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North-east Atlantic and Mediterranean species of the genus *Buffonellaria* (Bryozoa, Cheilostomata): implications for biodiversity and biogeography

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Received 9 March 2007; accepted for publication 12 June 2007

In this study we revise the cheilostome bryozoan genus *Buffonellaria* Canu & Bassler, 1927 and its Mediterranean and north-east Atlantic species, thereby addressing several existing problems. First, a lectotype for the type species, *Buffonellaria divergens* (Smitt, 1873) from Florida, is chosen, which proves to be distinct from the European species. Second, the two hitherto established north-east Atlantic species [*Buffonellaria nebulosa* (Jullien & Calvet, 1903) and *Buffonellaria porcellanum* Aristegui Ruiz, 1987], are redescribed, which were poorly documented until now. Third, close inspection of material, collected from Spitsbergen to tropical West Africa, using scanning electron microscopy reveals that the actual number of species, all previously referred to either *B. divergens* or *Stephanosella biaperta* (Michelin, 1848), is distinctly greater in the north-east Atlantic than has been previously acknowledged. As a result, seven new species are introduced (*Buffonellaria acorensis* sp. nov., *Buffonellaria antoniettae* sp. nov., *Buffonellaria arctica* sp. nov., *Buffonellaria harmelini* sp. nov., *Buffonellaria jensi* sp. nov., *Buffonellaria muriella* sp. nov., and *Buffonellaria ritae* sp. nov.), whereas two are left in open nomenclature. With the increase in number of species, the extremely broad geographical range of distribution assumed for *B. divergens* breaks down to numerous restricted areas. However, although most species have only been reported from a single location, *B. arctica* sp. nov. seems to have a fairly wide distribution in the Arctic region. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 152, 537–566.

ADDITIONAL KEYWORDS: Celleporidae – new species – ovicell development – taxonomy.

INTRODUCTION

The history of *Buffonellaria* Canu & Bassler, 1927 and its species is a very intricate one. From the High Arctic to the Mediterranean Sea and tropical West Africa, specimens belonging to *Buffonellaria* have usually been referred to either the type species of this genus, the Recent *Buffonellaria divergens* (Smitt, 1873), or to *Stephanosella* (or occasionally *Schizoporella*) *biaperta* (Michelin, 1848), a species described from the Late Miocene of France (e.g. Smitt, 1868; Waters, 1879; Nordgaard, 1906, 1918; Norman, 1909; Ryland, 1969; d'Hondt, 1970, 1975, 1978; Kluge, 1975; Hayward & Ryland, 1979, 1999; López de la

Cuadra & García-Gómez, 1988; Zabala & Maluquer, 1988; Harmelin & d'Hondt, 1992; Alvarez, 1994; Dahle *et al.*, 1998). However, even after Ryland (1969: 220) clarified some of the main controversies and the taxonomic status of these two taxa, showing that *Stephanosella* Canu & Bassler, 1917 is very different from *Buffonellaria*, and that the Recent species is distinct from the fossil *S. biaperta*, several problems remained. For instance, *B. divergens* was originally described from Floridan waters. Judging by the small number of species that have a circum-Atlantic distribution, most of which are likely to have been introduced to either the western or eastern Atlantic by man (e.g. Ryland, 1965; Hastings, 1968), it is arguable that an eastern Atlantic or Mediterranean congeneric would indeed belong to the same species. Furthermore, Smitt (1873: 47) described two species

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under *Hippothoa divergens*: a forma *laxa* (Smitt, 1873: fig. 177) that does not belong to *Buffonellaria*, and a forma *typica*, the figured specimen of which would be the type of *B. divergens*. There was no material of this species, however, in the Smitt Collection held at the Museum of Comparative Zoology (MCZ, Harvard University), which Winston (2005) recently redescribed. A thorough description and illustration of the type of *B. divergens* was therefore lacking until now, preventing a substantiated comparison between western and eastern Atlantic taxa. Thus, there are only two established species of *Buffonellaria* in the north-east Atlantic: *Buffonellaria nebulosa* (Jullien & Calvet, 1903) and *Buffonellaria porcellanum* Aristegui Ruiz, 1987. Both occur off the continental shelf, around the Azores and Canary Islands, respectively, and have never been recorded again since their discovery. Even before the common use of scanning electron microscopy (SEM) in bryozoan research, Ryland (1969) already indicated that there are other Recent species of *Buffonellaria* that have been assigned to *B. divergens*. As we are able to show here, the reasons for the repeated assignment of diverse material from various regions to *B. divergens* arise from the small morphological differences between species, which necessitate close examination using SEM. Strong intracolony variability, caused by extensive hypercalcification and the proliferation of frontal avicularia, also results in the diverse appearance of zooecia in different ontogenetic stages, and may disguise primary zooecial features. Furthermore, variability in orifice shape occurring even within colonies may complicate a precise delimitation of species.

A refined concept of (morpho-) species taxa based upon integrated genetic and morphological studies (Jackson & Cheetham, 1990), as well as extensive SEM work revealing fine but consistent morphological details, has led to a recent trend towards splitting of species complexes and 'cosmopolitan' species in cheilostome Bryozoa (e.g. Lidgard & Buckley, 1994; Soule, Soule & Morris, 2002; Taylor & Mawatari, 2005; Harmelin, 2006). This trend not only increases the diversity in many taxa, but also decreases the geographical species ranges, thereby finally approaching the biogeographical pattern expected for sessile organisms with brooded larvae that spend between mere seconds and hours in the water column before attachment to a substrate, as is the case in most Cheilostomata (e.g. Jackson, 1986; Taylor, 1988a; McKinney & Jackson, 1989; Goldson, Hughes & Gliddon, 2001; Watts & Thorpe, 2006).

The aim of the present paper is therefore to thoroughly describe material from different north-east Atlantic and Mediterranean regions of which *B.*

divergens auctt. and *S. biapertura* auctt. have been reported. The outcome is an unexpected increase in diversity in the genus *Buffonellaria*, which accompanies a drastic reduction in the range of geographical distribution of *B. divergens*, which was hitherto considered to occur throughout the North Atlantic.

MATERIAL AND METHODS

The studied material is stored in the following institutions: Natural History Museum in London (NHM), Natural History Museum in Paris (MNHN), Swedish Museum of Natural History in Stockholm (SMNH), Palaeontological Museum of Catania University (PMC), Senckenberg Research Institute and Natural History Museum in Frankfurt (SMF), Croatian Natural History Museum in Zagreb (CNHM), and in the Canadian Museum of Nature in Ottawa (CMN). If allowed, selected (type) specimens for photographic documentation were cleaned with diluted domestic bleach, and the uncoated material was photographed digitally with an LEO 1455VP SEM using the back-scattered electron (QBSD) mode, under variable pressure. Our bryozoan systematics follow the working classification of D. P. Gordon (pers. comm. 2006), who is currently developing the classification scheme for eventual use in the revised *Treatise on Invertebrate Paleontology*.

Zooecial measurements were made on micrographs using the image software imagej. Each measurement is given in the text with the mean \pm the standard deviation, the observed range, and (enclosed in brackets) the number of specimens used and the total number of measurements made. The measurements are given in microns (μm) unless otherwise stated, and zooecial characters are identified by the following acronyms and abbreviations: FAL, frontal avicularium length; FAW, frontal avicularium width; OAL, oral avicularium length; OAW, oral avicularium width; OL, orifice length; OW, orifice width; OVL, oecium length; OVW, oecium width; ZL, zooecium length; Zw, zooecium width.

SYSTEMATICS

In this section we revise the diagnoses of the family Celleporidae Johnston, 1838 and the genus *Buffonellaria* Canu & Bassler, 1927, based on findings of the present study on frontal-wall and oecium formation in *Buffonellaria* species. We then fully redescribe the type species, *B. divergens* from Florida, before describing other known species and introducing new species from the north-east Atlantic and Mediterranean Sea, arranged in order of morphological similar-

ity. To keep the differential diagnoses short, only the most striking characters that justify a distinction from the other species are given.

FAMILY CELLEPORIDAE JOHNSTON, 1838

Revised diagnosis: Colony encrusting, unilaminar to multilaminar, typically domed, mamillate or nodular; or erect, branching, occasionally bilaminar, often massive. Frontal shield of autozoid cryptocystidean, typically smoothly calcified, often thick, with marginal pores and occasionally also with central pseudopores. Primary orifice proximally concave or with a well-marked sinus; condyles distinct; oral spines present or absent. Peristome absent to well developed, usually with one or more columnar, suboral, or lateral suboral avicularia. Polymorphic adventitious and vicarious avicularia typical. Ovicell formed by maternal zooid or distal autozoid, with imperforate entoecium, forming a frontal tabula if exposed, ectoecium incompletely calcified; not closed by autozoid operculum. Small basal pore chambers present.

Remarks: The recent placement of taxa with a pseudoporous frontal wall (*Pourtalesella* Winston, 2005 – a very closely related taxon of *Buffonellaria*, see below) in the Celleporidae requires modification of the family definition, which was hitherto considered to accommodate taxa with marginal pores only (e.g. Gordon, 1984: 114; Hayward & Ryland, 1999: 318). Furthermore, as Hincks (1880a: 255) already observed, and as will be shown in more detail below, even in some species of *Buffonellaria* in which adult zooids have an imperforate frontal wall, pseudopores may initially be present during formation of the primary skeleton. Gordon (2000) presented evidence that the formation of pseudopores from imperforate lepralioid frontal shields is a derived character in, for example, the Celleporidae, in which most taxa produce imperforate frontal walls.

Another closely related genus is *Torquatella* Tilbrook, Hayward & Gordon, 2001, which includes species with pseudoporous frontal walls, and for which a new family, the Torquatellidae, has only recently been introduced by Tilbrook (2006: 286). Ovicell morphology, nevertheless, suggests a strong relation with the Celleporidae, and especially with the genera *Buffonellaria* and *Pourtalesella*. However, because further studies on the ontogeny of *Torquatella* would be necessary in order to relate the characteristic frontal calcification to any of the celleporid genera, a final decision on this case is beyond the scope of this paper.

The different types of ovicell formation and morphology are also incorporated into the new family

definition. In *Buffonellaria* and *Pourtalesella* the exposed entoecium was occasionally considered to have a row of pores along its margin (e.g. Aristegui Ruiz, 1987; Winston, 2005). However, a complete series of oecium formation in several species of *Buffonellaria* shows that the entoecium is imperforate. The apparent ‘pores’ in bleached specimens are produced by the exposure of the interoecial coelomic lumen between the entoecial ribs that marginally disappear underneath the ectoecium (see below).

In fact, in all Celleporidae the entoecium is imperforate. Pseudopores (or lacunae in *Turbicellepora* Ryland, 1963), which may develop in an incompletely calcified ectoecium, are filled with cuticular ‘plugs’. However, in some *Celleporina* species, there are real pores leading from the oecial coelom to coelomic canals, within thick irregular calcification deriving from the entoecium (A. Ostrovsky, pers. comm. 2007). Furthermore, although the formation of the oecium in *Buffonellaria* and *Pourtalesella* proceeds from an oecial pore situated in the frontal wall of an autozoid distal to the maternal one (see below), oecia in the remaining genera are terminal. Whether it rests on the frontal wall of a distal autozoid or not, each brood chamber starts its growth as a flat distal bud of the maternal autozoid, forming a basement of the ovicell. From this kenozooidal basement the vertical walls and the roof of the oecium are then formed. The entire brood chamber is therefore termed ‘oecial kenozooid’ in these taxa (A. Ostrovsky, pers. comm. 2007).

GENUS *BUFFONELLARIA* CANU & BASSLER, 1927

Original description: *Buffonellaria* Canu & Bassler, 1927: 8.

Synonyms: *Buffonellaria:* Hayward & Ryland, 1979: 204; Gordon, 1984: 117; Zabala & Maluquer, 1988: 127; Hayward & Ryland, 1999: 356.

Type species: *Hippothoa divergens* Smitt, 1873.

Revised diagnosis: Colony encrusting, unilaminar to plurilaminar, or erect rigid bilaminar. Basal pore chambers present, vertical zoecium walls with multiporous septula. Frontal wall with a single row of marginal pores, central shield usually imperforate in adult zooids but occasionally with tiny pseudopores, a distinct medioproximal oecial pore present in some zooids, extreme frontal hypercalcification masking primary frontal characteristics may occur. Primary orifice with sinus and condyles. No spines except on ancestrula and first generation autozooids. Oecium of the ovicell recumbent on distal zooid’s frontal wall, prominent first, later usually immersed by secondary

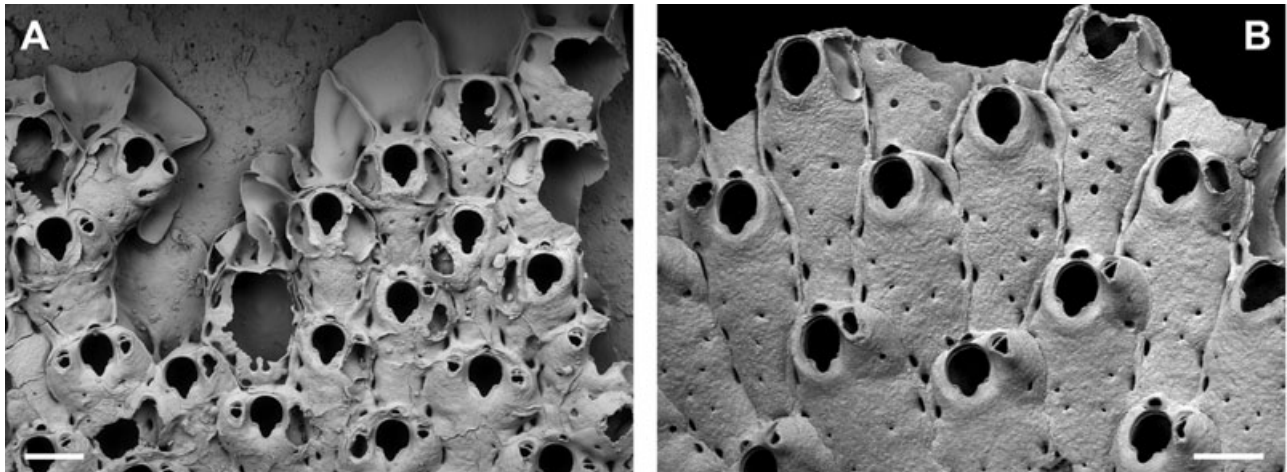


Figure 1. Frontal wall formation. A, note the presence of frontal-wall pores during early ontogeny in zoecia at the growth margin, and their subsequent closure in older, more proximal zoecia. *Buffonellaria muriella* sp. nov., NHM 2007.5.18.2, Guernsey; scale bar, 200 μ m. B, early ontogeny of the erect bilaminate *Buffonellaria* sp. 1, NHM 2007.5.18.12, Toulon, Mediterranean Sea; scale bar, 200 μ m.

calcification, emerging from the margin of the ooeial pore situated in proximal frontal wall of distal zooid, gymnocystal ectooecium with large noncalcified central window, exposed frontal area of entoecium imperforate, with more or less prominent radiating ribs that partly cover the intervening coelomic lumen between ento- and ectooecium; not closed by zooidal operculum. Avicularia adventitious, generally adjacent to orifice; additional enlarged dimorphic avicularia absent or present, occasionally frequent on frontal, with acute mandible. Ancestrula with well-developed proximal gymnocyst and a distally located opesia surrounded by spines.

Remarks: The diagnosis differs in several aspects from the latest account by Hayward & Ryland (1999), which is mainly due to the fact that these authors used the same diagnosis as in their earlier description of the *British Fauna* in 1979. In the latter work *B. armata* (Hincks, 1862) was included in the genus, which is, in contrast to *Buffonellaria*, characterized by the presence of oral spines, spatulate avicularia and a beaded orifice rim, and which is now placed in the genus *Stephanollona* Duvergier, 1921.

Furthermore, as for the Celleporidae, the genus *Buffonellaria* was hitherto considered to include species with an imperforate frontal wall only. SEM observations of the colony growth margin revealed, however, that in some species frontal pseudopores may exist during early ontogeny (Fig. 1), which soon become either completely closed, or remain open as frontal pseudopores of variable but generally very small size, depending on the taxon. A completely porous frontal shield may therefore be readily pro-

duced by pedomorphosis, i.e. when the early ontogenetic stage is retained in adult zooids. A clear line between species with and without a porous frontal wall (cf. *Pourtalesella*), may therefore be difficult to draw. In fact, the presence of a pseudoporous frontal wall is the only significant feature distinguishing the very recently erected genus *Pourtalesella* (type species *Schizopodrella incrassata* Canu & Bassler, 1928) from *Buffonellaria*. Orifice morphology and ovicell formation are identical in *Pourtalesella*, although Winston (2005: 95) mentions a 'marginally perforated entozooidal [sic] area' in the ooeium, but this is a mistake that has occasionally been made (see below). The larger, dimorphic, frontal avicularium typical for most species of *Buffonellaria* is absent in *P. incrassata*, in which only monomorphic oral avicularia are additionally budded during later ontogeny. However, the larger frontal avicularia are also lacking in *B. porcellanum* Arístegui Ruiz, 1987 but avicularia would, in any case, not constitute a character justifying the distinction of genera (D.P. Gordon, pers. comm. 2006). More information on frontal wall formation and functional morphology in both *Pourtalesella* and *Buffonellaria* species is clearly needed to clarify the status of *Pourtalesella*.

