

Research Article

Cite this article: Berning B, Spencer Jones ME (2023). Revision of the Cheilostomatida (Bryozoa) collected during the HMS ‘Challenger’ Expedition (1872–1876) in the central North Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **103**, e32, 1–22. <https://doi.org/10.1017/S0025315423000231>

Received: 5 August 2022
Revised: 10 December 2022
Accepted: 21 March 2023

Keywords:

Azores; biodiversity; Mid-Atlantic Ridge; taxonomy

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Revision of the Cheilostomatida (Bryozoa) collected during the HMS ‘Challenger’ Expedition (1872–1876) in the central North Atlantic

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Abstract

Of the 21 species recorded from the greater Azores region during the HMS ‘Challenger’ Expedition, 12 were newly introduced during the late 19th century. The respective types of these species are fixed, and eight species are redescribed based on scanning electron microscope analysis (*Notoplites bilobus*, *Raxifabia minuta*, *Hemicyclopora canalifera*, *Smittoidea oratavensis* comb. nov., *Buskea ovalis* comb. nov., *Buskea fayalensis* comb. nov., *Celleporina ansata* comb. nov. and *Reteporella atlantica* comb. nov.). Another four species are merely dealt with shortly either because the material is insufficiently preserved for a thorough revision (*Columnella gracilis*, *Carbasea pedunculata*), or because the species have recently been revised already (*Notoplites clausus*, *Microporella hastigera*). Moreover, two Azorean species that were introduced by later workers are synonymized with ‘Challenger’ species: *S. oratavensis* is considered a senior synonym of *Smittia ensifera*, and *Lekythopora laciniosa* is synonymized with *C. ansata*.

Introduction

The first scientific expedition to explore the organisms of the deep sea, the voyage on the British HMS ‘Challenger’ from 1872–1876, was also the first cruise upon which bryozoans were described from around the central North Atlantic archipelago of the Azores (Busk, 1881a, 1884; Waters, 1888). While a mere 21 species were recorded then, this pioneering expedition was quickly followed up by a series of French cruises to the archipelago in the late 19th and early 20th century, upon which the majority of the ~200 known Azorean bryozoan species were described (Jullien & Calvet, 1903; Calvet, 1906, 1907, 1931). Another set of scientific expeditions to the Azores took place during the second half of the 20th century (e.g. d’Hondt, 1975; Harmelin, 1978; Harmelin & Aristegui, 1988). Since then, only a few species have been added to the bryozoan diversity of the Azores (Harmelin, 2006; Reverter-Gil & Fernández-Pulpeiro, 2007; Berning & Kuklinski, 2008; Berning, 2013; Berning *et al.*, 2019; Harmelin *et al.*, 2019; Haugen *et al.*, 2020). This is despite a renewed interest in the archipelago’s marine fauna and ongoing sampling activities in the region (George *et al.*, 2018; Baptista *et al.*, 2022), which is often driven by the necessity to identify non-indigenous species (e.g. Cardigos *et al.*, 2006; Amat & Tempera, 2009; Micael *et al.*, 2014, 2019; Vieira *et al.*, 2014).

This work is another in a series of modern revisions of cheilostomatid Bryozoa from NE Atlantic islands and seamounts, a great number of which were introduced during the late 19th and early 20th century (e.g. Reverter-Gil & Fernández-Pulpeiro, 1999, 2007; Berning & Kuklinski, 2008; Souto *et al.*, 2011, 2016; Berning, 2012, 2013; Vieira *et al.*, 2013; Reverter-Gil & Souto, 2015; Reverter-Gil *et al.*, 2015; Berning *et al.*, 2017, 2019, 2021; Harmelin *et al.*, 2019; Madurell *et al.*, 2019). The modern species-taxon concept in bryozoans makes it necessary to reanalyse and redescribe the historical species, which were often insufficiently figured and described in the original literature, in order to correctly assess bryozoan diversity, ecology and geographic distribution. We here deal with 12 historical cheilostomatid species from the greater Azores region that were recovered from four ‘Challenger’ stations in 1873, ranging in depth from 90–3060 m.

Materials and methods

Type and comparative material of species from the ‘Challenger’ Expedition, which were described by Busk (1881a, 1884) and Waters (1888), and which are housed at the Natural History Museum London (NHMUK) and the Manchester Museum (MM), were studied using scanning electron microscopy (SEM). Material collected at the following HMS ‘Challenger’ stations in the vicinity of the Azores is considered here:

Station 70, 38°25′N 35°50′W (on the Pico Fracture Zone, i.e. ~400 km west of the Azores and therefore outside the Exclusive Economic Zone), 26/6/1873, 1675 fathoms (~3060 m), *Globigerina* ooze.



Station 75, 38°38'N 28°28'W (N of Pico Island), 2/7/1873, 450 fathoms (~820 m), volcanic mud and sand.

Station lacking a number and precise position, in the channel between the islands of Faial and Pico (here termed 'Station FP'), 2/7/1873, washings from dredge, 50–90 fathoms (~90–165 m).

Station 76, 38°11'N 27°9'W (between the islands of Pico and São Miguel), 3/7/1873, 900 fathoms (~1650 m), *Globigerina* and pteropod ooze.

Additional specimens from the Azores, also those collected during the late 19th century on French scientific cruises, were examined at the Manchester Museum (MM), the Muséum national d'Histoire naturelle at Paris (MNHN), the Musée océanographique at Monaco (MOM), and the Biology Centre of the Oberösterreichische Landes-Kultur GmbH (formerly Oberösterreichisches Landesmuseum, collection *Evertebrata varia*; OLL). A substantial amount of material from the Azores was subsequently collected during the French 'Biaçores' Expedition in the 1970s, which is kept at the MNHN. A thorough review of that material was, however, beyond the scope of the present paper, and only a few specimens are given in the material list of the respective species. The specimens from the MNHN analysed during this study are hyperlinked with the respective online Collection Database entries whenever available (<https://science.mnhn.fr/all/search>); if existing, additional SEM images can be viewed and downloaded there. While in the text only the holotypes, lectotypes and neotypes are given for the sake of brevity, a complete list of the para(lecto)types and all other studied specimens is provided in the Supplementary Material (S1).

Suitable bryozoan colonies were digitally photographed at the NHMUK using a LEO 1455VP SEM, and at the MNHN using a Tescan VEGA SEM. Both machines allowed imaging of uncoated specimens with back-scattered electrons in low vacuum mode. Morphometrics were made on these micrographs using the image software ImageJ (Schneider *et al.*, 2012), and are given in the descriptions as mean \pm standard deviation, minimum–maximum values and number of measurements (whenever >2 measurements were taken). Values are in μm unless otherwise noted. Character abbreviations: H = height (i.e. the zooid dimension normal to the basal surface), L = length, W = width.

Neither Busk (1881a, 1884) nor Waters (1888) explicitly designated type material, while several species were newly described based on material from two or more stations separated by hundreds or even thousands of kilometres. In this case, the selection of a lectotype and the type locality of the species is primarily based on the figured specimen if it could be ascertained, and secondarily on the first mentioned station in Busk's (1884) 'Habitat' list at the end of each species description. As Busk distributed the original material among his colleagues and to different institutions (e.g. Waters (1888: 1) mentioned that duplicate specimens of the 'Challenger' material exist in Edinburgh), it is possible that additional paralectotypes will be discovered in the future.

The longitudes of the sampling stations of the 'Talisman', 'Travailleur' and 'l'Hirondelle' cruises, as given by Jullien & Calvet (1903) and Calvet (1906, 1907), were initially measured with reference to the Paris meridian but have here been corrected to the Greenwich meridian. We also noted that the geographic position of 'Prince Albert' Station 882 (38°03'40"N 28°34'45"W, some 50 km south of Pico Island), as given by Calvet (1931: 134) for specimens of *Hemicyclopora canalifera*, *Buskea fayalensis* and *Reteporella atlantica* (see below), is not in accordance with the depth of 98 m at that station. The nature and number of species recorded at this station by Calvet (1931: 135) suggest that it is the geographic position that is erroneous. We thus presume that a transcription error has occurred in the minute reading, and that

the correct latitudinal position is 38°30'40"N, which is in the southern Pico-Faial Channel and corresponding with a depth of 98 m. The corrected position is thus given as 38°30.67'N 28°34.75'W.

Systematics

Superfamily CALLOPOROIDEA Norman, 1903

Family FARCIMINARIIDAE Busk, 1852

Genus *Columnella* Levensen, 1914

Columnella gracilis (Busk, 1884)

(Figure 1A, B)

Part *Farciminaria gracilis* Busk, 1884: 51, pl. 5, fig. 3.

Type material

Lectotype (here designated): NHMUK 1887.12.9.238, Busk coll., Station 70, several small fragments of a single colony, two with one ovicell each, ?figured specimen (Busk, 1884: pl. 5, fig. 3b), in Canada balsam.

Description

Colony erect, unjointed but probably flexible, dichotomously branching at an angle of about 20–30°, over 1.5 cm in height; branches slender (~300 μm) and slightly curved, quadrangular in cross section; colony base not observed. Zooids lightly calcified, rectangular, very elongated and narrow (L: ~1100 μm ; W: ~150 μm).

A small avicularium distal to every zooid.

Ovicell large and distinctly longer than wide (L: ~700 μm ; W: ~400 μm), hyperstomial, ooecium proximally constricted and with an elevated rim.

Remarks

From the syntype series, only two specimens exist in the NHMUK collection. Whereas specimen NHMUK 1944.1.8.132 (Busk bequest, Station 70, on slide) is missing, one of the slides (NHMUK 1887.12.9.238) comprises several small fragments from Station 70 west of the Azores (Figure 1A). None of these specimens can be unequivocally attributed to Busk's drawings, although two fragments from Station 70, which is mentioned first in Busk's (1884) habitat list, comprise ovicells, one of which was presumably imaged in his fig. 3b. A note on the slide by Busk also supports this notion, and it is likely that the fragile colony broke apart between production of the image and preparation of the slide. This specimen is therefore designated here as lectotype. Both specimens are mounted in Canada balsam on slides and cannot be studied using SEM, which renders impossible a thorough redescription of the morphospecies. The short description and morphometrics given above are based on optical microscope images (Figure 1B), which do not show any detailed characteristics, as well as on Busk's (1884) original account. Both need to be taken cautiously. Nevertheless, Busk's original description and images (1884: 51, fig. 3a, b) match with the morphology of the lectotype.

Another specimen referred to *Columnella gracilis* by Busk (NHMUK 1887.12.9.239) is a large colony fragment from Station 122 off Brazil (Figure 1D). A comparison of the colonies from the Azores and Brazil, however, shows that the branches in the Azorean specimen are more slender than in the Brazilian one (300 μm vs 500 μm ; Figure 1C), that the zooids are distinctly longer (~1100 μm vs ~300 μm), and that there are avicularia distal to every zooid, while these seem to be lacking in the southern Atlantic specimen. In concert with the geographic distance between the two stations, these morphometric differences suggest that the specimen from Brazil belongs to a different species.

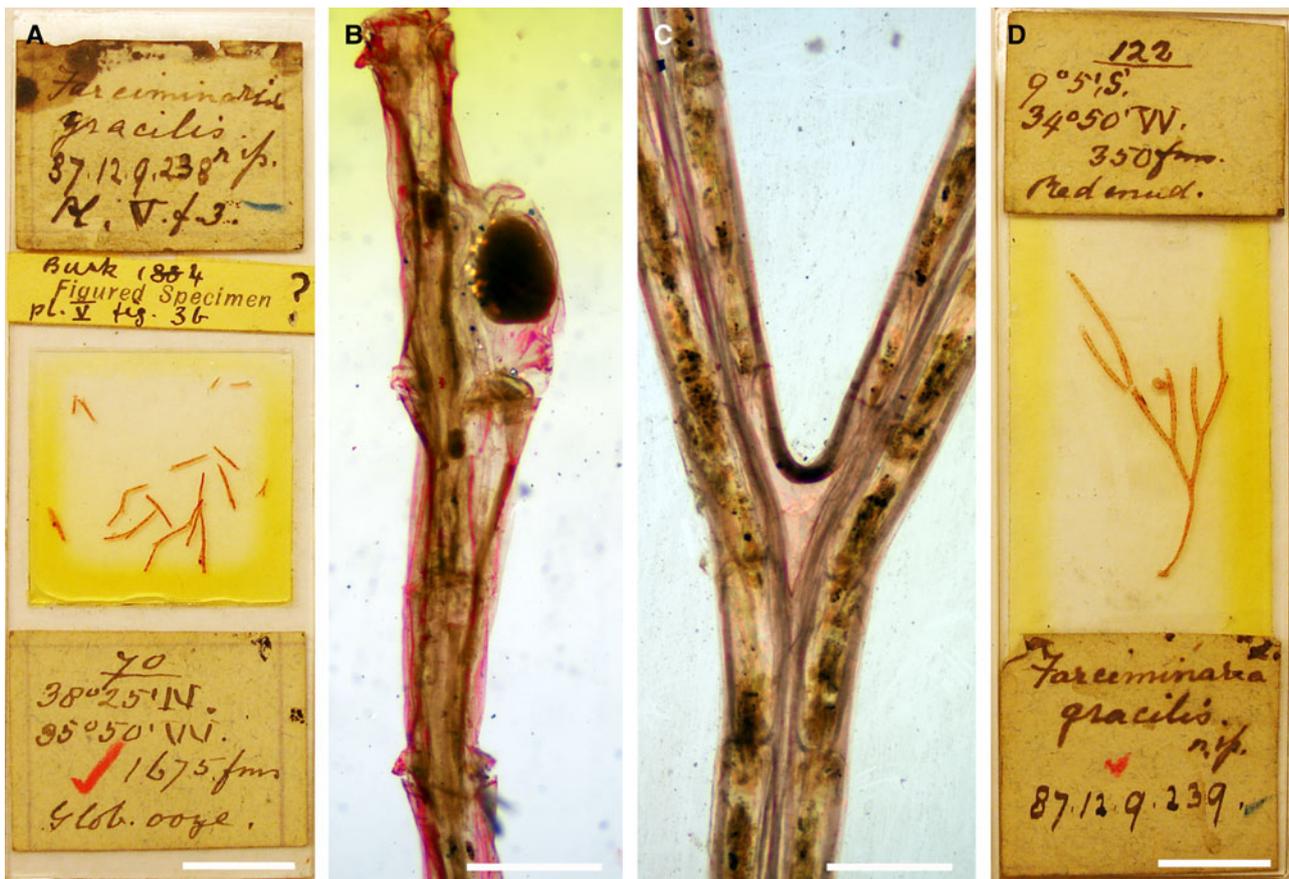


Figure 1. *Columnella gracilis* (Busk, 1884): (A) the lectotype NHMUK 1887.12.9.238 from west of the Azores (Station 70); (B) optical image of an ovicellate branch (lectotype, NHMUK 1887.12.9.238). *Columnella* sp.: (C) optical image of a bifurcating branch segment of NHMUK 1887.12.9.239 from off Brazil (Station 122), note the distinctly greater branch width and absence of avicularia in this specimen; (D) same specimen, image of the slide. Scale bars: A, D, 1 cm; B, C, 500 μ m.

Columnella gracilis was originally recorded from ~3000 m depth at the northern ridge of the Pico Fracture Zone, ~400 km WSW of the island of Flores, i.e. W of the Mid-Atlantic Ridge on the North American Plate. The conspecificity of subsequent records remains doubtful as most are, just like Busk's other specimen from Brazil, extremely far away from the type locality. For instance, d'Hondt (1981: 13; 1983: 75) recorded the species from off Argentina. Other reports from the North Atlantic are also at a distance of several hundred to a few thousand kilometres to the original position (d'Hondt, 1983, 1985). In the absence of thorough descriptions and detailed illustrations from all of the above-mentioned publications, however, it is impossible to make any statements on its geographic and bathymetric range at present.

