

Original Article

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Apprehending novel biodiversity redux – thirteen new genera and three new families of Zealandian Bryozoa, with the first living species of the Eocene–Miocene genus *Vincularia* (Vinculariidae)

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Abstract

Thirteen new genera and three new families of cheilostome Bryozoa are described from the New Zealand biogeographic region, centred on Zealandia, between 26.42° (northern Norfolk Ridge) and 54.02°S latitude (south-east Campbell Plateau) from coastal waters to bathyal depths (46–1676 m). The new genera, comprising 15 new and one previously described Zealandian species, are: *Elementella* (Elementellidae n. fam.), *Niwapora*, *Quascallopora*, *Quitocallopora*, *Judyella* (Calloporidae), *Ellisantropora* (Antroporidae), *Rhizellisina* (Ellisinidae), *Radixenia* (Calloporoidea incertae sedis), *Granomurus* (Granomuridae n. fam.), *Carolanna* (Bugulidae), *Borioplebs* (Borioplebidae n. fam.), *Seabournea* (Cribrilinidae) and *Waeschenbachia* (Romancheinidae). A new Recent species of the otherwise Eocene–Miocene genus *Vincularia* is also described from deep water on the Three Kings Ridge. Two new combinations are created – *Judyella precocialis* (Gordon, 1984) and *Ellisantropora aggregata* (Gordon, 1984). *Ellisantropora tilbrooki* sp. nov. is also introduced for a species from Torres Strait. Four of the deep-sea genera (three from one station on the northern Norfolk Ridge, one from a station on the Three Kings Ridge) have species with plesiomorphies or distinctive skeletal characters that suggest they are relict. Almost half of the new species form spot-like colonies on hard substrata.

Introduction

Under a paper title beginning with ‘Apprehending novel biodiversity’, Gordon (2014) described 15 new genera from the north-central to southernmost extension of the largely submerged geological continent of Zealandia as far as the seamounts near the Hjort Trench at 59°S. Zealandia ranges from north of New Caledonia to features associated with the southern margin of the subantarctic Campbell Plateau (Mortimer & Campbell, 2014) and includes a highly diverse described and known-undescribed bryofauna of 1266 species (current to April 2016) (Gordon *et al.*, 2019). Although Zealandia is very much smaller than the other continents including Australia (only 4.92 million km² total crustal area for Zealandia vs 14.16 million km² for Greater Australia (Sahul) (Mortimer & Campbell, 2014)), the known bryofauna of the latter realm presently comprises not many more species (1307), and both regions have more described and known-undescribed species than Europe (945) (current to 2016) (Gordon *et al.*, 2019).

Over and above varied historic and present taxonomic effort in the three continental regions is the contribution of seascape evolution to biodiversity. Zealandia is globally exceptional in its disproportionate area of seafloor (94%) relative to land (6%). Aotearoa/New Zealand, the major geographic and political component of Zealandia, spans 30 degrees of latitude, has a legally ‘extended continental shelf’ of potentially 1.7 million km² and one of the largest Exclusive Economic Zones in the world, of which about half the area is shallower than 2000 m. New Zealand’s subtropical to subantarctic latitudinal spread is accompanied by a fractal coastline (estimated 15,000–18,000 km) of inlets, headlands, spits, bays, harbours, fiords, sounds and estuaries, and the strikingly varied seafloor relief includes shelves, slopes, plateaus, seamounts, canyons, abyssal plains and two trenches, one exceeding 10 km deep (Gordon *et al.*, 2010). All this geological diversity is mirrored by the marine biodiversity, estimated at ~17,966 species (current to October 2013) (Gordon, 2013).

The collection of the National Institute of Water and Atmospheric Research (NIWA), Wellington has many undescribed bryozoan species from throughout the New Zealand EEZ and southern Zealandia, representing many habitats and almost all seascape areas other than the abyssal sea floor and trench depths beyond 4500 m (Gordon, 1987). The present paper describes 16 new Zealandian species in 14 genera (13 new) and 11 families, three of them new. Accordingly, the paper is titled with reference to the earlier one in this two-part series, ‘Apprehending novel biodiversity’, appended by ‘redux’, a word that means brought back, resurgent or revived. This title has a dual application because one of the new species represents the first Recent representative of the otherwise Eocene–Miocene genus *Vincularia*



(Defrance, 1829) and family Vinculariidae (Busk, 1852b). Further, one new genus, *Elementella* gen. nov., exhibits the simplest known skeletal morphology of any living cheilostome, resembling a Jurassic species, and three other species, suggestive of a relict Cenozoic fauna, show skeletal morphologies transitional or intermediate between different family-level taxa.

Materials and methods

Examined specimens were collected during numerous cruises carried out by NIWA and its predecessor, the New Zealand Oceanographic Institute (NZOI), between 1961 and 2015. Until 2007, all vessel-collected biological material, including bryozoans, was preserved in seawater–formalin before later transfer to 70% isopropanol or ethanol. After 2007, all such material was immediately preserved in 99% ethanol unless specific protocols dictated otherwise. Station locations are shown in Figure 1 and complete station data are given in Appendix 1. Registered examined specimens are lodged in the NIWA Invertebrate Collection, prefixed with NIWA registration numbers.

Specimens prepared for scanning electron microscopy (SEM) were bleached in sodium hypochlorite (NaClO) solution to reveal details of the skeleton. Some specimens were metal-coated in gold-palladium or left uncoated and photographed using a Hitachi TM3000 Tabletop SEM.

Measurements of morphological characters were made of scanned images using Fiji (ImageJ) software (Schindelin *et al.*, 2012). Metrics are given in μm as the range, followed by the mean and standard deviation (bracketed) and number of measurements. The key characters have the following abbreviations:

AnL, AnW	ancestrula length and width
AvL, AvW	avicularium cystid length and width
FOL, FOW	female orifice length and width
OL, OW	orifice length and width
OoL, OoW	ooecium length and width
OpL, OpW	operculum length and width
OpsL, OpsW	opesia length and width
PoL, PoW	peristomial orifice length and width
ZL, ZW	autozooid length and width

SYSTEMATICS

Class MYOLAEMATA Schwaha, Ostrovsky & Wanninger, 2020a
 Subclass GYMNOLAEMATA Allman, 1856
 Order CHEILOSTOMATA Busk, 1852a
 Suborder INCERTAE SEDIS
 Superfamily INCERTAE SEDIS
 Family ELEMENTELLIDAE fam. nov.

Type Genus. *Elementella* gen. nov.

Diagnosis. Colony encrusting, uniserial, sparsely branching. Autozooids simple, pyriform to clavate or parallel-sided with short non-filiform cauda. Cystid gymnocystal, smooth; cryptocyst absent. Opeal area and membranous frontal wall very extensive, with terminal single-layered flap-like operculum that has an inner marginal sclerotized rim. No spines, avicularia or ooecia. Basal pore-chambers present, shape variable. Kenozooids present where space limited for full autozooid development. Inferred ancestrula identical to other zooids, bipolar, budding daughter zooids mid-distally and mid-proximally.

Remarks

A new family and genus are introduced here for two deep-sea bryozoan species that have the simplest skeletal morphology of any known living cheilostomes. The large opesia is covered by a membranous frontal wall with a flap-like operculum that has an inner marginal sclerite and lateral flanges. There are no spines or tubercles, heterozooids and reproductive structures are apparently lacking, and the autozooidal cystid has no trace of a cryptocyst. The two species essentially have the appearance of simple runner-like ctenostomes that have calcified their lateral walls.

In existing classifications, *Elementella* gen. nov. would conventionally be classified in Electridae Stach, 1937, a family that currently includes the earliest and morphologically simplest cheilostomes. To do so appears problematic, however, for two main reasons. First, the type genus of Electridae has a well-developed pitted or/and porous gymnocyst that is bordered by a narrow cryptocyst and typically several conical non-articulated spines that are mostly cuticular – unlike *Elementella*, which lacks a cryptocyst and spines. Species of *Electra* Lamouroux, 1816 also have basal pore-chambers (in zooids near the ancestrula) as well as smaller round mural pore-chambers with multiporous pore-plates (within lateral walls of multiserial zooids) (Prenant & Bobin, 1966; Silén, 1987), whereas uniserial *Elementella* has so far been found only with somewhat irregular tiny basal pore-chambers. Overall, then, the two genera differ in significant aspects of skeletal morphology. Second, molecular sequencing has shown that some other genera morphologically closer to *Electra* than *Elementella* are not as closely related as hitherto thought (Taylor & Waeschenbach, 2015). For example, two species of *Einhornia* Nikulina, 2007, both previously included in *Electra*, are in a separate clade from one that comprises *Electra* in one branch and *Aetea* Lamouroux, 1812 and *Membranipora* de Blainville, 1830 in another. Further, the putative electrid genus *Conopeum* Gray, 1848 is basalmost in the same molecular tree and clearly not an electrid. A similar result for *Conopeum* had already been obtained by Nikulina & Schäfer (2008) (see also Gordon *et al.*, 2020). For these reasons, *Elementella* is not here included in Electridae.

Are there other nominal electrid genera that are morphologically closer to *Elementella* gen. nov.? Ironically, the species that comes closest is also the earliest – *Pyriporopsis pohowskyi* Taylor, 1994 from the late Jurassic (Oxfordian/Kimmeridgian: 157.1–152.1 mya) of Yemen. This species is one of two attributed to *Pyriporopsis* Pohowsky, 1973, the type species of which is *Pyriporopsis portlandensis* Pohowsky, 1973, also from the late Jurassic (Tithonian: 152.1–145.6 mya), but separated in time potentially by 6.5–11.5 my. Both species have the same uniserial to loosely pluriserial colony form, with pyriform to oval or parallel-sided zooids having a mean length of 630 μm and 550 μm , respectively, for the two species. Although the two species are very similar overall, Taylor (1994) observed two key differences – there is no trace of a cryptocyst or closure plates in *P. pohowskyi*, even in well-preserved zooids, whereas *P. portlandensis* has a distinctly striate (non-pustulose) cryptocyst and closure plates. These differences may be significant at genus level and more information on cheilostome diversity in the late Jurassic is desirable. Of the two species of *Pyriporopsis*, *Elementella* is morphologically closer to *P. pohowskyi*. Both *Pyriporopsis* species are here provisionally included in the Elementellidae. The status of *Pyripora* d'Orbigny, 1852 in this context is contingent upon better knowledge of the Miocene type species *Pyripora pyriformis* (Michelin, 1848). The Cretaceous–Eocene genus *Herpetopora* Lang, 1914 differs from *Elementella* in having more-discrete, less variably shaped autozooids in which the cauda is narrower, becoming filiform in runner-like branches. *Herpetopora* zooids

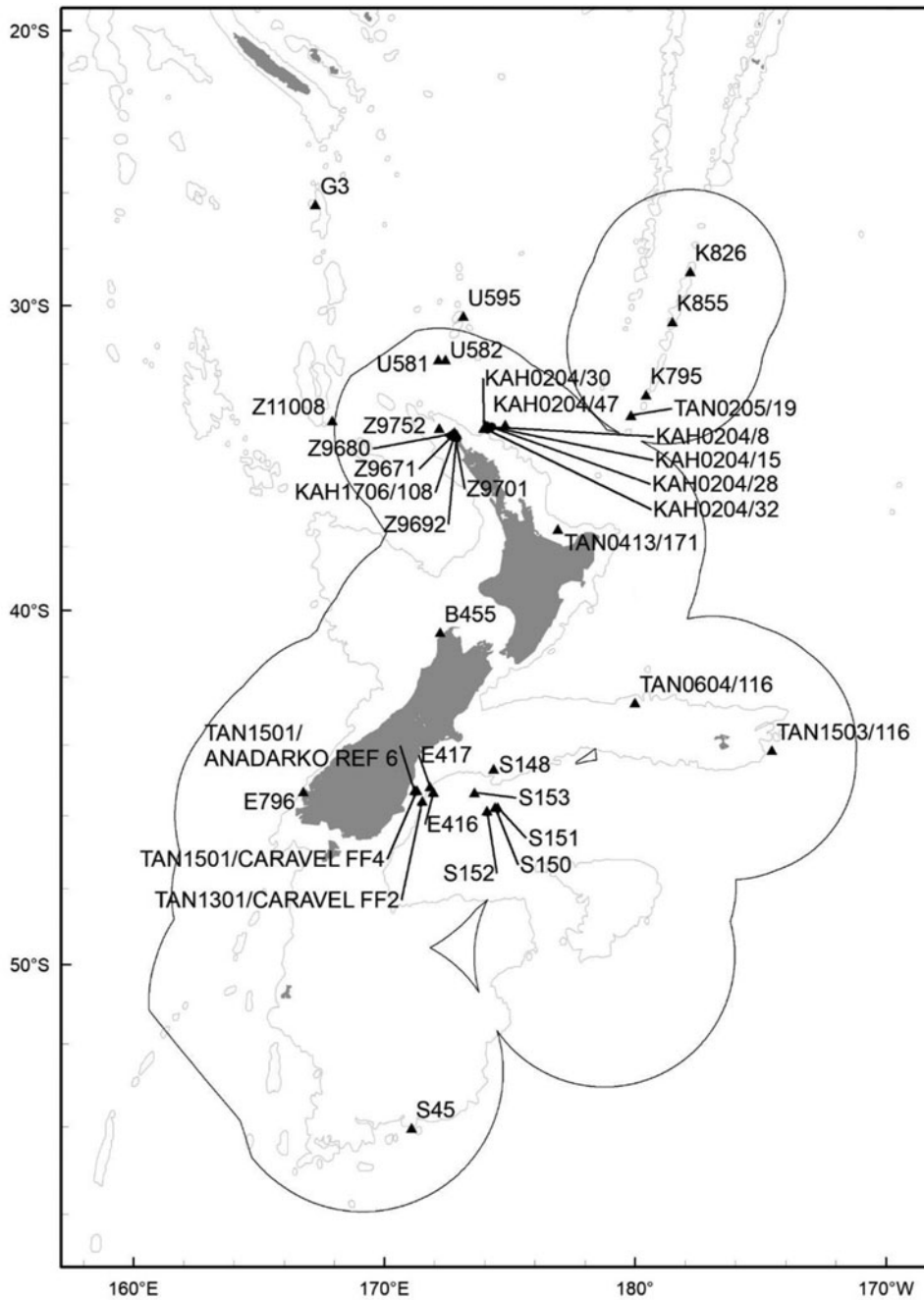


Fig. 1. Map of station distributions for the new species of Zealandian Bryozoa described herein, based on specimens in the NIWA Invertebrate Collection, Wellington. Bathymetry (light grey) at 1000 m depth intervals.

also lack basal pore-chambers. Taylor (1988) describes *Herpetopora* as lacking a ‘non-pustulose cryptocyst’ (in contradistinction to *Pyripora*) but close examination of pl. 43, figure 5 in Taylor (1988) shows that there is at least a very narrow cryptocyst-like opesial margin that is textured, quite unlike the thin, non-textured opesial margin in *Elementella*.

The ancestrula of *Elementella* is bipolar, i.e. budding of daughter zooids is both distopetal and proxipetal in the terminology of Nikulina (2002), an ancestral character state shared, inter alia, by *Pyripopsis*, *Conopeum*, *Herpetopora*, *Pyripora* and *Electra* (all Electridae s.l.), as well as *Aetea* (Aeteidae), *Eucratea* (Eucrateidae) and *Scruparia* (Scrupariidae) (see Silén, 1987, p. 32; Taylor, 1988; Nikulina, 2001, p. 510; Nikulina, 2002, p. S383). The ancestrula of *P. portlandensis* is very small and appears kenozooidal, though Taylor (1986) thought this unlikely, suggesting that fine micritic sediment may have concealed any trace of a closure plate. The ancestrula of *P. pohowskyi* is unknown.