In *Buffonellaria* and *Pourtalesella* (and possibly also in *Torquatella*) ooeium production is decoupled from the formation of maternal zooids, which are characterized by having a distinct, rimmed, round or oval ooeial pore immediately distal to the orifice, deriving from the proximal frontal wall of the succeeding autozooid (Fig. 2). From this ooeial pore the ooeium may later, after complete formation of the frontal wall of the succeeding zooid, be generated. Therefore, ovicell pro-

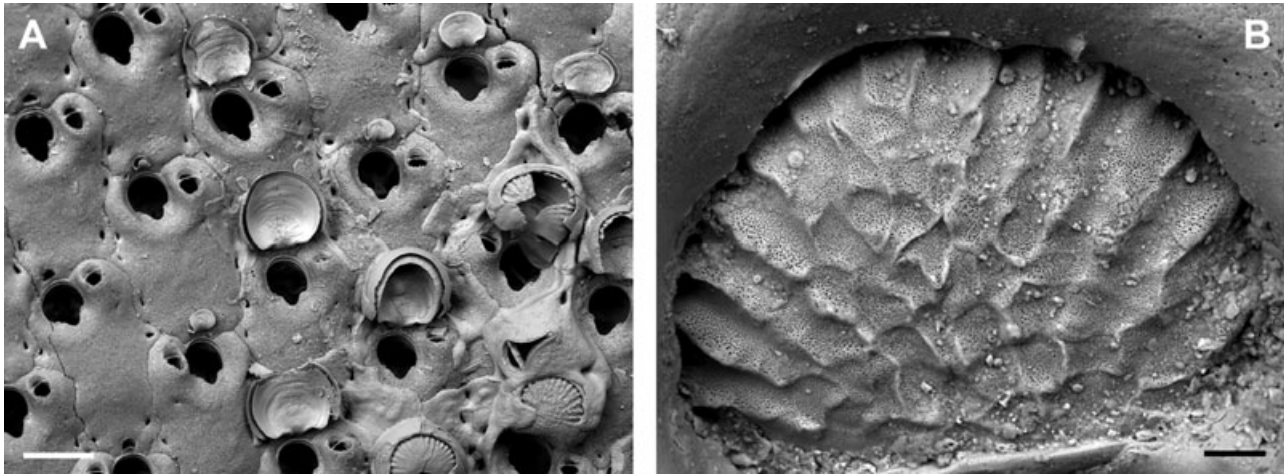


Figure 2. Oecium formation. A, colony with several ontogenetic stages of oecium formation, in which oocial pores are present in zooecia at the very left-hand side, but in which oecium formation has not yet commenced. The second series of zooecia further to the right, as well as two zooecia in the upper right-hand corner, show the earliest stages of oecium development, in which the fold of entoocium and ectoocium shows concentric growth. In the central series of zooecia, the basal oecium wall is completed and entoocium and ectoocium proceed to grow in a globular fashion. The intervening coelomic lumen is best visible in this stage. The frontal tabula of the entoocium is produced as the ectoocium ceases to grow, producing a central window (zooecium at centre right). Oecium growth is then completed, a frontal avicularium is budded, and secondary calcification begins to cover the colony surface (zooecia in lower right corner). *Buffonellaria muriella* sp. nov., CNHM Inv.br.27, Adriatic Sea; scale bar, 200 μ m. B, close-up of the finely pitted entoocial surface. *Buffonellaria antoniettae* sp. nov., paratype, PMC B16.30.6.2006b, Sicily; scale bar, 20 μ m.

duction does not take place at the extreme colony periphery and can potentially be delayed until, e.g. environmental conditions have become favourable, while then being able to proceed at a greater rate without the colony having to produce maternal zooids at that stage. The oecium is formed by evagination of the inner epithelial lining of the oocial pore, initially producing a flat cuticular fold with subsequent calcification of ento- and ectoocium. An intervening coelomic lumen is present between these calcified layers. Calcification of the ectoocium commences to proceed frontally at a certain point, leaving a central semicircular area of exposed entoocium (the tabula). The generally semicircular area of frontal entoocium is superficially densely perforated by minute pits ($\leq 0.5 \mu$ m), and usually bears radiating ribs. The entoocium is, nevertheless, imperforate, whereas it is the disappearing of the ribs and intervening grooves underneath the cuticular part of the ectoocium that wrongly gives the appearance of a row of pores along the exposed entoocial margin in bleached specimens. In several species frontal avicularia are budded and secondary calcification proceeds to grow immediately after completion of the ovicell – presumably for protective reasons because extreme types of hypercalcification are only observed in those colony parts where ovicells exist – thereby dramatically altering the zoarial surface morphology in this part.

An ancestrula was not observed in the present material due to overgrowth by later zooids during colony growth. According to Hayward & Ryland (1999) it has a well-developed gymnocyst and a distal semiorbicular opesia surrounded by a number of spines.

BUFFONELLARIA DIVERGENS (SMITT, 1873)
(FIG. 3A, B)

Original description: *Hippothoa divergens* forma *typica* Smitt, 1873: 47, pl. 9, fig. 179.

Synonyms: non *Buffonellaria divergens* (Smitt, 1873): Canu & Bassler, 1928: 88, pl. 8, figs 7, 8.

Material examined: *Lectotype* (designated here): SMNH 1880, Smitt Collection, leg. L.F. Pourtales 21.04.1869, Florida, off Key West, 250 m, on pebble; figured in Smitt (1873: pl. 9, fig. 179).

Measurements: ZL, 679 ± 70 , 530–773 (1, 13); ZW, 526 ± 50 , 413–587 (1, 13); OL, 134 ± 4 , 129–140 (1, 10); OW, 127 ± 6 , 117–136 (1, 10); oAL, 47 ± 5 , 39–55 (1, 11); oAW, 35 ± 4 , 28–42 (1, 11); fAL, 109 ± 6 , 102–113 (1, 3); fAW, 50 ± 3 , 47–53 (1, 3).

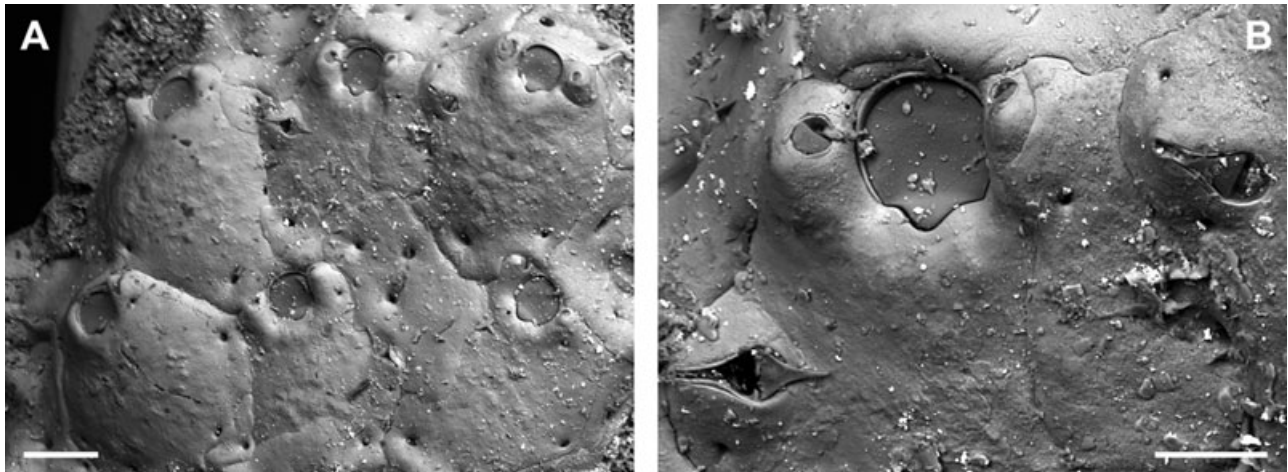


Figure 3. *Buffonellaria divergens* (Smitt, 1873): lectotype, SNHM 1880, Florida, off Key West. A, general aspect of autozoecia from the colony growth margin; scale bar, 200 μm . B, close-up of orifice, as well as of oral and frontal avicularia; scale bar, 100 μm .

Description: Colony encrusting, unilaminar, multiserial. Zoecia: hexagonal to polygonal, separated by shallow grooves. Frontal wall slightly convex, wrinkled, imperforate except for between two and five round or oval marginal pores. Primary orifice about as long as wide, surrounded by a very slightly raised but broad rim; anter broadly horseshoe-shaped, proximal margins short and straight with rounded shoulders, passing into a relatively narrow and widely U-shaped sinus, occupying about two-thirds of the total width.

Ovicells were not present in the available material.

Oral avicularia: usually paired, oval, lateral to orifice at about mid-distance, situated on a raised cystid with one or two small basal pores, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, directing proximolaterally. Additional frontal avicularia common, even on zooids at the colony periphery, situated at the lateral zooid margin just distal to mid-distance of zooid, on a very slightly raised cystid with two small areolar pores at the base, rostrum elongate triangular, parallel-sided and slightly downcurved distally, pointing laterally, at an acute angle to colony surface.

Remarks: When introducing the new genus *Buffonellaria*, Canu & Bassler (1927) chose *Hippothoa divergens* Smitt, 1873 as the type species. However, a lectotype of *B. divergens* did not exist, and there were no specimens of this species in the bryozoan collection at the MCZ, which formed the basis of Smitt's (1873) publication on 'Floridan Bryozoa', and which was recently redescribed by Winston (2005). The remaining material from Florida not stored at the MCZ, is stored in the Swedish Natural History

Museum, and we here designate the lectotype of *B. divergens* (SMNH 1880). The type specimen is the colony shown by Smitt (1873: pl. 9, fig. 179), as is evident from the location of the three frontal avicularia shown in Fig. 3A. Unfortunately, this specimen lacks ovicells, and bleaching of the type in order to observe orifice characteristics was, understandably, not allowed. The redescription is therefore restricted to superficial zoecial and avicularian morphology only.

As Winston (2005) rightly remarked, the *B. divergens* specimens from Florida differ from the eastern-Atlantic and Mediterranean specimens that are also referred to this species; this will be demonstrated in detail below. Consequently, *B. divergens* is not, as was hitherto assumed, a widely distributed, trans-Atlantic species, but is restricted to Floridan and, possibly, Caribbean waters. However, as Winston noted, even the specimens collected in the area of the Tortugas during a later *Blake* cruise, which were identified as *B. divergens*, differ significantly in zoecium size from the lectotype. Therefore, in light of the present results that show relatively restricted geographical species ranges, other records of this species even from nearby regions need to be considered cautiously.

Canu & Bassler's (1928: 88, pl. 8, figs 7, 8) *B. divergens* from Cuba is a distinct species because of the lack of frontal avicularia and the distally directing oral avicularia. Furthermore, as they do not mention or show the typical oecium, it is questionable whether this species belongs to *Buffonellaria* at all. The same applies to another species from the Gulf of Mexico they newly describe as *Buffonellaria reticulata* Canu & Bassler (1928: 89, pl. 8, fig. 5).

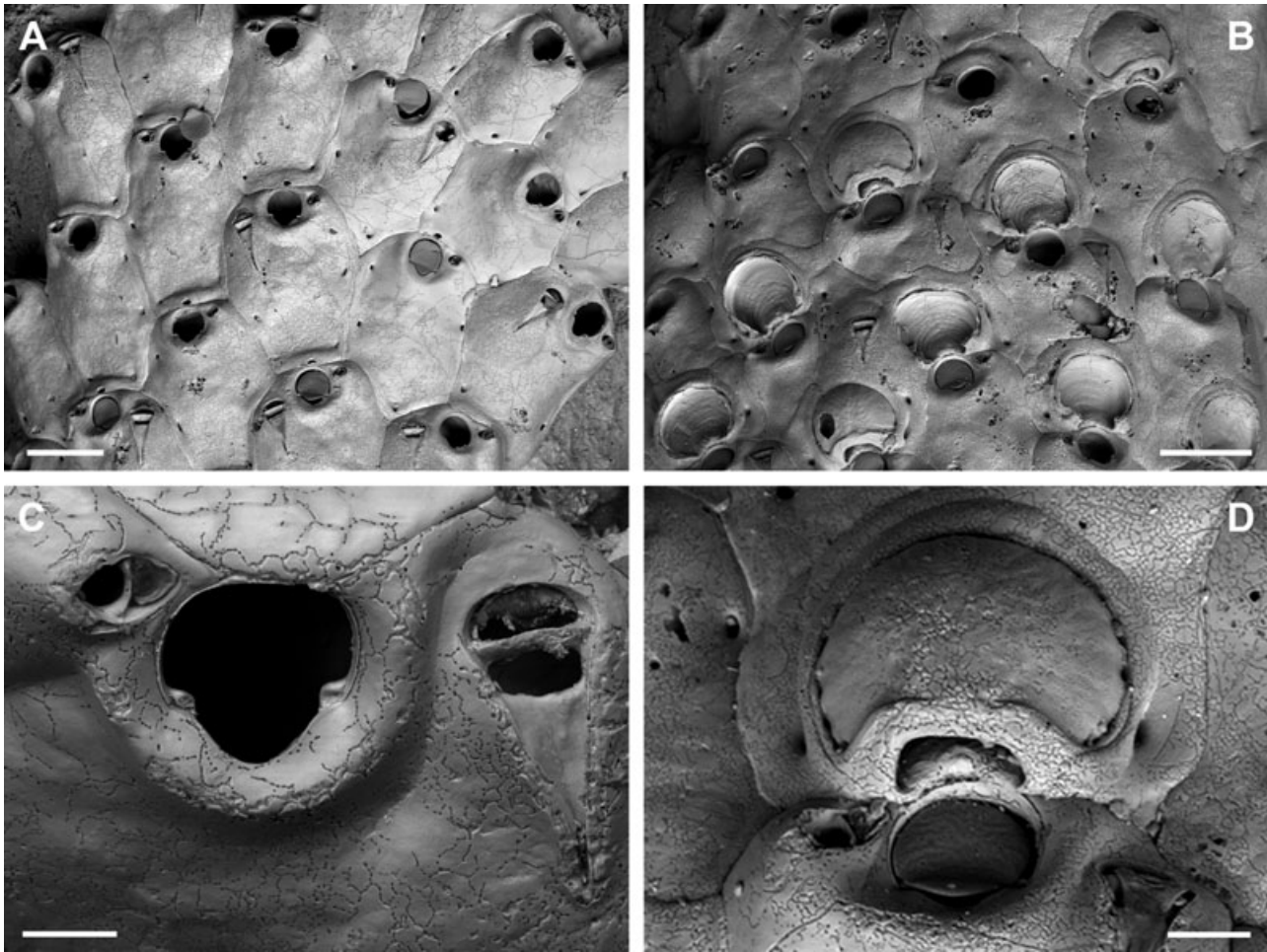


Figure 4. *Buffonellaria ritae* sp. nov.: holotype, NHM 2007.5.18.6, Madeira, off Santa Cruz. A, general aspect of autozooezia; scale bar, 200 μ m. B, ovicellate zoecia; scale bar, 200 μ m. C, close-up of orifice and oral avicularia; scale bar, 50 μ m. D, close-up of oecium; scale bar, 50 μ m.

***BUFFONELLARIA RITAE* SP. NOV.**
(FIG. 4A–D)

Material examined: Holotype: NHM 2007.5.18.6, off Santa Cruz, Madeira, ‘Blake’ Cruise, Stn 182, 210 m, on *Miniacina miniacea* Pallas, 1766.

Paratype: NHM 2007.5.18.7, off Santa Cruz, Madeira, ‘Blake’ Cruise, Stn 182, 210 m, occurring free of a substrate.

Other material: NHM 1911.10.1.1077, off Santa Cruz, Madeira, ‘Blake’ Cruise, Stn 182, 210 m; NHM 1911.10.1.1078, off Santa Cruz, Madeira, ‘Blake’ Cruise, Stn 182, 210 m, encrusting *M. miniacea*.

Differential diagnosis: *B. ritae* sp. nov. differs from all other species in the common presence of a dimorphic, proximally directing avicularium that develops during early ontogeny, and which is situated lateral to the orifice, as well as in its large and smooth exposed area of entoecium.

Etymology: Named in honour of the senior author’s mother, Rita Berning.

Measurements: ZL, 457 \pm 50, 351–521 (3, 20); ZW, 353 \pm 44, 248–427 (3, 20); OL, 97 \pm 7, 79–109 (3, 20); OW, 90 \pm 5, 78–99 (3, 20); OvL, 163 \pm 12, 146–186 (1, 8); OvW, 201 \pm 9, 190–213 (1, 8); oAL, 50 \pm 5, 37–47 (3, 20); oAW, 36 \pm 4, 25–31 (3, 20); fAL, 159 \pm 17, 135–188 (3, 20); fAW, 69 \pm 5, 56–79 (3, 20).

Description: Colony encrusting, laminar to plurilaminar, multiserial. Zoecia hexagonal, separated by shallow grooves. Frontal wall slightly convex, smooth, imperforate except for between three and five small round or slit-like marginal areolar pores; oecial pore slightly larger, round. Primary orifice slightly longer than wide; anter semicircular, proximal margins very short and sloping, passing into a deep, broad, and widely U-shaped sinus, occupying more than two-

thirds of the total width, condyles short and blunt; orifice surrounded by a low thickened rim incorporating the oral avicularium.

Ooecium, broader than long, shallowly vaulted, marginal band of ectooecium very narrow, exposed entooecium therefore large, with a smooth surface and 14–16 very low ribs, generally discernible only at the very margin; distinct proximal band of ectooecium paralleling and framing the semicircular aperture.

