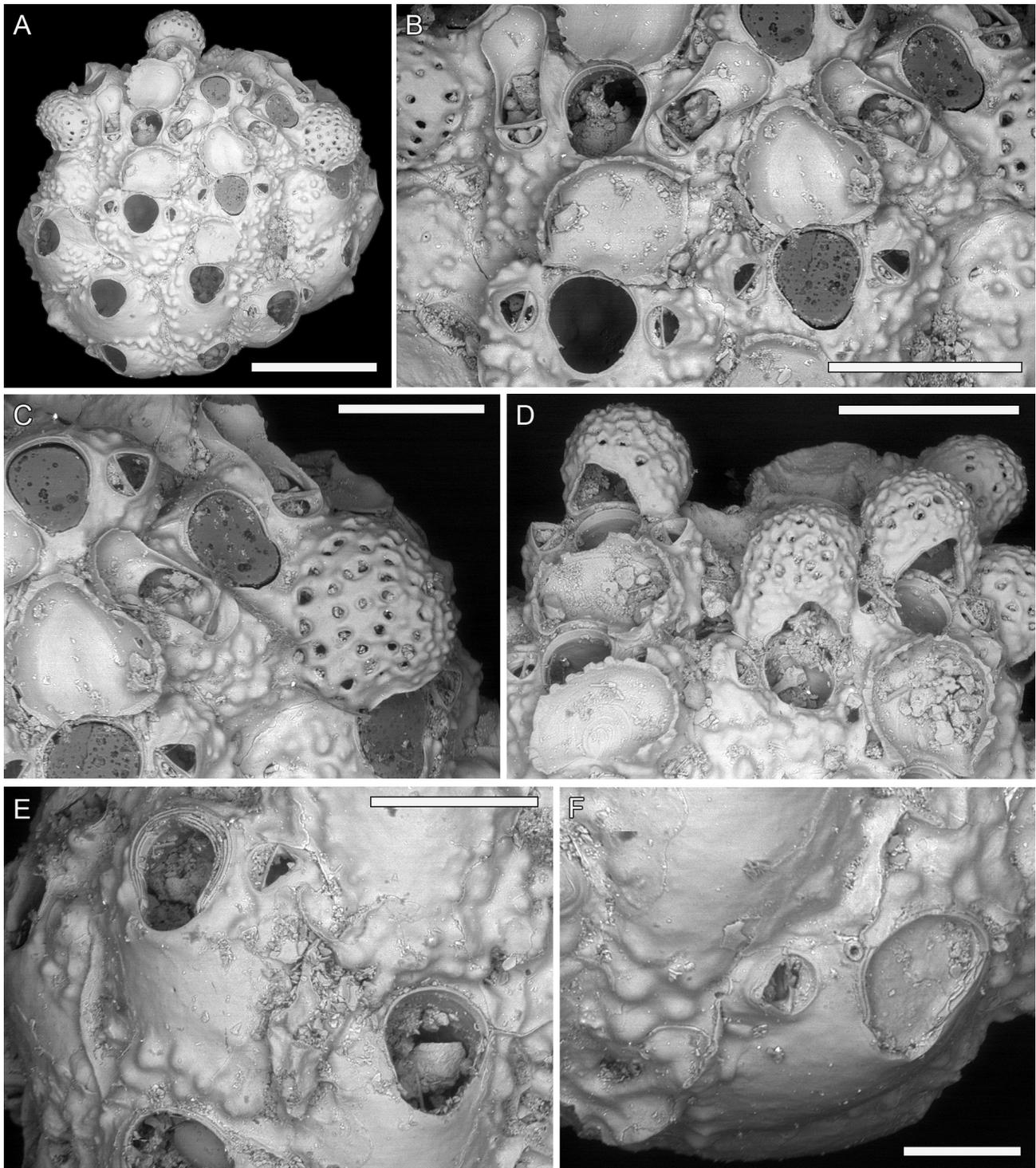


FIGURE 7. *Fedorella minima* Silén, 1947, Anguilla. A–C. Lectotype (designated here) SMNH-128088a. A. General view of the colony. B. Group of zooids, showing avicularian variability, the shape of the orifice and opercula. C. Close-up of a zooid with paired giant avicularia and lateral view of an ovicell. D. Paralectotype SMNH-128088b, group of ovicellate zooids showing the triangular opening of the oecium. E, F. Paralectotype SMNH-128088c. E. Close-up of two zooids with only one or completely lacking avicularia; the orifice of the zooid on the left shows signs of repetitive intramural budding. F. Close up of an orifice with closure plate. Scale bars: A = 500 μ m; B, D = 300 μ m; C, E = 200 μ m; F = 100 μ m.

Remarks. There is a discrepancy in the number of colonies and related depth ranges between the material currently available in the SMNH collection and the batches of specimens mentioned in Silén (1947). Silén listed 21 specimens from 150–375 m depth, 11 from 300–450 m depth, and two from 450–600 m depth, while the syntypes studied here include 13 colonies reported from a depth of 366–546 m, and eight colonies collected at 182–455 m. Another discrepancy is related to the year of collection, which is reported as 1861 by Silén (1947) but 1869 on the specimen labels. The colony figured in Silén (1947, pl. 4, fig. 24) in addition of not being identifiable among the specimens available, also lacked both the large spatulate avicularia and ovicells, which were instead described and drawn in his text-figs 47 and 48, making it, even if identifiable, not the ideal candidate as the type specimen. Based on the above-mentioned reasons, a lectotype (SMNH-128088a) is here designated, based on the best preserved colony, as well as the most complete character-wise (Fig. 7A–C).

In the original description, Silén (1947) considered each colony as an internode and speculated that the colony itself was made of several internodes connected by tubes. There are neither direct observations nor morphological characters supporting this hypothesis. The original record is the only one available for this species and the genus is also monospecific. However, based on observations of other genera with similar colony-form (e.g. *Fedora* in Ascosiidae), it seems more likely that each colony was independent and rooted to the substrate by rhizoids or a chitinous tube.

Cook & Lagaaïj (1976) listed *Fedorella* among conescharelliniform genera, i.e. colonies with frontally budded zooids with reversed orientations. Gordon & d’Hondt (1997) rejected this statement based on the description and illustrations already provided in Silén (1947) and confirmed here.