Thus, the sum of the characters exhibited by *Elementella* gen. nov., especially proxipetal budding from the ancestrula, suggests that the genus probably belongs in suborder Membraniporina. On the other hand, the possibility that it is a highly derived form that only superficially resembles primitive malacostegans cannot be ruled out. Inter alia, nothing is known about the mode of reproduction. Do the two new species of *Elementella* described here produce small eggs that develop into planktotrophic larvae in a deep-water environment? Evidence from a 5 km-deep ctenostome, *Haywardozoon pacificum* Grischenko, Gordon & Melnik, 2018, shows that is possible (Schwaha et al., 2020b). Or do ovicells or some other form of brooding occur in *Elementella* gen. nov. for which evidence is presently lacking? A putative new calloporid genus (*Niwapora* gen. nov.) is described below that somewhat resembles *Elementella* at the zooidal level but is multiserial and has vestigial oocelia.

Genus *Elementella* gen. nov.

Type Species. *Elementella simplex* sp. nov.

Etymology. Latin *elementum*, first principle, rudiment, plus diminutive suffix *-ella*, alluding to the very basic structure of the zooids.

Diagnosis. As for the family (above).

Elementella simplex sp. nov.

(Figure 2A–G)

Material Examined. Holotype: NIWA 22501, Station KAH0204/28, southern Three Kings Ridge, New Zealand, 490–515 m depth.

Paratype: NIWA 95665, Station G3, northern Norfolk Ridge, 710 m depth.

Etymology. Latin *simplex*, simple, alluding to the simple morphology of the colony and autozooids.

Description. Colony encrusting, uniserial, sparsely branching. Maximum length seen ~19 mm.

Autozooids fragile, very simply constructed, variable in shape but generally pyriform to clavate or parallel-sided with short non-filiform cauda (ZL 1382–1906 (1500 ± 207), N = 21; ZW 627–1041 (829 ± 89), N = 21). Cystid entirely gymnocystal (Figure 1A), thin, smooth, with no trace of cryptocyst along its inner margin; in frontal view gymnocyst comprising a transversely broad arcuate area distal and lateral of the orifice, very narrow steep-sided walls laterally, and frontolateral caudal portion. Basal wall apparently uncalcified except for thin margin adjacent to lateral walls. Relative to length and width, autozooids very low in profile (height). Opesial area and membranous frontal wall very extensive (OpsL 817–1473 (1114 ± 186), N = 21; OpsW 537–1369 (712 ± 182), N = 21).

Operculum (Figure 1D, E) terminal in frontal membrane, almost semicircular, in dry state appearing thin, single-layered, with slightly thicker outer marginal band and weakly sclerotized rim on inner margin, the sides of which are extended downwards (inwards) as short vertical flanges (OpcL 140–192 (170 ± 15), N = 21; OpcW 201–309 (252 ± 34), N = 21). No spines.

Each autozooid with 1–2 small (~64 µm) basal pore-chambers in angle of each lateral wall with substratum; pore-chambers (Figure 1F) with 2–4 pores. Lateral budding of new autozooids generally mid-distal, sometimes on each side distolaterally. Occasionally, if two zooid rows occur in close proximity and space is limited, a small operculate autozooid or non-operculate kenozooid may be interpolated between adjacent pore-chambers.

Avicularia and ooecia not encountered. No information on reproductive mode.

Inferred ancestrula identical to other zooids, budding daughter zooids mid-distally and midproximally (Figure 1B, C, G) (AnL 1611–1649 (1634 ± 20) N = 3; AnW 766–1041 (889 ± 140), N = 3).

Remarks

Apart from the exceptionally simple characters of the genus, *Elementella simplex* gen. et sp. nov. is also notable for its very large zooid size – up to almost 2 mm long. The depth of the zooid body cavity (i.e. zooid height as seen in profile) is very low relative to zooid length and the zooids are highly adaptable to surface irregularities in the substratum (rock and dead scleractinian coral), with the basal wall moulding itself into hollows and over bumps, regardless of the presumed disposition of the polypide; one zooid in the paratype even has a 90° bend midlength, which evidently had not affected its function in life.

The interpolation of a small operculate autozooid or non-operculate kenozooid between adjacent pore-chambers when space is limited was also observed in *Herpetopora* (Taylor, 1988).

A second species, *Elementella secunda* sp. nov., described below, differs in having shorter autozooids (mean 899 µm) that are proportionally narrower (mean 295 µm) with a relatively longer cauda; the substantially smaller operculum (and orifice) in *E. secunda* implies a significantly smaller tentacle crown, thereby supporting the distinction of two species. A third morphology, represented by a specimen (NIWA 3710) from Station KAH0204/15, southern Three Kings Ridge, 470–480 m, is somewhat intermediate between the two new species in autozooid size and proportions. Zooids have a mean length of 1037 µm and mean width of 499 µm. This intermediate form could potentially represent a third species but the zooids are all somewhat damaged and more material is needed for a fuller assessment.

Elementella simplex sp. nov. is so far known only from the northern Norfolk Ridge to southern Three Kings Ridge at 490–710 m depth.

Elementella secunda sp. nov.

(Figure 3A–C)

Material Examined. Holotype: NIWA 95666, Station Z11008, Norfolk Ridge, 710 m depth.

Etymology. Latin *secundus*, second, being the second described species of the genus.

Description. Colony encrusting, uniserial, very sparsely branching; material fragmented, longest uniserial portion 6 mm.

Autozooids fragile, clavate, with proximally tapering caudal portion (Figure 3A–C) (ZL 759–1088 (899 ± 132), N = 6; ZW 268–321 (295 ± 22), N = 6).

Cystid entirely gymnocystal, thin, smooth, with no trace of cryptocyst along its inner margin; in frontal view gymnocyst comprising lateral walls and frontolateral caudal portion. Basal wall very thin, apparently mostly cuticular. Opesial area and membranous frontal wall very extensive (OpsL 184–517 (399 ± 115), N = 6; OpsW 174–219 (199 ± 18), N = 6). Operculum terminal in frontal membrane, almost semicircular, in dry state appearing thin, single-layered, with slightly thicker outer marginal band and weakly sclerotized rim on inner margin (OpcL 53–62 (59 ± 5), N = 3; OpcW 76–82 (79 ± 3), N = 3). No spines.

Budding loci mid-distal and distolateral or mid-lateral; no evidence of proximolateral budding sites in the limited material. One kenozooid seen (Figure 3C), presumably connecting with a distolateral pore-chamber in an encroaching autozooid, obstructing further growth.

No avicularia or ooecia. No information on reproductive mode. Ancestrula not seen.

Remarks

Elementella secunda sp. nov. is most readily distinguished from *E. simplex* sp. nov. by its much smaller zooids that are clavate with a tapering cauda and by the absence of a moderately broad gymnocystal area distal of the orifice. Both species have extremely simple morphology, including the absence of a cryptocyst.

As mentioned above, a third morphology was seen that is intermediate in dimensions between *E. simplex* sp. nov. and *E. secundus* sp. nov. Like *E. simplex* it has a moderate area of gymnocyst distal to the orifice but the proximal caudate portion is proportionally broader. *Elementella secunda* sp. nov. encrusted deep-sea rock.

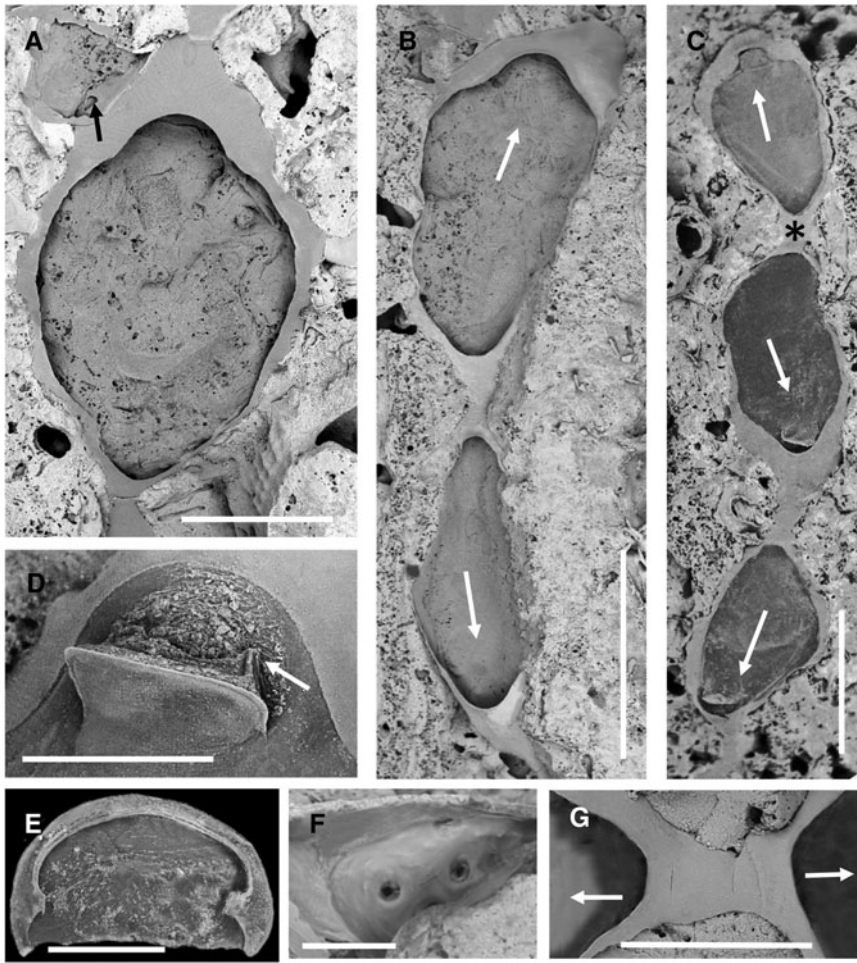


Fig. 2. *Elementella simplex* gen. et sp. nov., NIWA 22501, holotype, Station KAH0204/28, Three Kings Ridge: (A) autozooidal cystid; at top left is an aborted zooid (kenozooidal cystid) from an adjacent zooid that has established communication via a pore-chamber (opening arrowed). (B) bipolar pair, one of which (identity uncertain) is an ancestrula; arrows indicate growth direction. (C) linear group of three operculate zooids, the top two constituting a bipolar pair, one of which (identity uncertain) is an ancestrula; growth directions are arrowed; asterisk shows area magnified in G. (D) open operculum, with right-hand flange arrowed. (E) inner face of an operculum. (F) interior view of a biporous basal pore-chamber. (G) close-up of asterisked area of bipolar zooidal pair in C; there is no indication of fracture or repair. Scale bars: A, 0.5 mm; B, C, 1 mm; D, 200 μ m; E, 100 μ m; F, 30 μ m; G, 400 μ m.

The species is so far known only from the type locality on Norfolk Ridge, at 710 m depth.

Suborder FLUSTRINA Smitt, 1868
 Superfamily CALLOPOROIDEA Norman, 1903
 Family CALLOPORIDAE Norman, 1903
 Genus *Niwapora* gen. nov.

Type Species. *Niwapora grandis* sp. nov.

Etymology. From NIWA, acronym for the National Institute of Water & Atmospheric Research, Wellington, plus Latin *pora*, the feminized form of *porus*, hole, a common suffix in bryozoan generic names.

Diagnosis. Colony encrusting, multiserial, contiguous. Autozooids with very large opesia bordered by narrow gymnocyst and vestigial cryptocyst with single series of tiny tubercles. No spines or avicularia. Ovicell immersed, cleithral. Ooecium vestigial, derived from distal zooid, comprising transversely narrow flattened outfold. Sparse uniporous mural septula present. Ancestrula like autozooids.

Remarks

Niwapora gen. nov. is monotypic for a species that occurs on the Cavalli Seamount off north-eastern North Island. It is reminiscent of *Aplousina* Canu & Bassler, 1927 in its simple autozooidal morphology; the type species, *Aplousina gigantea* from the western Atlantic, likewise has a vestigial cryptocyst with a single series of beading, and the gymnocyst is so reduced as to be vestigial to

virtually absent. The ooecium differs, however, in its larger size, appearing as a moderately conspicuous bulge that extends under the distal zooidal margin into the proximal end of the daughter autozooidal cavity (Winston, 1982, 2010). In *Niwapora*, the reduced ooecium appears as a frontally inclined cap with a proximofrontal crest. It replaces the mid-distal area of gymnocystal wall, such that the underside of the ooecium can be seen from below.

It is moot whether or not *Niwapora* is a calloporid. It differs markedly from the type genus and species of the family, which is characterized by stout periopodial spines, adventitious avicularia, well-developed ooecia with a frontal skeletal exposure of endooecium, and basal pore-chambers. Calloporidae is morphologically heterogeneous, with ~81 living and fossil genera, and awaits comprehensive molecular sequencing of a range of genera that are putatively included in it. Calloporidae, as presently conceived, exhibits a varied range of expression of gymnocyst, cryptocyst, spines, avicularia, ooecia and pore-chambers, in various permutations and combinations. Presently, there is no other family in which *Niwapora* may be included.

Could *Elementella* gen. nov. and *Niwapora* gen. nov. be related? *Niwapora grandis* sp. nov. has such a microscopic cryptocyst that, if it were to disappear altogether, infertile zooids would resemble those of *Elementella* spp., which are otherwise caudate because of uniseriarity. *Elementella* gen. nov. lacks ovicells, but it is possible these have not been found yet or it is an internal brooder. Mediating against a possible relationship between the two genera are differences in ancestrular budding (unipolar in *Niwapora*, bipolar in *Elementella*) and interzooidal communications (uniporous mural septula in *Niwapora*, multiporous basal pore-chambers in *Elementella*).

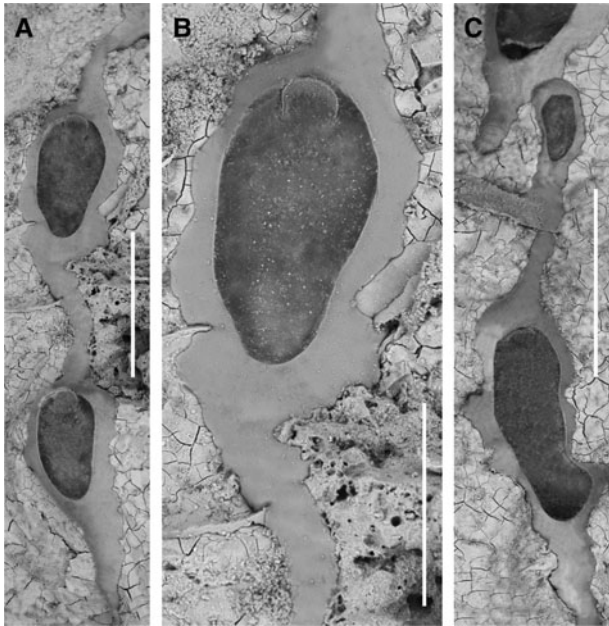


Fig. 3. *Elementella secunda* sp. nov., NIWA 95666, holotype, Station Z11008, Norfolk Ridge: (A) two operculate clavate autozooids. (B) enlargement of more-distal zooid in A. (C) an operculate autozooid that has encountered another zooid, producing an aborted zooid (kenozooid) at the point of contact. Scale bars: A, C, 500 μ m; B, 300 μ m.

Niwapora grandis sp. nov.
(Figure 4A–H)

Material Examined. Holotype: NIWA 95667, Station KAH0204/8, Cavalli Seamount, 610–640 m depth.

Etymology. Latin *grandis*, large, alluding to the large autozooid size.

Description. Colony encrusting, multiserial, initially unilamellar, but capable of self-overgrowth; sole colony 17 mm long, 9 mm wide.

Autozooids large, mostly more or less roundly subhexagonal in outline (Figure 4A), relatively thin-walled (ZL 935–1373 (1082 \pm 110), N = 23; ZW 679–1015 (791 \pm 92), N = 23). Opesia very extensive, occupying 92% of zooid length on average (OpsL 783–1029 (988 \pm 100), N = 15; OpsW 609–898 (716 \pm 81), N = 15). Gymnocyte very narrow, periopodial, slightly wider distolaterally and proximolaterally, a little elevated as distal oral rim. Cryptocyst periopodial, vestigial, comprising single series of microscopic tubercles along inner margin of gymnocyte (Figure 4F).

Operculum not seen. No spines or avicularia.