Small oral avicularia single, lateral to orifice with the crossbar usually located distal to mid-distance, oval, situated at the distal end of a slightly raised cystid, frontal plane at an acute angle to colony surface; rostrum semi-elliptical with a hooked tip, directing laterally or proximolaterally, proximal uncalcified area narrower, semicircular; crossbar complete, without columella. Typical, large, frontal avicularia often present in ontogenetically young zooids, situated lateral to orifice opposite to small avicularium, others may arise from marginal pore anywhere on frontal zooid surface during later ontogeny, located distally on large, slightly swollen, smooth and imperforate cystid; rostrum elongate triangular, narrowing slightly distal to crossbar, downcurved and becoming very slender and parallel-sided distally, oral avicularia point proximally, other frontal avicularia are irregularly orientated; proximal uncalcified area broadly semi-elliptical, distal area relatively small and restricted, and of varying shape; crossbar complete without columella.

Remarks: Although the specimens from Santa Cruz presented here are from Norman's Collection (NHM), as are the specimens of *Buffonellaria jensi* sp. nov. from Porto Santo (described below), he did not mention them in his paper on Madeiran bryozoans (Norman, 1909). Other specimens from Madeira identified as *Schizoporella biaperta* by Hincks (1880b: 76) are likely to belong to the genus *Stephanollona*, as Hincks already mentioned, which is evidenced by the presence of oral spines and spatulate avicularia.

Secondary calcification, and therefore variability in colony morphology, is not as prominent in this species compared with most other taxa, e.g. *B. jensi* sp. nov. Furthermore, because of the characteristic large avicularium situated lateral to the orifice, and because of the large and smooth entooecial area, *B. ritae* sp. nov. is easily distinguished from all other species.

BUFFONELLARIA NEBULOSA (JULLIEN & CALVET,
1903)

(FIG. 5A–E)

Original description: *Hippothoa nebulosa* Jullien & Calvet, 1903: 87, pl. 10, fig. 8.

Material examined: Lectotype: MNHN 3991a, Azores, RV 'Hirondelle', Stn 247, 318 m, on octocoral.

Paralectotype: MNHN 3991b, Azores, RV 'Hirondelle', Stn 226, 130 m, on a relict celleporid bryozoan.

Measurements: ZL, 629 ± 39, 563–696 (1, 15); ZW, 522 ± 31, 469–583 (1, 15); OL, 145 ± 4, 139–152 (1, 20); OW, 132 ± 7, 121–145 (1, 20); OvL, 295 ± 8, 286–309 (1, 6); OvW, 333 ± 5, 328–342 (1, 6); oAL, 69 ± 6, 55–76 (1, 12); oAW, 51 ± 5, 43–58 (1, 12); fAL, 185 ± 15, 171–217 (1, 16); fAW, 78 ± 6, 69–88 (1, 16).

Description: Colony encrusting, unilaminar, multiseriate. Zooecia quadrate to hexagonal, initially separated by shallow grooves, which are covered by thin layers of secondary calcification during later ontogeny. Frontal wall slightly convex to flat, granular, imperforate except for some three or four small, sickle-shaped, marginal areolar pores; oecial pore small and round. Primary orifice longer than wide; anter comprising two-thirds of a full circle, proximal margins short and slightly sloping, passing into rounded shoulders of a rounded V-shaped or U-shaped sinus, occupying about two-thirds of the total width, condyles conspicuous, as long as proximal margins and broad, slightly sloping, and with rounded edges.

Ooecia about as broad as long, initially globular, the lateral wall becoming covered by thin layers of secondary calcification during ontogeny, exposed entooecium relatively large, semicircular with a slightly concave proximal border, surface convex with 16–20 distinct, prominent, tubercular ribs meeting and levelling proximomedially, proximal ooecium margin slightly concave.

Small oral avicularia single or paired, distal to mid-distance of orifice, in close proximity of orifice rim, oval, situated at the distal end of a slightly raised and swollen cystid, with a tiny proximal pore, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, directing proximolaterally, proximal uncalcified area semicircular; crossbar complete, possibly with small columella. A single larger avicularium per zooid usually present, developing during early ontogeny, situated proximolateral to oral avicularium, others may arise from marginal pore anywhere on frontal zooid surface during later ontogeny, located distally on a slightly swollen and smooth cystid with a few, small, round pores; rostrum narrowing distal to crossbar, extremely long, thin, and parallel-sided distally, downcurved; frontal avicularia proximal to oral avicularia, point proximally, other frontal avicularia irregularly orientated; proximal uncalcified area semicircular, distal area arrowhead-shaped; crossbar complete with a stout bifid columella.

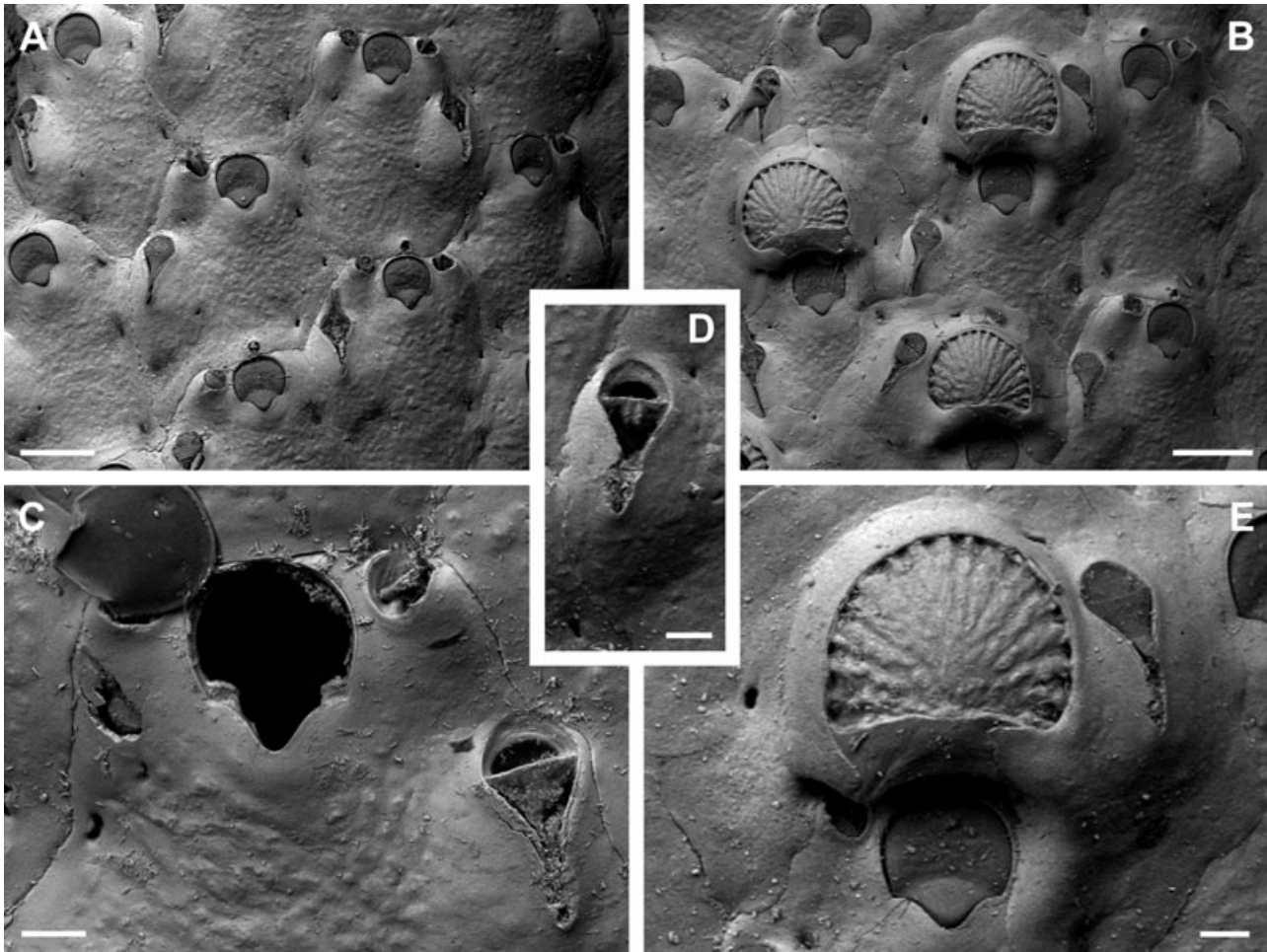


Figure 5. *Buffonellaria nebulosa* (Jullien & Calvet, 1903): lectotype, MNHN 3991a, Azores. A, general aspect of autozooecea; scale bar, 200 µm. B, ovicellate zooecea; scale bar, 200 µm. C, close-up of orifice showing a comparatively deep and V-shaped sinus; scale bar, 50 µm. D, close-up of frontal avicularium; scale bar, 50 µm. E, close-up of oecium and orifice with a rather U-shaped sinus; scale bar, 50 µm.

Remarks: Both specimens here designated as lectotype and paralectotype were stored in the same small glass vial with a handwritten label identifying them as 'type'. They also share the same collection number, although they derive from two different sample stations (Stn 247, Stn 226), but it is impossible to identify to which sample each specimen belongs. Therefore, as there are no characteristic elements in the original figure in Jullien & Calvet (1903) that can be related to any of the available type specimens, the larger colony containing ovicells is here designated as lectotype.

Four years after the introduction of this species, Calvet (1907: 423) recorded several specimens of *H. nebulosa* from the Azores. However, without a description or illustration of the material, it is not possible to judge whether these specimens are synonymous with *B. nebulosa* because another species (*Buffonellaria acorensis* sp. nov., see below) also occurs in this area.

Buffonellaria nebulosa is a deep-water species that has only been reported from the Azores archipelago, in depths of 130–320 m. In contrast to most other species, *B. nebulosa* develops distinctly less secondary calcification, and therefore achieves less ontogenetic morphological variability. However, orifice morphology, with the sinus being rather narrow and V-shaped or widely U-shaped, may be subject to considerable intracolony variability. The formation of a dimorphic avicularium with a determined position on the frontal wall during early ontogeny is shared with *B. divergens*, as well as with *B. ritae* sp. nov., *B. acorensis* sp. nov., and *Buffonellaria* sp. 2 (see below).

***BUFFONELLARIA ACORENSIS* SP. NOV.**

(FIG. 6A–D)

Synonyms: *Stephanosella biaperta* (Waters, 1879) [sic]; d'Hondt, 1975: 576.

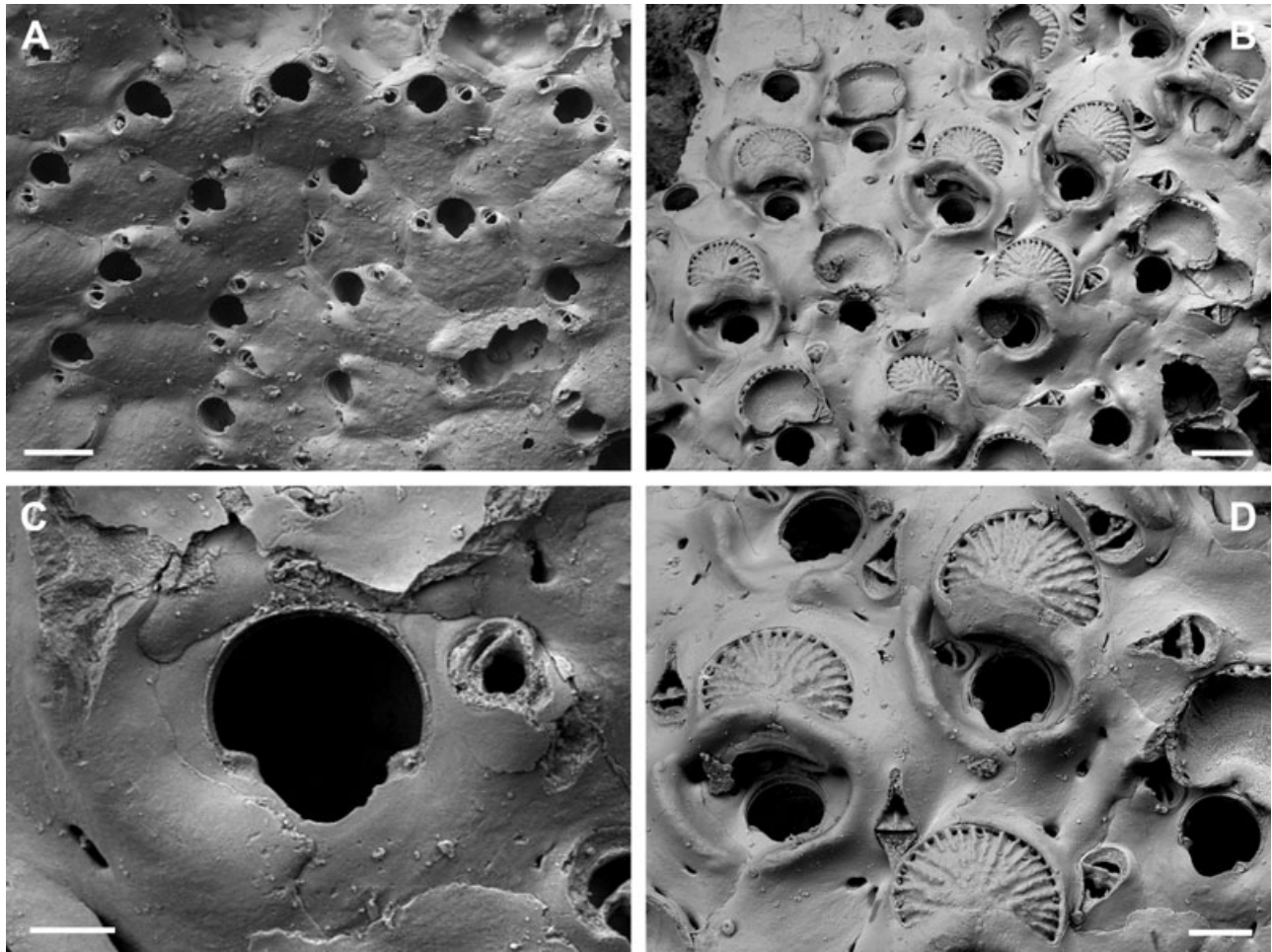


Figure 6. *Buffonellaria acorensis* sp. nov.: holotype, MNHN BRY-20057, Azores. A, autozoecia and two frontal avicularia; scale bar, 200 μ m. B, ovicellate zoecia in colony region with secondary calcification; scale bar, 200 μ m. C, close-up of orifice; scale bar, 50 μ m. D, close-up of ooecium and frontal avicularia; scale bar, 100 μ m.

Material examined: Holotype: MNHN BRY-20057, off São Miguel Island, Azores, RV 'Jean Charcot', Biaçores Expedition, Stn 145 (37°41'N, 25°37.5'W), 148–135 m, on rock.

Paratype: MNHN BRY-20058, off São Miguel Island, Azores, RV 'Jean Charcot', Biaçores Expedition, Stn 63 (38°37.5'N, 28°36.5'W), 220–165 m, on rock.

Other material: MNHN 7487, off Flores Island, Azores, RV 'Jean Charcot', Biaçores Expedition, Stn 109 (39°33'N, 31°17'W), 230–190 m, on shell.

Differential diagnosis: *B. acorensis* sp. nov. has a distinctly greater number of entoecial ribs than any other species, apart from *B. nebulosa*, from which it differs in having a broader, U-shaped sinus, frontal avicularia with a shorter and broader rostrum, and a more pronounced secondary calcification in ovicellate colony regions. The occasional occurrence of a frontal avicularium with a determined position on the frontal

wall further distinguishes this species from *B. jensi* sp. nov., *Buffonellaria muriella* sp. nov., *Buffonellaria harmelini* sp. nov., *Buffonellaria antoniettae* sp. nov., and *Buffonellaria arctica* sp. nov. (see below). *Buffonellaria divergens* has distinctly smaller oral and frontal avicularia, with the latter directing laterally.

Etymology: From the type locality, the Azores (Açores in Portuguese).

Measurements: ZL, 533 \pm 80, 395–686 (2, 20); ZW, 427 \pm 75, 282–529 (2, 20); OL, 131 \pm 13, 108–152 (2, 20); OW, 128 \pm 14, 104–154 (2, 20); OvL, 239 \pm 18, 218–268 (2, 9); OvW, 305 \pm 7, 296–320 (2, 9); oAL, 65 \pm 8, 48–84 (2, 20); oAW, 47 \pm 7, 37–62 (2, 20); fAL, 148 \pm 21, 116–200 (2, 20); fAW, 71 \pm 9, 56–86 (2, 20).

Description: Colony encrusting, unilaminar, multiseptal. Zoecia quadrate to hexagonal, initially separated by shallow grooves. Frontal wall very slightly

convex to flat, smooth, imperforate except for some three small, slit-like or sickle-shaped, marginal areolar pores, oocial pore larger, usually transversely elliptical. Primary orifice slightly longer than wide; anter semicircular, proximal margins short and sloping, passing into rounded shoulders of a widely opening and deep, rounded V-shaped or broadly U-shaped sinus, occupying a little less than two-thirds of the total width, condyles conspicuous, short but broad, blunt, very slightly sloping; orifice in ovicellate zooids commonly surrounded by a thickened rim of secondary calcification, with the oral avicularia incorporated into the interior side.

Ooecium broader than long, initially globular, becoming immersed during ontogeny, band of ectooecium relatively narrow, exposed entoecium therefore quite large, semicircular, surface convex with 18–21 distinct, prominent, tubercular ribs meeting proximomedially, proximal ovicell margin occasionally with a prominent rim of secondary calcification.