TABLE 5. Measurements in μm of *Fedorella minima* Silén, 1947, West Indies, Anguilla; SMNH-Type-8734 and SMNH-128088.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	20, 5	352	43	283	422
ZW	20, 5	347	35	302	417
OrL	20, 5	154	6	145	165
OrW	20, 5	140	8	130	157
Av1_L	20, 5	68	5	60	78
Av1_W	20, 5	66	6	53	76
Av2_L	8, 4	228	22	197	271
Av2_W	8, 4	103	10	90	113
OvL	10, 6	188	19	156	211
OvW	10, 6	253	18	230	284

Superfamily Schizoporelloidea Jullien, 1882

Family Cheiloporinidae Bassler, 1936

Genus *Cheilopora* Levinsen, 1909

Type species *Discopora sincera* Smitt, 1868

Cheilopora sincera (Smitt, 1868)

(Fig. 8; Table 6)

Discopora sincera Smitt, 1868: 28, pl. 27, figs 178–180.

Cheilopora sincera: Levinsen 1909: 353, pl. 24, fig. 4a.

not *Cheilopora sincera*: Grischenko *et al.* 2007: 1125, fig. 31.

Material examined. Lectotype (designated here) SMNH-Type-1733, North Atlantic Ocean, Finnmark, northern Norway, encrusting a bivalve shell. Leg. S. Lovén.

Description. Colony encrusting, multiserial, uni- to multilaminar, extensive, encrusting a fragment of a bivalve shell on both sides.

Autozooids arranged in alternating, longitudinal rows (Fig. 8A), distinct with narrow, shallow grooves and a thin rim of raised calcification, elongate rectangular sometimes acutely tapering proximally, twice as long as wide (mean L/W 2.12).

Frontal shield flat proximally, slightly convex centrally and distally raised as a pointed (Fig. 8A), rounded (Fig. 8B) or anvil-shaped (Fig. 8D) suboral process, nodular and finely granular, densely and evenly perforated by circular or funnel-shaped pseudopores, 20–25 µm in diameter, except for the suboral area and the raising peristome (Fig. 8A–C); marginal areolae distinguishable from pseudopores by being larger and elliptical to drop-shaped, about 80 µm long, placed lateral to the orifice (budding sites for avicularia) and at proximal corners (Fig. 8C).

Orifice cormidial, formed by two or more autozooids (e.g. the zooid to which it belongs plus the distal neighbour as seen in Fig. 8C or also the lateral neighbours as in Fig. 8D), bell-shaped, slightly larger in ovicellate zooids; oral spines absent; closure plates, nodular as the frontal shield, observed sealing the orifice (Fig. 8D).

Adventitious avicularia rare, single or paired, budded from the latero-oral marginal areolae, elliptical to pear-shaped; rostrum slightly raised, rounded, directed laterally, indenting the frontal shield of the lateral neighbours; crossbar lacking; mandible semi-elliptical (Fig. 8B).

Ovicells endozooidal, flat to slightly convex, formed by an elongation of the proximal frontal shield of the next distal zooid (Fig. 8A); oecium rounded trapezoidal or triangular, nodular as the frontal shield but much less pseudoporous (Fig. 8B).

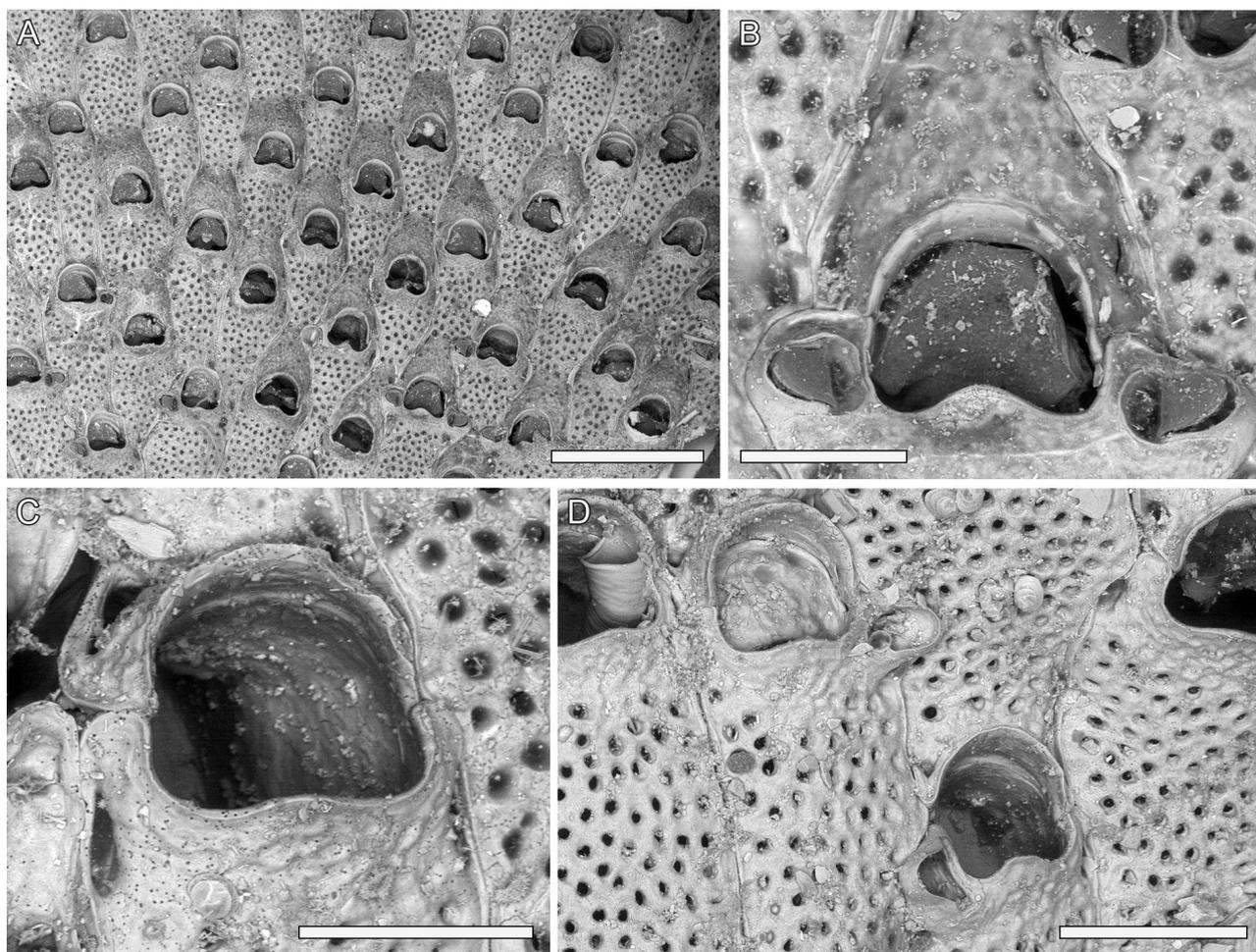


FIGURE 8. *Cheilopora sincera* (Smitt, 1868), Lectotype (designated here) SMNH-Type-1733, northern Norway. A. Group of zooids, most ovicellate. B. Close-up of an ovicell, orifice with operculum, and paired latero-oral avicularia with semielliptical mandibles. C. Close-up of an autozooidal orifice lacking avicularia. D. Close-up of two zooids with single avicularium and a closure plate. Scale bars: A = 1 mm; B, C = 200 µm; D = 300 µm.