Ovicell immersed, cleithral. Ooecium (Figure 4B–E, G, H) much reduced, wider than long, comprising transversely narrow hollow cap that is inclined frontalwards with proximofrontal crest; ectooecial surface smooth with thin transverse striae on each side. Developmentally derived from distal zooid via long slit, occupying/replacing mid-distal area of gymnocyte wall, such that underside of ooecium can be seen from below (OoL 77–136 (101 \pm 17), N = 11; OoW 305–422 (359 \pm 38), N = 11).

Sparse uniporous mural septula (Figure 4C, E) present; typically two on each lateral wall; only one in each transverse wall (pore-plate diameter 47–66 (56), N = 7; pore diameter 8–12 (11), N = 5). No distinction in size of pore-plate or pore between transverse and lateral walls.

Sole ancestrula like autozooids, except proximal margin more truncate (AnL 934, AnW 697). Budding of paired daughter zooids distopetal.

Remarks

The sole specimen encrusted a piece of rock collected during a rock-dredge tow from 640 to 610 m depth on the Cavalli seamount.

Genus *Quascallopora* gen. nov.

Type Species. *Quascallopora bathyalis* sp. nov.

Etymology. Latin *quasi*, appearing as if, simulating, plus *Callopora*, a related genus.

Diagnosis. Colony encrusting, unilaminar, multiserial. Some autozooids partly disjunct. Opesia extensive, frontally visible gymnocyte greatly reduced, cryptocyst periopodial, narrow throughout, with weak longitudinal lineations not pustules. Operculum proportionally large, terminal in membranous frontal wall. Spines articulated, sparse, long, not periopodial. No avicularia. Ovicell terminal, cleithral. Ooecium a kenozooid budded from maternal autozooid. Ectooecium almost completely membranous, endooecium with hexagonal reticulation; closure cleithral. Biporous mural septula present. Ancestrula like autozooids.

Remarks

Quascallopora gen. nov. resembles the type and other species of *Callopora* Gray, 1848 in general appearance and in having ooecia with an extensive endooecial surface, but differs in that the ooecia are terminal and kenozooidal, avicularia are lacking and there are multiporous mural septula instead of basal pore-chambers.

Callopora is also strictly a northern-hemisphere genus. Three austral species (one fossil) have been attributed to *Callopora* but these attributions are here considered erroneous. *Callopora precoalalis* Gordon, 1984, described from the Kermadec Ridge, is now included in *Judyella* gen. nov. (see below). South African *Callopora jamesi* O'Donoghue & de Wateville, 1944 needs further study but it appears not to belong to *Callopora* – it lacks avicularia and its cryptocyst is negligible. Further, if '*Crassimarginatella?* sp.' of Florence *et al.* (2007) is conspecific with *C. jamesi*, then the smooth skeletal surface of the ooecium in this species is endooecium, which is normally characteristically granular when not restricted to a small tabulate area. Palaeogene *Amphiblestrum moniliferum* Maplestone, 1901 from Australia, included in *Callopora* on the Bryozoa Home Page (Bock, 2016), likewise needs further study; ooecia were not described and the only avicularium was interpreted by Maplestone as vicarious.

Alderina Norman, 1903 resembles *Quascallopora* gen. nov. in lacking avicularia but it differs in also lacking lateral spines while possessing an ectooecial tabula and basal pore-chambers. *Allantocallopora* d'Hondt & Schopf, 1985 is a monotypic deep-sea genus, but differs from *Quascallopora* gen. nov. in being uniserial, with only distal spines, a weakly carinate ooecium and a laterally flared opesial margin. Species of *Copidozoum* Harmer, 1926 can have a large exposure of endooecium but the ovicell is acleithral and the genus is characterized by the presence of large interzooidal or subvicarious avicularia with a tapering rostrum.

Quascallopora bathyalis sp. nov.
(Figure 5A–C)

Material Examined. Holotype: NIWA 144896, Station TAN1501/CARAVEL FF4, head of Bounty Trough, eastern South Island, New Zealand, 1126 m depth.

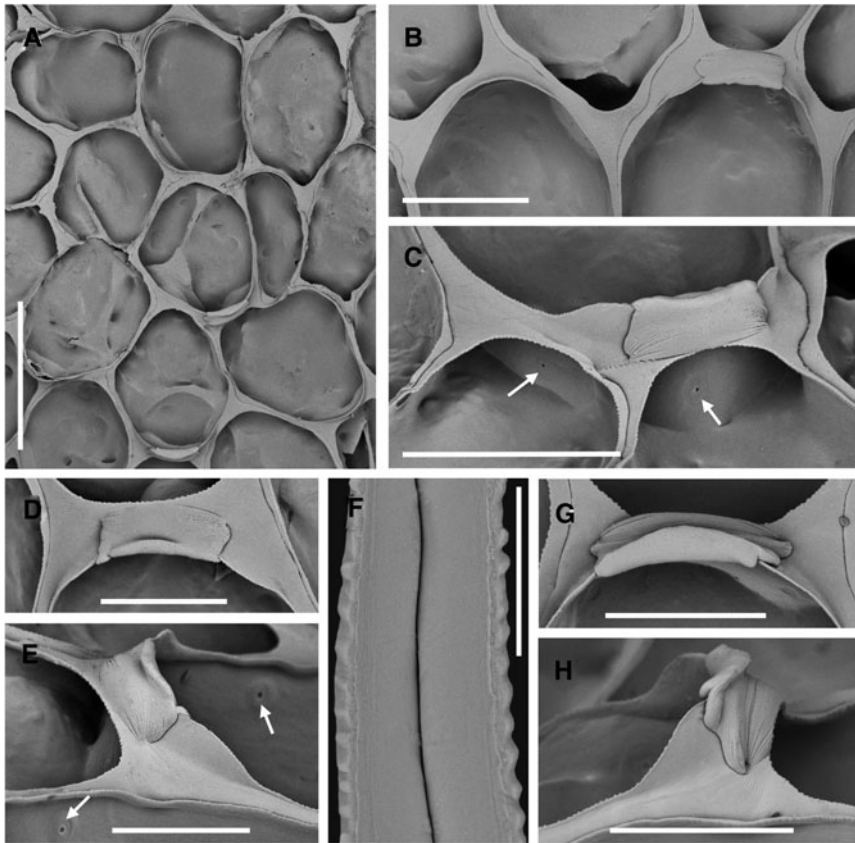


Fig. 4. *Niwapora grandis* gen. et sp. nov., NIWA 95667, Station KAH0204/8, Cavalli Seamount: (A) part of colony, showing self-overgrowth; some zooids ovicellate. (B) distal ends of non-ovicellate (left) and ovicellate (right) zooids. (C) distal view of an ovicellate zooid at the bifurcation of a zooid row; uniporous septula arrowed. (D, E) frontal and left-lateral views of the same oecium; uniporous septula arrowed. (F) frontal view of parts of adjacent autozooidal lateral walls showing minute cryptocystal beading. (G, H) frontal and right-lateral views of the same oecium. Scale bars: A, 1 mm; B, C, 500 μ m; D, E, G, H, 300 μ m; F, 50 μ m.

Paratypes: NIWA 146071, Station TAN1301/CARAVEL FF2, head of Bounty Trough near Karitane Canyon, eastern South Island, New Zealand, 1117 m depth; NIWA 146100, Station TAN1501/ANADARKO REF 6, head of Bounty Trough, eastern South Island, New Zealand 1024 m depth.

Other material: NIWA 22534, 95592, Station E416, 45.3500°S 171.9500°E, head of Bounty Trough, eastern South Island, New Zealand, 1225 m depth; NIWA 95593, Station E417, head of Bounty Trough, eastern South Island, New Zealand, 860 m depth; NIWA 95591, Station S148, SW Chatham Rise, New Zealand, 859 m.

Etymology. From latinized Greek, *bathys*, deep, alluding to the occurrence of the species at bathyal depths.

Description. Colony encrusting, unilaminar, multiserial, small comprising spots (Figure 5A) with maximum diameter 4 mm.

Autozooids elongate-oval (ZL 621–955 (789 \pm 88), N = 17; ZW 442–655 (536 \pm 60), N = 17), separated by deep interzooidal furrows, many slightly disjunct at corners, connected by very short broad tubes. Opesia extensive, occupying 74% or more of zooid length on average (OpsL 510–652 (584 \pm 60), N = 5; OpsW 349–430 (393 \pm 31), N = 5). Frontally visible gymnocyst greatly reduced, confined to small area between each pair of distolateral spines, steeply sloping proximal side walls and frontal surface of connecting tubes. Cryptocyst periopodial, narrow, of more or less equal width throughout, surface smooth or with weak, variable longitudinally wavy lineations, not pustulose as such.

Operculum proportionally large, terminal in membranous frontal wall, broadly semicircular (OpcL 115–135 (127 \pm 10), N = 3; OpcW 210–263 (237 \pm 27), N = 3).

Spines articulated, sparse, but conspicuous for their length; not periopodial but confined to distal half to two-thirds of zooid length; comprising two distolateral pairs and 1–2 lateral pairs, or one of the most proximolateral pair missing; elevated vertically

or slightly inclined distad if distolateral or outwards if lateral; length 355–665 μ m. No avicularia.

Ovicell (Figure 5C) well-developed, terminal, cleithral, not touching substratum when viewed in profile (OoL 189–220 (203 \pm 13), N = 5; OoW 274–323 (291 \pm 19), N = 5). Ectooecium almost completely membranous apart from narrow proximofrontal strip; endooecium with generally hexagonal reticulation. Closure cleithral.

Two widely separated mural septula on each lateral wall; typically biporous, rarely uniporous; a pair of side-by-side biporous septula on the distal transverse wall (biporous pore-plate diameter 45–60 (54), N = 5; uniporous pore-plate diameter 25–38 (32), N = 5; pore diameter 4).

Ancestrula (Figure 5B) like autozooids but slightly smaller (AnL 510–583 (547 \pm 51), AnW 387–437 (412 \pm 35), N = 2). One mid-distal and two distolateral daughter zooids. Proximal communications established with later zooids proximolaterally and proximally.

Remarks

Colonies of *Quascallopora bathyalis* gen. et sp. nov. were found solely on tubes of the arenaceous deep-sea foraminiferan *Rhabdammina major* de Folin. These occurred at the sediment surface at depths of 859–1225 m in the head of the Bounty Trough south and south-west of Banks Peninsula, South Island. Other undescribed cheilostome bryozoans occur on the same substratum, including a species of *Chaperiopsis* and one of *Fenestrulina*.

Genus *Quitocallopora* gen. nov.

Type Species. *Quitocallopora aviculata* sp. nov.

Etymology. Latin *quitus*, enabled, strong, alluding to the presence of robust interzooidal avicularia in the type species, plus *Callopora*, a related genus.

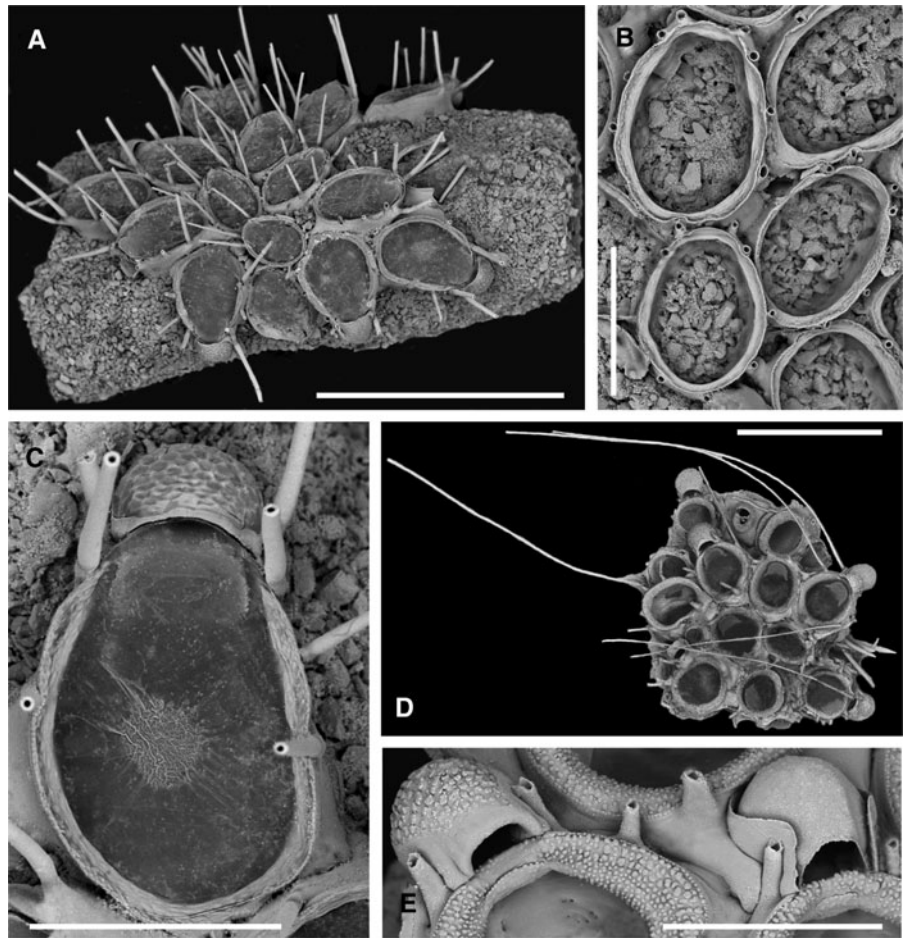


Fig. 5. *Quasicallopora bathyalis* gen. et sp. nov.: (A) NIWA 146071, Station TAN1301/CARAVEL FF2, Bounty Trough, ovicellate colony on tube of arenaceous foraminiferan *Rhabdammina major*. (B), NIWA 22534, Station E416, Bounty Trough, ancestrula (lower left) and daughter zooids. (C) close-up of lower-right ovicellate zooid in A. *Quitocallopora aviculata* gen. et sp. nov.: NIWA 95628, paratype, TAN0413/171, Bay of Plenty: (D) aviculariferous ovicellate colony; note the very long filiform spines. (E) NIWA 23244, TAN0413/171, Bay of Plenty, ooecia at two stages of development; note the ectooecium in the zooid at right. Scale bars: A, 2 mm; B, C, 500 μ m; D, 1 mm; E, 300 μ m.

Diagnosis. Colony encrusting, unilaminar, multiserial. Autozooids with large opesia. Cryptocyst periopiesial, narrow to moderate, of almost equal width throughout, granular. Gymnocyst scarcely visible laterally, more evident proximally and proximolaterally. Articulated spines in distal third of zooid or periopiesial. Avicularia, if present, interzooidal with sloping gymnocystal walls; rostral part and opesial parts almost equivalent in size, each semi-circular; rostrum with proportionately large foramen; pivot bar complete; opesia transversely crescentic bordered by granular crescentic cryptocyst. Ovicell hyperstomial. Ooecium formed from roof of distal zooidal/kenozooidal bud. Ectooecium membranous except for basal peripheral part, endooecium calcified, with granular-tubercular surface. Basal pore-chambers present. Ancestrula tatiform, with periopiesial spines and granular cryptocyst.

Remarks

Quitocallopora gen. nov. is established here for two deep-sea New Zealand species that form spot-type colonies. The genus appears closest to *Crassimarginatella* Canu, 1900 in its affinities. Gordon (2014) and Min *et al.* (2017) have discussed the range of morphological variation in *Crassimarginatella*, especially that expressed by ooecia and avicularia (see also Harmelin, 1973), concluding that, while splitting the genus appeared to have merit, more information was needed. The type species, *Crassimarginatella crassimarginata* (Hincks, 1880a), has, *inter alia*, avicularia with a stout pivot bar, basal pore-chambers and a tatiform ancestrula with spines, all features shared with the type species of *Quitocallopora* gen. nov. The ovicell in *Quitocallopora*, however, justifies recognition of a new genus; unlike *C. crassimarginata*, which has a cleithral ovicell

and a smooth, wholly ectooecial surface (Chimenz Gusso *et al.*, 2014, figure 33c, d), *Quitocallopora* has a non-cleithral ovicell and ectooecial calcification is restricted to a narrow band. The occurrence of some ooecia at the edge of the colony in the two new species described here shows them to be formed from the roof of the distal basal pore-chamber, which is, in fact, a zooidal bud with a membranous terminal part that can potentially grow into an autozooid. Its basal wall in the present material does not always rest on the substratum. *Quitocallopora* gen. nov. also differs from *Corbulella* Gordon, 1984 in having non-cleithral ovicells and a complete pivot bar in the avicularia.