Other *Columnella* species are certainly present in the greater Azores region. Silén (1951: fig. 1) reported a ~18 cm tall colony of *C. magna* (Busk, 1884) from 4540–4600 m depth 370 km WNW of Flores (as *Levinisella magna*). The type locality of that species is, however, in the southern hemisphere (the syntypes are from the Indian Ocean sector of Antarctica and from off southern Uruguay). Besides recording *C. magna*, d'Hondt (1975) also reported two other farciminariid species from 1250–4700 m depth in and around the Azores.

Superfamily FLUSTROIDEA Fleming, 1828
 Family FLUSTRIDAE Fleming, 1828
 Genus *Carbasea* Gray, 1848

Carbasea pedunculata Busk, 1884
 (Figure 2)

Carbasea pedunculata Busk, 1884: 56, pl. 16, fig. 4.

Type material

Lectotype (here designated): NHMUK 1887.12.9.288, Station 76, several large colony fragments, figured specimen (Busk, 1884: pl. 16, fig. 4).

Paralectotype: NHMUK 1887.12.9.286, Station 75, damaged colony base with rootlets.

Description

Colony erect, unilaminar, unjointed but flexible, dichotomously branching at an angle of ~20–30°, well over 2 cm in height (Figure 2A); branches ligulate, all in one plane, composed of three linear series of autozooids that are arranged in quincunx (Figure 2B), branches bordered on each side by a cuticular tube; colony fixed to the substratum by rootlets (Figure 3C). Zooecia very thinly calcified, rounded pentagonal to hexagonal, large (L: 1441 ± 91 , 1300–1584, 8; W: 869 ± 101 , 733–1044, 8). Polypide with some 24 tentacles. Operculum D-shaped, no oral or mural spines.

Avicularia absent.

Remarks

Busk (1884: 56) remarked that 'The single specimen included in the collection is unfortunately in a very imperfect condition – torn and ragged – so that the full dimensions of the growth cannot be determined from it.' The first part of the quote is



Figure 2. *Carbasea pedunculata* Busk, 1884: (A) slide with the lectotype, NHMUK 1887.12.9.288; (B) optical image of autozooids (lectotype, NHMUK 1887.12.9.288); (C) paralectotype NHMUK 1887.12.9.286, note that the specimens were remounted by S.F. Harmer and R. Kirkpatrick, respectively. Scale bars: A, C, 1 cm; B, 500 μ m.

dubious as he reported the species from two ‘Challenger’ stations, and there are, accordingly, two specimens of the syntype series in the NHMUK collection. While the sample from Station 76 (NHMUK 1887.12.9.288) consists of several fragments of the erect colony (Figure 2A), another torn rhizoidal colony base is present from Station 75 (NHMUK 1887.12.9.286; Figure 2C), which is marked as ‘Type’. A note in the NHMUK archive also says that some material was destroyed during remounting of these specimens in the 1920s, which were originally kept in ethanol. It is probable that more material was initially present, which Busk either kept in his own collection (and which later arrived at the NHMUK with the Busk bequest, such as NHMUK 1944.1.8.148 from Station 76, but this specimen is also lost today), or which he distributed among colleagues.

While there may be a slight chance that more syntype material may be present in other collections, sample NHMUK 1887.12.9.288 from Station 76 is here chosen as lectotype as it is the only one in which autozooids are preserved. As all available material is mounted on slides (in Canada balsam), the redescription given above is based on observation by optical microscopy. A detailed analysis of zoecial characters using SEM will need to be carried out on newly collected topotypic material.

The species was hitherto assigned to the genus *Flustra* Linnaeus, 1761 (see Bock, 2022). Based on its unilaminar colony growth as well as owing to the absence of spines and avicularia, however, Busk’s (1884) original systematic placement in the genus *Carbasea* was correct.

Carbasea pedunculata has never been reported again since its discovery. It is thus endemic to the Azores, occurring in depths from 800–1700 m. The species has remarkably large

zooids and polypides that are easily visible with the naked eye (Figure 2).

Superfamily BUGULOIDEA Gray, 1848

Family CANDIDAE d’Orbigny, 1851

Genus *Notoplites* Harmer, 1923

Notoplites bilobus (Busk, 1884)

(Figure 3)

Cellularia biloba Busk, 1884: 18, pl. 3, fig. 2.

Notoplites biloba (Busk): Harmer, 1923: 350.

Type material

Lectotype (here designated): NHMUK 1887.12.9.64, Busk coll., Station 76, a single specimen of >3 cm length with rootlet base, broken into several pieces, marked as ‘Type’ on the back, figured specimen (Busk, 1884: pl. 3, fig. 2b).

Description

Colony erect, jointed, dichotomously branching, widely ramified, over 3 cm in height with slender branches (Figure 3A), attached by numerous basal rhizoids produced from a proximal pore. Branches formed by two series of alternating autozooids, branching angle between 30–40°, zooids opening on one side only, colony white in dried state. Branching points composed of a single proximomedian zooid and two distolateral ones, with the nodes developing immediately distal to the latter zooids by breakage of the narrow proximal parts of the two subsequent zooids (Figure 3E). Autozooids very elongate (Figure 3D, G), narrowest and tubular proximally, widening distally with the distal half of zooids turned outwards at an angle of ~40° (L: 736 \pm 56, 640–812, 20; W: 212 \pm 16, 183–242, 20), usually (much) less than half of total autozooid length

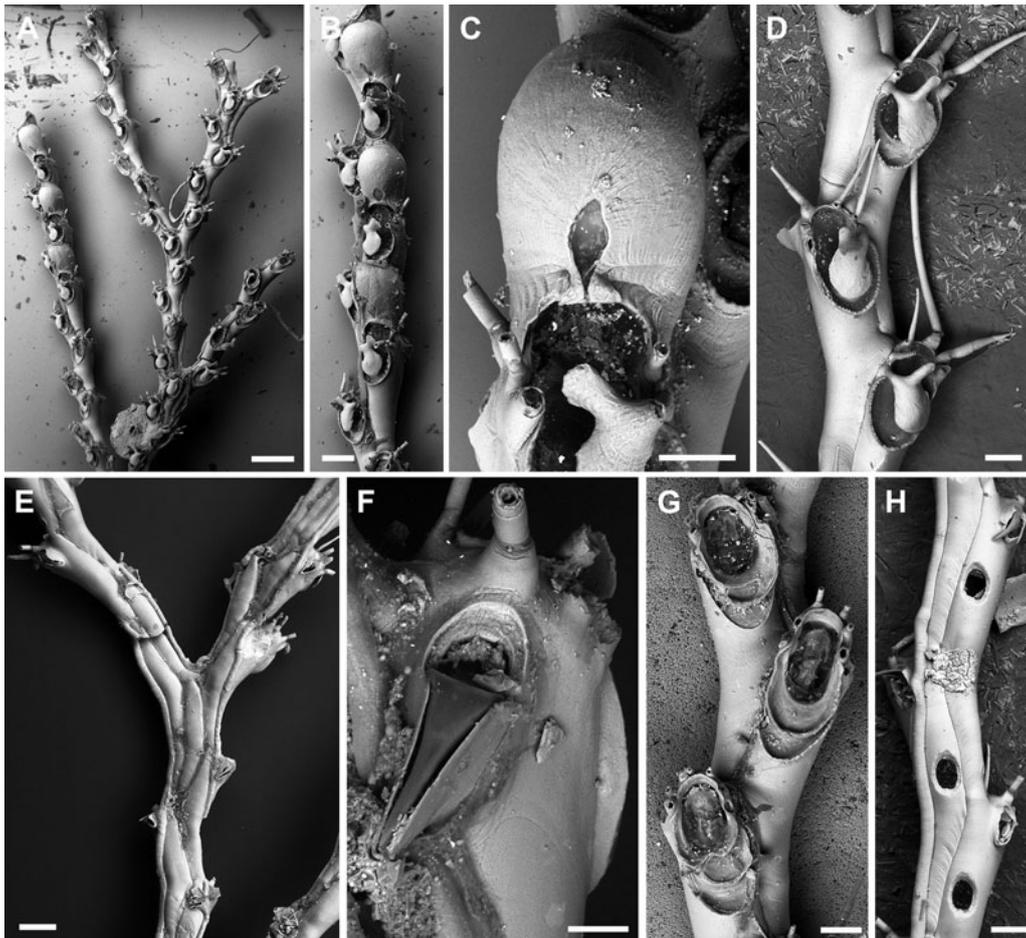


Figure 3. *Notoplites bilobus* (Busk, 1884): (A) overview of lectotype (NHMUK 1887.12.9.64); (B) several ovicellate zooids (lectotype, NHMUK 1887.12.9.64); (C) close-up of ovicell (lectotype, NHMUK 1887.12.9.64); (D) three autozooids, note the long distal spine (NHMUK 1945.9.14.1); (E) abfrontal, bifurcating branch with lateral rhizoidal tubes and distal avicularia on each zooid (paralectotype, NHMUK 1887.12.9.63); (F) close-up of abfrontal avicularium (paralectotype, NHMUK 1887.12.9.63); (G) intramural buds in zooids damaged by predation (paralectotype, NHMUK 1887.12.9.63); (H) abfrontal side of a branch, showing drill holes and damaged avicularia (NHMUK 1945.9.14.1). Scale bars: A, 500 μ m; B, E, 200 μ m; C, D, G, H, 100 μ m; F, 50 μ m.

occupied by the scutum/membranous area and orifice; skeletal surface smooth, convex, zooids separated by a distinct groove; ovicellate zooids slightly more bulky than autozooids. Rhizoids produced from a small oval pore near proximal end on the abfrontal side of some zooids, running along the lateral abfrontal side, basally closely approximated to form a single stalk; additional rhizoids are produced near branching points that run down on one interior side and up the other for some distance.

Opesia oval (L: 323 ± 21 , 270–356, 20; W: 184 ± 14 , 161–212, 20), proximal two-thirds on a distinctly raised rim (Figure 3D), outer cryptocystal rim thin and crenellate, the smooth inner cryptocyst steeply sloping towards a proximolateral shelf that is broadest proximally and gradually thinning distally to disappear in distal third (Figure 3G); outer distolateral opesial margin with 3 relatively thick spines that may be longer than an autozooid, proximal spine usually larger than the 2 distal ones, inner distolateral margin with 2 smaller and shorter spines plus scutum (Figure 3D); scutum on a short stalk at same level as proximal-most outer spine, arching over at some distance but not covering the entire opesia, much longer than wide (L: 237 ± 27 , 196–314, 20; W: 110 ± 15 , 82–150, 20), variably shaped but most often bilobed (Figure 3B–D), the slightly raised distal lobe generally shorter and narrower than proximal part, occasionally oval to reniform, surface with faint reticulate ridges; often slightly dimorphic in ovicellate zooids, with the distal lobe broadened.

A single adventitious avicularium placed near the bases of the oral spines at the distal abfrontal margin of every zooid (L: 214, 195–232, 2; W: 91, 88–93, 2), invisible in frontal view, directing towards the proximal end of zooid (Figure 3E, F, H), the proximal part of the avicularium (i.e. near the spine bases at the distal zooidal margin) forming a rim that is parallel with the abfrontal zooidal surface whereas the central and narrow distal part of rostrum is much raised, rostrum very elongate triangular (Figure 3F), distal part downcurved and with a hooked tip; mandible distally hooked, hinged on a pair of short lateral denticles, the semicircular area proximal to denticles with a narrow immersed proximal shelf and a semicircular opesia, palate (i.e. an immersed shelf in the rostrum) absent.

Ovicell hyperstomial, globular, large, distinctly longer than wide (L: 440 ± 24 , 410–474, 7; W: 310 ± 20 , 282–329, 7), covering the entire frontal shield of the distal zooid proximal of opesia (Figure 3B, C); ectooecium entirely calcified except for an elongated membranous fenestra of variable shape at the mid-proximal margin, surface smooth at first sight, faint reticulate ridges and growth marks visible at higher magnification, proximal oocel margin concave and widely arched over opesia, covering the distal spine of the inner distolateral margin; ovicell closure acleithral.

Ancestrula not observed.

Remarks

Some 43 *Notoplites* species are recognized worldwide at present, which are distributed from the tropics to polar latitudes, although most species are confined to cooler waters (i.e. deeper water at

lower latitudes). Besides *Notoplites bilobus*, two other *Notoplites* species are known to be present in the Azores: *N. clausus* (Busk, 1884) (see below) as well as *N. saojorgensis* Berning, 2013, which was newly described based on material erroneously reported as *N. marsupiatius* (Jullien, 1882) by Calvet (1931). Both species have a fimbriated scutum that covers the entire opesia and are therefore distinctly different from *N. bilobus*. Other species recognized in the NE Atlantic are *N. damicornis* Hayward & Ryland, 1978, *N. evocatus* (Jullien, 1882), *N. evocatus trispinosus* d'Hondt, 1987, *N. harmeri* Ryland, 1963, *N. marsupiatius* (Jullien, 1882), and *N. smitti* (Norman, 1868). *Notoplites bilobus* differs from all of these species by, among other characters, the bilobed scutum and the presence of a single, distal, abfrontal avicularium.

Notoplites bilobus has never been reported after its original introduction, besides in a revision of the genus *Notoplites* by Harmer (1923). It must therefore be regarded as endemic to the Azores, occurring at a depth of ~1600 m in the central group of islands. Many of the colonies' zooids are repaired and replaced by a second or occasionally even a third generation of intramural buds, which are distinctly raised above the level of the primary zooid (Figure 3G). The presence of drill holes in the abfrontal skeleton (Figure 3H), and also the structural damage to the abfrontal avicularia, shows that the formation of at least some of these intramural buds was induced by partial predators, most likely juvenile or micro-gastropods. This proves that predation pressure is also high in the bathyal, and that there is a necessity for the bryozoans to invest in defensive skeletal structures at these depths (see also Berning, 2008; Berning *et al.*, 2017), while in this case the protective scutum on the frontal colony surface was sidestepped by attacking the abfrontal side.

Notoplites clausus (Busk, 1884)

Menipea clausa Busk, 1884: 20, pl. 4, fig. 5.

Scrupocellaria marsupiatia Jullien: Waters, 1888: 9.

part *Notoplites marsupiatius* (Jullien): Harmer, 1923: 351.

?not *Scrupocellaria marsupiatia* Jullien: d'Hondt, 1973: 1212.

?part *Scrupocellaria marsupiatia* Jullien: d'Hondt, 1975: 556, figs 14–16.

Notoplites clausus (Busk): Souto *et al.*, 2011: 38, figs 16–20.

Type material

Lectotype (designated by Souto *et al.*, 2011): NHMUK 1887.12.9.83, Busk collection, Station 70, a single specimen of ~1.6 cm length with rootlet base, broken into several pieces.

Remarks

This species, which was considered to be a junior synonym of *Notoplites marsupiatius* (Jullien, 1882) since shortly after its introduction, has recently been resurrected and imaged by Souto *et al.* (2011: figs 16–20). It is possible that part or all of the material d'Hondt (1975: 556) recorded from a wide region around the Azores Archipelago as *Scrupocellaria marsupiatia* may belong to *N. clausus* (but see Souto *et al.*, 2011: 39; Berning, 2013: 5). Similarly, the material d'Hondt (1973) reported from south of the Azores may belong to *N. saojorgensis*. In the absence of images, these records have to be considered doubtful, and the type locality ~400 km W of the Azores, at a depth of ~3000 m, remains the only verified occurrence.