Ancestrula not observed.

Remarks. Smitt (1868) described this species as *Discopora sincera* based on the material collected by Prof. Lovén in Finnmark, Norway, and found between 19–60 m depth encrusting ascidians, bivalve shells (as the studied syntype), and volcanic rocks.

Levinsen (1909) introduced the genus *Cheilopora* to accommodate, in addition to Smitt's species, four further species, i.e. *Hippoporina circumcincta* Neviani, 1896, *Mucronella praelucida* Hincks, 1884, *Mucronella praelonga* Hincks, 1884, and *Lepralia grimaldii* Jullien, 1903 in Jullien & Calvet (1903). Of these species only two, namely *C. sincera* and *C. praelucida*, can be confirmed as belonging to *Cheilopora*, while Neviani's species became the type of *Cheiloporina* Canu & Bassler, 1923, and Jullien's species has been accepted as its junior synonym (see Reverter-Gil & Fernández-Pulpeiro 1999, p. 43). ?*Cheilopora praelonga* is only tentatively placed in this genus. Levinsen (1909), however, did not indicate a type species for his new genus; the selection was made a few years later by Canu & Bassler (1917).

The Japanese material described and illustrated in Grischenko *et al.* (2007, fig. 31) as *Cheilopora sincera* does not correspond with the type specimen. In addition to the absence of avicularia, which could be lacking for developmental or environmental reasons, the main difference is in the ovicell. In the Japanese species, the ovicell is hyperstomial and occupies most of the frontal surface of the next distal autozooids which appear packed and squat. In the type specimen, ovicells are endozooidal and flat, do not occupy the frontal of the neighbour zooid but seem to elongate it (Fig. 8A, B). Nevertheless, Bassler (1936) proposed the family Cheiloporinidae to accommodate genera with endozooidal ovicells, such as *Cheiloporina* and *Cheilopora*, initially placed in the Hippopodinidae, the type species of which had hyperstomial ovicells. A better fit for the Japanese specimen seems to be *Cyclicopora* Hincks, 1884. The type species, *C. longipora* (MacGillivray, 1882) lacks avicularia, the ovicells are large, hyperstomial and globular (Cook *et al.* 2018, p. 208, fig. 3.158), and some zooids can also develop a pointed mucro (see also SEM image of the type specimen NMV F45691 available from Bock (2022) at http://bryozoa.net/cheilostomata/cyclicoporidae/cyclicopora_longipora.html).

TABLE 6. Measurements in μm of *Cheilopora sincera* (Smitt, 1868), Norway; SMNH-Type-1733.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	15, 1	958	82	860	1115
ZW	15, 1	452	62	368	569
OrL	10, 1	213	17	194	250
OrW	10, 1	265	12	244	287
OrL*	10, 1	243	22	205	278
OrW*	10, 1	288	9	269	300
AvL	18, 1	150	13	120	167
AvW	18, 1	117	12	98	135
OvL	12, 1	274	26	213	306
OvW	12, 1	370	26	341	417

Family Gigantoporidae Bassler, 1935

Genus *Stenopsella* Bassler, 1952

Type species *Hippothoa fenestrata* Smitt, 1873

Stenopsella fenestrata (Smitt, 1873)

(Fig. 9; Table 7)

Hippothoa fenestrata Smitt, 1873: 47, pl. 6, fig. 142.

Stenopsella fenestrata: Bassler 1952: 385.

Material examined. Holotype by monotypy SMNH-Type-1800, North Atlantic Ocean, S of Tortugas, United States, depth 31 m. Leg. Gulf Stream Explorations 1868–69.

Description. Colony encrusting, multiserial, unilaminar (Fig. 9A).

Autozooids distinct with deep interzooidal furrows, salient, quincuncially or irregularly arranged, hexagonal or rhomboidal, longer than wide (mean L/W 1.44)

Frontal shield convex, finely granular and crenulated in young zooids at colony growing edge (Fig. 9D) but developing spinose frontal processes in older generations of autozooids (Fig. 9C), evenly and densely perforated, up to four-fifth of its length corresponding to the attachment line of the peristome; pseudopores circular, minute, 8–10 μm in diameter; marginal areolae undistinguishable.

Primary orifice subcircular with pointed triangular condyles separating a quadrangular anter from a shallow, bowl-shaped sinus (Fig. 9D), usually hidden by a tubular, imperforate peristome, directed upwards and frontally, forming a transversely elliptical secondary orifice, about 200 μm long by 300 μm wide (Fig. 9C, D); spiramen placed at the base of the peristome at the end of a short tube with a more or less flared rim, transversely elliptical or reniform, 170–215 \times 75–95 μm , facing frontally or downwards (Fig. 9B, C).

Avicularia single or paired, placed at the base of the peristome, drop-shaped with rounded, slightly raised rostrum directed distolaterally and inwards, and complete crossbar (Fig. 9D, E).