Quitocallopora aviculata sp. nov.
(Figures 5D, E; 6A–D)

Material Examined. Holotype: NIWA 23244, Station TAN0413/171, outer Bay of Plenty, North Island, New Zealand, 310–410 m depth.

Paratypes: NIWA 95628, 95629, same data as holotype.

Other material: NIWA 95630, same data as holotype.

Etymology. Alluding to the presence of avicularia.

Description. Colony encrusting, unilaminar, multiserial, small, comprising spots up to 3.7 mm diameter. Autozooids in quin-cunx, or one of the six surrounding zooids is an avicularium, or there are seven surrounding zooids, one an avicularium.

Autozooids mostly longer than wide, roundly subhexagonal to oval or pyriform, with deep interzooidal furrows between adjacent lateral walls (ZL 413–627 (487 ± 60), N = 20; ZW 331–447 (392 ± 39), N = 20). Opesia relatively large, bordered by conspicuously

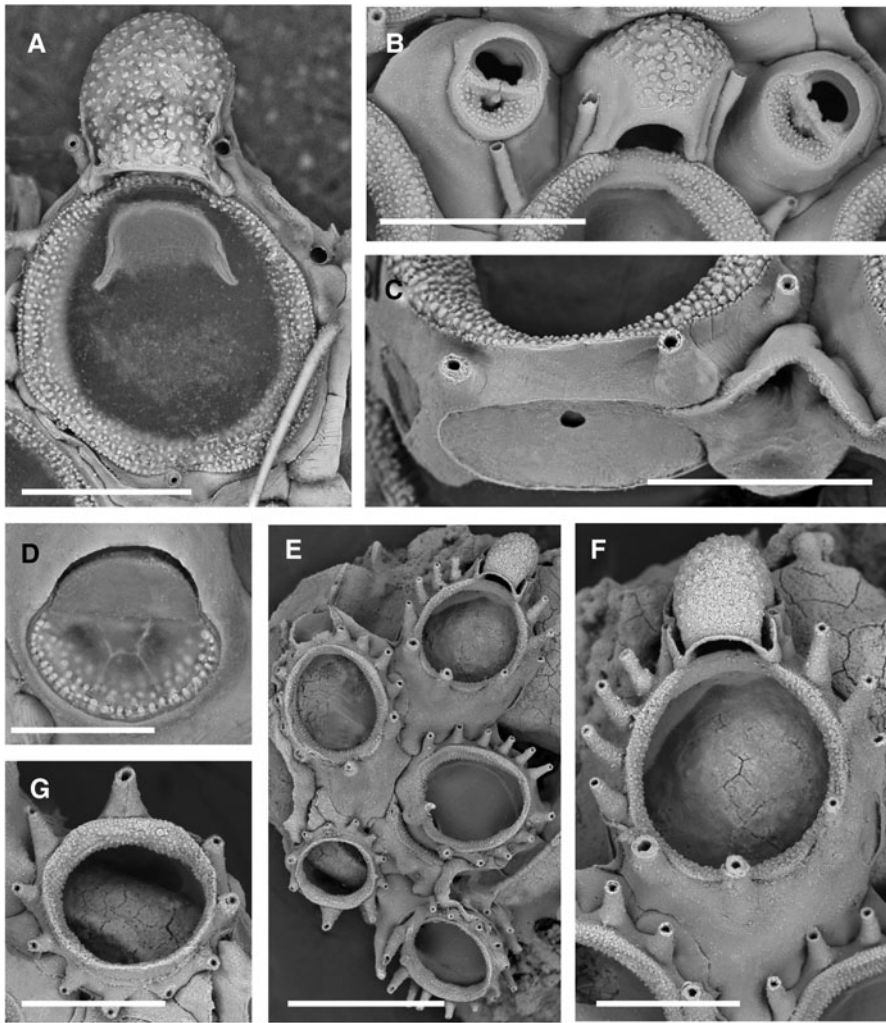


Fig. 6. *Quitocallopora aviculata* gen. et sp. nov.: (A) NIWA 95628, paratype, TAN0413/171, Bay of Plenty, operculate ovicellate zooid from colony in Figure 5D. (B) NIWA 23244, TAN0413/171, Bay of Plenty, fully developed ooeccium flanked by avicularia. (C), same, distal view of large uniporous pore-chamber. (D) NIWA 95628, avicularium with mandible in place. *Quitocallopora pusilla* sp. nov., NIWA 95618, Station TAN0205/19, Kermadec Ridge: (E) ancestrulate ovicellate spot colony. (F) ovicellate zooid in E. (G) close-up of ancestrula in E. Scale bars: A, C, F, G, 200 μ m; B, 300 μ m; D, 100 μ m; E, 500 μ m.

granular cryptocyst, this moderately wide, of almost equal width throughout, a little narrower distally; granules larger towards rim (OpsL 220–323 (272 ± 28), $N = 20$; OpsW 187–314 (245 ± 37), $N = 20$). Gymnocyst scarcely visible laterally, more evident proximally and proximolaterally. Typically two pairs of widely separated spines in distal third of zooid; usually a midproximal spine or this displaced to one side by an ooeccium. Some spines can be exceedingly long – up to 2.8 mm (Figure 5D). Opercular flap (Figure 6A) relatively large, the proximolateral corners turned slightly outwards (OpcL 100–126 (113 ± 10), $N = 7$; OpcW 162–202 (175 ± 14), $N = 7$).

Avicularia interzooidal (Figure 6B), conspicuous, reasonably numerous. Cystid roundly subquadrate to subrectangular with sloping gymnocrystal walls (AvL 219–319 (260 ± 31), $N = 9$; AvW 159–273 (210 ± 41), $N = 9$). Rostral part equal in size or slightly smaller than opesia part, semi-circular, with proportionately large foramen surrounded by narrow palatal margin and, on proximal side, a complete pivot bar with tiny tubercle(s) simulating midproximal ligula. Proximal part of avicularium semicircular, with small transversely crescentic opesia bordered by broadly crescentic cryptocyst with conspicuous granulation.

Ovicell hyperstomial, often terminal, acleithral [OoL 157–206 (181 ± 17), $n = 9$; OoW 189–218 (201 ± 11), $n = 9$]. Ooeccium (Figures 5E, 6A, B) formed from the roof of the large, distal basal pore-chamber. Most of frontal skeletal surface is endooecium with coarse granules, many tabulate; ectooecium mostly membranous, its calcareous part comprising a very narrow

band around periphery and proximofrontal rim. Opening flanked by distalmost pair of spines.

Interzooidal communications via relatively large and shallow lateral and distal pore-chambers (Figure 6C), each with a single small pore in the middle.

Ancestrula tatiform, with seven periopesia spines and granular cryptocyst encircling opesia.

Remarks

Quitocallopora aviculata gen. et sp. nov. occurred on rocky substrata. The largest (paratype, NIWA 95629) has 31 zooids (12 with ooeccia) and five avicularia. Zooidal basal walls are generally fully adherent to the substratum, but can produce short props – outpocketings of the basal wall – where zooids cross cavities or depressions. All eight colonies in the collection have some zooids that are produced by intramural reparative budding. New buds standing proud of the colony surface begin a new layer of zooids that overgrows the underlying layer. Ancestrular cystids bud autozooids, and both ancestrulae and autozooids can produce up to two stacked zooids frontally.

The species is so far known only from the type locality in the outer Bay of Plenty, North Island, at 310–410 m depth.

Quitocallopora pusilla sp. nov.

(Figure 6E–G)

Callopora precocialis Gordon, 1984: 26 (part).

Material Examined. Holotype: NIWA 1161, Station K795, mid-Kermadec Ridge, New Zealand, 350 m depth.

Paratypes: NIWA 22962, 95618, Station TAN0205/19, mid-Kermadec Ridge, New Zealand, 420–471 m depth.

Etymology. Latin *pusillus*, very little, alluding to the small spot-like colonies.

Description. Colony encrusting, unilaminar, multiserial, small, comprising spots up to 1.4 mm diameter; largest colony with nine zooids including ancestrula.

Autozooids longer than wide, subpyriform, with interzooidal furrows between adjacent lateral walls (ZL 315–583 (450 ± 84), $N = 11$; ZW 252–389 (321 ± 48), $N = 11$). Opesia relatively large, bordered by narrow granular cryptocyst, of almost equal width throughout, a little narrower and non-granular distally (OpsL 157–335 (256 ± 53), $N = 11$; OpsW 174–288 (223 ± 40), $N = 11$). Gymnocyst very narrow laterally, moderately developed proximally. Eleven or 12 well-developed periopodial spines (Figure 6E), sparser proximally, with proportionately stout bases and a high articulation point; acicular beyond this point. Spines straight, near-vertical to inclined slightly outwards distally and proximally, arching a little over opesia proximally; longest spine only $317 \mu\text{m}$. Opercular flap transversely D-shaped, almost parallel-sided, the proximolateral corners turned slightly outwards (OpCL 71–87 (79 ± 11), $N = 2$; OpsW 106–109 (108 ± 2), $N = 2$).

No avicularia seen. Ovicell hyperstomial, terminal, apparently acleithral. Ooecium (Figure 6F) formed from a distal kenozooid visible in lateral profile but not from above. Most of frontal skeletal surface a granular-tubercular endooecium; calcareous part of ectooecium comprising very narrow proximofrontal rim. Opening flanked by distalmost pair of spines (OoL 180–204 (190 ± 12), $N = 3$; OoW 165–182 (174 ± 9), $N = 3$).

Interzooidal communications via relatively large and shallow lateral pore-chambers, each with a single small pore in the middle. Ancestrula tatiform (Figure 6G), with 10–11 periopodial spines and granular cryptocyst encircling opesia (AnL 240–262 (251 ± 16), $N = 2$; AnW 205–256 (231 ± 37), $N = 2$).

Remarks

Quitocallopora pusilla sp. nov. occurred on small rocks and dead scleractinian coral. The two largest of three colonies have nine zooids, one of them with two oecia. Zooidal basal walls are generally fully adherent to the substratum, but, as in *Q. aviculata* sp. nov., can produce short props – outpocketings of the basal wall – where zooids cross cavities or depressions.

Quitocallopora pusilla sp. nov. differs most obviously from *Q. aviculata* sp. nov. in having a smaller colony size and smaller mean zooid size as well as lacking avicularia and possessing a larger number of periopodial spines. As in *Q. aviculata*, there is regeneration of zooids in autozooidal cystids.

The species is so far known only from the mid-Kermadec Ridge at 350–471 m depth.

Genus *Judyella* gen. nov.

Type Species. *Judyella corona* sp. nov.

Etymology. Honorary for Dr Judith E. Winston in recognition of her sterling contributions to bryozoology.

Diagnosis. Colony encrusting, unilaminar, uniserial to multiserial. Autozooids with moderately large subcircular to oval opesia. Cryptocyst periopodial, narrow, of almost equal width throughout, granular. Gymnocyst visible laterally, especially if uniserial, well developed proximally. Articulated spines numerous, upright,

periopodial, equally spaced apart. No avicularia. Ovicell hyperstomial, terminal, acleithral. Ooecium formed from distal kenozooid; ectooecium fully calcified with no frontal suture, furrow or fenestra. Interzooidal communications somewhat intermediate in size and position between mural and basal pore-chambers, uniporous. Ancestrula tatiform, with periopodial spines and granular cryptocyst.

Remarks

Judyella gen. nov. is established here for three New Zealand species that form shortly ramifying or small spot-like colonies. They appear most closely related to *Pyriporoides* Hayward & Thorpe, 1989 and *Olisthella* Gordon & Taylor, 2017, but differ in having an evenly rounded opesia (i.e. not constricted or parallel-sided), a uniformly narrow cryptocyst (i.e. no shelf) and a wholly smooth ectooecium (i.e. no median suture, furrow or fenestra). All three genera have in common an oecium that develops concurrently with a heterozooid, typically a kenozooid (rarely also an avicularium in the case of *Pyriporoides*). Following earlier work on uniserial calloporids (Rosso & Taylor, 2002), Gordon & Taylor (2017) used cladistic analysis to identify an apparent clade within or derived from Calloporidae that included *Pyriporoides* and *Olisthella* (*inter alia*). If molecular sequencing were to support this morphology-based clade, *Judyella* gen. nov. would almost certainly belong to it.

Judyella corona sp. nov.
(Figure 7A–E)

Material Examined. Holotype: NIWA 3714, Station KAH0204/32, Cavalli Seamounts, NE of North Island New Zealand, 780–810 m depth.

Paratypes: NIWA 95607, 95608, same data as holotype.

Other material: NIWA 3715, 95609, Station KAH0204/47, Cavalli Seamounts, NE of North Island New Zealand, 792–880 m.

Etymology. Latin *corona*, crown, alluding to the impressive corona of periopodial spines.

Description. Colony encrusting, uniserial, ramifying (Figure 7A), dichotomously branching, sometimes in small dense aggregations with self-overgrowth; linear colonies up to 9 mm long.

Autozooids more or less roundly subtriangular to pyriform (Figure 7C), widest in distal third (ZL 527–642 (596 ± 30), $N = 15$; ZW 390–527 (454 ± 40), $N = 15$). Opesia subcircular, surrounded by steep narrow cryptocyst with strong granulation except mid-distally where rim is thin and smooth with lamina descending towards basal wall (OpsL 159–258 (203 ± 26), $N = 15$; OpsW 141–221 (180 ± 17), $N = 15$). Cryptocyst surrounded by compact corona of 15–19 (mean 17) basally jointed periopodial spines, these vertical and slightly claviform in distal half of corona, more curved toward opesia and tapering towards spine tip in proximal half (Figure 7A, C, D). Gymnocyst comprising broad sloping sides of autozooidal cystid. No avicularia.

Ovicell hyperstomial, terminal. Ooecium (Figure 7A, E) formed from distal kenozooid that is concealed from frontal view, with smooth completely calcified ectooecium. Cystid of maternal zooid roundly subtriangular, ‘broad-shouldered’ distally, being the widest part of the zooid (OoL 191–223 (210 ± 27), $N + 2$; OoW 199–214 (206 ± 10), $N = 2$). Opesia of ovicellate zooids as in autozooids, with corona of 15 articulated periopodial spines interrupted by oecium; each proximolateral corner of oecium flanked by a pair of spines.

Interzooidal communications (Figure 7E) via pore-chambers that are intermediate between small mural and larger basal pore-chambers in size and position, each uniporous internally.