Small oral avicularia single or paired, lateral to orifice, oval, situated at the distal end of a slightly raised and swollen cystid with a tiny proximal pore, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, directing proximally or proximolaterally, rarely laterally, proximal uncalcified area semicircular; crossbar complete, with small columella. Additional larger avicularia single, sporadic to common, occasionally developing relatively early during ontogeny, usually situated proximolateral to oral avicularium, others may arise from marginal pore anywhere on frontal zooid surface during later ontogeny, located distally on a slightly swollen and smooth cystid, with a small, slit-like, proximal pore; rostrum elongate triangular, variable in length, narrowing distal to crossbar, downcurved, and occasionally becoming very slender and parallel-sided distally, frontal avicularia proximal to oral avicularia point in various proximal directions, other frontal avicularia irregularly orientated; proximal uncalcified area semi-elliptical, distal area arrowhead-shaped; crossbar complete, relatively thick, with stout columella.

Remarks: Although d'Hondt (1975: 576) cites Waters as the authority of *Stephanosella biaperta* when describing the present specimens, Waters (1879: 37) did not introduce a new species in his paper, but only omitted to state the authority of the species he identified as *Lepralia linearis* var. *biaperta*. However, whereas Waters' specimens closely resemble *B. muriella* sp. nov. (see below), they differ from *B. acorensis* sp. nov. in having a deeper sinus, narrower ovicells, and in producing less secondary calcification in colony regions with ovicellate zooids.

Colonies of MNHN 7487 differ from the holotype and paratype in having less marked ovicell ribs and

peristomes around orifices of ovicellate zooids. However, as all other characters correspond to those of the holotype, these differences are considered to reflect intraspecific variation. Genetic analyses may falsify this statement. The great variability in zooecium length and width is, to some extent, to the result of growth on an irregular substrate.

It is interesting to note that this is the second species recorded from the fairly isolated Azores archipelago, besides *B. nebulosa*. Apart from the occurrence of frontal avicularia during early ontogeny in both *B. nebulosa* and *B. acorensis* sp. nov., however, they do not seem to be very closely related morphologically. Concerning general zooecium morphology, *B. acorensis* sp. nov. is rather similar to *B. harmelini* sp. nov., *B. jensi* sp. nov., and *B. muriella* sp. nov. (see below), which makes it likely that *B. acorensis* sp. nov. and *B. nebulosa* have independently colonized the Azores from different source regions. Even more intriguing is that there was only a single *Buffonellaria* species present in each of the continental shelf locations covered in this study, whereas only the Madeiran archipelago also hosts two species (*B. jensi* sp. nov. and *B. ritae* sp. nov.).

***BUFFONELLARIA JENSI* SP. NOV.**

(FIG. 7A–D)

Synonyms: *Schizoporella biaperta* (Michelin, 1848) var. *divergens* (Smitt, 1873): Norman, 1909: 303, pl. 40, figs 3, 4.

Material examined: Holotype: NHM 2007.5.18.8, off Porto Santo, Madeira, on the benthic foraminifer *M. miniacea*.

Paratype: NHM 2007.5.18.9, off Porto Santo, Madeira, colony occurring free of a substrate.

Other material: NHM 1911.10.1.1080, off Porto Santo, Madeira, on *M. miniacea* and organic substrate.

Differential diagnosis: *B. jensi* sp. nov. is distinguished from *B. divergens*, *B. nebulosa*, *B. ritae* sp. nov., and *B. acorensis* sp. nov., in the absence of an early ontogenetic frontal avicularium, with a determined position on the frontal wall, as well as by a much more pronounced secondary calcification of colony regions with ovicellate zoecia. It differs from *B. muriella* sp. nov. in having a greater number of entoecial ribs, a relatively shorter rostrum in frontal avicularia, and a generally shallower and broader sinus (although sinus shape is subject to considerable variation in *B. muriella* sp. nov., see below). Differences between *B. jensi* sp. nov. and *B. harmelini* sp. nov. are found in the presence of more conspicuous marginal pores, a broader sinus, elliptical oral avicularia, a greater number of entoecial ribs, and in

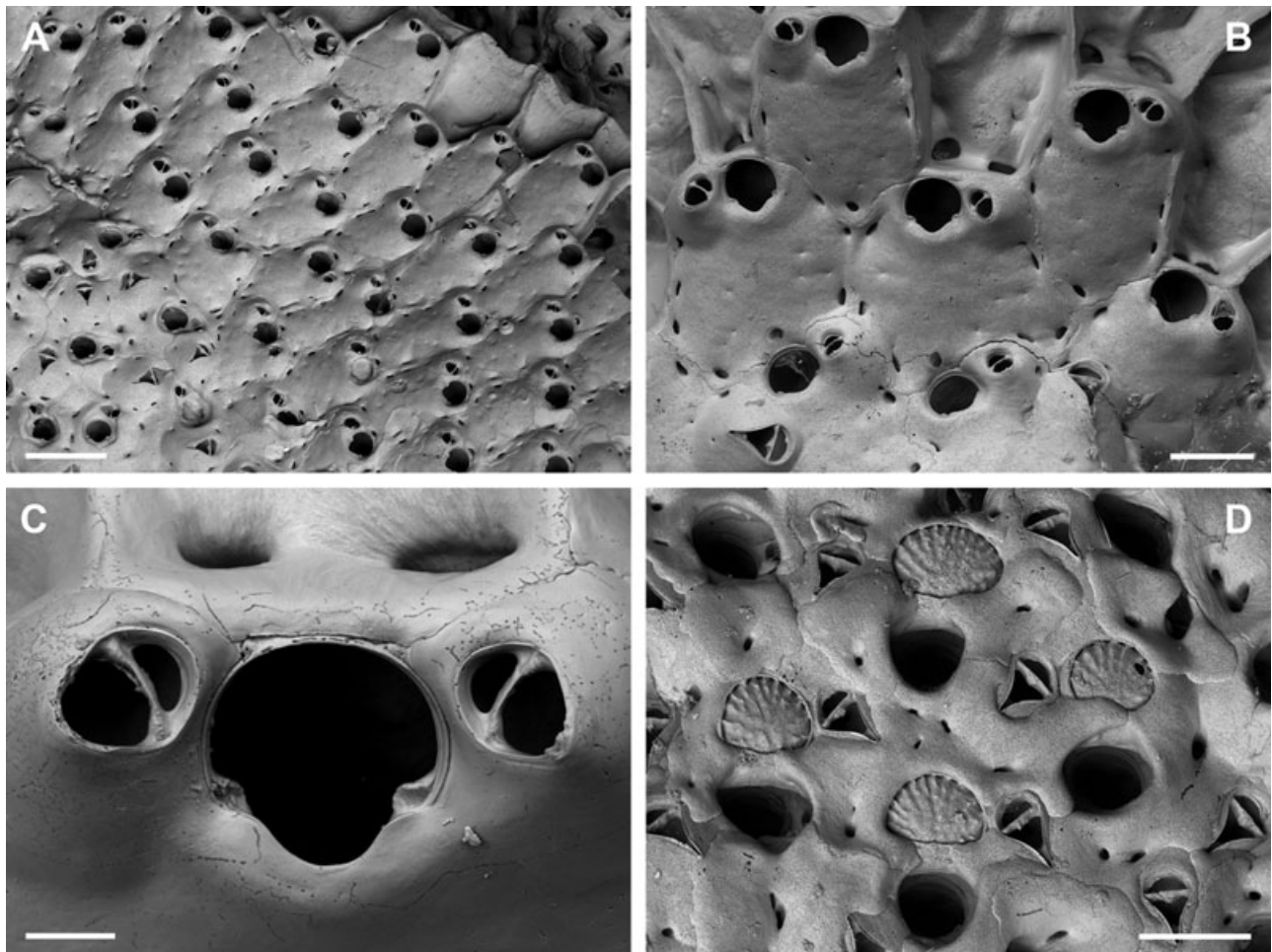


Figure 7. *Buffonellaria jensi* sp. nov.: holotype, NHM 2007.5.18.8, Madeira, off Porto Santo. A, general aspect; note formation of frontal avicularia and onset of secondary calcification in ontogenetically older zooecia, at lower left-hand corner; scale bar, 400 μ m. B, autozoecia at the colony growth margin; scale bar, 200 μ m. C, close-up of orifice and oral avicularia; scale bar, 50 μ m. D, ooecia and frontal avicularia in colony region covered by secondary calcification; note deeply immersed orifices; scale bar, 200 μ m.

thicker secondary calcification. *Buffonellaria antoniettae* sp. nov. has distinctly larger and elongate triangular oral avicularia, whereas *B. arctica* sp. nov. has a granular frontal wall, smaller oral and frontal avicularia, as well as larger ovicells, with an elliptical entoecial area. *Buffonellaria jensi* sp. nov. also differs from *B. porcellanum* in having a smooth frontal wall, larger zooecia oral avicularia, and ovicells with a greater number of entoecial ribs, as well as in developing frontal avicularia during later ontogeny.

Etymology: Named in honour of the senior author's father, Jens Berning.

Measurements: ZL, 549 \pm 43, 492–645 (1, 20); ZW, 387 \pm 65, 278–537 (1, 20); OL, 127 \pm 5, 116–135 (1, 20); OW, 129 \pm 8, 117–141 (1, 20); OvL, 208 \pm 20,

176–229 (1, 9); OvW, 232 \pm 22, 191–264 (1, 9); oAL, 84 \pm 8, 70–97 (1, 14); oAW, 61 \pm 5, 53–71 (1, 14); fAL, 150 \pm 10, 131–167 (1, 7); fAW, 92 \pm 8, 77–107 (1, 7).

Description: Colony encrusting, unilaminar, multiseriate. Zooecia quadrangular, initially separated by distinct sutures, soon covered by secondary calcification. Frontal wall very slightly convex, smooth, imperforate except for between four and seven small, oval to slit-like, marginal areolar pores, and a few tiny central pseudopores; ooecial pore slightly larger, transversely elliptical. Primary orifice on average about as long as wide, but length/width relationship variable; anter almost two-thirds of full circle, proximal margins short and slightly sloping, passing into rounded shoulders of a deep, broad, and widely U-shaped sinus, occupying a little less than two-

thirds of the total width, condyles conspicuous, short but broad, blunt; orifice encircled by a thickened rim of secondary calcification during later ontogeny, incorporating the oral avicularium.

Ooecium broader than long, initially globular, becoming immersed during ontogeny, band of ectooecium relatively narrow, exposed entoecium therefore quite large, semicircular, surface slightly convex with 13–17 prominent tubercular ribs meeting proximomedially.

Small oral avicularia single, occasionally paired, lateral to orifice, oval, situated at the distal end of a slightly swollen and raised cystid with a small proximal areolar pore, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, with a few low teeth distally, directing proximolaterally, proximal uncalcified area semicircular; crossbar complete, without columella. Additional larger avicularia frequently present in older parts of the colony, arising from a marginal pore anywhere on frontal zooid surface, located distally on large, slightly swollen, smooth cystid with few marginal areolar pores; rostrum elongate triangular, narrowing distal to crossbar, slightly downcurved, occasionally becoming very slender and parallel-sided distally, pointing in various directions; proximal uncalcified area semicircular, distal area arrowhead-shaped; crossbar complete with a median columella.

Remarks: The original illustration of these specimens published by Norman (1909) differs somewhat from the SEM photos presented here. Although he showed three autozooids with a pair of oral avicularia, only a single one is generally present. Another zooid has a long, distally directed, curved, and pointed oral avicularium, which was not observed to occur in these or other specimens. It may therefore be a broken cystid of an oral avicularium. Moreover, the sinus is somewhat deeper but narrower in Norman's drawings. However, the drawings are relatively simple, and other material from Madeira (see *B. ritae* sp. nov.), with which these specimens may have been mistaken, does not match this illustrated specimen either. As the sample location, as well as the note on the original label, which states that Senhor De Noronha donated the specimens, matches with Norman's (1909: 303) remarks, these specimens are chosen as types, in spite of these inconsistencies.

The co-occurrence of *B. ritae* sp. nov. and *B. jensi* sp. nov. around the Madeiran archipelago is, as the co-occurrence of *B. nebulosa* and *B. acorensis* sp. nov. around the Azores, worth mentioning because from all other locations studied, only a single species was recorded. In addition, morphological differences are even more pronounced in *B. ritae* sp. nov. and *B. jensi* sp. nov. than in the Azores species, thus indicating

independent colonization of the islands from different source regions, rather than *in situ* speciation after a single invasion event.

Whereas hypercalcification is pronounced in ovicellate colony regions in *B. jensi* sp. nov., profoundly changing the surface morphology, orifice variability is comparatively low. Unfortunately, the depth of occurrence around Madeira is not known. It was found growing on the encrusting foraminifer *M. miniacea* and on soft organic tissue.

BUFFONELLARIA MURIELLA SP. NOV.

(FIGS 1A, 2A, 8A–F)

Synonyms: *Schizoporella biaperta* (Michelin, 1848): Hincks, 1880: 255, pl. 40, figs 7–9.

Buffonellaria divergens (Smitt, 1873): Hayward & Ryland, 1979: 204, fig. 86; Hayward & Ryland, 1999: 356, fig. 167; fig. 183C, D (as *Stephanollona armata*).

Material examined: Holotype: NHM 2007.5.18.1, Guernsey, on bivalve, illustrated by Hayward & Ryland (1979: fig. 86).

Paratypes: NHM 2000.12.5.10, Greenwich Light, Western Channel, Stn 26A, on small pebble; NHM 1897.5.1.726, Hastings, UK, on pectinid, illustrated by Ryland (1969: fig. 2C).

Other material: NHM 1911.10.1.1082–1083, Guernsey, on bivalves; NHM 2007.5.18.2, Guernsey, on bivalves; NHM 2007.5.18.3, Adriatic Sea, off Puglia, Italy, occurring free of a substrate; CNHM Inv.br.27, off Lastovo, Adriatic Sea, Croatia, 10–15 m, on *Halimeda tuna* (Ellis & Solander, 1786); CNHM Inv.br.28, off Lastovo, Adriatic Sea, Croatia, 30–40 m, on non-calcifying algae and occurring free of a substrate; CNHM Inv.br.29, on Jabuka Shoal, Adriatic Sea, Croatia, 40–50 m, on *Pentapora fascialis* (Pallas, 1766), as well as on coralline and other noncalcifying algae.

Differential diagnosis: *B. muriella* sp. nov. lacks early ontogenetic frontal avicularia with a determined position on the frontal wall, and can therefore be distinguished from *B. divergens*, *B. ritae* sp. nov., *B. nebulosa*, and *B. acorensis* sp. nov., which also produce distinctly less secondary calcification in colony regions with ovicellate zooecia. *Buffonellaria muriella* sp. nov. differs from the morphologically closely related *B. jensi* sp. nov. in having a generally narrower and deeper sinus, with longer condyles (but see below), fewer entoecial ribs, and a relatively longer rostrum in frontal avicularia. Differences between *B. muriella* sp. nov. and *B. harmelini* sp. nov. are found in more conspicuous marginal pores, the smaller and elliptical oral avicularium, and in a slightly more extensive calcification of colony regions

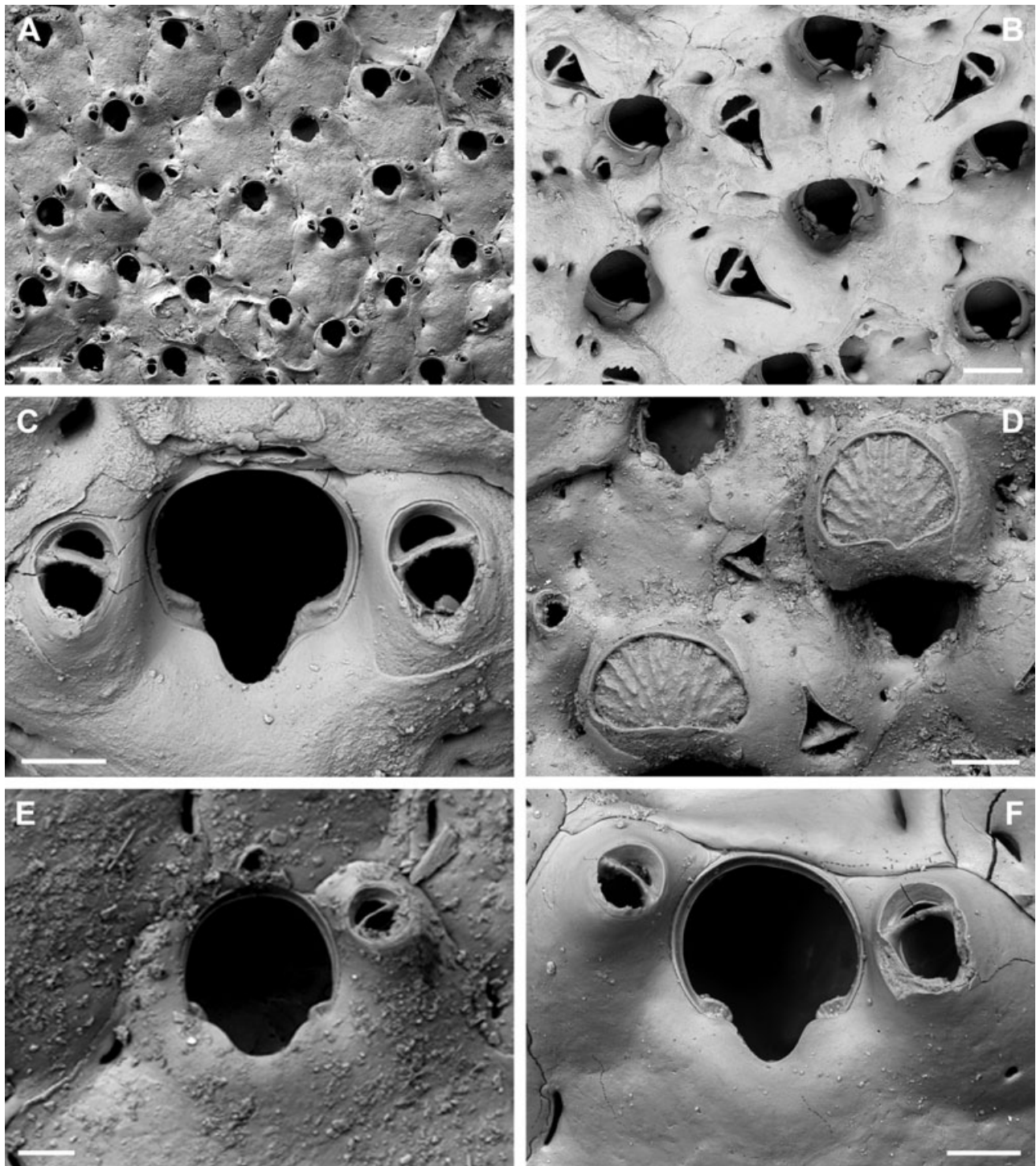


Figure 8. *Buffonellaria muriella* sp. nov. A, general aspect of autozoecia; note the formation of frontal avicularia at lower left, and the variability in orifice shape; NHM 1911.10.1.1082–1083, Guernsey; scale bar, 200 μ m. B, colony region with abundant formation of frontal avicularia and advanced frontal calcification immersing the orifices; holotype NHM 2007.5.18.1, Guernsey; scale bar, 100 μ m. C, close-up of orifice with deep, V-shaped sinus and long condyles; holotype; scale bar, 50 μ m. D, close-up of orifices and frontal avicularia prior to precipitation of secondary calcification; NHM 1911.10.1.1082–1083, Guernsey; scale bar, 100 μ m. E, close-up of orifice with broad, shallow, U-shaped sinus and shorter condyles; NHM 1911.10.1.1082–1083, Guernsey; scale bar, 200 μ m. F, close-up of orifice of an Adriatic specimen; CNHM Inv.br.28; scale bar, 50 μ m.