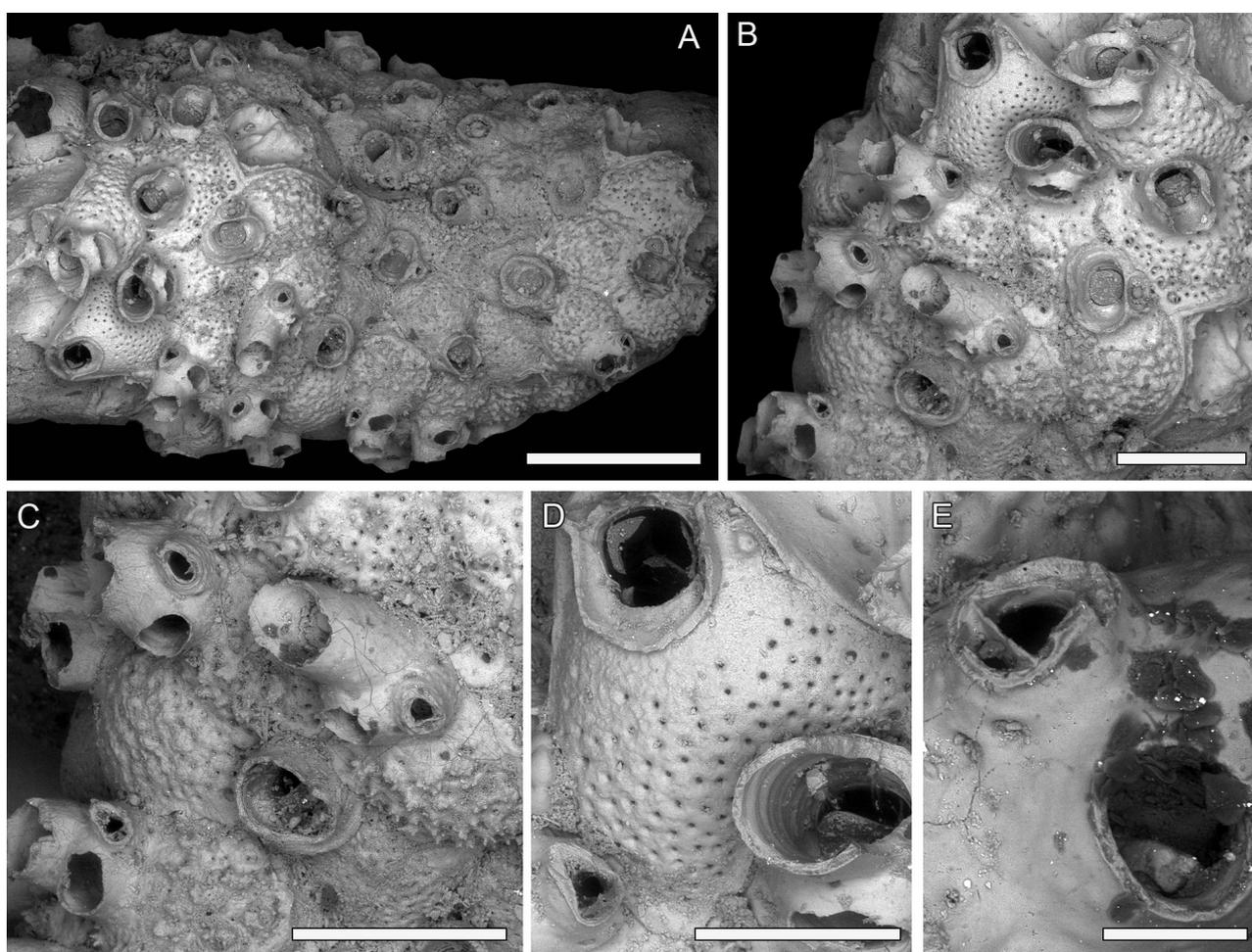


FIGURE 9. *Stenopsella fenestrata* (Smitt, 1873), Holotype SMNH-Type-1800, Tortugas, United States, here proposed as *Gigantopora fenestrata* **comb. nov.** A. General view of the colony. B. Group of zooids some in frontal and other in lateral view. C. Close-up of some zooids in lateral view, showing the development of the peristome, a variable position of the avicularium in relation to the spiramen, and the prickly appearance of the frontal shield. D. Close-up of a zooid with broken peristome and showing the primary orifice. E. Close-up of the adventitious, peristomial avicularium with complete crossbar. Scale bars: A = 1 mm; B, C = 500 μm ; D = 300 μm ; E = 100 μm .

Ovicells and ancestrula not observed.

Remarks. Smitt (1873) placed this species in *Hippothoa* Lamouroux, 1821 acknowledging that the small

encrusting colony (in agreement with the syntype illustrated here) available from Pourtales' collection lacked the most essential character of the genus, i.e. the orificial sinus. However, the observation of such a sinus on an erect fragment of what he thought was the same species but collected in the Pacific and housed at the British Museum (i.e. NHMUK), prevented him from creating a separate genus for the western Atlantic specimen.

A new genus, *Stenopsis*, was first mentioned in Canu & Lecointre (1925) as a nomen nudum and subsequently formally introduced in Canu & Bassler (1927) with type species Smitt's *H. fenestrata*. The name *Stenopsis* was preoccupied by *Stenopsis* Rafinesque, 1815 (a beetle of the family Tenebrionidae), and Bassler (1952) coined the replacement name *Stenopsella* to include, in addition to Smitt's species, two fossil species from the Eocene of North America initially identified as *Galeopsis* Jullien, 1903 in Jullien & Calvet (1903) by Canu & Bassler (1920).

However, *Stenopsella* seems to match the definition of *Gigantopora* Ridley, 1881 in having encrusting colonies, salient autozooids with nodular frontal shields pierced by pseudopores, a tubular peristome directed upwards and outwards, single or paired avicularia on the sides of the peristome, and a special roundish, transversely broad pore visible frontally (Ridley 1881, p. 47). The ooecium of the type species is also described as "small, globose, recumbent at back of cell proper, punctate" (Ridley 1881). Although Smitt's syntype lacks ovicells, they can be seen in the SEM image of a Gulf of Mexico specimen taken by J.E. Winston and available at http://bryozoa.net/cheilostomata/gigantoporidae/stenopsella_fenestrata.html (Bock 2022). The cap-like, perforated ooecium corresponds with the description of that in the type species but also with those of the numerous Recent and fossil species of *Gigantopora*. Based on these observations, *Stenopsella* is here proposed as junior synonym of *Gigantopora*, and the new combination *Gigantopora fenestrata* suggested. Judging by the images and description available in Canu & Bassler (1920), it is likely that both Eocene species currently attributed to *Stenopsella*, i.e. *S. cyclops* and *S. longicollis*, should also be placed in *Gigantopora*. In addition, some of the species in Canu & Bassler (1920) currently attributed (some tentatively) to *Galeopsis*, i.e. *G. erinaceus*, *G. convexa* and *G. verrucosa* appear to have pseudoporous frontal shields and, therefore, might better fit into *Gigantopora* as well.

TABLE 7. Measurements in μm of *Stenopsella fenestrata* (Smitt, 1873), Tortugas, United States; SMNH-Type-1800.

	N (zooids, colonies)	Mean	SD	Min	Max
ZL	7, 1	736	60	651	824
ZW	7, 1	510	73	430	644
OrL	5, 1	155	8	145	163
OrW	5, 1	144	4	140	150
AvL	5, 1	130	12	118	145
AvW	5, 1	88	9	79	102

Superfamily Smittinoidea Levinsen, 1909

Family Watersiporidae Vigneaux, 1949

Genus *Terwasipora* Reverter-Gil & Souto, 2019

Type species *Lepralia complanata* Norman, 1864

Terwasipora complanata (Norman, 1864)

(Fig. 10)

Lepralia complanata Norman, 1864: 85, pl. 10, fig. 4.

Terwasipora complanata: Reverter-Gil & Souto 2019: 2743, figs 5, 6.

Material examined. Holotype by monotypy SMNH-Type-1772, North Atlantic Ocean, Ireland, encrusting a rock. Leg. unknown.