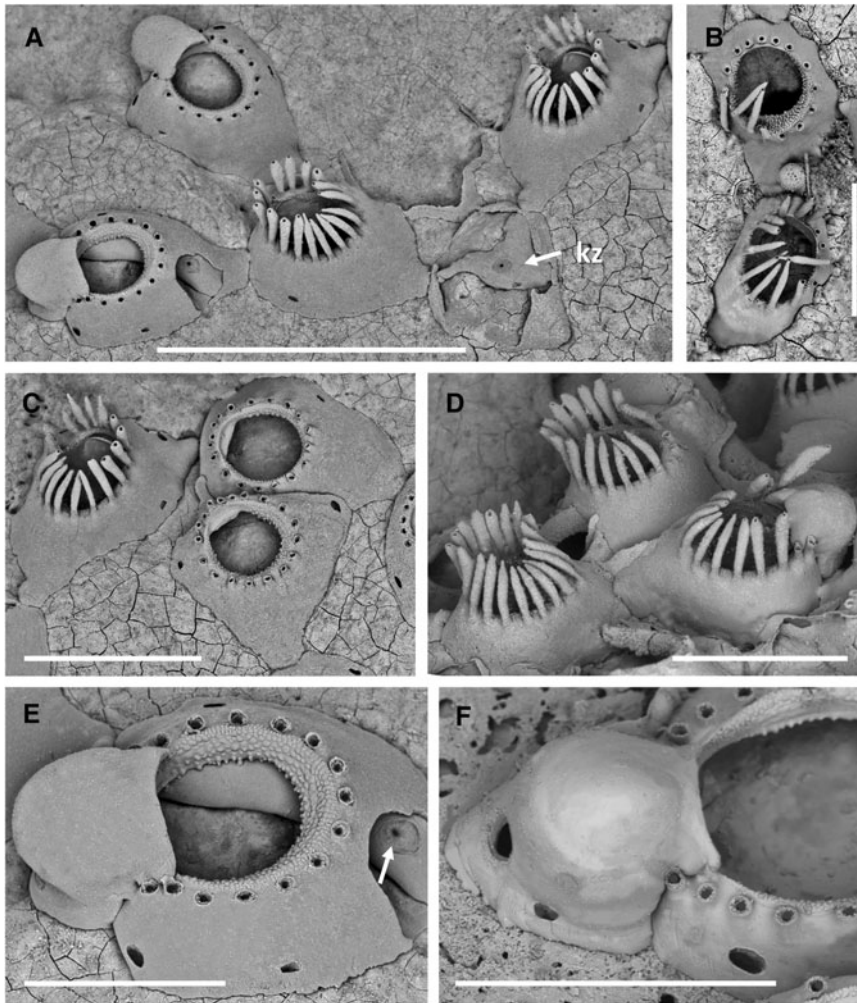


Fig. 7. *Judyella corona* gen. et sp. nov., NIWA 3714, holotype, Station KAH0204/32, Cavalli Seamount: (A) autozooids and ovicellate zooids; one broken autozooid with reparative kenozooid (kz). NIWA 95607, paratype Station KAH0204/47, Cavalli Seamount: (B) ancestrula and daughter zooid. (C) NIWA 3714, autozooids. (D) autozooids and ovicellate zooid. (E), close-up of lower-left ovicellate zooid in A; notice the kenozooid beneath the oecium; uniporous septulum arrowed. (F) *Judyella precocialis* (Gordon, 1984), NIWA 1160, holotype, Station K795, Kermadec Ridge: lateral view of oecium formed by distal kenozooid. Scale bars: A, 1 mm; B, E, 300 μ m; C, D, 500 μ m; F, 200 μ m.

Autozooids and ovicellate zooids budded at diverging angle from distolateral pair of pore-chambers; another pair of pore-chambers, not budding autozooids, present mid-laterally. In ovicellate zooids, pore-chambers present in distolateral shoulders, not budding further autozooids, but in one instance a small kenozooid budded from one such pore-chamber and curved around to distal side of oecium. In another instance, where an autozooid had encountered another autozooid in different branch, a tubular kenozooid passed from a mid-distal position to a lateral pore-chamber of the adjacent zooid. A triangular kenozooid (Figure 7A) budded in one broken autozooidal cystid connecting caudae of two daughter zooids.

Ancestrula (Figure 7B) like autozooids but with only 13 spines (AnL 380, AnW 232, N = 1).

Remarks

Judyella corona sp. nov. is notable for the dense corona of perioesial spines and the triangular, 'broad-shouldered' form of ovicellate zooids. It differs from the following species, *Judyella concordia* sp. nov., in having pyriform zooids and in lacking a spinose process from the oecial kenozooid.

Callopora precocialis Gordon, 1984, is also included in the genus, as *Judyella precocialis* comb. nov. It differs mainly from *Callopora* in that the ectooecium is wholly calcified (Figure 7F). In noting the oecial kenozooid (overlooked by Gordon (1984)), Gordon *et al.* (2009, p. 297) included the species in *Pyriporoides*, but, as noted above, in this genus the opesia is constricted, the cryptocyst has a proximal shelf and the oecium has a median suture of fissure. Scanning electron microscopy of the

paratype specimen of *C. precocialis* has revealed that it belongs to *Quascallopora pusilla* sp. nov. (described above).

Judyella concordia sp. nov.
(Figure 8A–C)

Material Examined. Holotype: NIWA 3709, Station KAH0204/30, Cavalli Seamounts, NE of North Island New Zealand, 800–825 m depth.

Etymology. Alluding to the spinous process of the oecial kenozooid, which resembles the 'droop-nose' of the Anglo-French supersonic passenger aircraft known as *Concorde*, retired in 2003.

Description. Sole colony (Figure 8A) incomplete, encrusting, tiny, comprising four intact zooids (three ovicellate) and tiny remains of two others; size 0.94 mm maximum dimension.

Autozooids broadly suboval to roundly subhexagonal, widest just proximal of midlength (ZL 248–377 (328 ± 57), N = 4; ZW 166–296 (217 ± 57), N = 4). Regeneration of autozooid seen in one older cystid. Opesia also broadly suboval, surrounded by narrow cryptocyst with strong granulation on short steep rim that flattens to smooth narrow shelf around entire opesia (OpsL 147–182 (168 ± 17), N = 4; OpsW 100–125 (114 ± 12), N = 4). Cryptocyst surrounded by ~18 spine bases (no whole spines remaining), most around opesial rim, a few lower on the gymnocyst wall. Gymnocyst comprising broad sloping sides of autozooidal cystid, especially proximally where it can be extended. No avicularia.

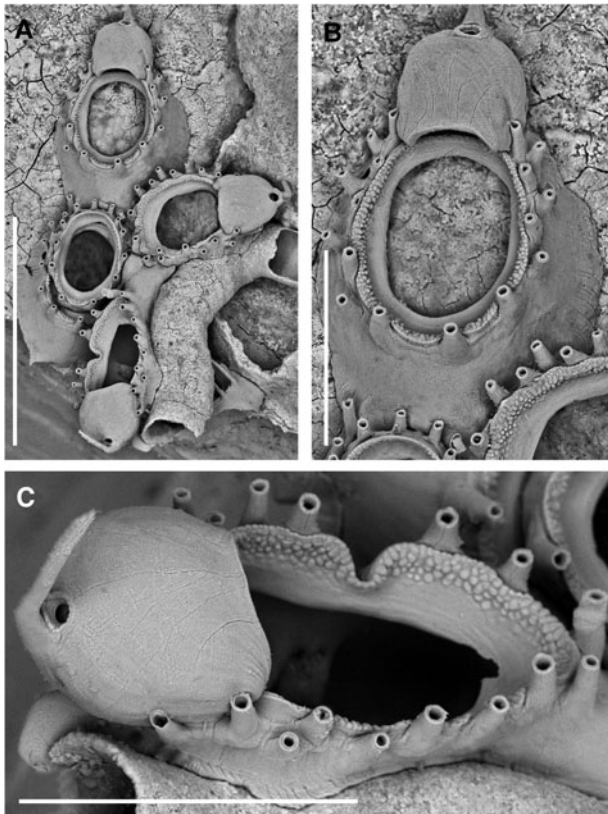


Fig. 8. *Judyella concordia* sp. nov., NIWA 3709, Station KAH0204/30, Cavalli Seamount: (A) ovicellate spot colony lacking ancestrula. (B) close-up of distal ovicellate zooid in A. (C) close-up of proximal ovicellate in A; note the normal disposition of the distal kenozooid spinose projection. Scale bars: A, 500 μ m; B, C, 200 μ m.

Ooecium (Figure 8B, C) with smooth ectooecial calcification, formed by distal kenozooid that is almost wholly concealed. A beak-like spine (Figure 8C) emerges distally below kenozooidal opesia opening and angles frontally over distal midline of ooecium (OoL 128–147 (139 ± 10), $N = 3$; OoW 130–132 (131 ± 1), $N = 3$). Cystid of ovicellate zooid as in autozooids, with 16–20 periopiesal spine bases.

Interzooidal communications via small basal pore-chambers, distributed distally and laterally.

Ancestrula not seen.

Remarks

Judyella concordia sp. nov. is notable for the spinose frontal extension of the ooecial kenozooid. The sole colony occurs on a rock taken from 800–825 m on the Cavalli Seamounts.

Family ANTROPORIDAE Vigneaux, 1949

Genus *Ellisiantropora* gen. nov.

Type Species. *Retevirgula aggregata* Gordon, 1984.

Etymology. A hybrid of the bryozoan genus names *Ellisina* and *Antropora*, alluding to some characters of both that are expressed in the new genus.

Diagnosis. Colony encrusting, unilaminar, multiserial, contiguous. Autozooids with elongate-oval opesia surrounded by very narrow granular cryptocyst of equal width throughout; gymnocyst narrow, confined to sloping lateral walls, a little larger proximally or proximolaterally. No spines. Avicularia comprising a small distolateral pair, interzooidal, with minute pivots, no pivot bar. Ovicell hyperstomial, ectooecium wholly calcified and carinate

with thin median-longitudinal suture line; closure subcleithral. Interzooidal communications via numerous small uniporous basal pore chambers. Ancestrula like later zooids but with periopiesal spines.

Remarks

A new genus is needed to accommodate two species whose affinities have been problematic. One is the nominated type species, *Retevirgula aggregata* Gordon, 1984, which, when described, was noted as lacking two key characters of the type species of *Retevirgula* Brown, 1948, viz connecting tubes between zooids and avicularian pivot bars. There is also no heterozooid associated with the ooecium. It is here renamed *Ellisiantropora aggregata* comb. nov. The second species is *Ellisiantropora tilbrookii* sp. nov. Tilbrook (1998, p. 36) noted that Harmer (1926) had included three morphologies under the name '*Antropora marginella* (Hincks, 1884)', only one of which accorded with Hincks's species (itself a junior synonym of *Antropora minor* (Hincks, 1880b) according to Tilbrook (1998)). One of the morphologies, NHMUK 1928.9.13.18 from Torres Strait, Queensland, was identified by Tilbrook (1998) as *Retevirgula aggregata*. In the event, it differs from *E. aggregata* comb. nov. most obviously in having far fewer avicularia and slightly shorter zooids. It was fully described by Tilbrook (1998, p. 44) in his review of *Antropora*.

The family attribution of *Ellisiantropora* is less straightforward. As indicated by the hybrid name, choices are Ellisinidae and Antroporidae, as well as Calloporidae. All genera currently included in Ellisinidae (see Cook *et al.*, 2018) have an ovicell associated with a heterozooid, either an avicularium (as in *Ellisina* Norman, 1903, *Retevirgula* Brown, 1948 and *Lamourouxia* Hondt d' & Gordon, 1999), a kenozooid (as in *Kenoaplousina* López Gappa & Liuzzi, 2013) or both, as in some species of *Ellisina* (see Hayward & Ryland, 1998, figure 56C, D) and *Retevirgula* (see Gordon, 1986, pl. 4B; but this genus probably needs splitting). If we solely consider the type species of the genera that typify families, *Ellisiantropora* gen. nov. is morphologically closest to Ellisinidae, exemplified collectively by the large, longitudinally oval opesia bordered by a very narrow granular cryptocyst of even width, narrow gymnocyst, basal pore-chambers, interzooidal avicularia lacking pivot-bars and cleithral ovicells that have a wholly calcified ectooecium. *Antropora granulifera* (Hincks, 1880a), typifying Antroporidae, shares some of these characters but has an extensive cryptocystal shelf and endozooidal ovicells with small and indistinct ooecia. *Callopora lineata* (Linnaeus, 1767), typifying Calloporidae, also shares some characters, but has a proportionally larger gymnocyst bearing an adventitious avicularium and the ooecium of the acleithral ovicell has a large exposure of endooecium.

Ellisiantropora gen. nov. also resembles the antroporid genus *Akatopora* Davis, 1934. Both the Eocene type species, *Akatopora clausentina* Davis, 1934 and Recent *Akatopora circumsaepa* (Uttley, 1951) have paired heterozooids that when autozooids are regularly in quincunx, each appears to have a complement of six, as in *E. aggregata*. The heterozooids comprise kenozooids and avicularia, the latter having a semicircular mandible in the Recent species. When bleached, some avicularia can resemble kenozooids owing to the absence of mandibular pivots. The main additional differences between the two genera are the lesser exposure of gymnocyst (vestigial in *A. circumsaepa*) and non-hyperstomial ovicells in *Akatopora*, as well as intramural frontal budding and multilamellar growth in the Recent species of this genus. Interestingly, a molecular-genetic study of New Zealand cheilostomes has shown that *Ellisiantropora aggregata* (as *Retevirgula aggregata*) and *Akatopora circumsaepa* group with total support in a monophyletic clade distant from a species

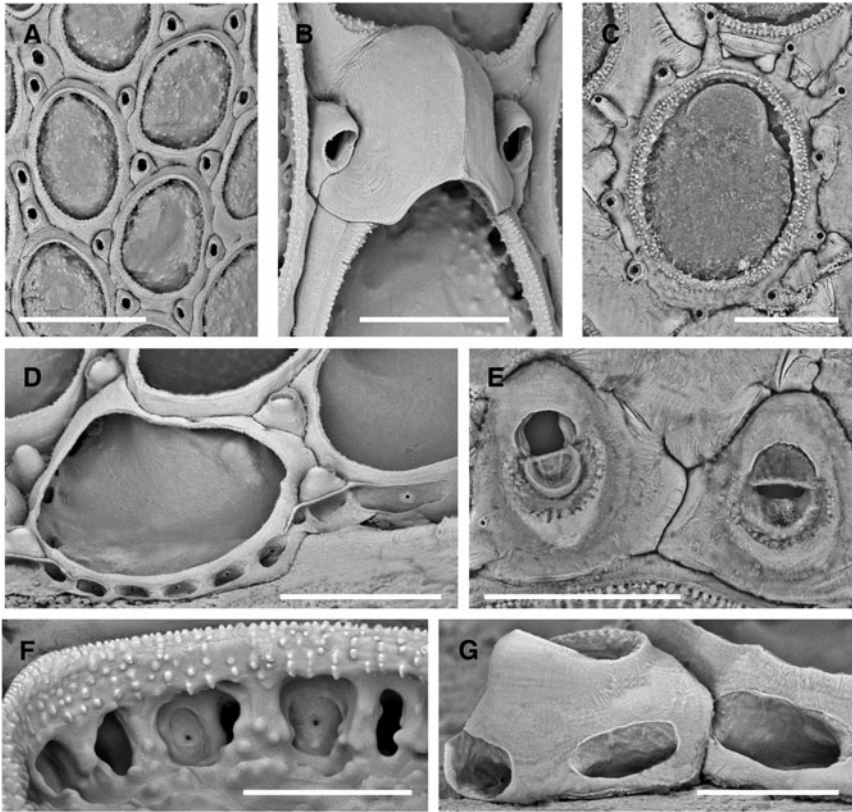


Fig. 9. *Ellisantropora aggregata* (Gordon, 1984): NIWA 120104, Station B455, NW South Island: (A) part of colony showing disposition of interzooidal avicularia. (B) carinate oecium. NIWA 120103, NW South Island: (C) tatiform ancestrula. (D) NIWA 120104, developing zooid at colony margin showing numerous basal pore-chambers. (E) NIWA 120103, interzooidal avicularia with mandibles in open (left) and closed (right) positions. (F) NIWA 120104, interior view of lateral wall showing recessed uniporous septula. (G) same, interzooidal avicularium with basal pore-chambers. Scale bars: A, 500 µm; B, 200 µm; C, E, F, 100 µm; D, 300 µm; G, 50 µm.

of *Ellisina* (Orr *et al.*, 2021). For this reason, *Ellisantropora*, which lacks the ellisinid character of an ooeial heterozooid, having instead its ooeium formed by the distal autozooid, is provisionally included in Antroporidae. Inasmuch as *Antropora* has yet to be sequenced, this association has yet to be confirmed.

Ellisantropora aggregata (Gordon, 1984)

(Figure 9A–G)

Retevirgula aggregata Gordon, 1984, p. 27, pl. 2D; Gordon, 1986, p. 30.

'*Retevirgula*' *aggregata*: Gordon *et al.*, 2009, p. 289.

Material Examined. Holotype: NIWA 1266, Station K855, Curtis Island, Kermadec Ridge, New Zealand, 115–125 m depth.

Paratype: NIWA 1267, same data as holotype.

Other material: NIWA 120103, 120104, Station B455, north-west South Island, New Zealand, 54 m.

Redescription. Colony encrusting, unilaminar, multiserial, contiguous, up to 6 mm maximum dimension.