Sharing the fimbriated scutum that covers the entire opesia, *Notoplites marsupiatius* from the continental slope of NW Spain

as well as *N. clausus* and *N. saojorgensis* from the Azores region seem to form a distinct clade within *Notoplites*.

Superfamily BIFAXARIOIDEA Busk, 1884

Family BIFAXARIIDAE Busk, 1884

Genus *Raxifabia* Gordon, 1988

Raxifabia minuta (Busk, 1884)

(Figure 4)

Bifaxaria minuta Busk, 1884: 81, pl. 13, fig. 5, 5a

?not *Sclerodomus minutus* Busk: d'Hondt & Schopf, 1984: 940.

Type material

Holotype (by monotypy): NHMUK 1887.12.9.380, Busk coll., Station 70, colony base with rootlets fixed in *Globigerina* sand, mounted on slide.

Description

Colony erect, rooted, biserial (Figure 4A, B), branching not observed, forming a single rod (~4.3 mm in length) with a lensoid cross section, tapering proximally, maximum width of lateral face ~350 µm, maximum width of frontal face ~220 µm. Zooids alternating back to back (Figure 4B), extremely elongate rectangular in frontal view (L: 751 ± 16, 735–777, 5; W: 217 ± 8, 210–227, 4), laterally compressed (i.e. the height of a zooid is greater than its width: H: 231 ± 21, 198–256, 8), resulting in narrower frontal colony faces (Figure 4C), separated by a groove on raised ridges; frontal shield smooth, with a median suture that is produced by merging of the pair of spinocysts, a distinct row of pores running along the suture with others scattered on the remaining shield, another pair of larger pores in the most proximal part via which the spinocysts and possibly also the rhizoids may be formed. Orifice suborbicular (Figure 4C, D), slightly wider than long (L: 123 ± 2, 119–125, 6; W: 132 ± 4, 127–136, 4), proximal margin shallowly concave, potential condyles not seen as obscured by the opercula.

Avicularia presumably interzooidal, paired, distolateral to every orifice and tightly framed by the spinocysts of the proximal and distal zooids (Figure 4D), oriented at almost 90° angle to zooidal frontal surface, i.e. with the frontal plane directing distally; outline oval, rostrum semi-elliptical (L: 62 ± 2, 60–65, 5; W: 51 ± 4, 46–56, 5), directing slightly outwards and toward zooidal frontal surface; the presence of a crossbar could not be determined in this unbleached specimen.

Ovicells and ancestrula not recognizable.

Remarks

The only specimen, from ~400 km W of the Azores at 3000 m depth, is a complete but small and immature colony with the basal rhizoidal part preserved. As the holotype could not be bleached, and the proximal part of the colony surface is completely covered by rhizoids, it was not possible to examine the potential ancestrula and early astogenetic colony. The same applies to the details of the orificial condyles and the avicularia as these are covered by the opercula and mandibles, respectively.

Gordon (1988: 287) included *Bifaxaria minuta* in the genus *Raxifabia*, which he newly introduced for bifaxariid species with a subcircular to schizoporelloid (i.e. sinusoidal) autozooidal orifice and a frontal shield that is formed by a single pair of spines. *Raxifabia minuta* is so far the only representative of the genus in the Atlantic while all other congeners occur in the Pacific. Considering the distance between localities, however, the specimens subsequently recorded by d'Hondt & Schopf (1984) from the equatorial Atlantic off West Africa and Brazil

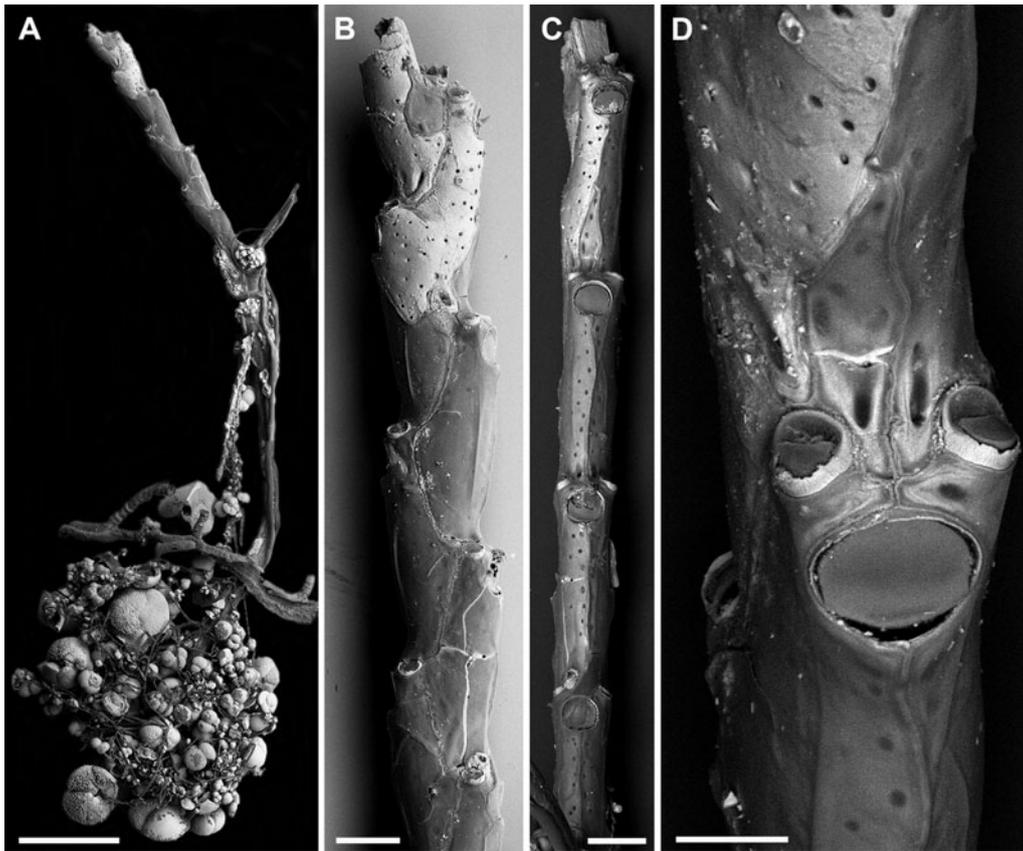


Figure 4. *Raxifabia minuta* (Busk, 1884), holotype, NHMUK 1887.12.9.380: (A) overview of colony with base rooted in foraminiferal sand; (B) colony in lateral view, note that the two distal zooids show evidence of repair by means of intramural budding (a secondary orifice rim is visible in one zooid), as well as by re-formation of the spinocysts, thus distorting the spinocystal characters in these zooids; (C) colony in frontal view; (D) oblique view on orifice and distal avicularia. Scale bars: A, 1 mm; B, C, 200 μ m; D, 100 μ m.

as *R. minuta* are very likely to belong to one or more distinct species.

Superfamily LEPRALIELLOIDEA Vigneaux, 1949

Family ROMANCHEINIDAE Jullien, 1888

Genus *Hemicyclopora* Norman, 1894

Hemicyclopora canalifera (Busk, 1884)

(Figure 5)

Mucronella (*Phylactella*?) *canalifera* Busk, 1884: 159, pl. 22, fig. 2.

Mucronella canalifera Busk: Waters, 1888: 24, pl. 3, fig. 44; Calvet, 1931: 93.

?part *Lepralia labiosa* (Jullien): Calvet in Jullien & Calvet, 1903: 134.

Lepralia labiosa (Jullien): Calvet, 1907: 410.

Lepralia canalifera (Busk): Calvet, 1907: 410.

?part *Hippoporina*? *labiosa* (Jullien): d'Hondt, 1975: 577.

Type material

Lectotype of *Mucronella canalifera* (here designated): NHMUK 1887.12.9.634, Busk coll., Station 75, from sand, figured specimen (Busk, 1884: pl. 22, fig. 2).

Description

Colony encrusting, unilaminar, multiserial, forming an irregular patch (Figure 5A, B). Autozooids oval to hexagonal (L: 650 ± 63 , $557\text{--}784$, 20; W: 460 ± 34 , $421\text{--}528$, 20), separated by distinct grooves (Figure 5B); frontal shield strongly and evenly convex, surface finely granular, with a single row of small marginal pores invisible from directly above, two rows lateral of the

orifice, frontal shield abruptly rising proximal of orifice to form a thick prominent lip that is variably curved and flared, highest usually proximally (Figure 5A–D); vertical walls much reduced, numerous basal pore-chambers present (Figure 5D), 4–7 combined into elongated areas framed by gymnocystal calcification, one area distally, two distolaterally and two laterally; basal wall only marginally calcified. Orifice suboval (Figure 5C), slightly longer than wide (L: 159 ± 12 , $138\text{--}178$, 20; W: 138 ± 10 , $123\text{--}159$, 20), proximal border variably concave, condyles thick and bluntly triangular, orifice margin usually with 6 (rarely 8) long outwardly bent spines (Figure 5B), the proximal-most pair just distal to condyles, early astogenetic zooids with 8 spines (Figure 5E).

Ovicellate zooids slightly dimorphic, differing in the presence of a gap between the distal-most pair of oral spines in which the ovicell is accommodated; ovicell produced by an encrusting kenozooid (Figure 5D), oecium prominent, globular, wider than long (L: 263 ± 27 , $226\text{--}306$, 14; W: 332 ± 15 , $314\text{--}360$, 14), endoecium entirely calcified, imperforate, surface finely granular as zooidal frontal shield, proximomedian margin with a distinctly raised triangular umbo with smooth proximal gymnocystal calcification; ovicell closed by the operculum (cleithral).

Ancestrula oval, presumably with extensive proximolateral gymnocystal calcification, opesia confined to distal part of frontal area, almost lenticular in outline, framed by a raised gymnocystal rim surrounded by 8–10 spines, proximal cryptocystal margin smooth and shallowly concave, proximally passing into an extensive shelf with a granular surface; first autozooid budded distally, second zooid distolaterally (Figure 5E).

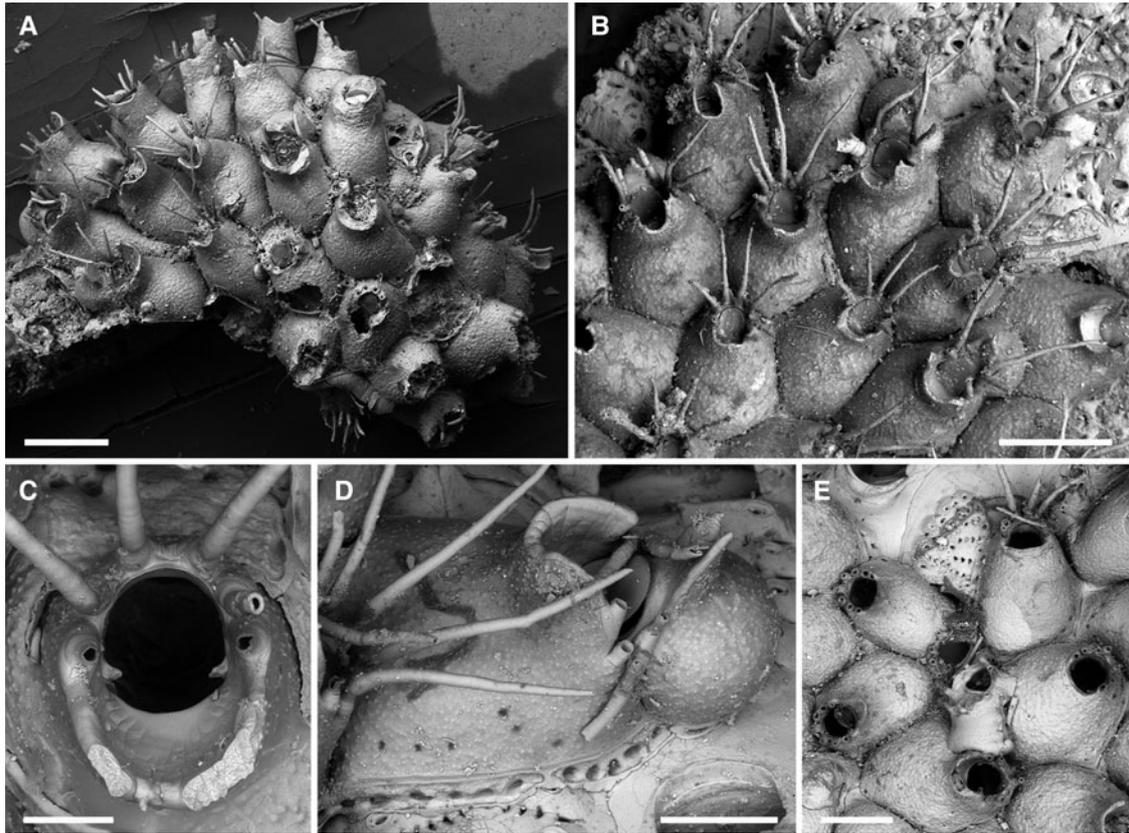


Figure 5. *Hemicyclopora canalifera* (Busk, 1884): (A) overview of lectotype (NHMUK 1887.12.9.634); (B) a specimen of *Lepralia labiosa* from the Calvet collection with the oral spines preserved (MOM INV-22496); (C) orifice (MNHN-IB-2008-2436), (D) maternal zooid and kenozooidal ovicell in lateral view showing the umbo on the proximal oocellar margin (MNHN-IB-2008-2436); (E) ancestrula (partly obscured by another ancestrula of an unknown species) and early astogenetic zooids with eight oral spines (MNHN-IB-2008-2436). Scale bars: A, B, 500 μ m; C, 100 μ m; D, 200 μ m; E, 300 μ m.

Remarks

When introducing *Mucronella canalifera*, Busk (1884: 159) also treated specimens from Madeira as synonymous, which he previously reported as *Lepralia mangnevillea* Audouin, 1826 (Busk, 1860: 284). It has recently been shown, however, that these Madeiran colonies are actually quite different and belong to *Saevitella peristomata* (Waters, 1899) (see Berning, 2012: 44).

Waters (1925: 543, pl. 29, fig. 10) described and figured the ancestrula of *Hemicyclopora canalifera* as normal tatiform, i.e. with a large oval opesia. The (albeit poorly preserved) ancestrulae observed in the material studied during this work suggest, however, that the opesia is restricted to the distal third of the frontal by an extensive immersed cryptocystal shelf, just like in the other species of the genus (Harmelin & Rosso, *in press*). Cook (1968: 217) already suggested that the proximal cryptocystal shelf may have been broken in Waters' specimen. Cook (1968: 216) further synonymized *H. canalifera* with *Hemicyclopora multispinata* (Busk, 1861) from Madeira but the latter is supposed to have 8–10 spines in adult zooids. Until the types of *H. multispinata* have been analysed based on SEM images this decision has to be rejected owing to the great distance between localities, and we here regard *Hemicyclopora canalifera* as a distinct entity. The species has also been cited from other North Atlantic regions (Calvet, 1931: Bay of Biscay, Norway, Spitsbergen), which most probably represent distinct species as well.