Remarks. The description of this species is omitted because accurate descriptions are available in several

papers, some very recent (e.g. Reverter-Gil & Souto 2019, Ramalho *et al.* 2022). However, the original material described by Norman (1864) has never been described and/or illustrated. The syntype SMNH-Type-1772 (Fig. 10A) consists of a fan-shaped colony, about 5.8 x 8.6 mm, encrusting a granitic rock, about 9 x 11.5 cm, sharing the substrate with spirorbid polychaetes.

Norman (1864) acknowledged having found the specimen in the collection of British Zoophytes of his late friend Mr. Barlee that he inherited. This information agrees with the label (Fig. 10B), as does the description of the substrate provided by Norman (1864) as coarse-grained granite. While Norman (1864) claimed not to have detailed information about the collecting locality, apart from being British, the label reports Ireland as the probable origin, which seems plausible given that the geology of the northern coast of Ireland is characterized by igneous rocks and granitic intrusions.



FIGURE 10. *Terwasipora complanata* (Norman, 1864), Holotype SMNH-Type-1772, Ireland. A. General view of the colony. B. Label on the underside of the rock substrate. Scale bars: A = 1 mm; B = 3 cm.

This species has a wide Atlanto-Mediterranean distribution. Confirmed records are from the Isles of Scilly (off Cornwall, England) encrusting shells and rocks (Hayward & Ryland 1999), several localities along the Atlantic Iberian coast (Reverter-Gil & Souto 2019), the Strait of Gibraltar (e.g. López de la Cuadra 1991), the Alboran Sea (Ramalho *et al.* 2022), and the western Mediterranean (Gautier 1962, Novosel & Pozar-Domac, 2001, Rosso & Di Martino 2016).

Discussion

The SMNH zoological collection includes a well-organised, rich bryozoan section with extensive geographical cover. This material was mainly accumulated during the late 19th and early 20th century from several Swedish or other expeditions (e.g. Swedish Arctic Expedition, Gulf Stream Explorations), and the bryozoan component was subsequently studied by eminent Swedish naturalists, expert bryozoan taxonomists and systematists, such as Fredrik Adam Smitt (1839–1904) (see Schopf & Bassett 1973 for in-depth information on Smitt's career) and later Lars Silén (1910–1999). With a few exceptions, their material, published in a number of works (e.g. Smitt 1868, 1872, 1873; Silén 1947) has not been restudied since the advent of SEM as a standard tool for bryozoan taxonomy. Here, the priority has been given to the type specimens of the type species of cheilostome genera available in the collection. They total eight but for two of them, *Doryporella* and *Terwasipora*, descriptions are omitted given that they were recently re-described based on different specimens (see Grischenko *et al.* 2000, 2004; Reverter-Gil & Souto 2019).

Additional genera for which the type material is housed at SMNH were not treated here for two reasons. First, SEM studies were conducted on these specimens in recent years, as it is the case for: (i) the type species of *Bryopesanser* Tilbrook, 2006, i.e. *Hippothoa pesanseris* Smitt, 1873 (SMNH-Type-1790 and SMNH-Type-1791) (see Tilbrook 2012); (ii) the type species of *Buffonellaria* Canu & Bassler, 1927, i.e. *Hippothoa divergens* Smitt, 1873, for which a lectotype was selected in Berning & Kuklinski (2008); and (iii) the type specimen of the type

species of *Gephyrotes* Norman, 1903, i.e. *Escharipora figularis* forma *nitido-punctata* Smitt, 1868 (SMNH-Type-1770) illustrated and redescribed in Di Martino & Rosso (2015). Second, they were part of the most extensive re-study of Smitt's "Floridan Bryozoa from the Gulf Stream Explorations in Winston (2005) based on the specimens that were eventually returned to the Museum of Comparative Zoology Harvard University (MCZ) after Smitt had studied them. This includes nine genera that in alphabetical order are: *Callistopora* Winston, 2005 (type species *Membraniporella agassizii* Smitt, 1873: SMNH-Type-1839); *Colatooecia* Winston, 2005 (type species: *Porina serrulata* Smitt, 1873: SMNH-Type-1840); *Gemelliporina* Bassler, 1936 (type species: *Gemellipora glabra* Smitt, 1873: SMNH-Type-1784 and SMNH-Type-1873); *Hippaliosina* Canu, 1918 (type species: *Escharella rostrigera* Smitt, 1872: SMNH-Type-1851); *Mamillopora* Smitt, 1873 (type species: *Mamillopora cupula* Smitt, 1873: SMNH-Type-9119); *Petraliella* Canu & Bassler, 1927 (type species: *Escharella bisinuata* Smitt, 1873: SMNH-Type-1777 and SMNH-Type-1802); *Therenia* David & Pouyet, 1978 (type species *Hippothoa porosa* Smitt, 1873: SMNH-Type-9103 and SMNH-Type-1789) (see also Berning *et al.* 2008); *Triporula* Canu & Bassler, 1927 (type species *Escharipora stellata* Smitt, 1873: SMNH-Type-9107 and SMNH-Type-1805); and *Vitrimurella* Winston, Vieira & Woollacott, 2014 (type species: *Gemellipora lata* Smitt, 1873: SMNH-Type-1785). Finally, a further type species, *Posterula sarsii* (Smitt, 1867) (SMNH-Type-1741), could not be located on the bivalve shell that it was supposed to encrust.

As type specimens are the fundamental units on which taxonomic works are based, and taxonomic works are (or should be) the baselines on which meaningful larger scale studies on biodiversity, ecology, evolution etc. should be grounded, availability of historical type specimens is of paramount importance. This revision, for instance, has allowed the identification of erroneous geographical records for some of the species examined, as well as the synonymy between two genera. The SEM micrographs produced, being publicly available, can be a tool to further improve taxonomic identification and correct published geographical records.

In the last two decades, the promotion of accessibility together with future preservation, has been one of the main priorities in museum strategies worldwide and several digitisation programmes have been started. Unfortunately, not all collections/specimens receive the same attention, and some groups that are not so well-known to the general public, such as bryozoans, have been severely neglected or, alternatively, digitised using techniques, such as photos made with standard camera settings, that are unsuitable. If the aim of digitisation programmes is to be more than just a mere cataloguing of what is included in the collections, but to produce digital data including detailed images that can provide virtual access to the specimens, taxonomists specialising in the different groups should be involved in digitisation projects. Programmes such SYNTHESYS+, that funded and made possible this visit, allow researcher from different disciplines and specialists of different taxonomic groups to access not only collections and specimens but also research facilities such as scanning electron microscopes. The data produced, shared via publications or museum online catalogues and repositories, can greatly contribute to this global digitisation effort.