with ovicellate zoecia. In contrast to *B. antonietae* sp. nov., *B. muriella* sp. nov. has smaller zoecia, fewer entoecial ribs, and distinctly smaller elliptical avicularia. *Buffonellaria muriella* sp. nov. differs from *B. arctica* sp. nov. in having a smooth frontal wall, a semicircular entoecial area, and a larger frontal avicularia. It is also distinguished from *B. porcellanum* by the smooth frontal surface, as well as by the presence of frontal avicularia, and larger zoecia, orifices, oecia (with a greater number of entoecial ribs), and oral avicularia, which are situated lateral to the orifice.

Etymology: Named after a good friend of the senior author, Muriel Kock.

Measurements: ZL, 526 ± 51 , 458–626 (2, 20); ZW, 366 ± 36 , 299–431 (2, 20); OL, 140 ± 8 , 118–153 (2, 20); OW, 124 ± 7 , 105–135 (2, 20); OvL, 217 ± 36 , 174–261 (2, 8); OvW, 248 ± 34 , 190–284 (2, 8); oAL, 67 ± 11 , 53–96 (2, 20); oAW, 54 ± 6 , 44–65 (2, 20); fAL, 154 ± 13 , 130–180 (2, 20); fAW, 86 ± 8 , 67–101 (2, 20).

Description: Colony encrusting, unilaminar to plurilaminar, multiserial, occasionally erect bilaminar (observed in material from the Adriatic Sea only). Zoecia hexagonal to elongate hexagonal, quadrangular, or oval, separated by shallow grooves that become obscured by secondary calcification during later ontogeny; frontal wall slightly convex, smooth, initially pseudoporous, becoming imperforate or with only tiny pseudopores remaining during later ontogeny; between four and seven slit-like, marginal, areolar pores; oecial pore rimmed, round or oval. Primary orifice variable in shape, and therefore in relation of length and width, usually longer than wide; anter more or less semicircular, proximal margins short, straight, and slightly sloping, passing into rounded shoulders of poster, varying in shape from generally deep and rounded V-shaped to relatively shallow and broadly U-shaped, occupying more than half of the total width; condyles variable in shape and size, usually conspicuous, relatively broad, blunt, more or less paralleling the proximal margin, occasionally smaller and shorter than the proximal margins.

Ooecium initially globular, prominent, slightly broader than long, frontal semicircular in outline during later ontogeny when it becomes almost completely immersed by secondary calcification; ectooecium a broad smooth band, exposed entoecium semicircular, relatively flat, marked with 11–13 radiating tubercular ribs slightly thickening towards margin.

Small oral avicularia single or paired, usually proximolateral or lateral to orifice, occasionally distal

to mid-distance of orifice, oval, situated on a slightly raised and swollen cystid, with a tiny, proximal, areolar pore, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, directing proximally or proximolaterally (rarely laterally), distally toothed and slightly raised; proximal uncalcified area semicircular; crossbar complete, occasionally with a small columella. Additional larger avicularia present in older areas of the colony, arising from marginal pores anywhere on frontal zooid surface, situated on large swollen cystid with marginal pores and a smooth surface; rostrum elongate triangular, narrowing distal to crossbar, becoming very slender and parallel-sided distally, pointing in various directions; proximal uncalcified area semicircular; crossbar complete with a median columella.

Remarks: Apart from colony growth type, the species description of *B. muriella* sp. nov. is based upon specimens from off south-east England only. Although there are no differences in discrete features between specimens from the north-east Atlantic and the Adriatic Sea, the latter are characterized by generally having somewhat smaller condyles (Fig. 8F), and slightly larger oral [oAL, 85 ± 10 , 68–103 (3, 17); oAW, 66 ± 8 , 55–85 (3, 17)] and frontal avicularia [fAL, 176 ± 16 , 150–197 (2, 15); fAW, 90 ± 6 , 82–102 (2, 15)], whereas zoecium, orifice, and ooecium sizes are all identical. Furthermore, Adriatic specimens have a greater number of ovicell ribs (15–17, see Fig. 2A), a less conspicuous columella in frontal avicularia, and, as mentioned above, occasionally exhibit erect bilaminar growth, which was not observed in north-east Atlantic specimens. However, we do not consider these differences a strong enough argument to separate these morphotypes into two species, because we cannot rule out local environmental conditions or intraspecific genetic differences between populations as causal mechanisms, especially considering the presence of strong intracolony variability (see below). Genetic analyses are certainly needed to clarify the relationship between these populations.

Although encrusting and erect parts of the colony in Adriatic specimens did not show any differences in zoecium morphology, this species stands out by its extreme variability in surface topography, which is, to a great extent, produced by secondary calcification during ontogeny. More importantly, the orifice shape is also prone to considerable variation, and, especially in the British specimens, may change from deep and rather V-shaped to shallow and broadly U-shaped within a single colony, approaching orifice shapes displayed in the closely related *B. jensi* sp. nov. and *B. harmelini* sp. nov. In addition, zoecium shape may vary between broadly hexagonal or quadrangular and

relatively elongated, with a narrow proximal region cramped by the proximal zooids. Under these conditions, defining species boundaries in this genus may occasionally prove to be a contentious issue.

During early ontogeny the frontal wall is, as Hincks (1880a: 255) already noted, centrally perforated by relatively large pseudopores (Fig. 1A). These are either rapidly closed by secondary calcification or remain present as tiny pseudopores, even during later ontogeny (see also *B. porcellanum*, as well as *Buffonellaria* sp. 1 and *Buffonellaria* sp. 2 below). Another feature observed in specimens from the Adriatic was that in the zooid distal to a maternal zooid, secondary calcification of the proximal frontal wall around the ooeial pore was suppressed, forming a shallow bowl in which the ooeium fits into at a later stage.

As it is unclear how many different Atlantic and Mediterranean species were lumped together under the former name *B. divergens*, very little certain information exists about the ecology of *B. muriella* sp. nov. Most of the specimens from the north-east Atlantic encrust pectinids and other bivalves. Colonies from the Adriatic Sea were observed to grow on *H. tuna*, corallinaceans, and fleshy algae, and the erect foliaceous bryozoan *P. fascialis* in depths of 10–50 m (M. Novosel, pers. comm. 2006). Erect growth was observed to occur in specimens of only one sample (CNHM Inv.br.28, 30–40 m), whereas the substrate was not preserved and therefore was presumably of ephemeral nature.

The presently affirmed range of geographical distribution of the north-east Atlantic populations of *B. muriella* sp. nov. extends from the Irish Sea (H. de Blauwe, pers. comm. 2006) via Guernsey to the eastern English Channel. In the Mediterranean Sea, *B. muriella* sp. nov. was recorded in southern Croatia and south-east Italy, and possibly also occurs along the south-west Italian coast as far as Naples, as Waters's (1879: 37, pl. 11, figs 1, 2) specimens closely resemble this species. Interestingly, in the Adriatic Sea its occurrence is restricted to the southern part, as it was not recorded by Hayward & McKinney (2002), who have thoroughly sampled the north-east Adriatic region off Croatia. However, minimum temperatures and mean annual temperatures in the northern part of the Adriatic Sea are comparable with those off south-west England, whereas temperatures in the southern Adriatic are distinctly higher (see Novosel, Pozar-Domac & Pasarić, 2004; Lombardi *et al.*, 2006). Thus, if the distribution of the Adriatic population is controlled by temperature, this may indicate that populations from southern England and the Adriatic Sea have different environmental preferences, and may, indeed, be different taxa.

BUFFONELLARIA HARMELINI SP. NOV.

(FIG. 9A–D)

Material examined: Holotype: NHM 2007.5.18.10, Gabinière islet, Port-Cros Island, Mediterranean Sea (42°53.16'N, 6°23.5'E), 58–50 m, on *Myriapora truncata* (Pallas, 1766).

Paratype: NHM 2007.5.18.11, Gabinière islet, Port-Cros Island, Mediterranean Sea (42°53.16'N, 6°23.5'E), 58–50 m, occurring free of a substrate.

Differential diagnosis: *B. harmelini* sp. nov. differs from all but one of the other species in having a larger oral avicularium with a triangular rostrum. The only exception is *B. antoniettae* sp. nov., which has triangular avicularia, but ones that are more elongated and therefore even larger than those in *B. harmelini* sp. nov., and which forms erect bilaminar colonies.

Etymology: Named after our appreciated colleague and collector of the specimens, Jean-Georges Harmelin.

Measurements: ZL, 470 ± 39, 396–552 (1, 18); ZW, 350 ± 29, 305–410 (1, 18); OL, 142 ± 10, 122–153 (1, 19); OW, 122 ± 7, 109–132 (1, 19); OvL, 213 ± 12, 187–239 (1, 13); OvW, 254 ± 18, 219–291 (1, 13); oAL, 88 ± 9, 72–104 (1, 14); oAW, 57 ± 6, 44–67 (1, 14); fAL, 172 ± 25, 140–219 (1, 20); fAW, 94 ± 12, 76–119 (1, 20).

Description: Colony encrusting, unilaminar, multiseriate. Zooecia rectangular in early ontogeny, separated by shallow grooves, soon altered by secondary calcification during ontogeny. Frontal wall slightly convex, initially even and smooth, imperforate except for between three and six small slit-like or sickle-shaped marginal areolar pores during early ontogeny; ooeial pore conspicuous, generally round. Primary orifice slightly longer than wide; anter two-thirds of a full circle, proximal margins short, straight or slightly sloping, passing into rounded shoulders of a variably deep, U-shaped to rounded V-shaped sinus, occupying about two-thirds of the total width, condyles short but distinct, blunt.

Ooeium initially globular, frontal rather hemispherical during later ontogeny when marginally covered by secondary calcification, wider than long; ectooecium a broad smooth band encircling a slightly convex, semicircular, frontal area of uncovered entooecium, marked by between nine and 13 distinct, tubercular, radiating ribs meeting proximomedially.

Oral avicularia single, rarely paired, lateral to orifice, with the crossbar located at mid-distance or slightly distal to it, oval, situated on a slightly raised cystid, frontal plane at an acute angle to colony

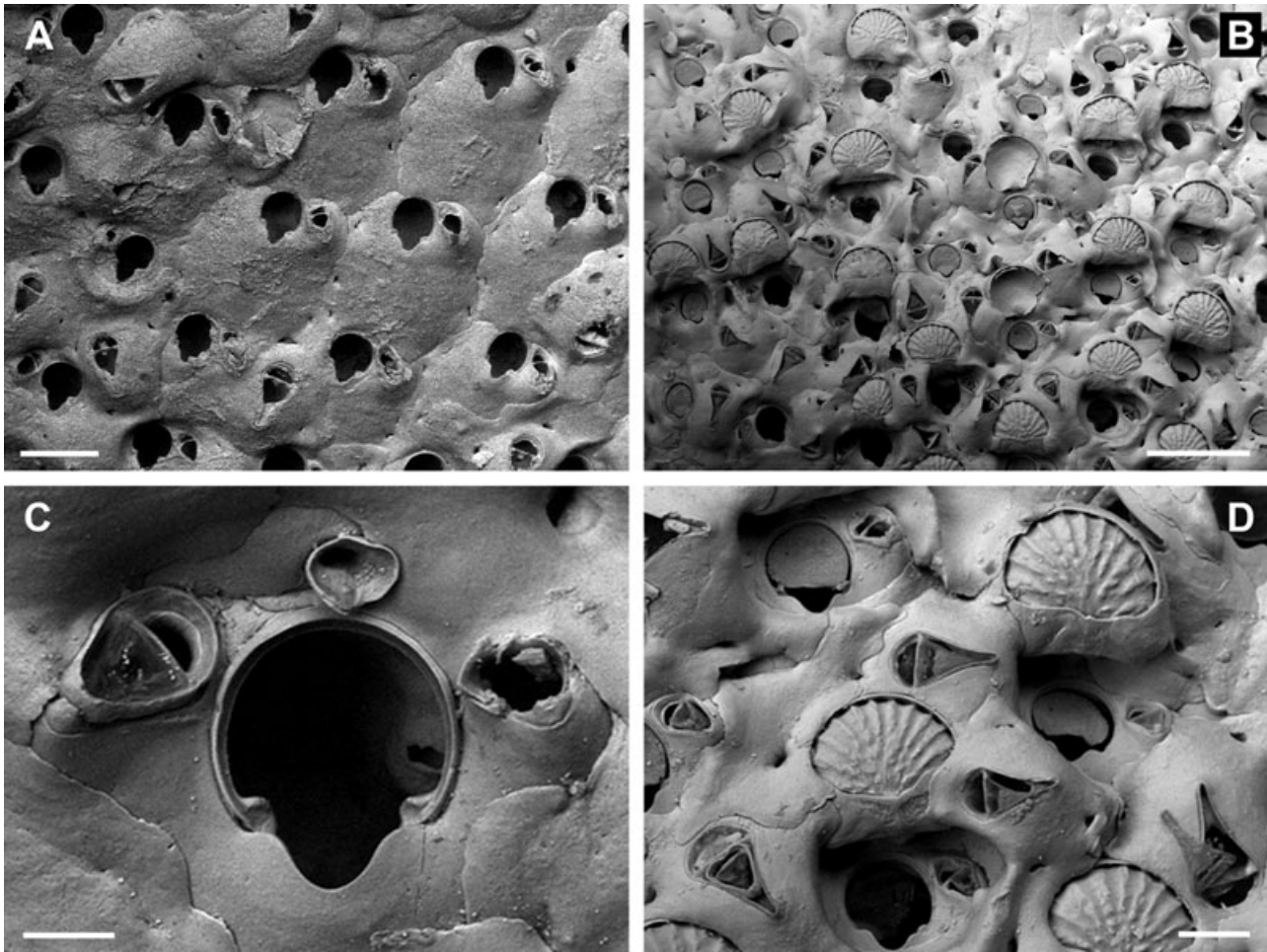


Figure 9. *Buffonellaria harmelini* sp. nov.: holotype, NHM 2007.5.18.10, off Port-Cros Island, Mediterranean Sea. A, general aspect of autozooeceia; scale bar, 200 μ m. B, ovicellate zooecia and frontal avicularia in colony region, affected by secondary calcification; scale bar, 400 μ m. C, close-up of orifice; scale bar, 50 μ m. D, ooecia, oral and frontal avicularia; note the damaged frontal avicularium regenerated as oral an avicularium at lower left; scale bar, 100 μ m.

surface; rostrum rounded triangular with a hooked tip, directing proximolaterally, proximal uncalcified area semicircular; crossbar complete, without columella. Additional larger avicularia present in older areas of the colony, arising from marginal pore anywhere on frontal zooid surface, situated on large swollen cystid with marginal pores and a smooth surface; rostrum elongate triangular, narrowing distal to crossbar, becoming very slender and parallel-sided distally, pointing in various directions, occasionally downcurved distally; proximal uncalcified area semicircular, triangular distally; crossbar complete with a median columella.