Most, or possibly even all, of the specimens referred to *Lepralia labiosa* Jullien, 1903 belong to *H. canalifera* (both having the same type locality, Pico Island). The status and morphology of the species is unclear as the syntypes from *Hirondelle* Station 247 (Jullien in Jullien & Calvet, 1903: 69) are lost (d'Hondt,

1975: 577; Tricart & d'Hondt, 2009). The case is complicated by the fact that the specimen figured in Jullien & Calvet (1903: pl. 9, fig. 6) as *L. labiosa*, which is kept in Calvet's collection at Monaco (MOM INV-22582, marked as 'Type'), is from *Hirondelle* Station 226. It can, therefore, not be regarded as a syntype because Jullien explicitly mentions only specimens from Station 247 as part of the type series. Calvet's action of choosing a figured specimen that Jullien has not seen when describing the species in the first part of their 1903 work represents another case in which he substantially interfered with the taxonomic decisions (e.g. Berning *et al.*, 2021: 344), in contrast to what he stated in the preface (Jullien & Calvet, 1903: 3).

Unfortunately, the specimen is also severely affected by Bynesian decay, which masks morphological details, and it could not be imaged using SEM. Jullien's original description agrees with the figure in that the ovicell is forming a little tubular peristome, while the distinct proximal umbo that is characteristic of *H. canalifera* is absent. All additional specimens from Station 226 available in the MOM collection, however, belong to *H. canalifera* (Figure 5B), as do all examined specimens from *Talisman* Station 125 (Faial-Pico Channel) that were later reported by Calvet (1907) as *Lepralia canalifera* and *Lepralia labiosa*.

In the Azores *H. canalifera* was recovered from 80–820 m depth. Whereas downslope transport may be responsible for the occurrence at great depths (see Discussion), the colonies from 'Challenger' Station 75 (820 m) were relatively well-preserved, while showing no morphological differences to specimens from shallower waters. Apart from its type locality, the Faial-Pico Channel, which also marks the shallowest record of the species, *H. canalifera* was recovered from Graciosa, another island of the

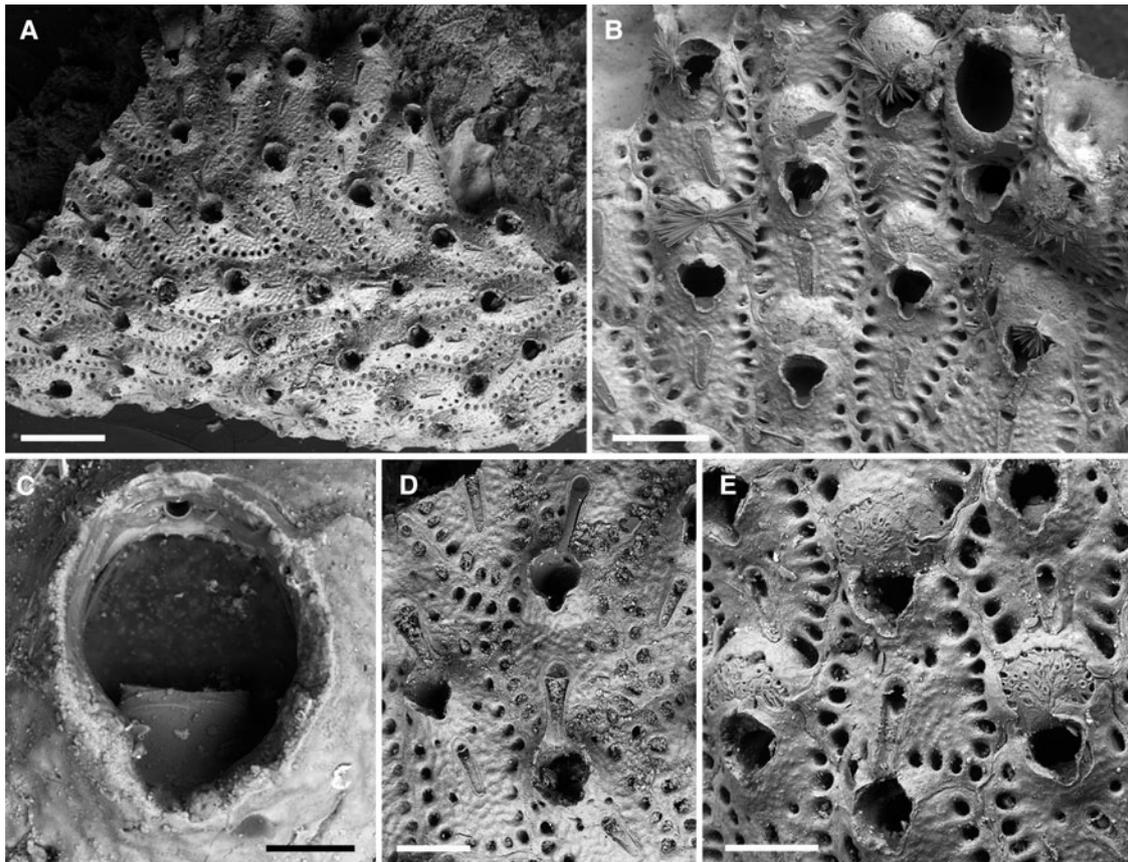


Figure 6. *Smittoidea oratavensis* (Busk, 1884): (A) overview of lectotype (NHMUK 1887.12.9.609); (B) lectotype of *Smittia ensifera* Jullien, 1903 (MOM INV-22514); (C) close up of orifice, note the toothed distal margin and the single oral spine base (lectotype, NHMUK 1887.12.9.609); (D) both types of avicularia (lectotype, NHMUK 1887.12.9.609); (E) ovicellate zooids (paralectotype, NHMUK 1944.1.8.293). Scale bars: A, 500 μ m; B, 300 μ m; C, 50 μ m; D, E, 200 μ m.

central group, at \sim 400 m depth (as *Hippoporina labiosa* by d'Hondt, 1975). The *Hemicyclopora* species present in São Miguel in the eastern group of islands, which was recorded as *Hippoporina discrepans* (Jullien, 1903) by d'Hondt (1975: 561), is distinct from both the nominal species and *H. canalifera*, and has recently been referred to as *Hemicyclopora* sp. 1 by Harmelin & Rosso (in press).

Superfamily SMITTINOIDEA Levinsen, 1909

Family SMITTINIDAE Levinsen, 1909

Genus *Smittoidea* Osburn, 1952

Smittoidea oratavensis (Busk, 1884) comb. nov.

(Figure 6)

Smittia oratavensis Busk, 1884: 153, pl. 22, fig. 1.

Smittia ensifera Jullien in Jullien & Calvet, 1903: 102, pl. 12, fig. 4; Calvet in Jullien & Calvet, 1903: 149, pl. 17, fig. 5.

Smittina ophidiana Waters: Calvet, 1907: 433;

Smittina ophidiana Waters: Calvet, 1931: 91; d'Hondt, 1975: 557 (listed).

Smittoidea ensifera Jullien: Wisshak *et al.*, 2015: 95 (listed).

Type material

Lectotype of *Smittia oratavensis* (here designated): NHMUK 1887.12.9.609, Busk coll., Station 75, sand, one colony on bioclast, ?figured specimen (Busk, 1884: pl. 22, fig. 1).

Lectotype of *Smittia ensifera* (here designated): MOM INV-22514, Calvet coll., 'Hirondelle'. 14/8/1888, Station 226, 38°31.32'N 28°34.52'W, Faial-Pico Channel, 130 m, colony on bioclast with free growth margin, on slide.

Description

Colony encrusting unilaminar, multiseriate (Figure 6A). Zooids elongated pentagonal to hexagonal, widest usually at mid-distance (L: 564 ± 48 , 464–634, 20; W: 356 ± 36 , 277–438, 20), separated by shallow grooves or sutures (Figure 6B, E); frontal shield flat to slightly convex, rising abruptly around orifice to form a peristome with a deep U-shaped proximal sinus and notch, surface faintly nodular, large central area imperforate, a single row of \sim 15–20 densely spaced round areolar pores along zooecial margins and 2 pores distolateral to central avicularium (Figure 6B, D, E); vertical walls extensive, with 3 or 4 uniporous septula per neighbouring zooid. Orifice suborbicular (Figure 6C), obscured by a peristome, distal rim with few fine teeth, a single or two distal oral spines in early ontogeny are quickly lost, the bases being incorporated into the peristome, condyles indistinct if present, lyrula large, forming a broad square about half of total orifice width; peristomial aperture slightly longer than wide (L: 168 ± 13 , 145–197, 20; W: 139 ± 7 , 124–154, 20).

Ovicell hyperstomial (Figure 6B, E), globular with a slightly flattened front (L: 227 ± 14 , 203–266, 20; W: 264 ± 22 , 231–300, 20), ectooecium smooth with numerous rimmed pseudopores of usually round shape, proximal margin rather straight and slightly overarching the distal orifice, the peristome encroaching the proximalateral margins while the distolateral ectooecium is marginally covered by secondary calcification of the distal zooid(s).

Avicularia dimorphic, always adventitious, single, central and proximally or slightly proximolaterally directed (Figure 6B, D, E); rostrum in the smaller avicularia extremely elongated triangular or even with parallel lateral margins and a rounded tip (L: 167 ± 20 , 133–205, 20; W: 46 ± 6 , 38–58, 20), mandible of same shape and length as rostrum; rostrum in larger avicularia distally flared

and open, downcurved and incorporated into distal peristomial margin of proximal zooid (L: 244 ± 20 , 207–280, 20; W: 73 ± 9 , 54–95, 20), mandible with downcurved bifid tip, exceeding length of rostrum and reaching into the peristome when close; both types having a palate with a depressed calcified shelf apart from a small semicircular opesia distal to crossbar and a suborbicular proximal window, crossbar thin and without columella.

Ancestrula tatiform, longer than wide (L: 360; W: 260), opesia reduced to distal half, suboval, only slightly longer than wide (L: 150; W: 130), framed by a thin raised rim abutting against 9 stout spines grouped in 3 relatively narrowly spaced distal pairs, and 3 more widely spaced proximal spines, with the most proximal spine being slightly thicker and presumably overarched the opesia; cryptocyst reduced to a narrow proximal shelf; proximal gymnocyst extensive, convex, surface smooth to slightly pitted.

Remarks

Although Busk (1884) named the species after the Port of Orotava (Tenerife Island, from where he had previously received specimens of apparently the same species), the type locality given in the original description is clearly meant to be Pico Island in the Azores ('Challenger' Station 75), while Orotava is merely listed in brackets subsequently. The syntypes present in the collection are also exclusively from the Azores, and the specimen that was presumably figured by Busk (1884: pl. 22, fig. 1) is here designated as lectotype (NHMUK 1887.12.9.609). Note that, while Busk correctly gave the name of the town Orotava, he termed the species *oratavensis*. As the same spelling was given in the figure caption, however, it cannot be regarded as a *lapsus calami* and is therefore considered as correct original spelling.

Smittoidea oratavensis has never been reported again after its discovery, and is unrecognized today (cf. Bock & Gordon,

2021a), presumably because it was synonymized with *Smittoidea marmorea* (Hincks, 1877a) soon after its establishment (Jelly, 1889: 249). *Smittoidea oratavensis* differs from that species, however, in producing a larger avicularium in some zooids, the tips of which are incorporated into the distal peristome of the proximal autozooid. Moreover, in *S. oratavensis* a single or a pair of distal oral spines are present during early ontogeny, while spines are absent altogether in *S. marmorea* (cf. Hayward & Ryland, 1999: 268), and the distal rim of the primary orifice bears several small denticles that are not reported to occur in *S. marmorea*.

The morphologically most closely related species of *S. oratavensis* rather seems to be the Mediterranean *Smittoidea ophidiana* (Waters, 1879) as all of the above mentioned characters are shared. Calvet (1907, 1931) and d'Hondt (1975) already noted their close similarity and reported specimens from the Azores under this name. A specimen from its type locality (Naples), which was collected in 1875 by Waters and is presumably part of the syntype series, was studied for comparison (NHMUK 1899.7.1.2345A). Distinct differences exist in that *S. ophidiana* has much larger autozooids (mean ZL 840 μ m, ZW 530 μ m), larger apertures (mean ApL 230 μ m, ApW 170 μ m), and more numerous areolar pores (~25). While the large frontal avicularia are also bigger (mean lAL 360 μ m, lAW 110 μ m) in *S. ophidiana*, the small avicularia are about the same size (mean sAL 50 μ m, sAW 46 μ m) as in *S. oratavensis*. Ovicells are unfortunately lacking in the *S. ophidiana* specimen studied, while the bifid tips of the mandible in the long avicularia seem to be longer in the Mediterranean species than in the Azorean population, in which, however, only a single mandible was preserved. These differences are, overall, important enough to maintain *S. ophidiana* and *S. oratavensis* as distinct species, and we therefore resurrect *Smittoidea oratavensis* (Busk, 1884).

Another *Smittoidea* species from the Azores, *Smittia ensifera* Jullien, 1903, was introduced ~20 years later, without making reference to Busk's species (Jullien & Calvet, 1903: 102, 149). Syntypes of *S. ensifera* from 'Hirondelle' Station 226 are absent from the MNHN (Tricart & d'Hondt, 2009), which is housing Jullien's collection. To fix the status of *S. ensifera*, which is also unrecognized today (Bock & Gordon, 2021a), a syntype from the same station that is kept in the Calvet collection at the MOM is designated here as lectotype (MOM INV-22514). As there are no morphological differences between *S. oratavensis* and *S. ensifera* (see Figure 6A and B, respectively), the former is here treated as a junior subjective synonym of the latter.

As the peristome conceals much of the orifice, making it difficult to measure its exact size, the length and width of the peristomial aperture was measured instead in all specimens. The bathymetric distribution of *S. oratavensis* ranges from 70–820 m, although the specimens from the deep 'Challenger' Station 75 are not very well preserved and may have been transported downslope. Wisshak *et al.* (2015: 95) have recently recorded living specimens from settlement panels at 150 m (as *S. ensifera*). Apart from the type locality, Pico Island, *S. oratavensis* was also recorded from other Azorean islands (d'Hondt, 1975): Graciosa (76–220 m), Terceira (220 m), São Miguel (130–260 m) and the Formigas Islets south of São Miguel (70–130 m). As synonymies with species from the NE Atlantic continental shelf and the Mediterranean Sea are rejected here, the species is regarded as endemic to the Azores.

Superfamily SCHIZOPORELLOIDEA Jullien, 1882
 Family MICROPORELLIDAE Hincks, 1879
 Genus *Microporella* Hincks, 1877b
Microporella hastigera (Busk, 1884)
 (Figure 7)



Figure 7. *Microporella hastigera* (Busk, 1884): Paralectotype (NHMUK 1887.12.9.548). Scale bar: 5 mm.

Flustramorpha hastigera Busk, 1884: 136, text-fig. 40, pl. 21, figs 7, 7a–c.

Diporula hastigera (Busk): Waters, 1888: 23, pl. 3, figs 28 & 29; Jullien in Jullien & Calvet, 1903: 51, pl. 1, fig. 3, pl. 6, fig. 3; Calvet in Jullien & Calvet, 1903: 129; Calvet, 1907: 407.

Microporella hastigera (Busk): Calvet, 1931: 87; d'Hondt, 1975: 577 (listed); Di Martino *et al.*, 2020: 8, figs 4–5.

Type material

Lectotype (designated by Di Martino *et al.*, 2020): NHMUK 1887.12.9.547, Busk coll., Station 75, volcanic mud, large fragment (1.6 cm in length), figured specimen (Busk, 1884: pl. 21, fig. 7).

Remarks

Microporella hastigera (Busk, 1884) is one of the few erect species in this genus, its lectotype has recently been designated, revised and figured using SEM by Di Martino *et al.* (2020: 8, figs 4 & 5). Owing to its erect growth, large colonies and strong calcification (Figure 7), this species is among the most conspicuous and ubiquitous bryozoans in the Azores, particularly comprising a significant amount of the biogenic sediment around the islands, and numerous specimens exist in the historical collections. A complete list of all available specimens is therefore not provided here, and the material given represents only those samples that have personally been examined.