Acknowledgements

This research received support from the SYNTHESYS+ Project <http://www.synthesys.info/> which is financed by European Community Research Infrastructure Action under the H2020 Integrating Activities Programme and Research Council of Norway (grant 314499 to EDM). The author is grateful to Sabine Stöhr (SMNH, Senior Curator of the Invertebrate Collection) for her support during the Synthesys application process and assistance in the collection during the two-week research visit, Margret Steinhorsdottir (SMNH and TAF leader for SYNTHESYS+) for helping arranging the visit, and Andreas Karlsson for assistance during SEM sessions. Antonietta Rosso (University of Catania, Italy), Paul D. Taylor (Natural History Museum, London, UK), and an anonymous reviewer provided useful comments that greatly improved the originally submitted manuscript.

References

- Allman, G.J. (1856) *A monograph of freshwater Polyzoa, including all known species, both British and foreign*. The Ray Society, London, 119 pp., 11 pls.
<https://doi.org/10.5962/bhl.title.9143>
- Bassler, R.S. (1935) Bryozoa. Generum et Genotyporum. Index et Bibliographica. In: Quenstedt, W. (Ed.), *Fossilium Catalogus*

I. Animalia. Vol. 67. W. Junk, s'Gravenhage, pp. 1–229.

- Bassler, R.S. (1936) Nomenclatorial notes on fossil and Recent Bryozoa. *Journal of the Washington Academy of Science*, 26, 156–162.
- Bassler, R.S. (1952) Taxonomic notes on genera of fossil and Recent Bryozoa. *Journal of the Washington Academy of Science*, 42, 381–385.
- Berning, B. & Kukiński, P. (2008) North-east Atlantic and Mediterranean species of the genus *Buffonellaria* (Bryozoa, Cheilostomata): implications for biodiversity and biogeography. *Zoological Journal of the Linnean Society*, 152, 537–566.
<https://doi.org/10.1111/j.1096-3642.2007.00379.x>
- Berning, B., Tilbrook, K.J. & Rosso, A. (2008) Revision of the north-eastern Atlantic and Mediterranean species of the genera *Herentia* and *Therenia* (Bryozoa: Cheilostomata). *Journal of Natural History*, 42, 1509–1547.
<https://doi.org/10.1080/00222930802109140>
- Bock, P. (2022) The Bryozoa Homepage. Recent and Fossil Bryozoa. Available at <http://bryozoa.net/> (accessed 2 February 2022).
- Busk, G. (1852) *Catalogue of marine Polyzoa in the collection of the British Museum. I. Cheilostomata*. Trustees of the British Museum, London, 120 pp.
- Busk, G. (1858) On some Madeiran Polyzoa. Collected by J. Yates Johnson, Esq. (Continued from No. XXII, p. 129.). *Quarterly Journal of Microscopical Science*, 6, 261–263.
- Canu, F. (1917) Bryozoaires. *Revue critique de Paleozoologie*, 21, 29–37.
- Canu, F. (1918) *Hippaliosina*, un nouveau genre de Bryozoaires. *Bulletin de la Société Géologique de France*, 18, 88–94.
- Canu, F. & Bassler, R.S. (1917) A synopsis of American Early Tertiary Cheilostome Bryozoa. *United States National Museum Bulletin*, 96, 1–87.
<https://doi.org/10.5479/si.03629236.96.1>
- Canu, F. & Bassler, R.S. (1920) North American early Tertiary Bryozoa. *United States National Museum Bulletin*, 106, 1–879.
<https://doi.org/10.5479/si.03629236.106.i>
- Canu, F. & Bassler, R.S. (1923) North American later Tertiary and Quaternary Bryozoa. *United States National Museum Bulletin*, 125, 1–302.
<https://doi.org/10.5962/bhl.title.159661>
- Canu, F. & Bassler, R.S. (1927) Classification of the cheilostomatous Bryozoa. *Proceedings of the U.S. National Museum*, 69, 1–42.
<https://doi.org/10.5479/si.00963801.69-2640.1>
- Canu, F. & Bassler, R.S. (1928) Fossil and Recent Bryozoa of the Gulf of Mexico region. *Proceedings of the U.S. National Museum*, 72, 1–199.
<https://doi.org/10.5479/si.00963801.72-2710.1>
- Canu, F. & Bassler, R.S. (1929) Bryozoa of the Philippine region. *United States National Museum Bulletin*, 100, 1–685.
- Canu, F. & Lecointre, G. (1925) Les Bryozoaires cheilostomes des Faluns de Touraine et d'Anjou. *Mémoires de la Société Géologique de France*, New Series, 3, 1–18.
- Cheetham, A.H. & Sandberg, P.A. (1964) Quaternary Bryozoa from Louisiana mudlumps. *Journal of Paleontology*, 38, 1013–1046.
- Cook, P.L. & Lagaaij, R. (1976) Some Tertiary and Recent conescharelliniform Bryozoa. *Bulletin of the British Museum (Natural History)*, 29, 317–376.
- Cook, P.L., Bock, P.E., Gordon, D.P. & Weaver, H.J. (2018) *Australian Bryozoa Volume 2. Taxonomy of Australian Families*. CSIRO Publishing, Melbourne, 320 pp.
<https://doi.org/10.1071/9781486306831>
- David, L. & Pouyet, S. (1978) Le genre *Herentia* Gray, 1848 (Bryozoa, Cheilostomata). Systématique et phylogénèse, biostratigraphie et biogéographie. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon HS 4*, 'Livre Jubilaire Jacques Flandrin', 167–193.
- Di Martino, E. & Rosso, A. (2015) Revision of the bryozoan genus *Gephyrotes* Norman, 1903 (Cheilostomata, Cribrilinidae) with the description of two new taxa. *Zootaxa*, 3941 (2), 261–283.
<https://doi.org/10.11646/zootaxa.3941.2.7>
- Di Martino, E. & Taylor, P.D. (2017) Some Miocene cheilostome bryozoan genera of Michel Vigneaux—systematic revision and scanning electron microscopic study. *Geodiversitas*, 39, 783–796.
<https://doi.org/10.5252/g2017n4a7>
- Di Martino, E., Taylor, P.D. & Portell, R.W. (2017) Bryozoans from the lower Miocene Chipola Formation, Calhoun County, Florida, USA. *Bulletin of the Florida Museum of Natural History*, 53, 97–200.
- Di Martino, E., Taylor, P.D. & Portell, R.W. (2019) *Anomia*-associated bryozoans from the upper Pliocene (Piacenzian) lower Tamiami Formation of Florida, USA. *Palaeontologia Electronica*, 22.1.11. [published online]
<https://doi.org/10.26879/920>
- Duvergier, J. (1921) Note sur les Bryozoaires du Néogène de l'Aquitaine. *Actes de la Société linnéenne Bordeaux*, 72, 145–182.
- Ehrenberg, C.G. (1831) *Symbolae Physicae, seu Icones et descriptiones Corporum Naturalium novorum aut minus cognitorum*,

- quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam...studio annis 1820–25 redirentur.* Berolini, Berlin. [Pars Zoologica, v. 4. Animalis Evertebrata exclusis Insectis]
- Gabb, W.M. & Horn, G.H. (1862) The fossil Polyzoa of the Secondary and Tertiary formations of North America. *Journal of the Academy of Natural Sciences of Philadelphia*, 5, 111–179.
- Gautier, Y.V. (1962) Recherches écologiques sur les Bryozoaires chilostomes en Méditerranée occidentale. *Recueil des travaux de la Station marine d'Endoume*, 38, 1–434.
- Gordon, D.P. (1993) Bryozoan frontal shields: studies on umbonulomorphs and impacts on classification. *Zoologica Scripta*, 22, 203–221.
<https://doi.org/10.1111/j.1463-6409.1993.tb00352.x>
- Gordon, D.P. & d'Hondt, J.-L. (1997) Bryozoa: Lepraliomorpha and other Ascophorina from New Caledonian waters. *Mémoires du Muséum National d'Histoire Naturelle. Résultats des Campagnes MUSORSTOM*, 18 (176), 9–124.
- Gray, J.E. (1848) *List of the specimens of British animals in the collections of the British Museum. Part 1. Centrionae or radiated animals.* Trustees of the British Museum, London, 151 pp.
- Grischenko, A.V., Dick, M.H. & Mawatari, S.F. (2007) Diversity and taxonomy of intertidal Bryozoa (Cheilostomata) at Akkeshi Bay, Hokkaido, Japan. *Journal of Natural History*, 41, 1047–1161.
<https://doi.org/10.1080/00222930701391773>
- Grischenko, A.V., Mawatari, S.F. & Taylor, P.D. (2000) Systematics and phylogeny of the cheilostome bryozoan *Doryporella*. *Zoologica Scripta*, 29, 247–264.
<https://doi.org/10.1046/j.1463-6409.2000.00038.x>
- Grischenko, A.V., Taylor, P.D. & Mawatari, S.F. (2004) *Doryporella smirnovi* sp. nov. (Bryozoa: Cheilostomata) and its impact on phylogeny and classification. *Zoological Science*, 21, 327–332.
<https://doi.org/10.2108/zsj.21.327>
- Harmer, S.F. (1926) The Polyzoa of the Siboga Expedition, 2. Cheilostomata Anasca. *Siboga Expedition Reports*, 28b, 183–501.
- Harmer, S.F. (1957) The Polyzoa of the Siboga Expedition, Part 4. Cheilostomata Ascophora II. *Siboga Expedition Reports*, 28d, 641–1147.
- Hayward, P.J. & Ryland, J.S. (1999) *Cheilostomatous Bryozoa. Part 2. Hippothoidea—Celleporoidea. Synopses of the British Fauna. New Series. Vol. 14.* Field Studies Council, Shrewsbury, 416 pp.
- Hedrick, B.P., Heberling, J.M., Meineke, E.K., Turner, K.G., Grassa, C.J., Park, D.S., Kennedy, J., Clarke, J.A., Cook, J.A., Blackburn, D.C., Edwards, S.V. & Davis, C.C. (2020) Digitization and the future of Natural History Collections. *Bioscience*, 70, 243–251.
<https://doi.org/10.1093/biosci/biz163>
- Hincks, T.A. (1884) Contributions towards a general history of the marine Polyzoa. XIII. Polyzoa from Victoria (continued). *Annals and Magazine of Natural History*, Series 5, 14, 276–285.
<https://doi.org/10.1080/00222938409459809>
- Johnston, G. (1838) *A history of British Zoophytes.* W.H. Lizars, Edinburgh, London and Dublin, 341 pp.
<https://doi.org/10.5962/bhl.title.110844>
- Jullien, J. (1882) Note sur une nouvelle division des Bryozoaires Cheilostomiens. *Bulletin de la Société zoologique de France*, 6, 271–285.
- Jullien, J. & Calvet, L. (1903) Bryozoaires provenant des campagnes de l'Hirondelle (1886–1888). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert I^{er}, prince souverain de Monaco*, 23, 1–188.
- Lamouroux, J.V.F. (1821) *Exposition méthodique des genres de l'ordre des polypiers, avec leur description et celles des principales espèces figurées dans 84 planches; les 63 premiers appartenant à l'histoire naturelle des zoophytes d'Ellis et Solander.* V. Agasse, Paris, 115 pp.
<https://doi.org/10.5962/bhl.title.11328>
- Levinsen, G.M.R. (1909) *Morphological and systematic studies on the cheilostomatous Bryozoa.* Nationale Forfatterers Forlag, Copenhagen, 431 pp.
<https://doi.org/10.5962/bhl.title.5690>
- Levinsen, G.M.R. (1917) Danmark-Ekspeditionen til Grønlands Nordstkyst 1906–1908. Bind. III, nr 16, Bryozoa. *Meddelelser om Grønland*, 43, 431–472.
- Linnaeus, C. (1767) *Systemae naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis Regnum Animale.* Laurentii Salvii, Holmiae, pp. 533–1327.
<https://doi.org/10.5962/bhl.title.157601>
- López de la Cuadra, C.M. (1991) *Estudio sistemático de los Briozoos Queilostomados (Bryozoa: Cheilostomida) del Estrecho de Gibraltar y áreas próximas.* PhD Thesis. Universidad de Sevilla, Sevilla, 239 pp.
- MacGillivray, P.H. (1882) Descriptions of new or little-known Polyzoa, Part 1. *Transactions and Proceedings of the Royal Society of Victoria*, 18, 115–121.
- Nelson, G. & Ellis, S. (2018) The history and impact of digitization and digital data mobilization on biodiversity research. *Philosophical Transaction of the Royal Society B*, 374, 20170391.
<https://doi.org/10.1098/rstb.2017.0391>
- Neviani, A. (1896) Briozoi postpliocenici di Spilinga (Calabria). *Atti dell'Accademia Gioenia di Scienze Naturali in Catania*,