Autozooids more or less elongate-oval to roundly subhexagonal (ZL 365–702 (523 ± 105), N = 15; ZW 322–489 (371 ± 45), N = 15). Elongate-oval opesia (Figure 9A) surrounded by very narrow and steep granular cryptocyst of equal width throughout (OpsL 247–523 (388 ± 83), N = 15; OpsW 247–406 (297 ± 43), N = 15). Operculum semicircular, terminal in membranous frontal wall. Gymnocyst narrow, smooth, confined to sloping lateral walls, a little larger proximally or proximolaterally. No spines.

Avicularia (Figure 9A, B, D, E, G) small, interzooidal, comprising a small distolateral pair; hence, when autozooids are in regular quincunx, each appears to be surrounded by six avicularia – a distolateral pair, lateral pair, proximolateral pair – but this pattern can vary at the bifurcation of zooid rows (AvL 112–194 (139 ± 23), N = 15; AvW 61–137 (79 ± 18), N = 15). A few accessory identical or smaller such avicularia budded adventitiously from interzooidal avicularia (Figure 9A). Rostral part of avicularium a little smaller than postmandibular part, semicircular, elevated

frontalwards, the proximolateral corners projecting as tiny pointed cusps; no pivot-bar. Avicularian opesia bordered by steep crescentic cryptocyst with granular outer margin, with minute pivots. Rarely an interzooidal space is available that is occupied by either a kenozooid, larger-than-usual avicularium or very small autozooid.

Ovicell (Figure 9B) hyperstomial, appearing subcleithral in dried material. Ectooecium wholly calcified and carinate with thin median-longitudinal suture line; proximal corners of ooeium flanking operculum; ovicell closure subcleithral (OoL 201–265 (239 ± 33), N = 3; OoW 251–297 (271 ± 24), N = 3).

Interzooidal communications via numerous small uniporous basal pore chambers; these laterally narrow, each internal opening recessed and flanked by irregular buttresses (Figure 9F). Interzooidal avicularia also with small basal pore-chambers (Figure 9G).

Ancestrula (Figure 9C) like later zooids but with 11 periopiesial spines (AnL 236–251 (243 ± 10), N = 2; AnW 209–220 (215 ± 8), N = 2).

Remarks

Mean zooid length and width in *Ellisantropora aggregata* comb. nov. are 523 µm and 371 µm, respectively, compared with 410 µm and 300 µm in *Ellisantropora tilbrooki* sp. nov. from Torres Strait (Tilbrook, 1998). The size difference could be a consequence of higher temperatures in Torres Strait, but *E. tilbrooki* sp. nov. also has far fewer avicularia. In New Zealand, *E. aggregata* occurs on molluscan shell fragments from 54–490 m depth from north of Raoul Island (Kermadec Ridge) to north-west South Island. No information is given in Harmer (1926) or Tilbrook (1998) concerning substratum or depth for *E. tilbrooki* sp. nov.

Family ELLISINIDAE Vigneaux, 1949

Genus *Rhizellisina* gen. nov.

Type Species. *Rhizellisina rhizoidea* sp. nov.

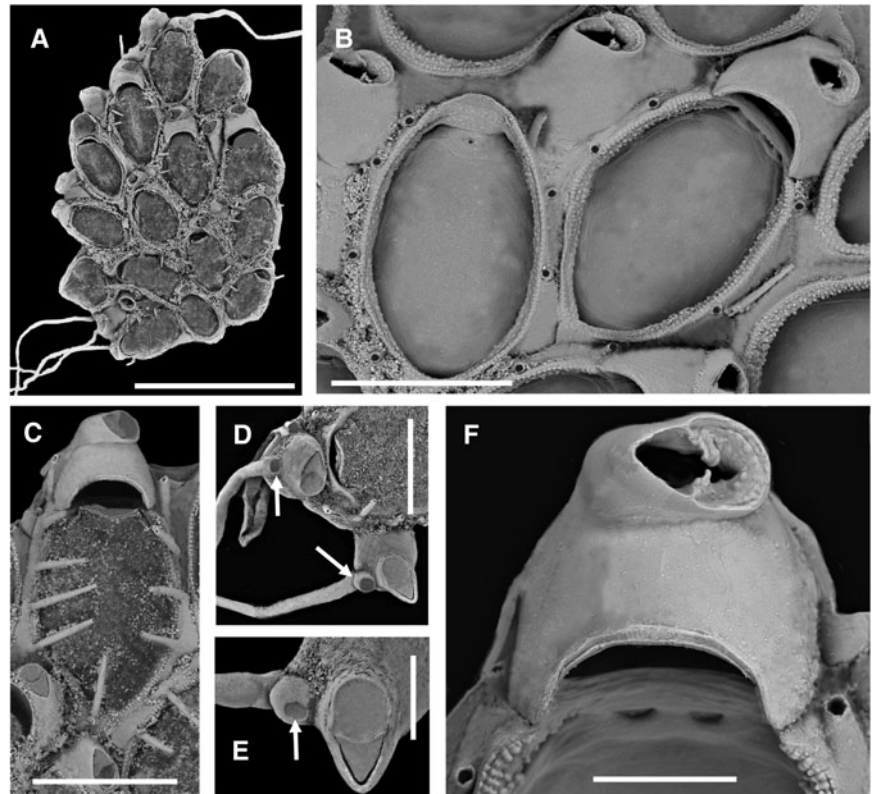


Fig. 10. *Rhizellisia rhizoidea* gen. et sp. nov.: (A) NIWA 95627, Station E416, Bounty Trough: operculate ovicellate colony with some rootlets evident. (B) same, bleached fragment with ovicellate zooid, avicularia and spine bases. (C) NIWA 95624, Station S150, Bounty Trough: ovicellate zooid with periopodial spines. (D, E), same, showing cuticular window on geniculations where rootlets issue from avicularia. (F), NIWA 95627, close-up of oocelial avicularium. Scale bars: A, 1 mm; B, C, 300 μ m; D, E, 200 μ m; F, 100 μ m.

Etymology. Greek, *rhiza*, root, plus *Ellisina*, a bryozoan genus, alluding to the presence of rootlets (rhizoids).

Diagnosis. Colony small, unilaminar, multiserial, supported on soft sediment by slender rootlets that issue from basal pore-chambers in autozooids and avicularia. Sparse articulated spines bordering distal half of opesia. Avicularia interzooidal, with mandibular pivots only. Ovicell hyperstomial, cleithral. Ooecium associated with avicularian cystid, which forms its floor and crowns its summit; closure subcleithral, ectooecium wholly calcified, smooth. Basal pore-chambers present, with uniporous septula on interior walls. Ancestrula like later zooids.

Remarks. A new genus is required for a deep-sea species resembling *Ellisina* but having very small colonies of 16 autozooids or fewer that are planar and unilaminar but elevated horizontally above a very-fine sediment surface by slender rootlets. Articulated spines, borne on the gymnocyst, are also present. These are lacking in the type and other species of *Ellisina* Norman, 1903.

Rhizellisia rhizoidea sp. nov.
(Figure 10A–F)

Material Examined. Holotype: NIWA 95622, Station S151, Bounty Trough, eastern South Island, New Zealand, 1586 m depth.

Paratypes: NIWA 96523, same data as holotype; NIWA 95624, Station S150, Bounty Trough, 1640 m; NIWA 95625, Station S152, Bounty Trough, 1676 m; NIWA 95626, Station S153, Bounty Trough, 1386 m.

Other material: NIWA 95627, Station E416, head of Bounty Trough, eastern South Island, New Zealand, 1225 m.

Description. Colony small, planar, unilaminar, multiserial, supported horizontally above soft sediment by slender rootlets (Figure 10A). Delicate, suboval to slightly flabellate in shape.

Largest colony with 16 feeding zooids (including ancestrula), diameter 2.3 mm.

Autozooids mostly rounded elongate-subhexagonal (ZL 475–593 (516 ± 47), $N = 18$; ZW 328–433 (349 ± 29), $N = 18$). Opesia large, elongate-oval, sometimes a little acute proximally, bordered by very narrow steeply descending granular cryptocyst of equal width throughout (OpsL 393–443 (413 ± 19), $N = 7$; OpsW 245–319 (267 ± 26)). Operculum terminal in membranous frontal wall, semicircular. Gymnocyst smooth, very narrow, or a little more visible in proximal half of zooid; bearing bases of 4–9 slender articulated spines (Figure 10B, C), mostly in distal half of zooid though occasionally a spine may occur in mid-proximal position.

Avicularia interzooidal (Figure 10B), cystid smooth, base four-sided to triangular; frontal face orientated transversely, rostrum inclined obliquely frontalwards, triangular with virtually no palate, tip slightly rounded; mandibular pivots stout; post-mandibular cryptocyst relatively broad, steep, granular, opesial part of avicularian foramen much smaller than rostral part (AvL 73–250 (176 ± 71), $N = 12$; AvW 124–207 (176 ± 71), $N = 12$).

Ovicell hyperstomial, cleithral. Ooecium formed by avicularium (Figure 10B, C, F), the cystid of which constitutes its floor and projects transversely on distal summit of ooecium; ectooecium wholly calcified, smooth. Each proximolateral corner flanked by a spine (OoL 130–168 (143 ± 13), $N = 10$; OoW 170–229 (213 ± 17), $N = 10$).

Basal pore-chambers small, two on each lateral wall of autozooid, each opening to interior via a uniporous septulum; distal transverse wall with 1–2 uniporous septula ($\sim 16 \mu$ m diameter) communicating with distal autozooid or avicularium, but having 2–3 such septula ($\sim 22 \mu$ m diameter) when communicating with oocelial avicularium.

Rootlets each issuing from a basal pore-chamber, typically pertaining to an avicularium, but some autozooids may have a rootlet. One partly broken isolated zooid (not an ancestrula) with one lateral rootlet plus three associated avicularia, each with 1–2

rootlets. These rootlets geniculate at point of attachment with parent autozoid/heterozoid, each with a cuticular window on the 'knee' (Figure 10D, E).

Ancestrula like later zooids, usually with six spines and a distal avicularium. Daughter zooids can be budded on each side distolaterally and laterally or these positions occupied by one or more avicularia (AnL 396; AnW 254; N = 1).

Remarks

The bottom sediment at the stations where *Rhizellisia rhizoidea* gen. et sp. nov. occurred comprised a mix of fine terrigenous and planktonic particles. Colonies were presumably elevated above the sediment surface (rather than lying sideways) by the cluster of rhizoids, which are up to 3.7 mm long in some colonies. Some 20–38% of zooids in the largest colonies were ovicelled.

The species is so far known only from a relatively small area of the Bounty Trough, off eastern South Island, New Zealand, at depths of 1225–1676 m.

Family VINCULARIIDAE Busk, 1852b

Genus *Vincularia* Defrance, 1829

Type Species. *Vincularia fragilis* Defrance, 1829.

Remarks. The family Vinculariidae and genus *Vincularia*, long regarded as extinct, are included in this account in order to validate their existence in the Recent marine biota, accompanied by a full description and illustrations. Previously, the existence of *Vincularia* had been noted in the New Zealand-region bryofauna only in a list of taxa (Gordon *et al.*, 2009, 2019).

Cheetham (1966) clarified the status of *Vincularia*, affirming that it was known with certainty only from the Eocene of England and Europe (Cheetham, 1966). Subsequently, additional species were recognized in the Eocene and Oligocene of the USA and Oligocene of France (Cheetham, 1973). Several species were described from the early to late Miocene of Indonesia (Di Martino & Taylor, 2014) and an undescribed putative species of *Vincularia* has been recognized from the early to middle Miocene of the Dominican Republic (<https://nmita.rsmas.miami.edu/database/bryozoa/systemat/vincusp.htm>). Di Martino & Taylor (2014) also referred an Indian Miocene species to *Vincularia* and noted the existence of an undescribed Miocene species from Tanzania.

Busk (1852b, p. 2; 1854, p. 95, pl. 65, figure 2) was the first to name the family Vinculariidae (as Vinculariadae), validly basing it on monotypic *Vincularia* Defrance, 1829 and including some other fossil and living genera in the family. Judging from his sole illustrated species attributed to *Vincularia*, which appears to be a species of *Ogivalia* Jullien, 1882, Busk's understanding of the genus did not conform to the type species of *Vincularia*, which is hardly surprising, given the inadequacy of Defrance's (1829) description and illustrations. Canu (1907), who noted that Defrance's type material was housed at the University of Caen, gave the first comprehensive description of *V. fragilis* based on additional new material, highlighting the asymmetrical nature of the abfrontal polymorphs. Because they were 'divergent', Canu called them 'zoécies D', i.e. D-zooids. Bizarrely, he unnecessarily introduced a new genus, *Heterocella*, for four French Eocene species with D-zooids, nominating *V. fragilis* as type species. Cheetham (1966) was uncertain of the avicularian status of the D-zooids, whereas Di Martino & Taylor (2014) referred to them as 'avicularian autozooids', in contradistinction to the very small adventitious avicularia that are also typical. The large asymmetrical avicularian polymorphs are absolutely characteristic of the genus and family and occur in *Vincularia regia* sp. nov., a

living species restricted to deep water on the Three Kings Ridge north of New Zealand.

Vincularia regia sp. nov.

(Figure 11A–D)

Vincularia sp. Gordon *et al.*, 2009, p. 290; Gordon *et al.*, 2019, p. 16.

Material Examined. Holotype: NIWA 146137, Station U595, Three Kings Ridge north of Tui Seamount, New Zealand, 1474 m.

Paratype: NIWA 146136, same data as holotype.

Other material: NIWA 146101, Station U581, Three Kings Ridge, New Zealand, 1170 m; NIWA 146135, Station U582, Three Kings Ridge, New Zealand, 790 m.

Etymology. Latin *rex, regis*, king, alluding to the Three Kings Ridge.

Description. Colony fragments erect, quadri- to multiseriate, to 10 mm long and 1.3 mm wide.

Stems basally quadriseriate, comprising a pair of autozooids and a pair of avicularian morphs, expanding progressively into 5–6 longitudinal autozooidal series frontally (Figure 11A) while the abfrontal surface comprises increasingly larger avicularia in just the two series (Figure 11B, D). Increase in number of longitudinal autozooidal series achieved by simultaneous distal bifurcation (Figure 11C) of both avicularia of an alternating pair into a distal daughter avicularium and a laterodistal autozoid precursor of transitional morphology; these latter, one on each side, in turn bud a daughter autozoid that is proximal-most in its longitudinal series. Autozooids elongate-subhexagonal, symmetrical, with raised cryptocystal margin steeply surrounding an elongate-oval opesia (Figure 11C); proximal third of autozoid a concave lightly granular cryptocystal shelf (ZL 893–1064 (992 ± 63), N = 14; ZW 433–532 (485 ± 30), N = 14; OpsL. 618–716 (670 ± 34), N = 14; OpsW 202–293 (248 ± 30), N = 14). Distal zooidal wall sloping obliquely inwards toward basal wall, with a conspicuous pair of occlusor muscle scars and, below them, a pair of distobasal communication pores. No gymnocyst. No oral spines.

Large vicarious avicularia abfrontal only (Figure 11 B–D), slightly alternating, in two longitudinal series except where bifurcation of a new longitudinal series laterally interpolates a third avicularium. Cystids asymmetrical, curving outwards towards margin of stem on each side, with raised rims. Cryptocyst granular, shelf-like proximally, moderately broad laterally, tapering abruptly distally. No differentiation into separate rostral or opesial parts and no trace of condyles. Opesia elongate-oval to round, bounded distolaterally by cystid rim (AnL 857–1652 (1219 ± 227) N = 14, AvW 560–1137 (812 ± 213) N = 14). Mandibles not seen. Small adventitious structures, interpreted to be avicularia also present, 1–2 at proximal corner(s) of large avicularian cystids. No condyles or pivot bar.

Ooecia not seen. Ancestrula not seen.