Previously also assigned to the genus *Diporula* Hincks, 1879, *M. hastigera* has originally been recorded from off western and northern Pico Island from depths between 80 and 820 m. Particularly during the French 'Biaçores' expedition (see d'Hondt, 1975), the species was also reported from around the islands of Flores (105–170 m), Graciosa (190–406 m), São Jorge (245 m), Terceira (90–220 m), São Miguel (61–550 m) and the Formigas Islets south of São Miguel (190–220 m). Curiously, however, *M. hastigera* was not recorded from settlement panels recently brought out in the Faial-Pico Channel in depths down to 500 m for up to two years, although other *Microporella* species were present on the panels (Wisshak *et al.*, 2015). Calvet (1931: 87) reported *M. hastigera* to also occur in the Cape Verde Islands at 52 m depth but, considering the distance between the archipelagos, that population is probably not conspecific.

A fossil species that is closely related to, and probably the direct ancestor of, *M. hastigera* was recently found in lower Pliocene sediments of Santa Maria (Ávila *et al.*, 2015: 68; as *Microporella* sp. 2). The fossil differs from the modern species in a few aspects and will be described in more detail elsewhere.

Superfamily CELLEPOROIDEA Johnston, 1838

Family CELLEPORIDAE Johnston, 1838

Genus *Buskea* Heller, 1967

Buskea ovalis (Busk, 1881) comb. nov.

(Figure 8)

Cellepora ovalis Busk, 1881a: 352; Busk, 1884: 202, pl. 28, fig. 5; pl. 35, fig. 6.

Part *Palmicellaria skenei* Ellis and Solander: Jullien & Calvet, 1903: 154; Calvet, 1907: 431.

Harmerella dichotoma (Hincks): d'Hondt, 1975: 558 (listed).

Type material

Lectotype (here designated): NHMUK 1887.12.9.793, Station 75, figured specimen (Busk, 1884: pl. 28, fig. 5), two colony fragments presumably of the same colony, one large branching fragment (1.3 cm long) and a small branch tip, from sand.

Description

Colony initially uni- to multilaminar encrusting, soon producing an erect colony with irregular conical branch tips that become massive and subcylindrical by means of frontal budding (Figure 8A, B), colony may reach several cm in size, branches up to 4 mm in diameter. Autozooids in younger parts of erect colony elongated oval in outline (L: 636 ± 44 , 593–697, 4; W: 379 ± 24 , 358–414, 4), frontal shield convex, thicker branches often covered by extremely broad and relatively flat polygonal autozooids or kenozooids during late astogeny (Figure 8H, I), zooids separated by fine sutures, that may be disguised by frontal thickening; frontal shield smooth with a single row of conspicuous areolar pores, suborally forming a broad pointed umbo on left or right (Figure 8D, E). Primary orifice suborbicular (Figure 8C), slightly broader than long (L: 134 ± 7 , 125–142, 8; W: 154 ± 14 , 129–171, 8), with a broad ($\sim 2/3$ of proximal orifice width) and very shallow ($\sim 1/6$ of total orifice length) sinus, condyles indistinct, very short and blunt; orifice becoming immersed by a peristome during ontogeny, aperture with a large drop-shaped pseudosinus or labial notch on one side, formed by a raised flap of the proximolateral peristomial margin and a blunt tooth produced by the proximolateral avicularian cystid (Figure 8D–F), pseudosinus occasionally closed in by these projections to form a circular foramen.

Ovicells hyperstomial during early ontogeny (L: 222 ± 23 , 186–282, 16; W: 262 ± 20 , 231–292, 16), later becoming subimmersed due to secondary calcification (Figure 8D, E), produced by the zooid distal to the maternal one; ectooecium smooth, proximomedially perforated by 5–7 large round, oval or drop-shaped pseudopores, proximal margin slightly concave, arched high above the orifice, not closed by the operculum.

Avicularia dimorphic (Figure 8E–G). Suboral adventitious avicularia single, positioned terminally on suboral umbo, directing distolaterally, oblique or even perpendicular to frontal zoecial surface, oval in outline (L: 102 ± 19 , 62–138, 20; W: 77 ± 12 , 51–97, 20); rostrum semielliptical, crossbar complete with or without short blunt columella. Frontally budded avicularia of variable size, occasionally almost as large as autozooid (L: 221 ± 43 , 140–279, 17; W: 127 ± 19 , 85–150, 17), oval in outline, often slightly narrower distally; rostrum slightly raised distally, pointing in various directions, crossbar complete, with or without short stout columella, uncalcified areas semicircular (proximally) and semielliptical (distally).

Ancestrula and early astogenetic encrusting part not observed.

Remarks

Although *Buskea ovalis* (Busk, 1881) is recognized in this combination today (Bock & Gordon, 2021b), to our knowledge the species was never cited again after its discovery by Busk (1881a, 1884), and it has not been formally assigned to the genus *Buskea* before, which we do here. The specimen figured by Busk (1884: pl. 28, fig. 5; pl. 35, fig. 6) is designated as lectotype (NHMUK 1887.12.9.793). The material from the Faial-Pico Channel recorded as *Palmicellaria skenei* Ellis & Solander, 1786 by Calvet (1907) is identical with *Buskea ovalis*. The same applies to the specimens that were collected during the 'Biaçores' cruise, which d'Hondt (1975) recorded as *Harmerella dichotoma* (Hincks, 1862), a species that is today also placed in the genus *Buskea*.

In contrast to the type species of *Buskea*, *B. nitida* Heller, 1867, the branches in *B. ovalis* are not composed of regular zooid series. Instead, frontal budding prevails just proximal to the young branch tips. Its colony growth form is thus rather reminiscent of species in the genus *Turbicellepora* Ryland, 1963, although *B. dichotoma* from the eastern Atlantic and Mediterranean Sea is also reported to produce frontally budded zooids, at least in proximal colony regions (Hayward & Ryland, 1999: 348). It is

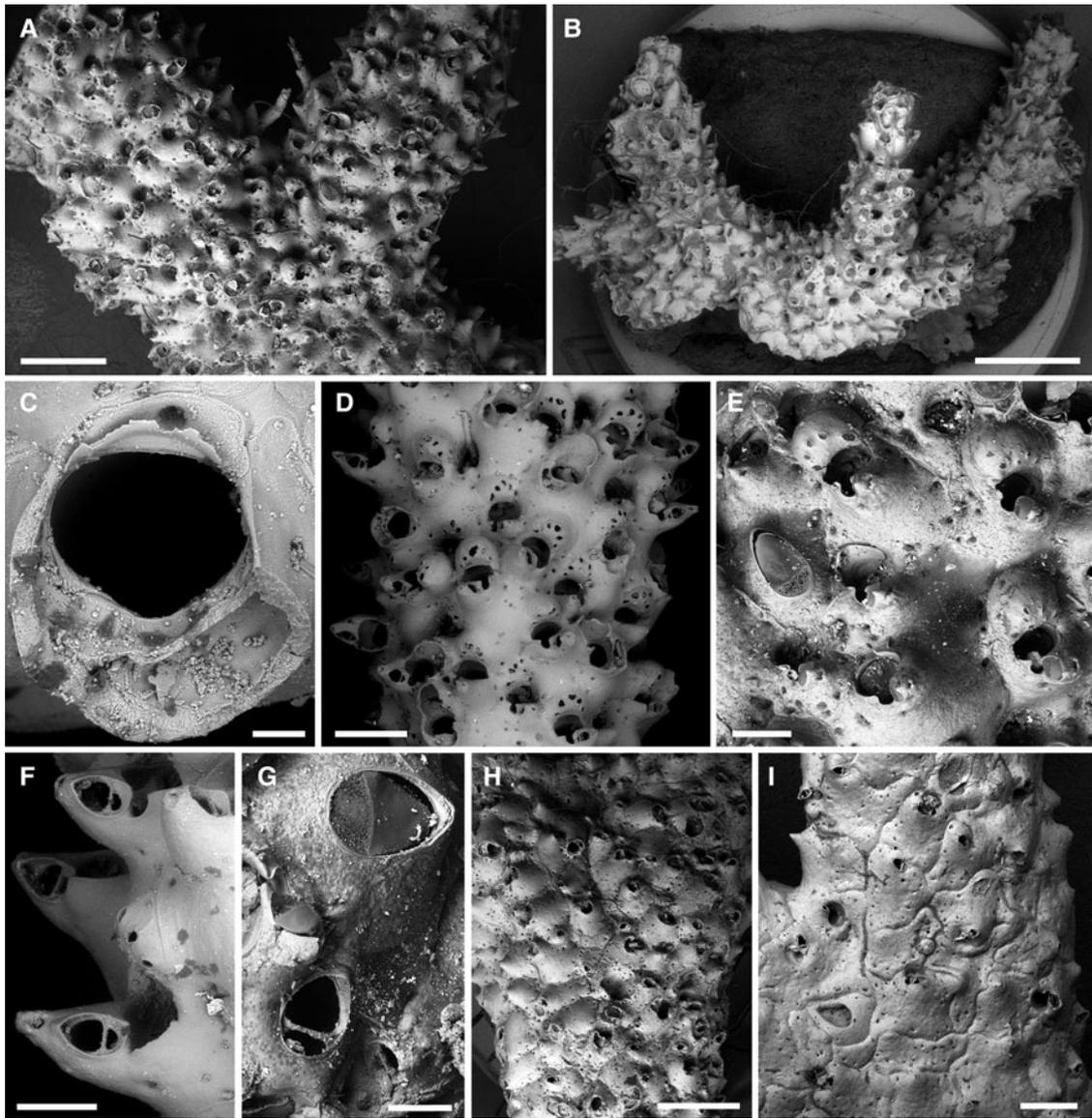


Figure 8. *Buskea ovalis* (Busk, 1881): (A) overview of lectotype (NHMUK 1887.12.9.793); (B) encrusting basal part of colony beginning to form erect branches (MNHN-IB-2008-2498); (C) orifice (MNHN-IB-2008-7449); (D) cylindrical branch with ovicellate zooids (MNHN-IB2008-7449); (E) ovicells and a large frontal avicularium (lectotype, NHMUK 1887.12.9.793); (F) close-up of suboral avicularia (MNHN-IB-2008-7449); (G) close-up of frontal avicularia, note that the crossbar in the lower avicularium is lacking a crossbar (lectotype, NHMUK 1887.12.9.793); (H) part of an older branch (NHMUK 1887.12.9.795); (I) basal part of an old colony with surface formed by kenozooids and frontal avicularia (NHMUK 1899.7.1.3454). Scale bars: A, H, 1 mm; B, 2 mm; C, 50 μ m; D, I, 500 μ m; E, F, 200 μ m; G, 100 μ m.

therefore difficult to morphologically distinguish *Buskea* from *Turbicellepora*, while *Galeopsis* Jullien, 1903, though apparently encrusting, is another genus with a very similar colony morphology (see below).

Zooid length and width in *B. ovalis* were measured in early ontogenetic zooids at branch tips; frontally budded zooids in more proximal colony regions are distinctly broader. As most colonies available were either unbleached or poorly preserved, the crossbars of only a few suboral and frontally budded interzooidal avicularia could be observed. While a columella seems to be absent in some adventitious and interzooidal avicularia, in other avicularia it was present, being small and short in suboral avicularia, and distinctly larger and stout in interzooidal avicularia. More bleached material needs to be screened in order to determine the frequency of columella occurrences in the two avicularium types.

As already noted by Busk (1881a: 352, 1884: 202), *B. ovalis* often uses the basal parts of thecate hydroids for settlement and support of its erect colony part, a habit shared with *Celleporina*

ansata (Busk, 1881a) described below. *Buskea ovalis* is endemic to the Azores, occurring from 57–1135 m depth. While most records were from 50–400 m depth, the specimens recovered from over 823 m (lectotype) and down to 1135 m (Jullien & Calvet, 1903) are likely to be allochthonous. Colonies were reported from around the central Azorean islands of Pico, Faial, São Jorge, Terceira and Graciosa, as well as from around São Miguel, the Formigas islets and off W Flores (cf. d'Hondt, 1975), although material from the latter three localities could not be examined during this study and have to be regarded as uncertain.

Buskea fayalensis (Waters, 1888) comb. nov.
(Figure 9)

Part *Haswellia*(?) *auriculata* Busk var. *fayalensis* Waters, 1888: 31.
Part *Haswellia auriculata* Busk: Jullien & Calvet, 1903: 145, not pl. 17, fig. 3; Calvet, 1907: 446; Calvet, 1931: 77.

Not *Buchneria fayalensis* (Busk): Gautier, 1962: 217, fig. 19; Zabala & Maluquer, 1988: 155, text-fig. 421.

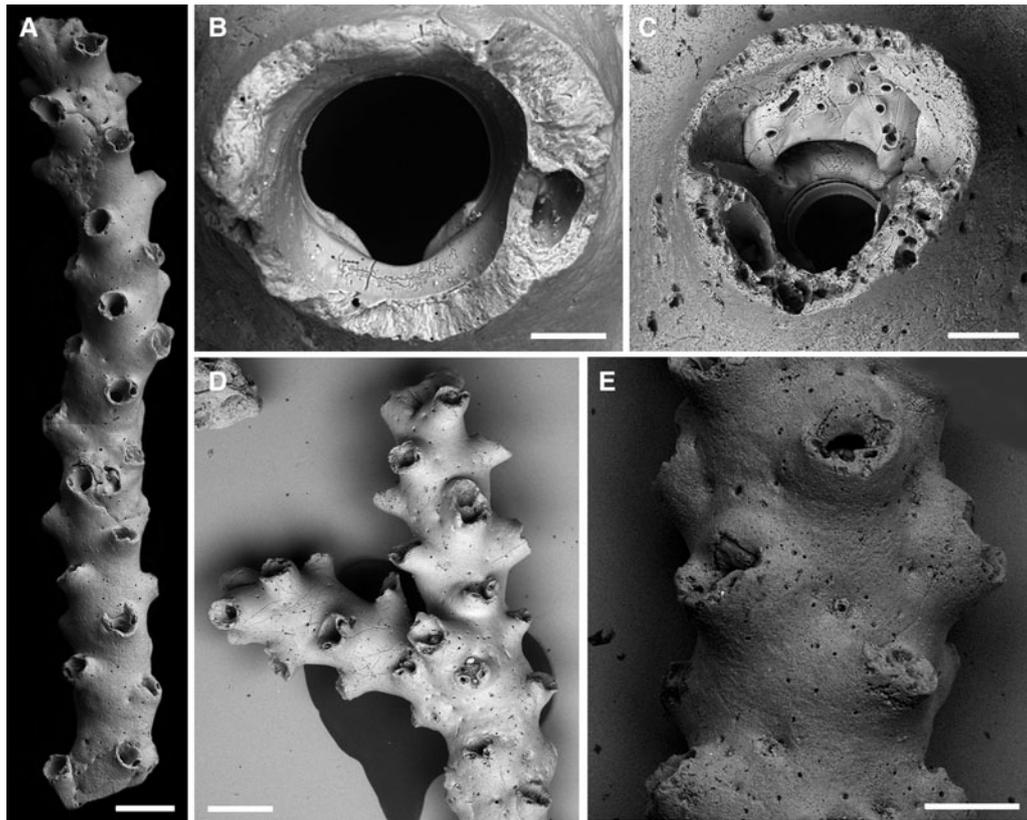


Figure 9. *Buskea fayalensis* (Waters, 1888): (A) branch overview (lectotype, NHMUK 2022.8.5.1); (B) orifice with the base of a single peristomial avicularium (lectotype, NHMUK 2022.8.5.1); (C) ovicell (paralectotype, NHMUK 1934.2.12.4a); (D) branching colony, note that some of the zooids have paired avicularia on the peristome (paralectotype, MM 2768d); (E) older ovicellate branch, note that, while secondary calcification has thickened the branch, the peristomes are still protruding from the surface (paralectotype, MM 2769b). Scale bars: A, D, 500 μ m; B, 50 μ m; C, 100 μ m; E, 300 μ m.