Remarks: As in most other species, the orifice shape is quite variable in *B. harmelini* sp. nov., but secondary calcification in ovicellate colony regions does occur, but is not as extreme as in, e.g. *B. antoniet-*

tae sp. nov. (see below). Apart from the rounded triangular oral avicularium, *B. harmelini* sp. nov. is morphologically closely related to *B. acorensis* sp. nov. (this species differs in having a greater number of entoocelial ribs and in producing frontal avicularia during early ontogeny), as well as to *B. jensi* sp. nov. and to *B. muriella* sp. nov. (both of which have more conspicuous marginal pores and produce more extensive frontal calcification during later ontogeny). Another species with a triangular oral avicularium of intermediate size between *B. harmelini* sp. nov. and *B. antoniettae* sp. nov. is *Buffonellaria* sp. 1, which also occurs in the north-west Mediterranean Sea, and is discussed below.

The colonies often show repaired avicularia (Fig. 10D). Commonly, the large frontal avicularia are then replaced by smaller oral-type ones. The geographical range of *B. harmelini* sp. nov. within the

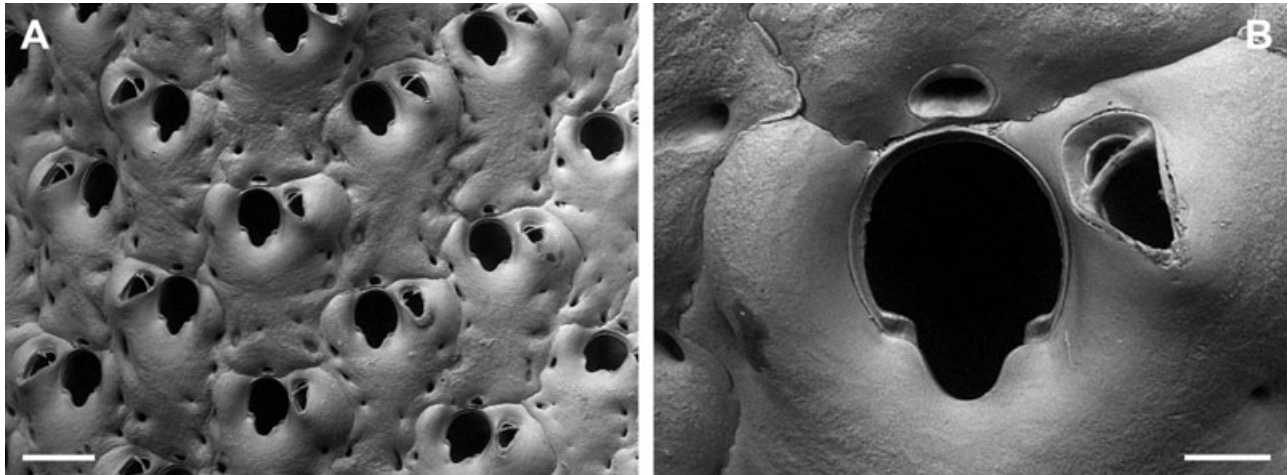


Figure 10. *Buffonellaria* sp. 1: NHM 2007.5.18.12, off Toulon, Mediterranean Sea. A, general aspect of autozooeccia; scale bar, 200 μm . B, Close-up of orifice; scale bar, 50 μm .

Mediterranean Sea is not known, as descriptions and illustrations of other records of *Buffonellaria* are insufficient for a precise determination (e.g. Gautier, 1962: 155; Zabala & Maluquer, 1988: 127, fig. 286).

BUFFONELLARIA SP. 1
(FIGS 1B, 10A, B)

Material examined: NHM 2007.5.18.12, off Toulon, Grande Rade, Mediterranean Sea, 53 m, occurring free of a substrate.

Measurements: ZL, 655 ± 80 , 533–738 (1, 20); ZW, 350 ± 34 , 262–404 (1, 20); OL, 156 ± 8 , 143–167 (1, 16); OW, 123 ± 4 , 118–135 (1, 16); oAL, 120 ± 11 , 104–138 (1, 15); oAW, 64 ± 5 , 54–71 (1, 15).

Description: Colony erect, bilaminar, foliaceous. Zooecia elongate rectangular, usually narrower proximally, initially separated by sutures on thin ridges, zooecial boundaries become wavy later, and are obscured by secondary calcification. Frontal wall with up to eight marginal areolar pores, and several pseudopores during early ontogeny, most of which soon become closed by secondary calcification, some tiny pores occasionally persist during later ontogeny, surface slightly convex, smooth. Primary orifice slightly longer than wide; anter about two-thirds of a full ellipse, proximal margins short and sloping, passing into a broad, deep, U-shaped sinus, occupying about two-thirds of the total width, condyles broad, blunt, more or less paralleling the proximal margins.

Ovicells were not observed.

Oral avicularia single, situated lateral to orifice, slightly distal to mid-distance of orifice, on a proxi-

mally raised cystid with a small proximal pore; rostrum triangular, directing proximolaterally, acute to frontal plane; crossbar complete, without columella, proximal uncalcified area more or less semi-circular. Additional frontal avicularia were not observed.

Remarks: As no ovicells and larger frontal avicularia are present in the only colony fragment available for study, we refrain from introducing a new species. Concerning general zooecial morphology and size, *Buffonellaria* sp. 1 is very closely related to *B. antoniettae* sp. nov. (see below), and is, besides *B. antoniettae* sp. nov. and Adriatic specimens of *B. muriella* sp. nov., the only other species with an erect bilaminar branching or foliaceous growth form encountered in this study. The erect growth type is therefore only observed in taxa from the Mediterranean Sea. Without being able to compare oecium morphology, *B. antoniettae* sp. nov. differs from *Buffonellaria* sp. 1 in a slightly more proximally positioned oral avicularium, with a significantly longer and distally thinner rostrum, as well as a slightly thicker crossbar. In addition, the sinus is generally deeper and more V-shaped in *B. antoniettae* sp. nov. Furthermore, orifice and oral avicularium morphology are also almost identical to those of *B. harmelini* sp. nov. However, the latter was only observed to form unilaminar encrusting colonies, has significantly smaller zooecia and oral avicularia, and has less conspicuous marginal pores. Although we cannot rule out the possibility that erect growth also occurs in *B. harmelini* sp. nov., the differences in several characters make it unlikely that *Buffonellaria* sp. 1 belongs to either *B. antoniettae* sp. nov. or *B. harmelini* sp. nov.

***BUFFONELLARIA ANTONIETTAE* SP. NOV.**

(FIGS 2B, 11A–F)

Material examined: Holotype: PMC B16.30.6.2006a, off south-east Sicily, 'Vega' 9, 118 m, colony fragment occurring free of a substrate.

Paratypes: PMC B16.30.6.2006b, off south-east Sicily, 'Vega' 9, 118 m, three colony fragments occurring free of a substrate.

Differential diagnosis: *B. antoniettae* sp. nov. differs from all other known and newly introduced species in its erect bilaminar growth form, and its large, elongate triangular, oral avicularium.

Etymology: Named after our appreciated colleague and collector of the specimens, Antonietta Rosso.

Measurements: ZL, 627 ± 66 , 504–731 (2, 20); ZW, 411 ± 33 , 316–450 (2, 20); OL, 151 ± 6 , 139–160 (2, 20); OW, 127 ± 6 , 116–141 (2, 20); OvL, 209 ± 9 , 198–223 (1, 15); OvW, 263 ± 11 , 247–286 (1, 15); oAL, 178 ± 10 , 161–198 (3, 15); oAW, 81 ± 6 , 72–96 (3, 15); fAL, 194 ± 17 , 149–219 (2, 12); fAW, 111 ± 9 , 98–126 (2, 12).

Description: Colony erect, bilaminar branching, branches some 3-mm wide. Zooecia elongate hexagonal, quadrangular, or oval, separated by indistinct meandering sutures; frontal wall slightly convex, imperforate and smooth, but initially with few pits and tiny pseudopores that soon become obscured by secondary calcification; initially between five and ten round or elongate, relatively small, marginal, areolar pores, and in some zooecia a round rimmed oecial pore of approximately the same size. Primary orifice variable in shape; anter about two-thirds of a full circle, proximal margins short and sloping, condyles short, but broad and slightly sloping, blunt, median margin straight, poster generally deep, broad, and a rounded V-shape, occasionally shallower and rather U-shaped.

Ooecium initially globular, slightly flattened frontally, central exposed entoecium large, semicircular, first with a relatively narrow proximal band of ectoecium, later slightly immersed by a thick rim of secondary calcification; surface of entoecium with 15–17 distinct, thin, radiating ribs, occasionally fusing towards the centre forming a meshwork, proximal margin straight in frontal view.

Oral avicularia large, single, occasionally absent (especially in zooids at branch margins), situated directly lateral to orifice on a broad and very slightly raised cystid that has a tiny proximal pore, frontal plane at an acute angle to colony surface; rostrum elongate triangular, directing proximolaterally, distal tip slightly downcurved; uncalcified area semicircular

proximally, elongate triangular distally; crossbar complete, without columella; oral avicularia are completely covered by secondary calcification in ovicellate colony regions. Additional larger avicularia present in older areas of the colony, arising from marginal pore anywhere on frontal zooid surface, situated on large swollen cystid, with marginal pores and a smooth surface; rostrum elongate triangular, narrowing distal to crossbar, becoming very slender and parallel-sided distally, pointing in various directions, occasionally slightly downcurved distally; uncalcified area semicircular proximally, rounded triangular distally; crossbar complete with a median columella.

In older ovicellate parts of the colony, hypercalcification completely covers the oral avicularia and deeply immerses the orifice; the frontal is then composed of larger areolar pores, the slightly immersed entoecial area, frontally budded avicularia, and semicircular, round or irregular apertures.

Remarks: *B. antoniettae* sp. nov. is easily distinguished from the other European *Buffonellaria* species by its large oral avicularia. Furthermore, it has well-developed and bifurcating branches, whereas most other species are mainly or solely encrusters, and seldom form organized bilaminar branches, such as the Adriatic specimens of *B. muriella* sp. nov. The fragments of dead colonies, here chosen as types, are from a suite of specimens that were recovered from off of south-east Sicily, and the geographical distribution is therefore restricted to this region at present. Although always in subordinate numbers, *B. antoniettae* sp. nov. was present in all 18 samples taken from muddy to silty sediments, ranging in depth between 115 and 130 m, and co-occurring in this thanatocoenosis with some 20 other (mostly erect) bryozoan species (Rosso, 1989). However, information on early astogeny, the initial (presumably) encrusting stage, as well as regarding the overall colony shape, is unfortunately not available, although we believe that change of growth type is not likely to have a great effect on zoecium morphology (see Remarks in *B. muriella* sp. nov.). Hypercalcification in ovicellate colony regions during later ontogeny is conspicuous in this species, completely covering the oral avicularia, and deeply immersing the orifices.

***BUFFONELLARIA ARCTICA* SP. NOV.**

(FIG. 12A–D)

Synonyms: *Schizoporella biaperta* (Michelin, 1848): Nordgaard, 1906: 15, pl. 1, figs 12–14; Kluge, 1975: 579, fig. 320; Gostilovskaya, 1978: 188, fig. 112.

Material examined: Holotype: NHM 2007.5.18.4, Spitsbergen, no locality details, on balanid plate.

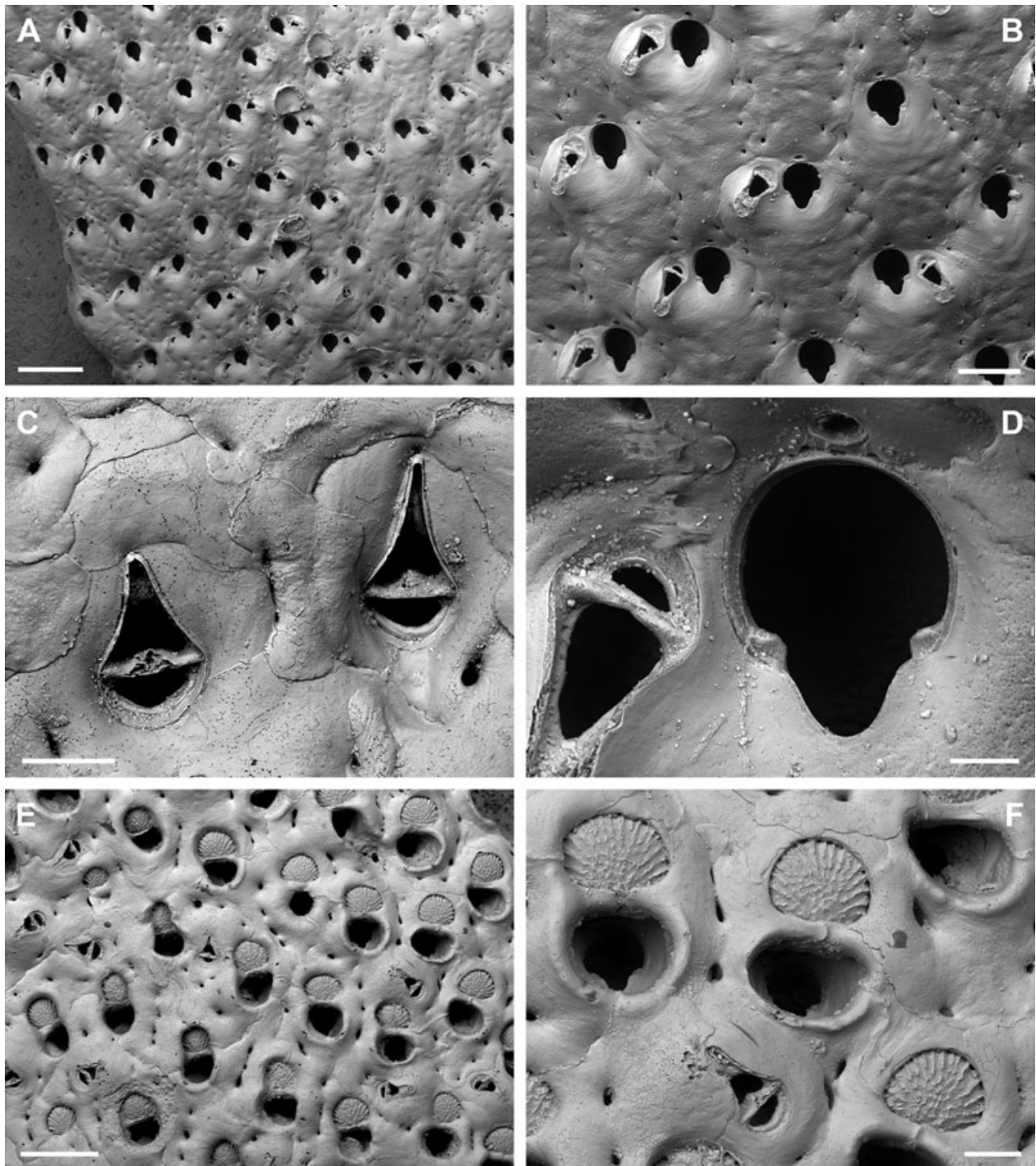


Figure 11. *Buffonellaria antoniettae* sp. nov.: Sicily. A, general aspect of bilaminar colony, with a branch margin at the left-hand side; holotype, PMC B16.30.6.2006a; scale bar, 500 μ m. B, autozooea with and without oral avicularia; note that the rostrum tips appear spatulate as a result of abrasion; holotype; scale bar, 200 μ m. C, close-up of frontal avicularia; paratype, PMC B16.30.6.2006b, scale bar, 100 μ m. D, close-up of orifice; holotype; scale bar, 40 μ m. E, proximal colony region with ooea and frontal avicularia extensively covered by secondary calcification; paratype.; scale bar, 400 μ m. F, close-up of ooea and deeply immersed orifices; paratype; scale bar, 100 μ m.