- Norman, A.M. (1864) On undescribed British Hydrozoa, Actinozoa and Polyzoa. *Annals and Magazine of Natural History*, 13, 82–90.
<https://doi.org/10.1080/00222936408681578>
- Norman, A.M. (1903) Notes on the natural history of East Finmark. *Annals and Magazine of Natural History*, Series 7, 11, 1–32.
<https://doi.org/10.1080/00222930308678717>
- Novosel, M. & Požar-Domac, A. (2001) Checklist of Bryozoa of the Eastern Adriatic Sea. *Natura Croatica*, 10, 367–421.
- Orr, R.J.S., Di Martino, E., Gordon, D.P., Ramsfjell, M.H., Mello, H.L., Smith, A. & Liow, L.H. (2021) A broadly resolved molecular phylogeny of New Zealand cheilostome bryozoans as a framework for hypotheses of morphological evolution. *Molecular Phylogenetics and Evolution*, 161, 107172.
<https://doi.org/10.1016/j.ympev.2021.107172>
- Orr, R.J.S., Di Martino, E., Ramsfjell, M., Gordon, D.P., Berning, B., Chowdhury, I., Craig, S., Cumming, R.L., Figuerola, B., Florence, W., Harmelin, J.-G., Hirose, M., Huang, D., Jain, S.S., Jenkins, H.L., Kotenko, O.N., Kuklinski, P., Lee, H.E., Madurell, T., McCann, L., Mello, H.L., Obst, M., Ostrovsky, A.N., Paulay, G., Porter, J.S., Shunatova, N.N., Smith, A.M., Souto-Derungs, J., Vieira, L.M., Voje, K.L., Waeschenbach, A., Zágóršek, K., Warnock, R.C.M. & Liow, L.H. (2022) Paleozoic origins of cheilostome bryozoans and their parental care inferred by a new genome-skimmed phylogeny. *Science Advances*, 8, eabm7452.
<https://doi.org/10.1126/sciadv.abm7452>
- Osburn, R.C. (1952) Bryozoa of the Pacific coast of America, part 2, Cheilostomata-Ascophora. *Report of the Allan Hancock Pacific Expeditions*, 14, 271–611.
- Rafinesque, C.S. (1815) *Analise de la nature ou Tableau de l'univers et des corps organisés*. Self-published, Palermo, 224 pp.
<https://doi.org/10.5962/bhl.title.106607>
- Ramalho, L.V., Rodrigues-Aporta, R. & Gofas, S. (2022) Preliminary account on the bryozoans of the Alboran platform (Western Mediterranean), with description of two new species. *Zootaxa*, 5094 (1), 53–91.
<https://doi.org/10.11646/zootaxa.5094.1.2>
- Reverter-Gil, O. & Fernández-Pulpeiro, E. (1999) Some records of bryozoans from NW Spain. *Cahiers de Biologie Marine*, 40, 35–45.
- Reverter-Gil, O. & Souto, J. (2019) Watersiporidae (Bryozoa) in Iberian waters: an update on alien and native species. *Marine Biodiversity*, 49, 2735–2752.
<https://doi.org/10.1007/s12526-019-01003-4>
- Ridley, S.O. (1881) Account of the zoological collections made during the survey of H.M.S. Alert in the straits of Magellan and on the coast of Patagonia. *Proceedings of the Zoological Society of London*, 1881, 44–61.
- Rosso, A. & Di Martino, E. (2016) Bryozoan diversity in the Mediterranean Sea: an update. *Mediterranean Marine Science*, 17, 567–607.
<https://doi.org/10.12681/mms.1706>
- Schopf, T.J.M. & Bassett, E.L. (1973) F.A. Smitt, Marine Bryozoa, and the introduction of Darwin into Sweden. *Transactions of the American Philosophical Society*, 63, 1–30.
- Silén, L. (1947) Conescharellinidae (Bryozoa Gymnolaemata) collected by Prof. Dr. Sixten Bock's expedition to Japan and the Bonin Islands 1914. *Arkiv för zoologi*, 39A, 1–59.
- Smitt, F.A. (1867) Kritisk förteckning öfver Skandinaviens Hafs-Bryozoeer. II. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 23, 395–534
- Smitt, F.A. (1868) Kritisk förteckning öfver Skandinaviens hafs-Bryozoeer. Part 4. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 25, 2–230.
- Smitt, F.A. (1872) Floridan Bryozoa collected by Count L.F. de Pourtales, Part 1. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 10, 1–20.
- Smitt, F.A. (1873) Floridan Bryozoa collected by Count L.F. de Pourtales, Part 2. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 11, 1–83.
- Soule, J.D., Soule, D.F. & Chaney, H.W. (1991) New tropical Pacific and Indian Ocean Cleidochasmatidae (Cheilostomata: Ascophora). In: Bigey, F.P. & d'Hondt, J.-L. (Eds.), *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France Mémoire HS 1*. Société des Sciences Naturelles de l'Ouest de la France, Nantes, pp. 465–486.
- Taylor, P.D., Martha, S.O. & Gordon, D.P. (2018) Synopsis of 'onychoceclid' cheilostome bryozoan genera. *Journal of Natural History*, 52, 1657–1721.
<https://doi.org/10.1080/00222933.2018.1481235>
- Tilbrook, K.J. (2006) Cheilostomatous Bryozoa from the Solomon Islands. *Santa Barbara Museum of Natural History, Monographs 4 (Studies in Biodiversity Number 3)*, 1–386.
- Tilbrook, K.J. (2012) Review of the bryozoan genus *Bryopesanser* Tilbrook, 2006 (Escharinidae: Cheilostomata) with the description of 11 new species. *Zootaxa*, 3165 (1), 39–63.
<https://doi.org/10.11646/zootaxa.3165.1.3>
- Tilbrook, K.J., Hayward, P.J. & Gordon, D.P. (2001) Cheilostomatous Bryozoa from Vanuatu. *Zoological Journal of the Linnean*

Society, 131, 35–109.

<https://doi.org/10.1006/zjls.2000.0249>

Vigneaux, M. (1949) Révision des Bryozoaires néogènes du Bassin d'Aquitaine et essai de classification. *Mémoires de la Société Géologique de France*, New Series, 28, 1–153.

Winston, J.E. (2005) Re-description and revision of Smitt's Floridan Bryozoa in the collection of the Museum of Comparative Zoology, Harvard University. *Virginia Museum of Natural History Memoir*, 7, 1–147.

Winston, J.E. (2016) Bryozoa of Floridan Oculina reefs. *Zootaxa*, 4071 (1), 1–81.

<https://doi.org/10.11646/zootaxa.4071.1.1>

Winston, J.E., Vieira, L.M. & Woollacott, R.M. (2014) Scientific Results of the Hassler Expedition. Bryozoa. No. 2. Brazil. *Bulletin of the Museum of Comparative Zoology*, 161, 139–239.

<https://doi.org/10.3099/MCZ14.1>