Type material

Lectotype (here designated): NHMUK 2022.8.5.1, Station FP, formerly part NHMUK 1934.2.12.4, of John Murray bequest, one colony fragment.

Paralectotypes: MM 2767, Waters coll., Station FP, sections of two colony fragments in Canada balsam, on slide. MM 2768, Waters coll., Station FP, five colony fragments (here sub-numbered a–e) on slide. MM 2769, Waters coll., Station FP, of the four colony fragments on a slide (here sub-numbered a–d), only specimens b and d are *Buskea fayalensis* while specimens a and c belong to a distinct *Buskea* species. NHMUK 1889.12.12.6, Waters coll., Station FP, four colony fragments in vial (sub-numbered a–d). NHMUK 1934.2.12.4, Station FP, John Murray bequest, three colony fragments in vial (here sub-numbered a–c).

Description

Colony erect, rigid, vinculariiform (i.e. with cylindrical branches, Figure 9A), branching irregular and at an angle between ~ 60 – 90° (Figure 9D), branches between bifurcations fairly long (>1 cm) and slender (~ 700 μ m in diameter, not including the peristomes) and usually rather straight, zooids opening on all sides. Zooids arranged in 4 alternating longitudinal series, ideally back to back but often horizontally and/or vertically displaced (Figure 9A, D, E); zoecia distinctly longer than wide (L: 750 ± 64 , 623–860, 20; W: 442 ± 45 , 365–521, 18), frontal shield smooth, slightly convex, abruptly rising around orifice to form a prominent and thickly calcified peristome, entire peristome directing somewhat distally (Figure 9D); zoecial boundaries invisible, covered by secondary calcification, ~ 10 tiny pores faintly indicating the zoecial outline. Orifice only slightly longer than wide (L:

129 ± 5 , 123–134, 7; W: 138 ± 1 , 137–140, 7), anter transversely elliptical, poster usually with a rounded V-shaped sinus though occasionally wider U-shaped, framed by a pair of narrow but long and sloping condyles that disappear underneath the proximal orifice margin (Figure 9B).

Ovicell hyperstomial during early ontogeny, soon becoming incorporated into the peristome that is larger than in autozooids and which covers the distal part of the oocidium (Figure 9C), later further immersed by secondary calcification (Figure 9E), proximal half of oocidium exposed, showing the smooth ectoocidium that is perforated by numerous pseudopores of varying size and shape, opening suborbicular, highly arched above orifice, not closed by the operculum.

Avicularia adventitious, most often single, occasionally absent or paired on (proximo)lateral peristomial rim (Figure 9C, D), directing distolaterally, crossbar complete, often with a distinct columella.

Ancestrula and early astogenetic encrusting part not observed.

Remarks

The histories of this and several superficially similar species are intricate. Busk (1884: 173) described *Haswellia auriculata* from the Tristan da Cunha Archipelago in the South Atlantic without any reference to specimens from the Azores. When later revising some of the ‘Challenger’ material, Waters (1888) vaguely attributed hitherto undetermined specimens from the Faial-Pico Channel to that species and suggested that this variety be termed *H. auriculata* var. *fayalensis*. In several subsequent works, Calvet (in Jullien & Calvet, 1903; Calvet, 1907, 1931) recorded the species again from the Azores. Although referring to Busk’s species *H. auriculata* and not to Water’s subspecies in the synonymy,

Calvet clarifies in the text that he accepts that the Azorean specimens belong to *H. auriculata* var. *fayalensis* (Jullien & Calvet, 1903: 145). Not so Brown (1952: 216), who considered the Azores material identical to both *H. auriculata* and *Vincularia pentagona* d'Orbigny, 1842 from the Malvinas (Falkland Islands), with the latter being the potential senior synonym of the three species. Considering the enormous distances between each of the three localities, however, the species are certainly all distinct. Whereas *H. auriculata* var. *fayalensis* has been treated as a distinct species since the second half of the 20th century, though temporarily assigned to the genus *Buchneria* Harmer, 1957 by e.g. Gautier (1962) and Zabala & Maluquer (1988), *V. pentagona* and *H. auriculata* are still regarded as synonymous (Gordon, 1984: 116; Bock & Gordon, 2021c).

Both *Buchneria fayalensis* (Waters) and *V. pentagona* are currently placed in the genus *Galeopsis* Jullien, 1903 (Gordon, 1984; Bock & Gordon, 2021d). This assignment is also problematic, however, and needs yet to be clarified, as the type species of *Galeopsis*, *G. rabidus* Jullien, 1903 from the Azores, is not well defined, while the holotype (by monotypy) seems to be lost (Tricart & d'Hondt, 2009). According to Jullien & Calvet (1903: 145), the specimen is a unilaminar encrusting colony from 'Hirondelle' Station 247 that lacks ovicells and grows on a reteporiform bryozoan. Another specimen from the Paris collection (MNHN-IB-2008-3721), doubtfully from the same station and encrusting a coral, does not seem to be the figured colony, and may even belong to a different species (BB, pers. observ.). In any case, the preservation of this colony, as well as of another specimen from an unknown station filed under *G. rabidus* (MNHN-IB-2008-843), does not allow the species to be precisely identified and characterized. Additional specimens present at the MOM could, unfortunately, not be studied using SEM as a new directive, which became effective during the course of this work, does not permit to take on loan specimens from the Calvet collection any more.

The reason for the affiliation of the erect-growing *B. fayalensis* to the genus *Galeopsis* with encrusting colonies was the discovery by Gordon (1984: 116, pl. 46, fig. C) of the transitional colony stage in a species from New Zealand he referred to *V. pentagona*. The zooids in both colony stages are similar to the erect *B. fayalensis* and the encrusting *G. rabidus* from the Azores, changing considerably in morphology from the encrusting to the erect part, and Gordon thus placed *V. pentagona*, *B. fayalensis* as well as another southern hemisphere species in *Galeopsis*. The problem with this decision is, however, that the southern hemisphere species (see also Moyano, 1985) are characterized by ovicells with an incompletely calcified ectooecium that centrally exposes the endooecium (i.e. producing a tabula as in *Celleporina* Gray, 1848 or *Buffonellaria* Canu & Bassler, 1927). In contrast, both *Galeopsis fayalensis* (Figure 9C) and presumably also *G. rabidus* (as identified by Calvet, 1931: 78) have an entirely calcified yet pseudoporous ectooecium as in *Buskea* (see above) and *Turbicellepora* Ryland, 1963. The southern hemisphere taxa should therefore not be congeneric with the Azorean species.

With its smittinid-type oecium, the morphology of the orifice and suboral avicularium as well as its erect colony form and structure, *G. fayalensis* in fact conforms to the characters of the North Atlantic genus *Buskea* Heller, 1867. While the suboral pseudosinus or spiramen is lacking in the erect colony part, in contrast to the hitherto described *Buskea* species, a thick prominent peristome encircles the entire orifice instead, incorporating the suboral avicularium. This difference, however, may be regarded as only of minor systematic importance, and the sinus may be lacking only as a result of the avicularia being placed more distally on the peristome than in other *Buskea* species. Although the morphology of zooids in the encrusting parts of *Buskea* species is not

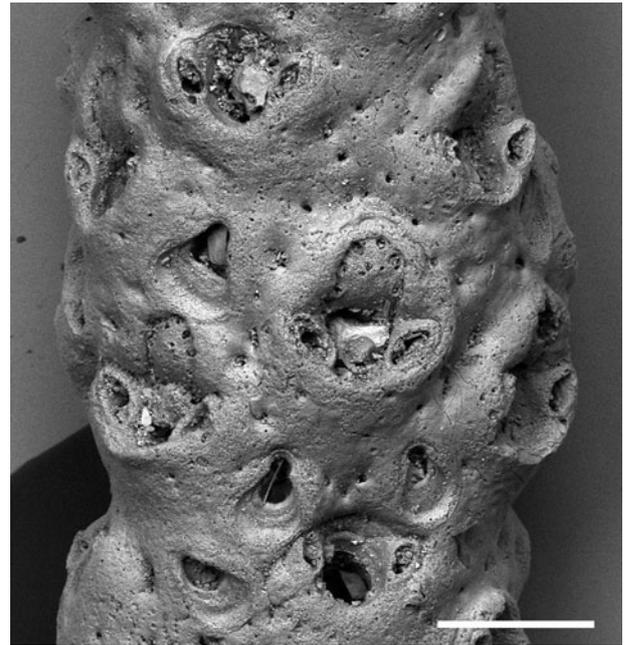


Figure 10. *Buskea* sp.: An older branch fragment with ovicellate zooids, paired peristomial avicularia, and frontal spatulate avicularia (MM 2769a). Scale bar: 300 μ m.

known, there are no apparent character differences that justify the exclusion of the erect *G. fayalensis* from *Buskea*, and we here assign the species to that genus. In order to come to a conclusion concerning the synonymy of *Buskea fayalensis* and *G. rabidus* on the one hand, and the characterization of the genus *Galeopsis* on the other, new material showing a transition from the encrusting to the erect colony part needs to be collected from the Azores, a neotype with an ovicell should be selected for *G. rabidus*, and the morphology of encrusting zooids in other *Buskea* species needs to be determined.

When introducing the species, Waters (1888) considered *Buskea fayalensis* to also occur off Capri (Mediterranean Sea). Potential specimens from Capri in the Waters collection have thus to be regarded as syntypes. Based on (1) the geographic distance between the Azores and the Mediterranean Sea, (2) the fact that the species grows in depths where rafting of adult colonies is unlikely, and (3) the figures provided by Zabala & Maluquer (1988) and Gautier (1962), however, we regard the Mediterranean population as a distinct species.

Even in the Azores several other *Buskea* species are present: besides *B. ovalis* and *B. fayalensis*, d'Hondt (1975) recorded *Buskea billardi* (Calvet, 1906), originally described from NW Africa, and the Mediterranean/NE Atlantic *Buskea dichotoma* (Hincks, 1862) was reported by Jullien & Calvet (1903) and Calvet (1907, 1931). Several additional morphotypes, including encrusting colonies with smittinid-type ovicells, were observed among the historical and newly collected material during this study. In fact, in one sample among Waters' syntypes (MM 2769) two of the four colony fragments (specimens MM 2769a, c) belong to a distinct and as yet undescribed species, *Buskea* sp. (Figure 10): the branches are composed of up to six alternating zooidal series while the zooids are smaller, frontal spatulate avicularia occur, the peristomial avicularia are usually paired, the oecium differently exposed, and the orificial sinus is distinctly wider. It may be that the image of, and remarks on, the specimens Jullien & Calvet (1903: 145, pl. 17, fig. 3) reported may also represent this species, while specimen MOM INV-22602 (identified as *Haswellia auriculata*) belongs to *B. fayalensis*.

In the absence of images of the species in Waters (1888), we here select the most well-preserved specimen from the syntype series (NHMUK 2022.8.5.1) as lectotype of *B. fayalensis*.

Although the specimen is from the Robert Murray bequest (NHMUK1934.2.12.4), which came to the museum later than Waters' bryozoan collections, Waters (1888: 1) stated that he had seen Murray's specimens in Edinburgh. The material thus has to be considered as syntypic.

Although Waters described the operculum, all of the Azorean colonies that remain in the collections today are dead, often physically damaged and bioeroded, with no organic tissue preserved. Branching occurs seldom and often at an angle of $\sim 90^\circ$, which may suggest that the new branch budded from a fragment that was lying on the seafloor rather than representing a natural bifurcation of an undamaged colony. Zooecia with undamaged frontal shields often exhibit a second or more orifice rims, indicating the presence of one or more intramural buds, the formation of which are likely to have been induced following predation of the zooids (cf. Berning, 2008). Owing to the damaged peristomes, none of the terminal avicularia are entirely preserved; measurements could therefore not be taken. Also, the larger part of the ovicells is covered by the peristome, obscuring their dimensions.

Buskea fayalensis is regarded as endemic to the Azores and was recorded from depths between 90–1260 m in the Faial-Pico Channel.

Genus *Celleporina* Gray, 1848
Celleporina ansata (Busk, 1881a) comb. nov.
 (Figure 11)

Part *Cellepora ansata* Busk, 1881a: 356.

Cellepora ansata Busk, 1881b: pl. 27, fig. 1.

Part *Cellepora ansata* Busk: Busk, 1884: 204, pl. 30, fig. 4; pl. 36, fig. 17.

Part *Schizoporella costazii* (Audouin): Jullien & Calvet, 1903: 84, 137.

Lekythopora laciniosa Calvet, 1906: 166; Calvet, 1907: 445, pl. 29, figs 13 & 14; Souto *et al.*, 2014: fig. 3.

Part *Costazzia costazii* [sic] (Audouin): Calvet, 1931: 115.

Osthimosia ansata Busk: Pouyet, 1973: 46 (listed).

Celleporina laciniosa Calvet: Wisshak *et al.*, 2015: 94 (listed).

Celleporina cf. *laciniosa* Calvet: Wisshak *et al.*, 2015: 94 (listed).

Type material

Lectotype of *Cellepora ansata* (here designated): NHMUK 1887.12.9.806b, Station 75, figured specimen (Busk, 1884: pl. 30, fig. 4), the central one of three colonies on thecate hydroid stem, from sand.

Lectotype of *Lekythopora laciniosa* (here designated): MNHN-IB-2008-55, Calvet coll., *Talisman*, 13/8/1883, Station 125, Faial-Pico Channel (no exact position provided), 80–115 m, one spindle-shaped colony on the stem of a thecate hydroid, on slide.

Description

Colony initially encrusting unilaminar and biserial (on hydroid stems) to multiseriate, later developing either spindle-shaped or massive celleporiform to branching colonies owing to frontal budding (Figure 11A, B). Autozooids in encrusting parts of colony flask-shaped, distinctly longer than wide (L: 608 ± 70 , 497–717, 20; W: 292 ± 51 , 221–383, 20), with a rhomb-like proximal part and a narrower distal peristome with parallel lateral margins that comprises almost half of the total zooid length; peristome at an acute angle to frontal surface and pointing distally; in frontally budded zooids the proximal part is much reduced in length and the peristome is almost perpendicular to frontal surface (Figure 11C); zooids separated by narrow grooves, lateral walls with several basal pore chambers per neighbouring zooid,

communication pores uniporous. Frontal shield slightly convex, surface faintly to distinctly nodular, initially with a single row of 4–8 small areolar pores that become more distinct during ontogeny. Peristome well developed, frontally compressed, aperture therefore distinctly wider than long, distal and proximal apertural margins usually with a variably developed bow framed by a pair of terminally positioned avicularia (Figure 11E); distal part of the peristome formed by the frontal shield of the distal autozooid or kenozooidal oecium. Primary orifice suborbicular (Figure 11D), almost as broad as long (L: 120 ± 19 , 105–164, 12; W: 116 ± 16 , 99–143, 12), with a broad ($\sim 2/3$ of total orifice width) and deep (almost $1/4$ of total orifice length) sinus, condyles indistinct.