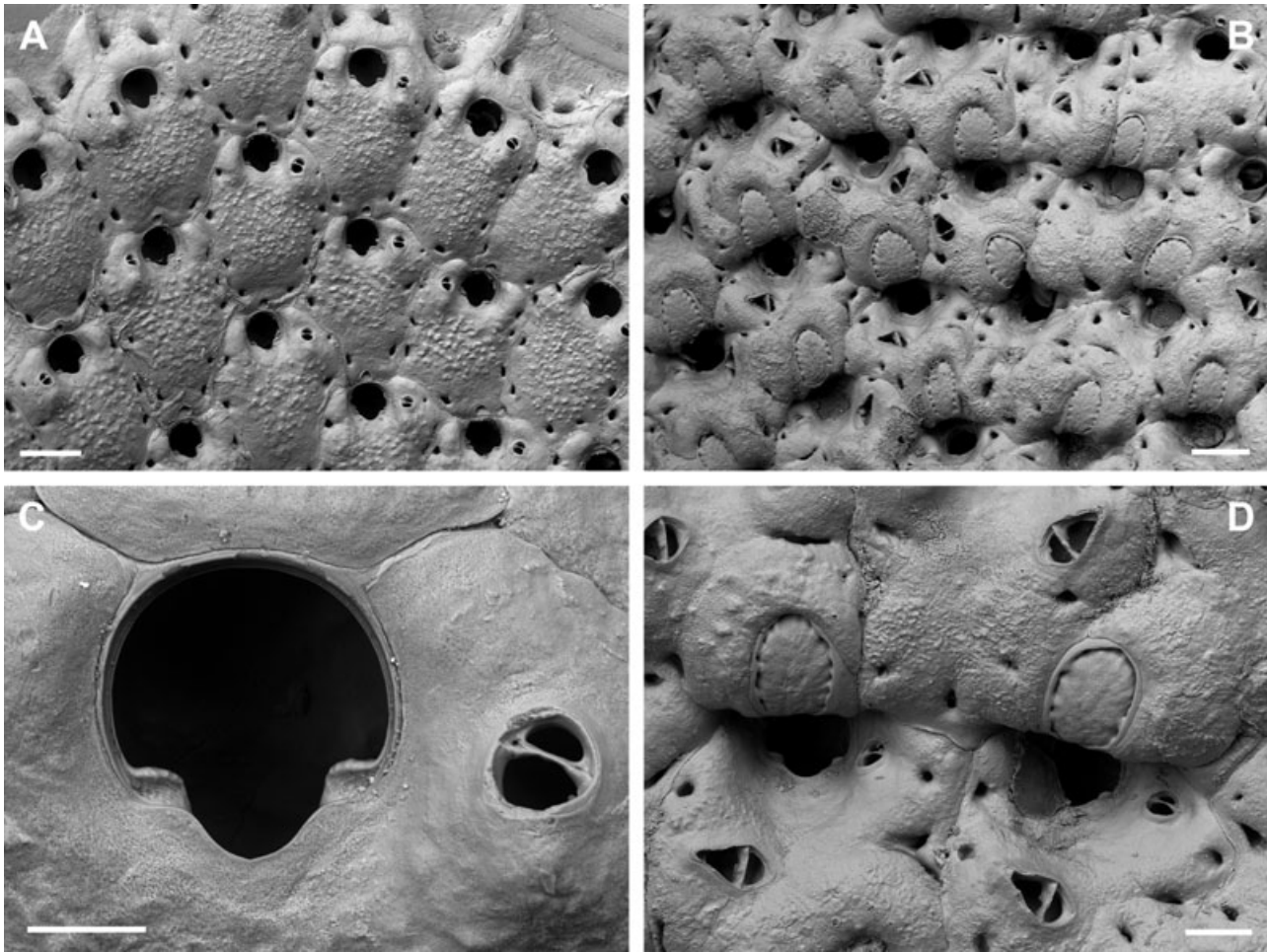


Figure 12. *Buffonellaria arctica* sp. nov. A, autozoecia from the colony growth margin; holotype & NHM 2007.5.18.4, Spitsbergen; scale bar, 200 μ m. B, ovicellate zoecia and frontal avicularia, orifices immersed by secondary calcification; holotype; scale bar, 200 μ m. C, close-up of orifice and oral avicularium; paratype & NHM 2007.5.18.5, Spitsbergen; scale bar, 50 μ m. D, close-up of ovicellate zoecia and frontal avicularia; holotype; scale bar, 100 μ m.

Paratype: NHM 2007.5.18.5, Grey Hook, Spitsbergen, 165 m, on rock.

Other material: NHM 1911.10.1.1073, Greenland, no locality details, 110 m; NHM 1911.10.1.1075, Grey Hook, Spitsbergen, 165 m, two colonies on rocks; NHM 1911.10.1.1079, Greenland, no locality details, on bivalve shells; NHM 1911.10.1.1081, Spitsbergen, no locality details, four colonies on rocks and balanid plates; NHM 2007.02.02.1, Kongsfjorden, Spitsbergen, on rock; CMN (2006)–0004, Nunavut, Forbes Sound, Canada, Calanus Expedition, 25 July 1962 (60°22'N, 69°26'W), Powell Collection; SMNH 1742, Edge Island (Storfjord, Whalers Point), Svalbard, Swedish Arctic Expedition 1864, Stn 6 (77°20'N, 20°30'E), 55–73 m; illustrated by Smitt (1868: pl. 24, figs 71–73).

Differential diagnosis: *B. arctica* sp. nov. differs from all other species in having a distinctly elliptical area of exposed entoecium. Granulation of the frontal

wall is also much more distinct in this species, and the marginal pores are larger and/or more numerous than in the previously described species (*B. porcellanum* has larger but fewer pores).

Etymology: For its wide geographical distribution in Arctic waters.

Measurements: ZL, 583 \pm 40, 503–656 (2, 20); ZW, 441 \pm 43, 366–534 (2, 20); OL, 129 \pm 6, 122–141 (2, 20); OW, 127 \pm 6, 114–137 (2, 20); OvL, 297 \pm 23, 236–324 (2, 16); OvW, 300 \pm 39, 206–344 (2, 16); oAL, 57 \pm 4, 51–69 (2, 20); oAW, 46 \pm 5, 38–59 (2, 20); fAL, 111 \pm 11, 96–134 (2, 20); fAW, 70 \pm 6, 60–86 (2, 20).

Description: Colony encrusting, unilaminar, multiseriate. Zoecia oval to quadrate or hexagonal, initially separated by shallow grooves, disguised by secondary

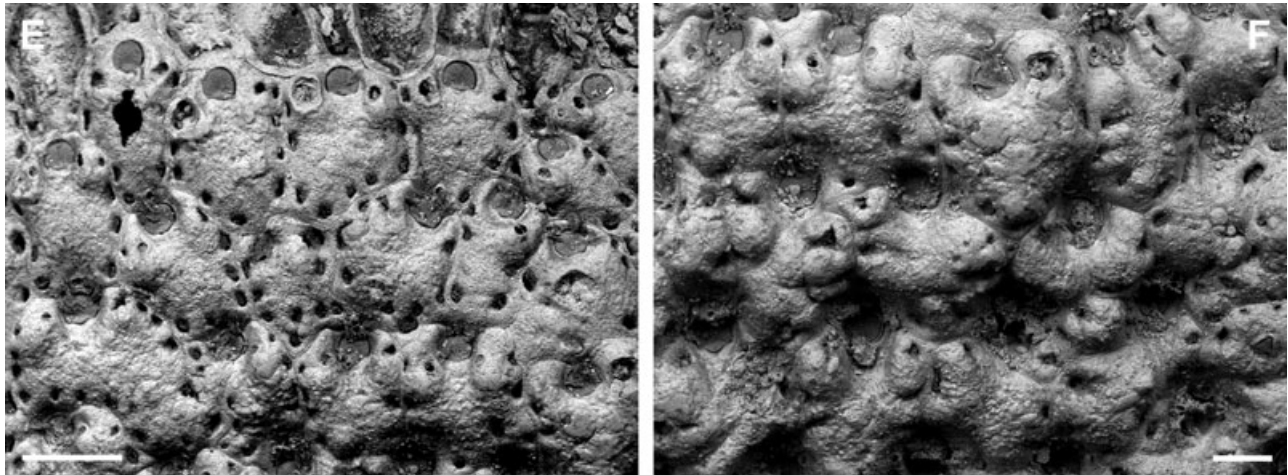


Figure 13. *Escharella linearis* (Hassall, 1841) forma *biaperta* (Michelin, 1848): SNHM 1742, Svalbard, Edge Island, illustrated by Smitt (1868: pl. 24, figs 71–73), uncleaned specimen. A, autozooids at colony margin; note the large areolar pores compared with *Buffonellaria arctica* sp. nov.; scale bar, 400 µm. B, autozooids with thick secondary calcification; scale bar, 200 µm.

calcification during ontogeny, as are most other frontal characteristics; distolateral vertical walls with between five and eight relatively large, widely spaced, distolateral communication pores, separated by broad and thick calcification. Frontal wall slightly convex, coarsely granular, imperforate, except for between five and eight round or oval marginal areolar pores, ooeccial pore of about same size, round or oval, rimmed. Primary orifice about as long as wide; anter two-thirds of a full circle, proximal margins short and slightly sloping, passing into a variably broad, deep and widely U-shaped sinus, occupying more than half of the total width, condyles conspicuous, variable, generally short but broad, square, blunt; orifice flanked laterally by a slightly swollen, rather smooth and elongated hump, one or each carrying an oral avicularium.

Ooecium variable in outline, on average as long as wide, initially globular, later immersed by thick, broad, and bulging secondary calcification around the margin; ectooecium extensive, exposed entoecium usually (semi) elliptical, surface relatively smooth with 12–16 very low ribs, usually confined to the very margin.

Oral avicularia single or paired, oval, lateral or proximolateral to orifice at midway to zooid margin, and on a slightly raised cystid with one or two small areolar pores, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, directing proximally or proximomedially, proximal uncalcified area narrower and more or less semicircular; crossbar complete, without columella. Additional avicularia frequent, budding from marginal pore anywhere on frontal during later ontogeny, situated on a swollen

cystid, surface smooth and imperforate, except for two areolar pores; rostrum triangular, relatively short, with a blunt tip, pointing in various directions; proximal uncalcified area more or less semicircular, distal area rounded triangular; crossbar complete without columella, but occasionally slightly thickened centrally.

Remarks: The confusion associated with the use of Michelin's name *biaperta* for modern Arctic *Buffonellaria* dates back to 1868 when Smitt, assuming his specimens were synonymous with the Pliocene species that Busk (1859: 47, pl. 7, fig. 5) identified as (?) *Lepralia biaperta*, applied this name to a recent species for the first time (Smitt, 1868: 14, pl. 24, figs 70–73). However, although Ryland (1969: 220, fig. 2A) showed that Michelin's fossil taxon is not only a distinct species, but also belongs to a different genus, authors have continued to name Arctic specimens *biaperta* to date.

Smitt (1868) originally illustrated two specimens as *Escharella linearis* (Hassall, 1841) forma *biaperta* (Michelin, 1848), one with autozooids covered by extensive secondary calcification (Smitt, 1868: figs 71–73; SMNH 1742), which we examined using SEM (Fig. 13A, B), and one with autozooids lacking frontal calcification (Smitt, 1868: fig. 70). Neither specimen contains ovicells; however, we decided not to choose these specimens as types for *B. arctica* sp. nov. for two reasons. First, specimen SMNH 1742 differs from all other studied material in having distinctly larger marginal pores, as well as non-ovicellate zooids that are covered by thick and bulgy secondary calcification. Although the size of the marginal pores was

to some extent also variable in the types chosen here, and in other specimens, these marginal pores were, generally, distinctly smaller, and secondary calcification was only observed in ovicellate zooids. Second, we were not allowed to clean specimen SMNH 1742. Comparison of important subcuticular characters (such as condyles) was therefore impossible. Thus, we cannot rule out the possibility that two species exist in the Arctic, and we cautiously decided not to synonymize Smitt's material with *B. arctica* sp. nov.

Nevertheless, all studied specimens of *B. arctica* sp. nov. are morphologically consistent throughout, despite displaying general variability in orifice morphology, and intracolony differences in sinus and condyle shape, which seems to be typical in *Buffonellaria*. Owing to thick calcification around ovicells, colony regions with ovicellate zooids have a conspicuously bulgy topography during later ontogeny, with interspersed, typically elliptical areas of exposed entoecia.

Material examined with SEM comprises specimens from Spitsbergen and Greenland. *Buffonellaria arctica* sp. nov. thus has, compared with most other species presented here, a fairly wide geographical range of distribution. Although not observed with SEM, specimens from north-east Canada (CMN 2006-0004; see Nordgaard, 1906; Powell, 1968) and the figures of specimens from north-west Russia (Kluge, 1975; Gostilovskaya, 1978) do not show any significant differences, therefore supporting this scenario. Whether further records from the Laptev Sea, the Sea of Okhotsk (Kluge, 1975; Dahle *et al.*, 1998), the Sea of Japan (Androsova, 1958: 132, fig. 52), and the Pacific coasts of North America (e.g. Osburn, 1952: 368, pl. 42, figs 1, 2) indeed belong to this taxon is yet to be proven.

In its type area, the archipelago of Svalbard, *B. arctica* sp. nov. is a fairly rare species, as it occurs in only 2% of the samples collected by Kuklinski (2002). It encrusts shells and rocks in depths between 40 and 200 m (Kuklinski, 2002; Kuklinski *et al.*, 2005), which is in agreement with records from other Arctic regions, where it was also observed to grow on hydroids and calcareous algae (e.g. Kluge, 1975). Kluge furthermore reported this species to grow in water temperatures of down to -1.3°C .

BUFFONELLARIA PORCELLANUM ARÍSTEGUI RUIZ,
1987

(FIG. 14A–D)

Original description: *Buffonellaria porcellanum* Aristegui Ruiz, 1987: 530, figs 4, 10–14.

Material examined: Holotype: NHM 1987.1.3.2, Playa los Cancajos, La Palma, Canary Islands.

Measurements: ZL, 427 ± 65 , 345–590 (1, 20); ZW, 318 ± 40 , 263–396 (1, 20); OL, 92 ± 4 , 86–97 (1, 15); OW, 92 ± 5 , 84–104 (1, 15); OvL, 147 ± 14 , 131–155 (1, 3); OvW, 196 ± 21 , 174–216 (1, 3); oAL, 43 ± 4 , 36–51 (1, 11); oAW, 28 ± 5 , 20–37 (1, 11).

Description: Colony encrusting, unilaminar, multiserial. Zoecia hexagonal to polygonal, separated by distinct grooves that may be altered by secondary calcification during ontogeny. Frontal wall slightly convex, initially even and smooth, later with gentle irregular ridges and/or umbos, usually associated with four small pseudopores; between three and five large, conspicuous, marginal areolar pores; oocial pore small, oval, encircled by a thick rim of calcification. Primary orifice as long as is wide; anter two-thirds of a full circle, proximal margins very short, passing into rounded shoulders of a shallow but broad and widely U-shaped sinus, occupying about four-fifths of the total width, condyles short and blunt, comparatively small. A low peristome develops during ontogeny, formed by a raised ridge of secondary calcification of mother zooid and distal zooid, steeply sloping towards orifice distally, and extending proximolaterally, incorporating the suboral avicularium.

Ooecium initially globular, frontal being reduced to a semicircular outline during later ontogeny, when marginally covered by secondary calcification, ectooecium a broad smooth band encircling a rather flat, semicircular, frontal area of uncovered entoecium, marked by between six and ten prominent radiating ribs that thicken towards the margin; aperture orbicular.

Adventitious avicularia single, small, oval, located proximolateral to orifice, situated on a slightly raised cystid that becomes incorporated into peristome during ontogeny, frontal plane at an acute angle to colony surface; rostrum semi-elliptical, directing proximolaterally or laterally, proximal uncalcified area semicircular; crossbar complete, without columella. Larger frontal avicularia were not observed.

Remarks: Arístegui Ruiz (1984: 373, fig. 80b, c; pl. 31, figs 1–3) originally introduced this species as *Lagenipora macroavicularia* in his PhD thesis, and only three years later, using the same material and photos without referring to his previous account, erected *B. porcellanum* (Arístegui Ruiz, 1987). However, as the thesis was never officially published, and this species has never been cited thereafter, the name *macroavicularia* is suppressed here for *porcellanum*.

This species is characterized by its uneven frontal wall that develops during ontogeny, its large and round areolar pores, its asymmetrical peristome, the proximolateral position of the suboral avicularium, the absence of frontal avicularia, and by the few but

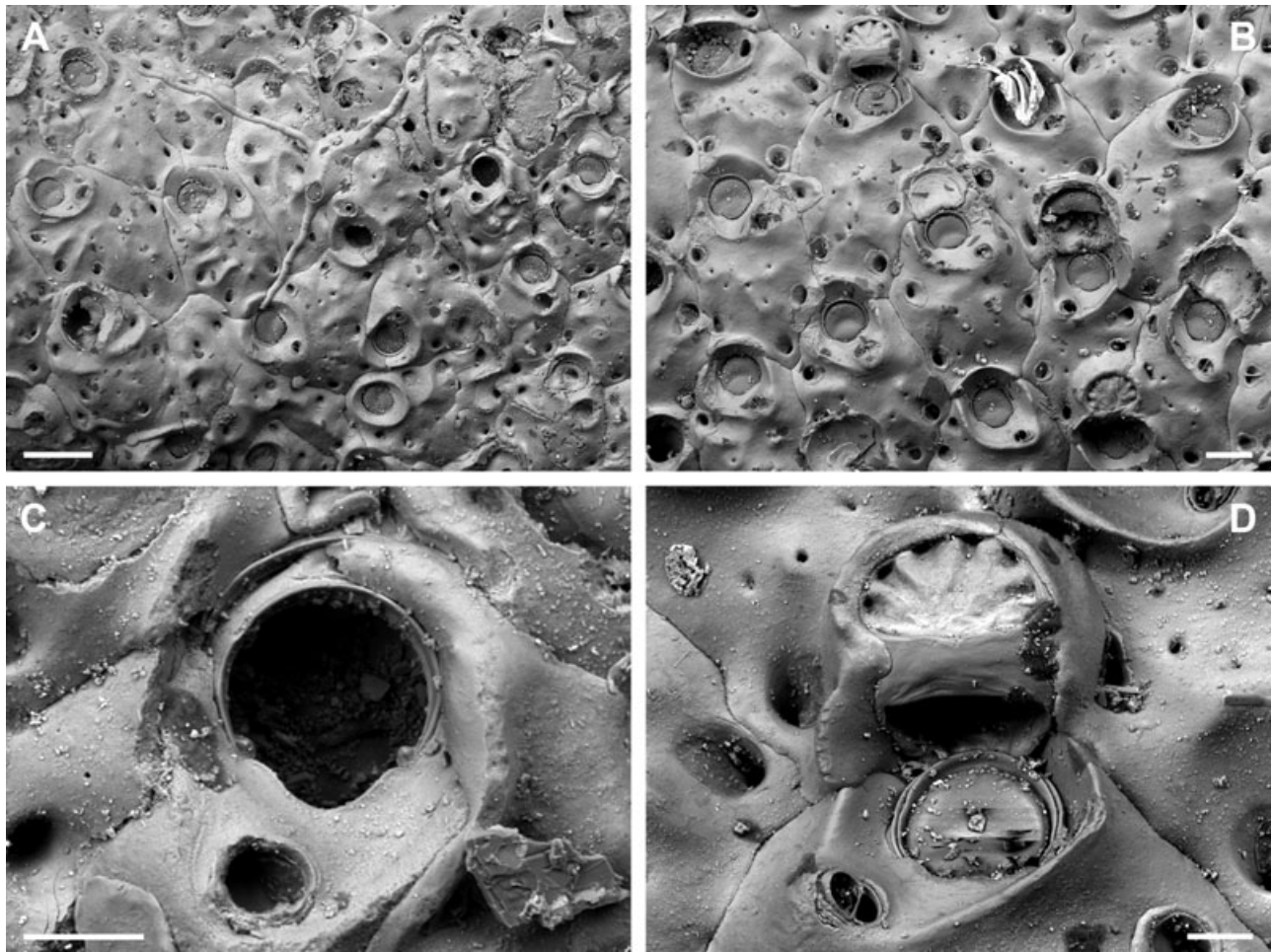


Figure 14. *Buffonellaria porcellanum* Arístegui Ruiz, 1987: holotype, NHM 1987.1.3.2, Canary Islands. A, general aspect; note the reparative growth in zooecia on the right, and the reversed polarity growth of two zooecia at the centre; scale bar, 200 μm . B, autozoecia and ovicellate zooecia; scale bar, 100 μm . C, close-up of orifice; scale bar, 50 μm . D, close-up of oecium; scale bar, 40 μm .

prominent ribs on its small exposed entoecial area. Although not directly observed, we assume that, similar to *B. muriella* sp. nov. and *Buffonellaria* sp. 1 (Fig. 1), pseudopores are formed during early development of the frontal wall of the primary skeleton. Together with *Buffonellaria* sp. 2 (see below), *B. porcellanum* is one of the species that retain small but relatively conspicuous pseudopores, even in later ontogeny.