Remarks

All available stems are unbranched, slightly eroded and lacking cuticular parts and were clearly transported. Regrettably, this means that there is no information on mode of attachment, maximum colony size, articulation or the nature of the avicularian polymorphs (do they have polypides?) and their mandibles. The new Indonesian Miocene species described by Di Martino & Taylor (2014) had large avicularian morphs that were relatively little differentiated from autozooids and it is possible, perhaps even highly likely, that they had polypides. The triangular nature of the small adventitious polymorphs in these species, exquisitely

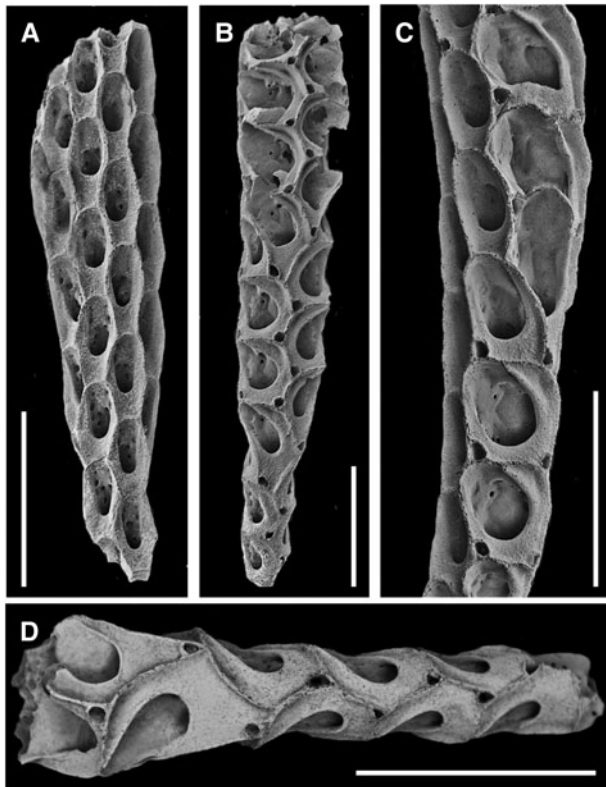


Fig. 11. *Vincularia regia* sp. nov.: NIWA 146101, Station U581, Three Kings Ridge: (A) frontal side of a stem showing autozooids. (B) abfrontal side of a stem showing avicularia. (C) partly lateral view of a stem showing bifurcation of an avicularian zooid row into a longitudinal series of autozooids to the left and an avicularian series to the right (cystids damaged). NIWA 146137, Station U595, Three Kings Ridge: (D) proximal end of a stem showing abfrontal surface with abrupt change in avicularian dimensions. Scale bars: A–D, 2 mm.

preserved, confirm that they were avicularia without pivots, in contradistinction to rootlet pores, which were present in one species and round. In contrast, Cheetham (1973) illustrated the small adventitious avicularia in *Vincularia fragilis* with distinct pivot bars. Whereas the Miocene species illustrated by Di Martino & Taylor (2014) had large avicularian morphs that, like *V. fragilis*, were relatively little differentiated, these morphs in *V. regia* sp. nov. are rather more like those in Eocene *Vincularia monstrosa* (Canu, 1907), which were more-expanded and asymmetrical; furthermore, they became distally transformed into female zooids with vestigial oecia, which is not the case in *V. regia* sp. nov.

Ordinary autozooids in *V. regia* sp. nov. strongly resemble those in *Bryopastor* Gordon, 1982 (family Bryopastoridae) and the two families may have diverged from a common stem. That stem may include Quadricellariidae, species of which have quadriserial branches. Interestingly, Cheetham (1966) included both *Nellia* Busk, 1852b (currently in Quadricellariidae) and *Vincularia* in the same family (Farciminariidae). While species of *Farciminaria* Busk, 1852b are quadriserial, they lack a cryptocyst, have conspicuous spines, and the kenozooidal oecium is large and conspicuous with a spinose endooecium and wholly membranous ectooecium, so Farciminariidae appears wholly unrelated to *Vincularia*. '*Vincularia*' *anceps* Brown, 1952 from the early Miocene of New Zealand does not belong to *Vincularia*, as noted by Brown – it appears to be a bryopastorid, possibly related to *Bryopastor* or *Pseudothyracella* Labracherie, 1975.

The three stations on the Three Kings Ridge are geographically isolated and in deep water and the chances of obtaining fresh material are presently remote. Nevertheless the finding of a living

example of *Vincularia* in the New Zealand region highlights the possibility that there might be other, yet-undiscovered, species elsewhere in the deep-sea. Given the widespread distribution of the genus in the Miocene, it is not improbable.

Family Incertae sedis
Genus *Radixenia* gen. nov.

Type Species. *Radixenia radians* sp. nov.

Etymology. From Latin *radius*, ray, spoke, plus Greek *xenos*, stranger, alluding to the radial arrangement of the zooids in the colony of a strange new bryozoan.

Diagnosis. Colony small, encrusting, unilaminar, comprising clavate autozooids attached to and radiating outwards from ancestrula, with some budding beyond these. Cystid with gymnocystal surface, especially proximally. Opesia elongate-oval, bordered by granular-tubercular cryptocyst that may be a little broader mid-proximally. Basal wall interior nodular, with a pair of large opercular occlusor-muscle scars. No spines. Avicularia interzooidal with open-channelled rostrum and minute pivots. Ovicells not seen. Basal pore-chambers present. Ancestrula kenozooidal.

Remarks

A new genus is required for an unusual encrusting cheilostome that has multiple zooids (nine in life) produced from the ancestrula. These radiate outwards all around the ancestrula, budding additional autozooids and interzooidal avicularia between them. A cirlet of multiple daughter zooids appears to be unique in Cheilostomata but is known in Ctenostomata. Silén (1942, figure 38) illustrated multiple stolon segments (kenozooids) attached to the non-feeding ancestrula of a vesiculariid. In particular, Silén (1942, 1944) described *Labriostomella gisleni* Silén, 1941 as having a small (100 µm diameter), flattened kenozooidal ancestrula with 10–15 tubular autozooids arising from it, each autozooid comprising the basis of an erect, bifurcating branch. When originally described, the species was interpreted as a cheilostome, but Silén (1944, pp. 7, 8) admitted that he had been mistaken in stating that the species was calcified.

Some cheilostomes produce an ancestrular complex, with 2–6 zooidal components depending on the species (e.g. Cook, 1973, 1985; Cheetham *et al.*, 2007; Ferretti *et al.*, 2007), but this differs from what is seen in *Radixenia radians* gen. et sp. nov., in which the ancestrula must be formed first, there surely not being enough nutrient reserves to support the simultaneous formation of nine daughter zooids. Silén (1942) interpreted the multiple autozooidal buds in the ancestrula of *L. gisleni* as analogous to, and originating from, spines, such that the ancestral cheilostome should have had an erect colony formed by means of frontal budding, an interpretation that is not presently supported by the fossil record (Taylor, 1990).

Although multiple zooidal budding from the ancestrula in *R. radians* sp. nov. would seem to be a plesiomorphic feature, the interzooidal avicularia, almost certainly setiform in life, are a fairly derived feature. The autozooids, with large oval opesiae, in conjunction with the heterozooids, recall those in such families as Heliodomidae Vigneaux (1949) and Biselenariidae Håkansson & Zágorský (2020). In these families, however, which are morphologically very close, ancestrulae resemble autozooids. In Heliodomidae, ancestrulae directly bud two autozooids and two avicularia (Hayward & Cook, 1979); in Biselenariidae, ancestrulae are cormidial and always associated with an avicularium of unique morphology when metamorphosed. A larger avicularium is

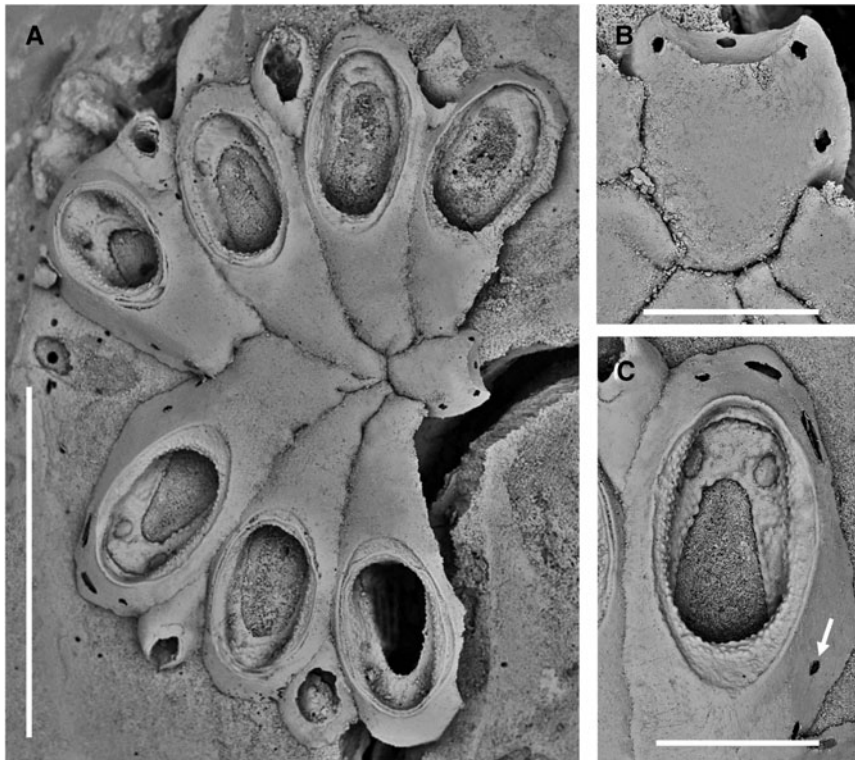


Fig. 12. *Radixenia radians* gen. et sp. nov., NIWA 127657, Station G3, Norfolk Ridge: (A) sole ancestrulate specimen, with clavate autozooids and interzooidal avicularia (all damaged). (B) kenozooidal ancestrula with proximal ends of five daughter autozooids and communication pores where four others had been connected. (C) best-preserved autozooid, showing window in basal wall and two large opercular occlusor-muscle scars; note fractures in thin distolateral wall; a pore-chamber opening is seen at lower right (arrow). Scale bars: A, 1 mm; B, 200 μ m; C, 300 μ m.

budded laterally from the ancestrula, and the two avicularia each had a concentric spiral of autozooids, all of which have a distolateral avicularium. Heliodomids are ovicellate, whereas ovicells have not been seen in Biselenariidae. Inasmuch as *Radixenia* gen. nov. has a kenozooidal ancestrula, multiple ancestrular budding, caudate autozooids, no spiral growth and no ovicells seen, inclusion in these two families is precluded. Establishment of a new family to accommodate *Radixenia* would be premature based on one incomplete colony so the genus remains *incertae sedis*.

Radixenia radians sp. nov.
(Figure 12A–C)

Material Examined. Holotype: NIWA 127657, Station G3, northern Norfolk Ridge, 710 m.

Etymology. Latin *radians*, radiating, alluding to the radial arrangement of zooids.

Description. Colony small, encrusting, unilaminar; partly broken, but when intact would have comprised nine clavate autozooids attached to and radiating outwards from ancestrula (Figure 12A). Some additional zooids budded between the most proximal pair, conferring asymmetry in budding and overall sub-oval shape to colony. Maximum diameter 2.12 mm.

Autozooids elongate, narrowing proximally. Cystid (Figure 12C) mostly with gymnocrystal surface, narrowest distally and along sloping lateral walls, extensive in caudate part of zooid; proximally very narrow and tapering toward point of attachment with ancestrula or, if budding from another autozooid, truncate proximally (ZL 723–1063 (940 \pm 124), N = 7; ZW 341–395 (372 \pm 20), N = 7). Opesia elongate-oval, bordered by inward sloping granular-tubercular cryptocyst that may be a little broader mid-proximally; surface smoother in arcuate mid-distal portion (OpsL 322–478 (412 \pm 48), N = 7; OpsW 185–246 (215 \pm 19), N = 7). Basal wall with fairly large elongate-oval to pyriform

window; interior surface of basal wall unusually nodular, with a pair of large opercular occlusor-muscle scars. No spines.

Avicularia (Figure 12A) inserted in distolateral angles between adjacent autozooids; each more or less teardrop-shaped, with distal margin of opesia damaged, but one example showing an apparent open channel distally, flanked by an indication of minute pivots for a probable setiform mandible (AvL238–341 (305 \pm 39), N = 5; AvW 176–229 (201 \pm 20), N = 5).

No oecia seen.

Interzooidal communications apparently via basal pore-chambers judging by external openings in distolateral gymnocrystal.

Ancestrula kenozooidal (Figure 12B), somewhat shield-shaped in outline, i.e. mostly rounded but with concave distal margin; relatively large communications pores showing where autozooids have become detached. Frontal surface gymnocrystal, smooth (AnL 300, AnW 249, N = 1).

Remarks

The sole colony encrusts a small piece of thin shell that broke, revealing the relationship between the ancestrula and autozooids. The colony was dead and partly eroded, with no cuticular structures remaining. Some partly broken lateral walls indicate that they are triangular in cross section and hollow, with basal pore-chambers delimited within the hollow space. If this interpretation is correct, then it is a very curious arrangement. The genus *Villicharixa* Gordon, 1989, nominally an electrid, is known to have a continuous hollow space running within the lateral walls, but there is no delimitation of pore-chambers within that space. Taylor (2020) recently described separated hollow spaces in lateral walls in *Wawalia* Dzik, 1975, also nominally an electrid.

One side of the ancestrula of *Radixenia radians* gen. et sp. nov. has a concave facet, indicating that the daughter zooid produced from the communication pore in that facet may have been larger than the others, or that the holotype specimen conserves only the distalmost part of a larger colony.

Superfamily MICROPOROIDEA
Family GRANOMURIDAE fam. nov.

Type Genus. *Granomurus* gen. nov.

Diagnosis. Colony encrusting, unilamellar, multiserial. Autozooids with extensive convex, granular cryptocyst underlying the membranous frontal wall; imperforate or with a few marginal pores. No frontal gymnocyst. Opesia small; operculum occupying half opesial length. Articulated spines tiny, ephemeral and lateral to opesia or short, permanent and distal. No avicularia. Ovicell hyperstomial, acleithral. Ooecium escharelliform, formed by distal autozoid and having fully calcified endooecium and continuity of wholly membranous ectooecium with membranous frontal wall. Basal pore-chambers well developed. Ancestrula not seen.

Remarks

Granomuridae is established for two genera – *Granomurus* gen. nov. and *Reussinella* Gordon, 2009. Both conform to the family diagnosis above; in *Granomurus* the opesia is wider than long with a raised distolateral rim and there are only tiny ephemeral spine bases lateral to the opesia and no frontal cryptocystal pores; in *Reussinella* the opesia is longer than wide with a proportionately larger operculum and no surrounding rim, there are two short oral spines distally, and the cryptocyst has sparse perforations near the proximolateral margin. Whereas *Granomurus* is neozelanic, *Reussinella* is Arctic-Boreal. The ooecium is described according to the terminology of Ostrovsky (2013).

When Gordon (2009) established *Reussinella* he noted the challenge of family attribution, pointing out that it did not wholly conform to the Calloporidae, Aspidostomatidae or Microporidae while provisionally including it in the latter. In the strict sense, as based on the type genus, species of Microporidae should have a combined opesia-orifice. Circumscription of Microporoidea, and which families may be included, is more problematic. It is almost certain that the superfamily as presently conceived comprises several lineages having calloporoidean ancestry, thus comprising a polyphyletic assemblage. Until these relationships are resolved in space and time, the scope of Microporoidea is uncertain; at present, taxa that exhibit an extensive cryptocyst, small opesia and little or no gymnocyst, including Granomuridae, may provisionally be included in the superfamily. Granomuridae differs from Aspidostomatidae and Microporidae in lacking a combined opesia-orifice and avicularia; it differs further from Aspidostomatidae in having basal pore-chambers and oral spines (ephemeral or well developed).

Genus *Granomurus* gen. nov.

Type Species. *Granomurus convexus* sp. nov.

Etymology. Latin *granum*, seed, *granosus*, seedy, grainy, and *murus*, wall, alluding to the granular surface of the zooidal frontal cryptocyst.

Diagnosis. As for the family diagnosis, with a wider-than-long opesia in which the opercular sclerite occupies the distal part, a raised opesial margin, tiny spine bases lateral to opesia, and no cryptocystal pores.

Remarks

The genus is presently monotypic.