Ovicells prominent or subimmersed depending on position and age of the neighbouring zooids, produced by a much reduced kenozooid at the base of the peristome, oecium hemispherical, almost twice as wide as long (L: 116 ± 16 , 91–153, 14; W: 215 ± 26 , 154–255, 14), tabula relatively flat and smooth with a single series of marginal pores and some scattered central ones when larger, proximal margin raised and occasionally forming a mucro (Figure 11C, E), ovicell opening arched high above the orifice, not closed by the operculum. Ovicells may already be produced by zooids in the encrusting part of the colony, and also during very early astogeny (from 4th generation zooids onwards).

Avicularia polymorphic (Figure 11C, E), adventitious avicularia paired, small (L: 60 ± 15 , 35–87, 20; W: 46 ± 11 , 29–61, 20), positioned terminally on proximolateral peristome, directing distolaterally or laterally, oblique to frontal zoecial surface, oval in outline; rostrum semielliptical, distally denticulate, crossbar complete, without columella, proximal uncalcified area semicircular, distal area semielliptical. Frontally budded avicularia of variable size and shape (L: 162 ± 47 , 88–269, 20; W: 70 ± 19 , 41–110, 20), either with parallel lateral margins or slightly spatulate; mandible relatively weakly sclerotized and somewhat shrivelled in dried specimens, rostrum distally raised and denticulate, pointing in various directions; crossbar complete, without columella but occasionally thickened centrally on its proximal side, an immersed calcified shelf comprising over half of palate length, distal uncalcified area suborbicular to elliptical, proximal area elliptical to reniform.

Ancestrula oval (L: 266 ± 18 , 252–286, 3; W: 187 ± 39 , 151–229, 3), convex, surface densely pitted (Figure 11F); opesia reduced to a distal D-shaped area entirely covered by an operculum, widest at about mid-distance (L: 67 ± 2 , 64–69, 4; W: 96 ± 7 , 90–106, 4), proximal margin straight, 7 spines surrounding the aperture with a distinct gap between the distalmost pair where the first generation autozooid is formed.

Remarks

Unfortunately, the only three-dimensionally preserved syntypes of *Cellepora ansata* Busk, 1881, which all encrust stems of thecate hydroids, are covered by glue, concealing many of the species' characters. The least affected colony has here been designated as lectotype.

The drawing Busk provided in the 'Challenger' report in 1884 (pl. 30, fig. 4), after having introduced *C. ansata* in 1881, does not bear much resemblance with the actual specimens. Unsurprisingly, Calvet (1906) newly described the same species again ~ 20 years later, with his *Lekythopora laciniosa* being easily recognizable from his images (Calvet, 1907: pl. 29, figs 13 & 14). In his next work on Azorean bryozoans, Calvet (1931: 115) then synonymized *L. laciniosa* with the ubiquitous *Costazzia costazii* [sic] (Audouin, 1826) (now regarded as *Celleporina costazii*), specimens of which he also reported from the Mediterranean Sea and Gorrige Bank in the eastern Atlantic besides the Azores. *Celleporina costazii* is a species complex, however, and the Azorean specimens are

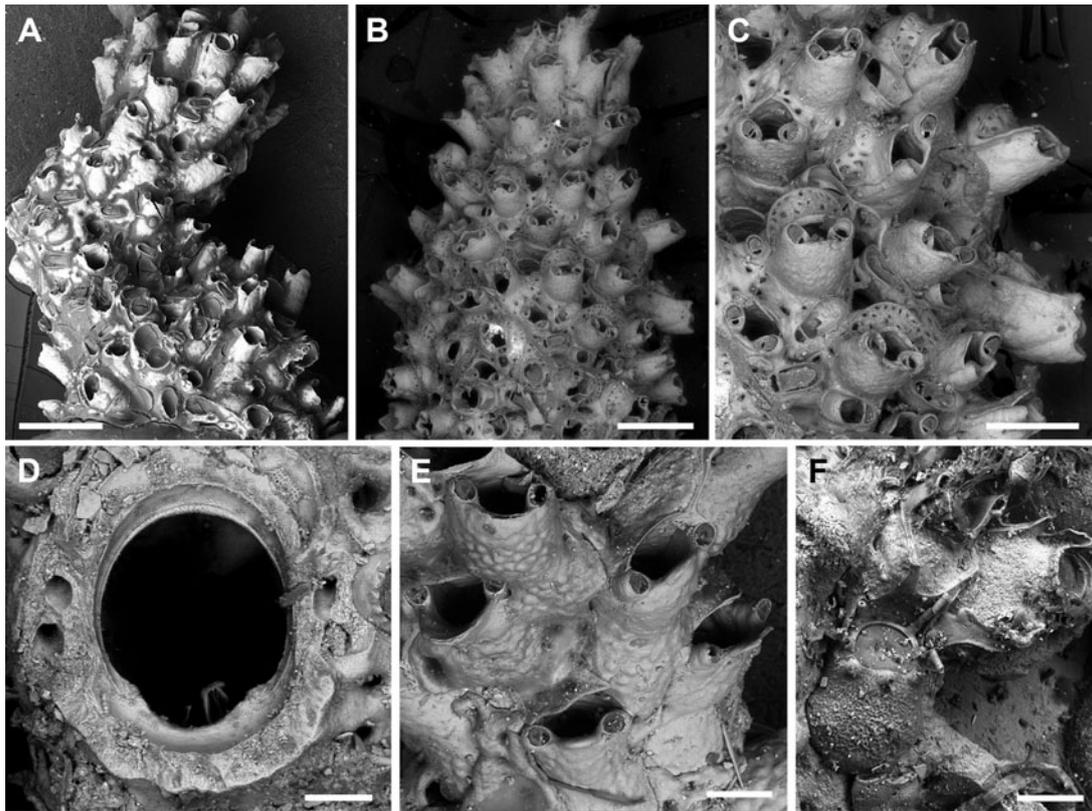


Figure 11. *Celleporina ansata* (Busk, 1884): (A) overview of lectotype (NHMUK 1887.12.9.806b); (B) overview of lectotype of *Lekythopora laciniosa* Calvet, 1906 (MNHN IB-2008-55); (C) ovicellate zooids and interzooidal avicularia (MNHN-IB-2008-55); (D) orifice (MNHN-IB-2008-55); (E) close-up of autozooidal apertures (parallectotype, NHMUK 1887.12.9.806c); (F) ancestrula (NHMUK 1887.12.9.795). Scale bars: A, B, 500 μ m; C, 300 μ m; D, 50 μ m; E, F, 100 μ m.

specifically distinct from the European ones assigned to that species. As no morphological differences were observed at zooidal level between the types of *C. ansata* and *L. laciniosa* (for which a lectotype has here been designated), we regard the latter as junior subjective synonym of the former. Pouyet (1973: 46) later transferred *C. ansata* to the genus *Osthimosia* Jullien, 1888, under which the species was known until today, but this decision is not upheld here as the ovicell is clearly that of a *Celleporina*, and the species is accordingly transferred to that genus.

While one specimen among material recorded as *Schizoporella costazii* (Audouin, 1826) from the Fayal-Pico Channel by Jullien & Calvet (1903: 84, 137) proved to be *Celleporina ansata*, it is also likely that some or all of the specimens recorded as *Costazia costazii* by d'Hondt (1975: 558), are conspecific with Busk's species. Among Busk's syntype specimens there is one misidentified colony (NHMUK 1899.7.1.3231, Station 75), however, demonstrating that there is at least another *Celleporina* species present in the central Azores. The zooids in this pisiform colony have, among other differences, a single lateral avicularium on the peristome, and the vicarious avicularia are distinctly spatulate.

Wisshak *et al.* (2015: 94) recently reported *C. ansata* as *Celleporina laciniosa* from 60 and 150 m depth, and as *C. cf. laciniosa* from 150 m depth off Faial. The latter taxon, which formed biserial, vine-like colonies on thecate hydroid stems, was initially thought to differ slightly from the former, which produced massive branching colonies on hard substrata at 60 m after two years of exposure, as well as broad, encrusting unilaminar and multiserial colonies on the settlement panels at 150 m. Close inspection of the zooids, however, and comparison with the types of *C. ansata*, suggests that all specimens belong to Busk's species. The different colony growth forms may thus be a response to growth on different substrata and in different environments (i.e. nutrient regimes).

The relatively short exposure times of up to two years was likely not enough for larger colonies to form at greater depths.

Measurements of zooid length and width were taken on zooids encrusting the flat substrate of settlement panels (Wisshak *et al.*, 2015). Frontally budded zooids in celleporiform parts of the colony are significantly shorter and usually partly covered by neighbouring zooids, making it difficult to measure them. Most characters are highly variable in size, particularly the length of the frontal avicularia varies threefold, and the largest adventitious peristomial avicularium is more than twice the size of the smallest one recorded. *Cellepora ansata* has so far only been recorded in the central Azores from 60–820 m depth.

Family PHIDOLOPORIDAE Gabb & Horn, 1862

Genus *Reteporella* Busk, 1884

Reteporella atlantica (Busk, 1884) comb. nov.

(Figure 12)

Retepora atlantica Busk, 1884: 116, text-fig. 15, pl. 28, fig. 1, 1a, 1b; Waters, 1888: 20; Calvet, 1907: 452.

Retepora marsupiata Smitt: Calvet, 1931: 102.

?part *Sertella marsupiata* – d'Hondt 1975a: 580.

Reteporella sp.: Wisshak *et al.*, 2015: 95 (listed).

Type material

Lectotype (here designated): NHMUK 2016.6.9.5, Station 75, one colony fragment, figured specimen (Busk, 1884: pl. 28, fig. 1, erroneously given as *Retepora cellulosa* in the caption), formerly part of NHMUK 1899.7.1.2904.

Description

Colony erect, rigid, fenestrate (Figure 12A), irregularly cup-shaped with a widely lobed and infolded rim, >7 cm in diameter

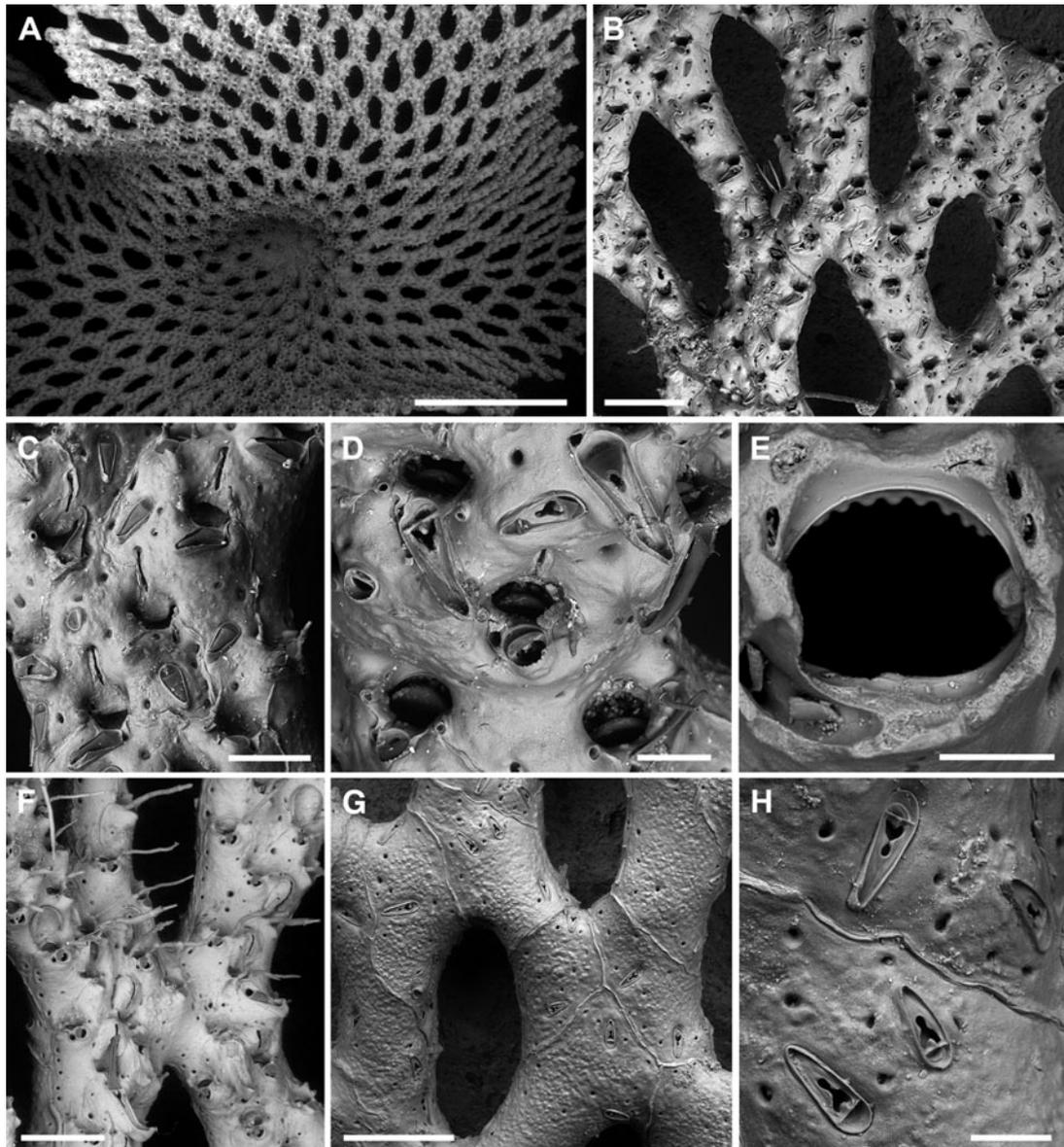


Figure 12. *Reteporella atlantica* (Busk, 1884): (A) overview of a colony (MNHN-IB-2008-4296); (B) overview of lectotype (NHMUK 1899.7.1.2904); (C) ovicellate zooids during relatively late ontogeny as evidenced by the presence of frontal avicularia (lectotype, NHMUK 1899.7.1.2904); (D) close-up of the different types of suboral and frontal avicularia (lectotype, NHMUK 1899.7.1.2904); (E) orifice (MNHN-IB-2008-4296); (F) spines in lateral view and a giant suboral avicularium at lower centre; (G) abfrontal side of lectotype (NHMUK 1899.7.1.2904); (H) close-up of abfrontal avicularia (lectotype, NHMUK 1899.7.1.2904). Scale bars: A, 5 mm; B, 500 μ m; C, F, 200 μ m; D, H, 100 μ m; E, μ m; G, 1 mm.

and height, of whitish/pearly colour at greater depth and bright orange in shallower water; outer abfrontal surface covered by kenozooids, inwards-facing surface bearing autozooids, trabeculae with 2–4 or occasionally 5 alternating longitudinal autozoid series (W: 460 ± 110 , 297–788, 75) (Figure 12B), fenestrulae variably shaped but most often elongate oval (L: 1076 ± 177 , 750–1540, 55; W: 440 ± 101 , 203–667, 55). Autozooids initially elongate rectangular to polygonal (distance between midpoints of orifices of obliquely adjacent zooids: 265 ± 33 , 192–321, 47), separated by narrow grooves but zooid boundaries soon obliterated owing to secondary calcification, zoecial surface relatively smooth in some parts but mostly nodular (Figure 12D), early ontogenetic zooids with a single row of small lateral areolar pores that become larger and more scattered on the surface during ontogeny; interzooidal communication via uniporous septula.

Orifice rounded D-shaped, broader than long (L: 72 ± 8 , 63–85, 10; W: 97 ± 6 , 89–107, 10), distal margin denticulate, proximal

margin straight to shallowly concave (Figure 12E); condyles short but broad, blunt, situated at about mid-distance of orifice, lateral orifice margin in early ontogenetic zooids equipped with 4 long spines (Figure 12F), with a distinct gap between the distalmost pair while only the proximal pair persists in ontogenetically older auto- and ovicellate zooids. Peristome formed by two proximalateral flaps in early ontogeny, the larger one incorporating the suboral avicularium, the proximal end of which merging with the tip of the opposing flap to form a short suture-zone and a round or drop-shaped pseudosinus (L: 48 ± 8 , 30–71, 40), the central avicularium cystid occasionally producing one or more short peristomial denticles distally.