Buffonellaria porcellanum is recorded from depths of 3–31 m on rocks, shells, and other calcareous substrates. It has not been reported from areas other than the Canary Islands.

BUFFONELLARIA SP. 2
(FIG. 15A, B)

Material examined: SMF 3015, Sierra Leone, RV 'Meteor' cruise 1973, Stn 196 (7°27'N, 13°7'W), 81 m, on shell.

Measurements: ZL, 445 \pm 28, 384–489 (1, 20); ZW, 376 \pm 41, 294–464 (1, 20); OL, 101 \pm 6, 92–113 (1, 13); OW, 92 \pm 4, 83–96 (1, 13); oAL, 43 \pm 3, 37–47 (1, 14); oAW, 28 \pm 2, 25–31 (1, 14); fAL, 100 \pm 7, 88–108 (1, 7); fAW, 44 \pm 3, 40–47 (1, 7).

Description: Colony encrusting, unilaminar, multiseriate. Zooecia hexagonal, separated by shallow grooves. Frontal wall slightly convex, surface rough with several pustules developing during ontogeny, each pierced by a tiny pseudopore, and between three and six oval or slit-like, marginal, areolar pores. Primary orifice slightly longer than wide; anter horseshoe-shaped, proximal margins very short and sloping, passing into a deep, broad, and widely U-shaped or rounded V-shaped sinus, occupying about two-thirds of the total width, condyles conspicuous, short but broad, blunt.

Ovicells were not observed.

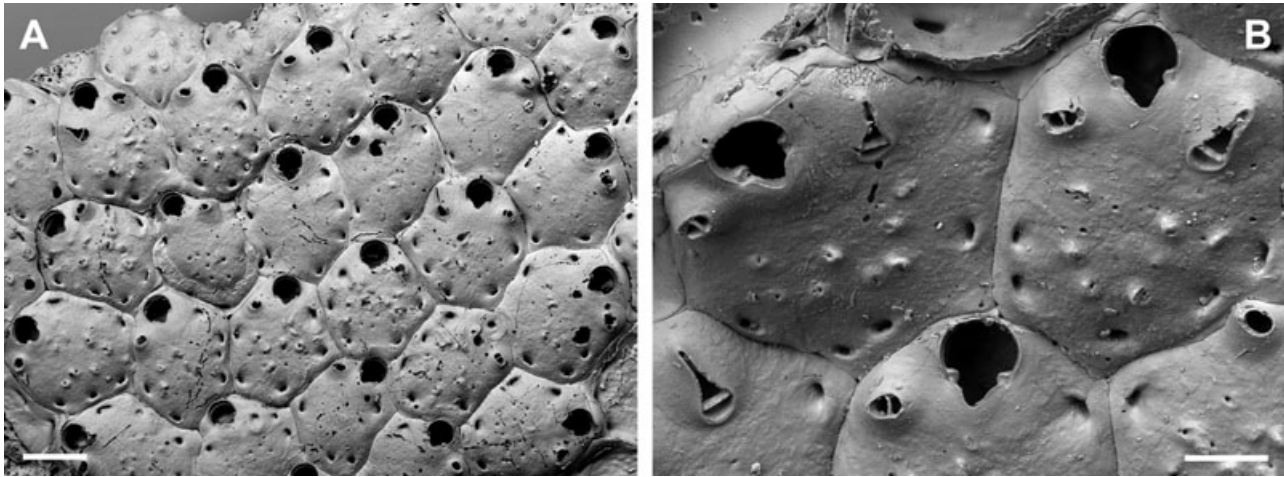


Figure 15. *Buffonellaria* sp. 2: SMF 3015, off Sierra Leone. A, general aspect; scale bar, 200 μm . B, Close-up of auto-zoecia; scale bar, 100 μm .

Small oral avicularia, single, situated proximolateral to orifice, close to the zooid margin, oval, situated on a slightly raised cystid; rostrum semi-elliptical, directing laterally or proximolaterally; crossbar complete, without columella but slightly curved, proximal uncalcified area therefore sickle-shaped. Additional larger avicularia occasionally present, also in ontogenetically young zooids, situated opposite to small avicularium, albeit slightly more proximally, on a relatively small imperforate cystid; rostrum elongate triangular, slightly acute to frontal plane, narrowing distal to crossbar, and becoming very slender and parallel-sided, pointing distally or distolaterally; proximal uncalcified area semicircular, distal area elongate triangular; crossbar complete, without columella.

Remarks: This taxon differs from the species described above in having a pustulose frontal surface, conspicuously large and rounded condyles, a small single avicularium situated lateral or proximolateral to the orifice, and in having a larger frontal avicularium, with a long and thin rostrum directing distally or distolaterally, located proximolaterally to the orifice. However, because only a single colony lacking ovicells was available for study, this species is kept in open nomenclature. The frontal wall in *Buffonellaria* sp. 2 retains small pseudopores throughout its ontogeny, penetrating the small pustules.

Several zoecia in this colony display regeneration features, some of which have an intact skeleton, but a second or even third orifice implanted in the primary one. This suggests that these zooids were fed upon by a partial predator, possibly a nudibranch gastropod boring through the operculum and sucking out the internal organs without damaging the skel-

eton (e.g. McKinney, Taylor & Lidgard, 2003), after which a new zooid – an intramural bud (see Taylor, 1988b) – was produced within the older one.

DISCUSSION

Considering that only two species were previously recognized from the continental shelf, the great diversity of *Buffonellaria* in European waters was, indeed, an unexpected finding. Especially so in the western and central Mediterranean Sea, where bryozoan faunas have been under intense and constant investigation since the 18th century (e.g. Pallas, 1766), and which can be regarded as one of the best-studied regions in the world. The diversity in the Mediterranean Sea is particularly astonishing considering the fact that the evolution of marine faunas initiated with the reflooding of the Mediterranean basins and the invasion of an eastern Atlantic stock after the latest Miocene Messinian salinity crisis, some 5.3 Myr ago (e.g. Krijgsman *et al.*, 1999; Berning, 2006). As only a single species is known from the Late Miocene Atlantic region directly west of the Strait of Gibraltar [reported as *B. cf. entomostoma* (Reuss, 1848) by Berning, 2006: 114], the presence of a number of species in today's Mediterranean Sea may suggest an adaptive radiation has taken place since the Early Pliocene. Although more species may have entered the Mediterranean during and after the reflooding, the close relationship between *B. harmelini* sp. nov., *B. antoniettae* sp. nov., and *Buffonellaria* sp. 1 suggests the presence of a common ancestor. Based on observations of other specimens, which could not be included in this work because of time restrictions, at least two more Mediterranean species are yet to be described.

One of the reasons for not noticing this great diversity before is certainly because of the occurrence of extreme morphological variability within colonies. The proliferation of large avicularia and associated secondary calcification may lead to a different surface topography in ontogenetically older areas, in which zoecial boundaries are obscured, and the orifice becomes slightly immersed. Colony morphology may be even more drastically altered in parts of the colony in which ovicells are produced. Here, extensive hypercalcification may double the thickness of encrusting unilaminar or erect bilaminar colonies. The surface is then characterized by variably shaped apertures containing the deeply immersed orifice at its bottom, as well as by the hemispherical entoecial areas, and the larger frontal avicularia (occasionally the smaller oral avicularia are also exposed). This substantial investment in superficial calcification and frontal avicularia is most probably made for protective reasons, to prevent the maternal zooids and ovicells from being grazed by predators.

Another source of intraspecific and even intracolony variation is orifice morphology, which may be quite distinct as, for instance, in *B. muriella* sp. nov. Thus, when introducing new species of *Buffonellaria*, the type specimens should comprise colonies that consist of both ontogenetically young and old zooids, and as many colonies as possible should be screened in order to detect intra- and intercolonial variability.

Furthermore, without SEM images it is difficult, or even impossible, to reliably identify species in this genus (see Table 1 for a compilation of the main distinguishing characters). Thus, as SEM images are not even provided in most of the recent publications, to which species the specimens belong that were recorded by Waters (1879: 37), Calvet (1928: 6); Osburn (1933: 39, pl. 15, figs 5, 6) Gautier (1962: 155), d'Hondt (1970: 240; 1978: 453), López de la Cuadra & García-Gómez, 1988: 24), Zabala & Maluquer (1988: 127, fig. 286), Harmelin & d'Hondt (1992: 30), or Alvarez (1994: 131) cannot be deduced. Considering the fairly restricted geographical range of distribution of each species (Fig. 16), and the intermittent spatial coverage of the present study (no records from the eastern Mediterranean Sea or off northern Spain, western France, and southern Norway), there are almost certainly more species yet to be described. Furthermore, considering the number of species present in European waters, and the fact that *Buffonellaria* occurs worldwide from the Arctic to the Antarctic, the total number (eight) of hitherto known species from the rest of the world must be regarded as a mere fraction of the true global diversity of *Buffonellaria*. The same certainly applies to many other bryozoan genera, which, if thoroughly revised, will then result in a drastic increase in the number of species in this phylum (see also Lidgard &

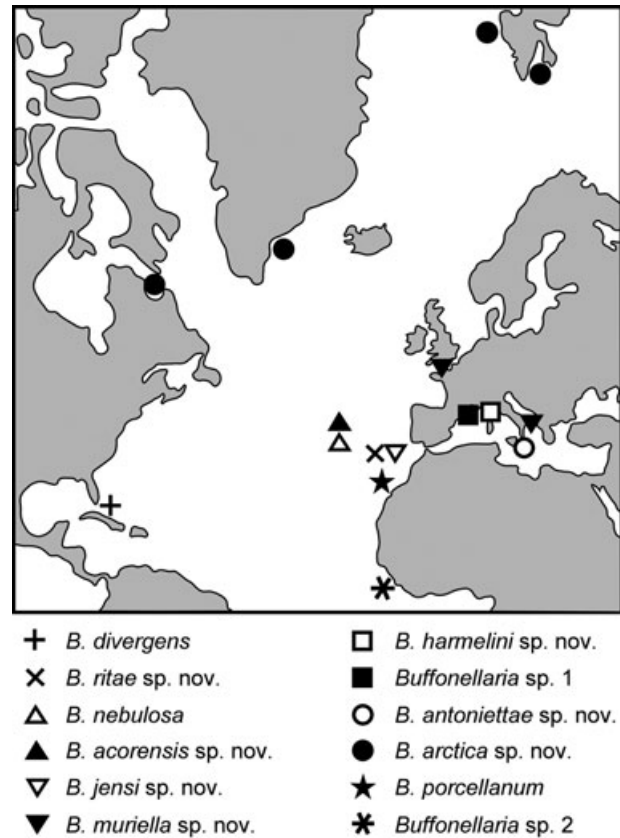


Figure 16. Distribution of North Atlantic and Mediterranean *Buffonellaria* species. Note that the Greenland location of *Buffonellaria arctica* sp. nov. was randomly chosen, as these samples lack specific locality information.

Buckley, 1994; Soule *et al.*, 2002; Taylor & Mawatari, 2005; Harmelin, 2006).

On the other hand, the restricted range of distribution of each *Buffonellaria* species now much more realistically reflects the true dispersal capabilities of sessile organisms with a nonplanktotrophic larval stage, than the previous notion of the presence of only one or two circum-Atlantic species. This study therefore helps disentangle the paradox in Bryozoa, which brood their larvae, yet (used to) comprise a relatively high number of (hitherto assumed) cosmopolitan species, and will assist in refining our concepts of the definition of species taxa, bryozoan diversity and evolution, and use of bryozoans for palaeobiogeographical purposes.

The genera *Buffonellaria* and *Pourtalesella* also provide another example for close systematic relationship between taxa with porous and nonporous frontal walls, which was hitherto considered a character with which to separate higher taxa, as well as for the independent and repeated evolution of (pseudo-)porous frontal shields within a family, as put forward

Table 1. Comparison of main characters and morphometric data of *Buffonellaria* species from the North Atlantic and Mediterranean Sea

Species	Mean ZL		Mean oAL		Shape of oral avicularia	Orientation of oral avicularia	Frontal avicularia per zooid	Orientation of frontal avicularia	Mean fAL		Number of oocelal ribs	Additional comments
	OL	1	OL	1					fAL	OvL		
<i>divergens</i> Fig. 3	679	134	1–2	47	Ellipt.	pl	0–1	l	109	–	–	fA situated in lateral corner of zooid
<i>ritae</i> sp. nov. Fig. 4	457	97	1	50	Ellipt.	l–pl	0–1	p	159	163	14–16	fA situated lateral to orifice
<i>nebulosa</i> Fig. 5	629	145	1–2	69	Ellipt.	pl	0–1	p	185	295	16–20	Entoecium smooth, extensive
<i>acorensis</i> sp. nov. Fig. 6	533	131	1–2	65	Ellipt.	p–pl	0–1	p (variable)	148	239	18–21	fA situated proximolateral to oA
<i>jensi</i> sp. nov. Fig. 7	549	127	1–2	84	Ellipt.	pl	None	–	–	208	13–17	
<i>muriella</i> sp. nov. Figs 1A, 2A, 8	526	140	1–2	67	Ellipt.	p–l	None	–	–	217	11–13	
<i>harmelini</i> sp. nov. Fig. 9	470	142	1–2	88	Triang.	pl	None	–	–	213	9–13	
sp. 1 Figs 1B, 10	655	156	1	120	Triang.	pl	None	–	–	–	–	Erect bilaminar growth
<i>antoniettae</i> sp. nov. Figs 2B, 11	627	151	0–1	178	Triang.	pl	None	–	–	209	15–17	Erect bilaminar growth
<i>arctica</i> sp. nov. Fig. 12	583	129	1–2	57	Ellipt.	p–pm	None	–	–	297	12–16	Entoecial area elliptical
<i>porcellanum</i> Fig. 14	427	92	0–1	43	Ellipt.	pl–l	None	–	–	147	6–10	Frontal wall with ridges and peristome.
sp. 2 Fig. 15	455	101	1	43	Ellipt.	l–pl	0–1	d–dl	100	–	–	oA situated proximolateral to orifice
												Frontal wall with tubercles

The 'Frontal avicularia per zooid' considered here are only those avicularia that are produced during early zooid ontogeny and that have a determined position on the frontal wall. In contrast, the 'Mean fAL' (length of frontal avicularia) comprises measurements of avicularia formed during both early and later ontogeny, as there are no differences in size. Measurements are in μm .

Abbreviations: d, distally; dl, distolaterally; Ellipt., elliptical; fA, frontal avicularium length; l, laterally; oA, oral avicularium; oAL, oral avicularium length; OL, orifice length; OvL, oecium length; p, proximally; pl, proximolaterally; pm, proximomedially; Triang., triangular; ZL, zoecium length.

by Gordon (2000). Although more work is clearly needed to clarify the (functional morphological) differences in frontal-wall formation between these genera, the presence of pseudopores in early ontogeny, and the occasional retention of these pores during later ontogeny in some species of *Buffonellaria*, suggests that a pseudoporous frontal wall may more easily be obtained, and may have less systematic significance, than was previously acknowledged.

ACKNOWLEDGEMENTS

We are grateful to Hans De Blauwe, Jean-Georges Harmelin, Jean-Loup d'Hondt, Carlos López-Fé de la Cuadra, Maja Novosel, Antonietta Rosso, and Karin Sindemark Kronestedt for loans of specimens or photos thereof, as well as Mary Spencer Jones for valuable assistance at the NHM. Dennis Gordon, Andrei Ostrovsky, and Paul Taylor are thanked for discussions and comments on earlier versions of the manuscript, and the present version greatly benefited from constructive remarks by two anonymous reviewers. BB gratefully acknowledges a SYNTHESYS grant (GB-TAF-1381), which enabled a visit to the NHM. Present funding is provided by the Austrian FWF (P18189 to Werner Piller). PK thanks the EU Marie Curie programme BRYOARC for the financial support of a research fellowship at the NHM.

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