Ovicells recumbent on frontal shield of the distal zooid, becoming (sub)immersed and almost completely covered by secondary calcification during ontogeny (Figure 12C), oecium globular, slightly longer than wide (L: 197 ± 20 , 163–231, 15; W: 169 ± 8 , 155–182, 15), not closed by the operculum; ectooecium entirely calcified except for a narrow central fissure

Table 1. Cheilostomatid and cyclostomatid bryozoan species collected on the 'Challenger' cruise from the greater Azores region, and cited from the archipelago thereafter. Species investigated here in bold

Current taxon name	Original taxon name	Station	References
<i>Adeonellopsis</i> cf. <i>distoma</i> (Busk, 1859)	<i>Adeonella distoma</i> (Busk, 1859)	FP, 75	Busk (1884), Waters (1888), Jullien & Calvet (1903), Calvet (1907, 1931), d'Hondt (1975)
<i>Buskea fayalensis</i> (Waters, 1888)	<i>Haswellia auriculata</i> var. <i>fayalensis</i> Waters, 1888	FP	Waters (1888), Jullien & Calvet (1903), Calvet (1907, 1931)
<i>Buskea ovalis</i> (Busk, 1881a)	<i>Cellepora ovalis</i> Busk, 1881a	75	Busk (1881a, 1884), Jullien & Calvet (1903), Calvet (1907), d'Hondt (1975)
<i>Carbacea pedunculata</i> Busk, 1884	<i>Carbacea pedunculata</i> Busk, 1884	75, 76	Busk (1884)
<i>Celleporina ansata</i> (Busk, 1884)	<i>Cellepora ansata</i> Busk, 1884	75	Busk (1881a, 1881b, 1884), Jullien & Calvet (1903), Calvet (1907, 1931), Wisshak et al. (2015)
<i>Chaperiopsis</i> n.sp.	<i>Membranipora galeata</i> var. <i>multifida</i> Busk, 1884	75	Busk (1884)
<i>Columnella gracilis</i> (Busk, 1884)	<i>Farciminnaria gracilis</i> Busk, 1884	70	Busk (1884)
<i>Cribrilaria bathyalis</i> Harmelin and Aristegui, 1988	<i>Cribrilina radiata</i> (Moll, 1803)	75	Busk (1884), Jullien & Calvet (1903)
? <i>Defrancia striatula</i> Busk, 1859	<i>Defrancia striatula</i> Busk, 1859	FP	Waters (1888)
<i>Hemicyclopora canalifera</i> (Busk, 1884)	<i>Mucronella (Phylactella) canalifera</i> Busk, 1884	FP, 75	Busk (1884), Waters (1888), Jullien & Calvet (1903), Calvet (1907, 1931), d'Hondt (1975)
<i>Hincksina alicae</i> (Jullien, 1903)	<i>Membranipora albida</i> Hincks, 1880	75	Busk (1884), Jullien & Calvet (1903), Calvet (1907), Berning et al. (2021)
<i>Hippothoa</i> n.sp.	<i>Hippothoa divaricata</i> Lamouroux, 1821	FP, 75	Busk (1884), Waters (1888), Jullien & Calvet (1903)
? <i>Idmonea bifrons</i> Waters, 1884	<i>Idmonea bifrons</i> Waters, 1884	FP	Waters (1888)
<i>Micropora</i> n.sp.	<i>Micropora coriacea</i> (Esper, 1791)	75	Busk (1884), Jullien & Calvet (1903), Calvet (1907, 1931)
<i>Microporella hastigera</i> (Busk, 1884)	<i>Flustramorphia hastigera</i> Busk, 1884	FP, 75	Busk (1884), Waters (1888), Jullien & Calvet (1903), Calvet (1907, 1931), d'Hondt (1975), Di Martino et al. (2020)
<i>Notoplites bilobus</i> (Busk, 1884)	<i>Cellularia biloba</i> Busk, 1884	76	Busk (1884)
<i>Notoplites clausus</i> (Busk, 1884)	<i>Menipea clausa</i> Busk, 1884	70	Busk (1884), Waters (1888), d'Hondt (1975), Souto et al. (2011)
<i>Phidolopora</i> n.sp.	<i>Retepora imperati</i> Busk, 1884	75	Busk (1884)
<i>Raxifabia minuta</i> (Busk, 1884)	<i>Bifaxaria minuta</i> Busk, 1884	70	Busk (1884)
<i>Reteporella atlantica</i> (Busk, 1884)	<i>Retepora atlantica</i> Busk, 1884	FP, 75	Busk (1884), Waters (1888), Calvet (1931), Wisshak et al. (2015), Baptista et al. (2022)
<i>Smittoidea oratavensis</i> (Busk, 1884)	<i>Smittia oratavensis</i> Busk, 1884	75	Busk (1884), Jullien & Calvet (1903), Calvet (1907, 1931), d'Hondt (1975), Wisshak et al. (2015)

FP, unnamed 'Challenger' station in the Faial-Pico Channel.

extending for more than half its length and staying exposed throughout ontogeny (L: 114 ± 14 , 91–143, 28), a short proximal labellum with a straight edge overhanging the orifice.

Avicularia adventitious, polymorphic (Figure 12D, F), positioned suborally, frontally and abfrontally. Three morphotypes of single suboral avicularia present, all pointing proximolaterally and with the frontal plane obliquely positioned relative to colony surface; suboral avicularium in most zooids small (L: 58 ± 5 , 47–64, 21; W: 57 ± 5 , 42–63, 21) and round to oval with a semicircular rostrum, distal margin toothed and raised, crossbar complete with a very short, broad and blunt columella, palate a narrow immersed shelf, uncalcified area distal to crossbar D-shaped, proximal uncalcified area semicircular; semicircular mandible with a tiny round lucida. Other zooids produce a triangular suboral avicularium of intermediate size (L: 157 ± 20 , 126–210, 21; W: 59 ± 5 , 50–67, 21), rostrum very elongate, distally distinctly hooked, crossbar complete with a long straight columella, palate occupied by an immersed calcified shelf apart from a proximal triangular-trifoliate opesia, uncalcified area proximal to crossbar

oval to semicircular; mandible very weakly sclerotized and with a round lucida at its proximal end. In yet a few other zooids the suboral avicularium is gigantic (L: 320 ± 19 , 294–348, 9; W: 91 ± 7 , 81–101, 9) while being similar in general morphology to the smaller triangular one; in most cases positioned distal to an ovicell with the cystid covering the entire frontal shield of the zooid, rostrum very elongate triangular, distally conspicuously hooked and distinctly projecting beyond the trabecular surface, mandible also very weakly sclerotized and with a small proximally placed lucida.

Another two types of adventitious avicularia, which are morphologically similar to the oval as well as the triangular suboral avicularia of intermediate size yet being smaller on average, may additionally be budded anywhere on the surface of the frontal autozooids during various ontogenetic stages (Figure 12C, D, H). The small round to oval avicularia may be obliquely positioned relative to the plane of the zooids (L: 44 ± 7 , 36–54, 8; W: 42 ± 5 , 36–49, 8). The larger elongate-triangular avicularia are parallel to the zooidal surface and very variable in size (L:

140 ± 35, 93–230, 30; W: 51 ± 9, 39–77, 30), the rostrum is only slightly hooked distally and the uncalcified area distal to the cross-bar is more distinctly trifoliate than in the suboral avicularium; in shorter avicularia the lateral margins of the rostrum are often not straight but slightly incurved.

On the abfrontal surface these two types are present as well: while the small round to oval avicularium is of similar size than the frontal one (L: 44 ± 4, 39–47, 3; W: 39 ± 3, 36–42, 3), the triangular one is about the same size as the intermediate suboral one (L: 152 ± 39, 100–232, 26; W: 50 ± 9, 38–73, 26). Mandibles in all of the triangular avicularia very weakly sclerotized.

Abfrontal kenozooids of variable size and shape, irregularly positioned, separated by slightly raised and straight or undulating vibices, surface granular with several small scattered pores (Figure 12G).

Ancestrula and early astogeny not observed in the available material.

Remarks

With its large, erect and reticulate colonies, *Reteporella atlantica* is one of the most conspicuous and ubiquitous bryozoans in the Azores, and has been recorded several times after its discovery, though occasionally under the name *Sertella marsupiata* (Smitt, 1873), with which *R. atlantica* has once been synonymized. Smitt's species from Florida has recently been redescribed as *Reteporellina marsupiata* by Winston (2005: 115), however, and is clearly distinct. A comparison with other species of the genus is as yet difficult as most historical taxa have never been revised and figured using SEM.

Characteristic of *R. atlantica* and several other morphologically related species is the great variability in size and morphology of suborally and frontally budded adventitious avicularia. Most common is a small elliptical avicularium, the same type of which is also occurring on the frontal and abfrontal surfaces, though somewhat smaller in dimensions. Particularly, but not exclusively, in ovicellate regions of the colony, an elongated triangular suboral avicularium of variable size replaces the smaller elliptical one. This type is again budded also on both the frontal and abfrontal surfaces during ontogeny, with the frontally budded avicularium being slightly smaller in size than the suboral and abfrontal ones. In a few zooids in ovicellate parts of the colony, a gigantic, distally conspicuously hooked avicularium may be produced suborally (Figure 12F). In this type, the avicularian cystid covers the autozoid's entire frontal surface.

A similarly large avicularium has been reported to occur in *Reteporella grimaldii* Jullien, 1903 from the eastern Atlantic (Reverter-Gil & Fernández-Pulpeiro, 1999: fig. 5D, E), as well as in species from the Mediterranean Sea reported under this name (Hayward & KcKinney, 2002: fig. 42D, and references therein), which are, however, very likely specifically distinct from the nominal species (see Baptista *et al.*, 2022). Several characters, such as the absence of frontal avicularia with pointed rostra in the *R. grimaldii* species complex, testify for the distinctness of these taxa and *R. atlantica*, however.

A curious fact concerning the mandibles in all of the suboral, frontal and abfrontal triangular avicularia in *R. atlantica* was already noted by Busk (1884: 117). Despite the often enormous size of the rostra, the mandibles are very weakly sclerotized and the occlusor muscles attach at their extreme proximal ends. This is in contrast to other *Reteporella* species in which strong muscles attach to the centre of the mandible, forming a distinct foramen for insertion. Thus, despite the large rostrum and avicularian cystid size, the mandibles in the Azorean species do not seem to be able to act as a forceful anti-predator defence. As with so many other avicularium types (e.g. the small, oval suboral ones), their function, as well as the reasons for the species to

invest so much energy into such large structures, remain unknown to date.

Reteporella atlantica was originally reported from off northern Pico at ~820 m, and particularly from between the islands of Faial and Pico at depths of ~60–130 m (Waters, 1888). D'Hondt (1975) later recorded the species from all three island groups. Preliminary results of a molecular genetic study on Azorean *Reteporella* suggests that the species is indeed widespread in the archipelago (Baptista *et al.*, 2022). Without an analysis of the historical material, however, it is impossible to judge whether all or only part of the specimens belong to *R. atlantica* as several closely related species co-occur in each group of islands. Accordingly, we here regard as *R. atlantica* only those specimens from around the type locality, pending further studies.

Owing to the geographic distance to the Azores, it is highly unlikely that specimens reported as *Retepora atlantica* from Madeira (Waters, 1899: 16), and as *Sertella atlantica* from Cape Verde (Cook, 1968: 200), the Canary Islands (Cook, 1968: 200; Aristegui Ruiz, 1984: 204), northern Iberia (d'Hondt, 1977: 61) and the Strait of Gibraltar (Harmelin & d'Hondt, 1992: 30), are indeed conspecific with the Azorean species.

Discussion

Of the 21 species recorded from the greater Azores region during the HMS 'Challenger' cruise (Table 1), which represent ~10% of the bryozoan species hitherto described from the archipelago, 12 are here considered to have been validly introduced as new taxa by Busk (1881a, 1884) and Waters (1888), and are accordingly revised or reported above. The remaining nine species comprise taxa that were recorded under the names of previously established taxa from elsewhere, or were newly described based on a type from a distinct geographic locality but considered to also occur in the Azores (Table 1). As such, *Membranipora galeata* var. *multifida* Busk, 1884 (nowadays regarded as *Chaperiopsis multifida*) was introduced for a specimen from the Cape of Good Hope (Busk, 1884: 64). The figured specimen (and therefore the potential lectotype) of *Retepora imperati* Busk, 1884, which is placed in the genus *Schizoretopora* Gregory, 1893 today, is from Cape Verde (Madurell *et al.*, 2019), while the Azorean specimens of the syn-type series belong to the genus *Phidolopora* Gabb & Horn, 1862 (BB, pers. observ.). Comparison between colonies from the respective type localities and material from the Azores suggests that the non-Azorean populations are specifically distinct. The same applies to the Azorean taxa assigned to previously established species from the European continental shelf, such as *Micropora coriacea* (Esper, 1791) and *Hippothoa divaricata* Lamouroux, 1821 (BB, pers. observ.). The Azorean representatives remain to be newly described and are accordingly given as 'n.sp.' in Table 1.

One result of this revision, adding to other previous taxonomic works on the archipelago's bryozoan fauna (e.g. Berning, 2013; Berning *et al.*, 2019, 2021; Harmelin *et al.*, 2019; Haugen *et al.*, 2020), is an increase in the number of species endemic to the Azores, further substantiating the biogeographic distinctness of the archipelago within the wider Macaronesian region that was recently highlighted by Freitas *et al.* (2019). In an ongoing study, the remaining historical species as well as newly collected material (George *et al.*, 2018) will be examined in order to more comprehensively understand the archipelago's bryozoan diversity (e.g. Baptista *et al.*, 2022). Moreover, the presence of fossil bryozoans in early Pliocene strata in the island of Santa Maria (Ávila *et al.*, 2015) will aid in comprehending the origin of the Azorean fauna. The recent taxonomic efforts are therefore a prelude to our comprehension of the true richness, geographic distribution, evolution and ecology of Azorean bryozoans.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315423000231>.

Acknowledgements. We would like to acknowledge Michèle Bruni (MOM) for help with the collection at Monaco, as well as Pierre Lozouet and Jérôme Mainguy at the MNHN in Paris. Rachel Petts and Henry McGhie (MM) gratefully sent on loan the Waters material from Manchester. As usual, Dennis Gordon (NIWA) and Phil Bock are thanked for sharing their bryozoan wisdom, and BB is grateful for Sérgio Ávila's (Universidade dos Açores) long-term support in his quest to better understand the Azorean bryozoans, Recent and fossil.

Author contributions. BB formulated the research question, designed the study, carried out the study, analysed the data, interpreted the findings, and wrote the article. MESJ formulated the research question, designed the study, carried out the study, and wrote the article.

Financial support. This study was funded by the SYNTHESYS Project (<http://www.synthesys.info/>), which is financed by the European Community Research Infrastructure Action under the FP7 'Capacities' Program, and which enabled BB to study Azorean type material at the NHMUK (GB-TAF-3347) and the MNHN (FR-TAF-1902, -5579). Additional financial support was provided by the Portuguese Funds through FCT – Foundation for Science and Technology under the UID/BIA/50027/2013 and POCI-01-0145-FEDER-006821.

Competing interests. The authors declare none.

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