Granomurus convexus sp. nov.
(Figure 13A–C)

cf. *Aspidostoma* sp. Gordon, 1986, p. 74, pl. 28F.

Material Examined. Holotype: NIWA 27763, Station TAN0604/116, north slope, central Chatham Rise, 950–1045 m.

Paratype: NIWA 95594, same data as holotype.

Other material: NIWA 146151, Station S45, SE Campbell Plateau, 1262 m. Unregistered, Station E796, Fiordland coast, 226–251 m.

Etymology. Latin *convexus*, convex, alluding to the convex frontal cryptocyst.

Description. Colony encrusting, unilaminar, multiserial, contiguous, up to 7 mm maximum diameter.

Autozooids (Figure 13A) subhexagonal (ZL 741–979 (891 ± 71), N = 17; ZW 558–905 (722 ± 97), N = 17). Opesia small (Figure 13B), c. one quarter zoid length, wider than long, with inner distal and proximal margins subparallel; outer distal and lateral margins elevated, slightly flared with granular rim; narrow skeletal surface surrounding opesia smooth (OpsL 175–248 (201 ± 22), N = 17; OpsW 243–286 (266 ± 16), N = 17). Cryptocyst convex, densely granular, with no pores or opesiules. Operculum semicircular, occupying half opesial length. No frontal gymnocyst. Spine bases very tiny, one either side of opesia on zooidal margin.

No avicularia.

Ovicell (Figure 13C) hyperstomial; ooecium formed by distal autozoid; skeletal surface endooecial, continuous with cryptocyst of distal zoid and equally granular; ectooecium wholly cuticular, continuous with membranous frontal wall (OoL 270–308 (292 ± 11), N = 8; OoW 307–351 (330 ± 14), N = 8). Acleithral; opening high-arched, subvertical or inclined a little distad.

Interzooidal communications via basal pore chambers; these fairly widely open, with cuticular surface.

Ancestrula not seen.

Remarks

Gordon (1986) described a small infertile colony of this species from the Fiordland coast and noted its similarity not only to *Aspidostoma* Hincks, 1881 but also to *Reussinella arctica* (Osburn, 1950) (as *Euritina*). More material has confirmed its relationship to *Reussinella*, but not to *Aspidostoma*, and expanded knowledge of its geographic and depth range, from the north slope of the Chatham Rise to the southern Campbell Plateau at depths of 226–1262 m. The genus and species are presently endemic to New Zealand.

Superfamily BUGULOIDEA Gray, 1848

Family BUGULIDAE Gray, 1848

Genus *Carolanna* gen. nov.

Type Species. *Carolanna schackae* sp. nov.

Etymology. Honorific for Dr Carolann Schack, a bryozoologist of exceptional talent.

Diagnosis. Colony erect, supported by rootlets, uniserial, with branch bifurcations at intervals. Autozooids elongate, arranged in chains, each zooid slightly overlapping daughter zooid distally, separated by joint. Opesia occupying entire frontal surface, bordered by non-articulated spines. No avicularia. Ovicellate zooid wider distally than autozoid. Ovicell hyperstomial, terminal, cleithral, closed by large dimorphic operculum; ooecium kenozooidal, budded from maternal zooid; endooecial calcification smooth, ectooecium cuticular. Ovicellate zooid with only 6 pairs of spines, the distal pair stoutest, flanking ooecium. Ancestrula erect, proximally attached.

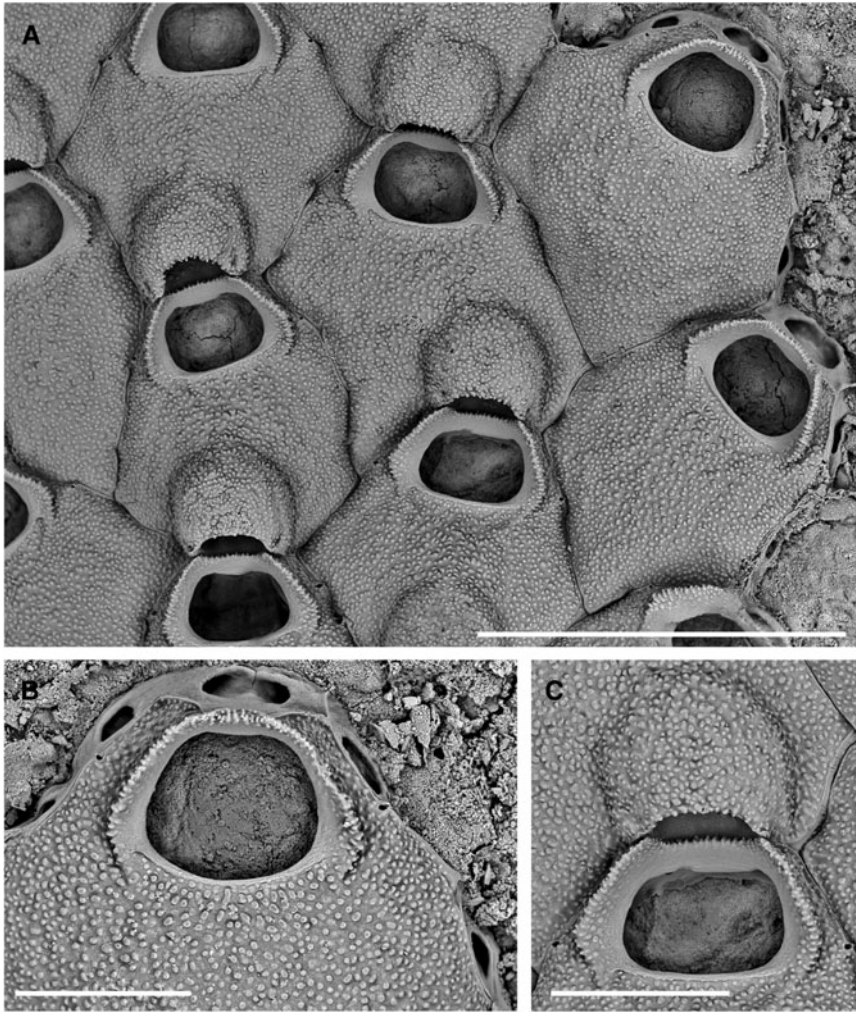


Fig. 13. *Granomurus convexus* gen. et sp. nov., NIWA 27763, holotype, Station TAN0604/116, Chatham Rise: (A) ovicellate and non-ovicellate zooids. (B) autozooidal opesia and adjacent basal pore-chambers; notice the very tiny spine bases, one either side of the opesia on the zooidal margin. (C) close-up of oecium and opesia. Scale bars: A, 1 mm; B, C, 300 μ m.

Remarks. *Carolanna* gen. nov. is one of relatively few genera of Bugulidae that are strictly uniserial. Of these, only *Bugulella* Verrill, 1879 and *Falsibugulella* Liu, 1984 have periopodial spines. *Bugulella* differs from *Carolanna* in having clavate zooids and bird-head avicularia; *Falsibugulella* differs in having only a distal opesia, a different mode of budding daughter zooids, and rootlets issuing from a distobasal (not proximolateral) position on the zooid. In the New Zealand region, *Luguba* Gordon, 1984 is similar in having well-developed spines around an elongate opesia and a broad-based oecium, but differs in being biserial and unjointed and in having bird-head avicularia. South-west Atlantic *Xenoflustra* Moyano, 2011 lacks avicularia and has similar spinose zooids and broad-based oecium, but colonies are semiflustrine with multiserial branches.

Carolanna gen. nov. may also be compared with species of Beaniidae inasmuch as zooids in a majority of beaniid species can have many lateral spines. But no beaniid produces erect, dichotomously branching colonies and their oecia are never as large and conspicuous as in *C. schackae* sp. nov., which also lacks the grappling-hook rhizoidal attachments that are characteristic of all beaniids.

Carolanna schackae sp. nov.

(Figure 14A–F)

Luguba n. sp. Gordon *et al.*, 2009, p. 289.

Material Examined. Holotype: NIWA 132787, Station KAH1706/108, off Spirits Bay, North Island, New Zealand, 54 m.

Paratypes: NIWA132784, Station Z9687, 48 m; NIWA 132786, Station Z7901, 76 m; both off Spirits Bay, North Island, New Zealand.

Other material: NIWA 132782, Station Z9671, 55 m; NIWA 132783, Station Z9680, 46 m; NIWA 132785, Station Z9692, 52 m; NIWA 132788, Station KAH1706/108, off Spirits Bay, North Island, New Zealand, 54 m.

Etymology. Eponymous for Dr Carolann Schack.

Description. Colony erect, uniserial, with branch bifurcations at intervals (Figure 14A); maximum height 31 mm.

Autozooids elongate (Figure 14B), widest in distal half, narrowest proximally, arranged in chains of at least five zooids before bifurcating. Each zooid slightly overlapping its daughter zooid distally, separated from its neighbour by a distobasal gap in calcification that functions as a joint (Figure 14C) (ZL 527–602 (557 ± 22), N = 18; ZW 179–219 (196 ± 18), N = 6). All skeletal surfaces gymnocrystal. Opesia extensive, occupying virtually entire frontal surface. Operculum comprising discrete flap in distal end of membranous frontal wall. Opesia bordered by 6–9 non-articulated spines; the distalmost pair points distad, all others arch across frontal wall, mostly without interdigitating; each spine with distal pore.

No avicularia.

Ovicell hyperstomial (Figure 14D, E), terminal, with helmet-like kenozooidal oecium budded from maternal autozooid, as wide as long or wider and deeper-bodied in distal half than in autozooids. Endoecial calcification smooth, ectoecium almost wholly cuticular. Cleithral, closed by dimorphic operculum that is wider than in autozooids (OoL 175–212 (199 ± 14), N = 5; OoW 231–248 (239 ± 9), N = 3). Ovicellate zooid with only 6 pairs of spines, the distal pair stoutest, flanking oecium.

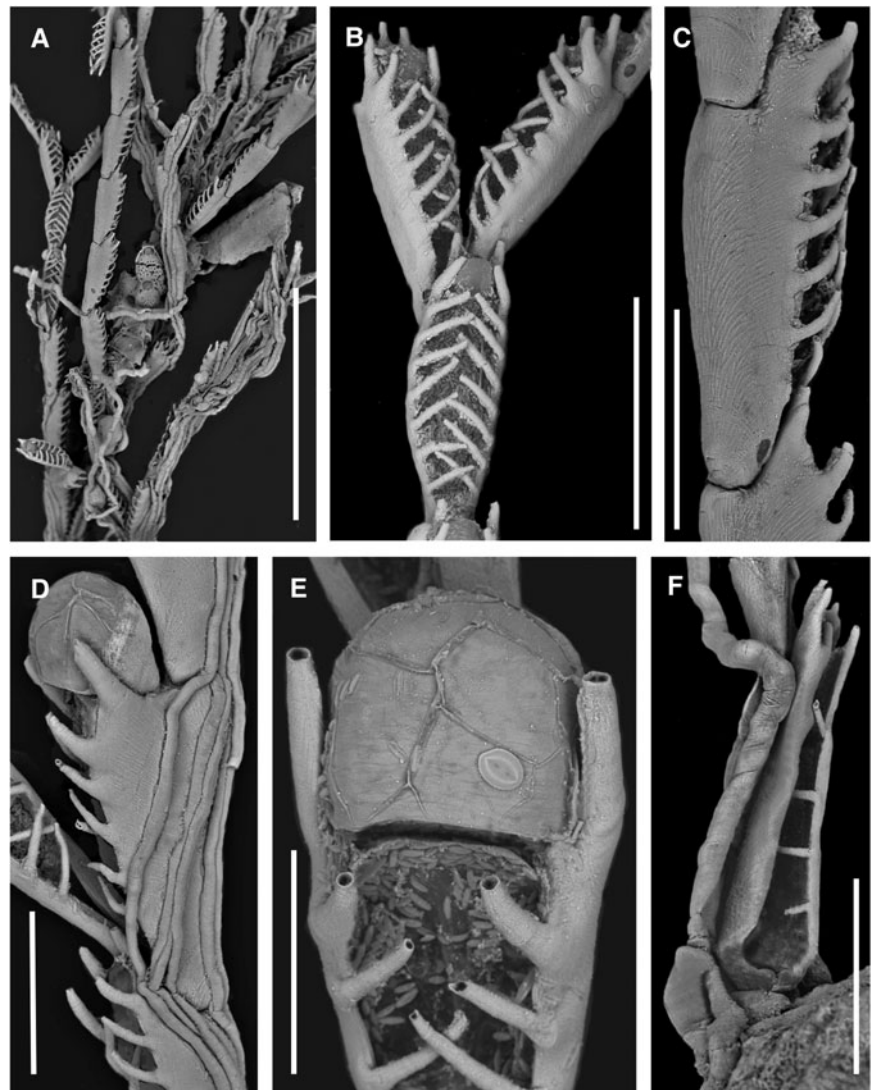


Fig. 14. *Carolanna schackae* gen. et sp. nov.: NIWA 132787, Station KAH1706/108, Spirits Bay: (A) bifurcating uniserial branches with rootlet bundles. (B) branch bifurcation. (C) lateral view of autozooid showing joints where connected to neighbours. (D) lateral view of ovicellate zooid. (E) frontal view of oocidium, with creases in collapsed ectooecium. NIWA 146134, Station KAH1706/108, Spirits Bay: (F) ancestrula, flanked by rootlet from daughter zooid. Scale bars: 2 mm; B, 500 µm; C, D, F, 300 µm; E, 200 µm.

A rootlet pore in the proximolateral corner of many zooids; rootlets descending the sides of zooid branches, forming a tangled proximal cord toward the base of the colony.

Ancestrula erect (Figure 14F), attached to substratum directly, budding single daughter zooid from distobasal pore, supportive rootlets developing from the daughter zooid (AnL 579, AnW 168, N = 1).

Remarks. Colonies are slender and delicate. Fewer zooid widths were measured than zooid lengths because zooid lateral margins tended to inroll when preserved in ethanol or prepared for SEM, thereby causing zooid narrowing. The oocidium is similar to that in the genus *Bryocalyx* Cook & Bock, 2000, and in both genera can be considered as the sum of a flattened distal kenozooid producing a helmet-like oocial outfold (cf. Ostrovsky *et al.* 2009). *Carolanna schackae* gen. et sp. nov., monotypic for the genus, is so far known only from the outer reaches of Spirits Bay, Three Kings Shelf, northern New Zealand, where colonies attach to small shell fragments at depths of 46–76 m.

Superfamily incertae sedis
Family BORIOPLEBIDAE fam. nov.

Type Genus. *Borioplebs* gen. nov.

Diagnosis. Colony squat, comprising short cylindrical branches from oligoseriate basal zooids. Autozooids thick-walled,

lageniform, with elevated funnel-like peristomial rim in which opesia-orifice is set at lower level. Wholly cryptocystal; no cryptocystal ridges. Opesia-orifice roundly transversely D-shaped. No oral spines, condyles, avicularia or oecia. Recessed uniporous mural septula. Ancestrula like autozooids.

Remarks. This monogeneric family is difficult to place. Although external morphology did not suggest that *Borioplebs* gen. nov. might be ascophoran in nature, an internal examination was made of the cryptocystal wall. Not only are areolar-septular pores lacking externally and internally, there is no indication of an umbonuloid shield. The zooids alone are somewhat suggestive of Cellariidae, especially the genus *Syringotrema* Harmer, 1926, a genus ranging from the Oligocene to the present day. No known cellariid has an encrusting phase, however; instead, colonies are erect and anchored by rootlets. The form of the colony in the sole species of *Borioplebs* (see below) is reminiscent of that seen in *Inversaria* von Hagenow, 1851 (Onychocellidae), a genus of perhaps 10 species, all Cretaceous except for one from the latest Paleocene of New Zealand (Taylor *et al.*, 2018). No species of *Inversaria*, however, has peristomial orifices like that in *Borioplebs*. *Borioplebs* has erect cylindrical stems from an encrusting base, and despite the absence of cryptocystal ridges, nevertheless constitutes somewhat of a conceptual morphological intermediate between Onychocellidae and Cellariidae. Had it been discovered in the Cretaceous, its morphology would be

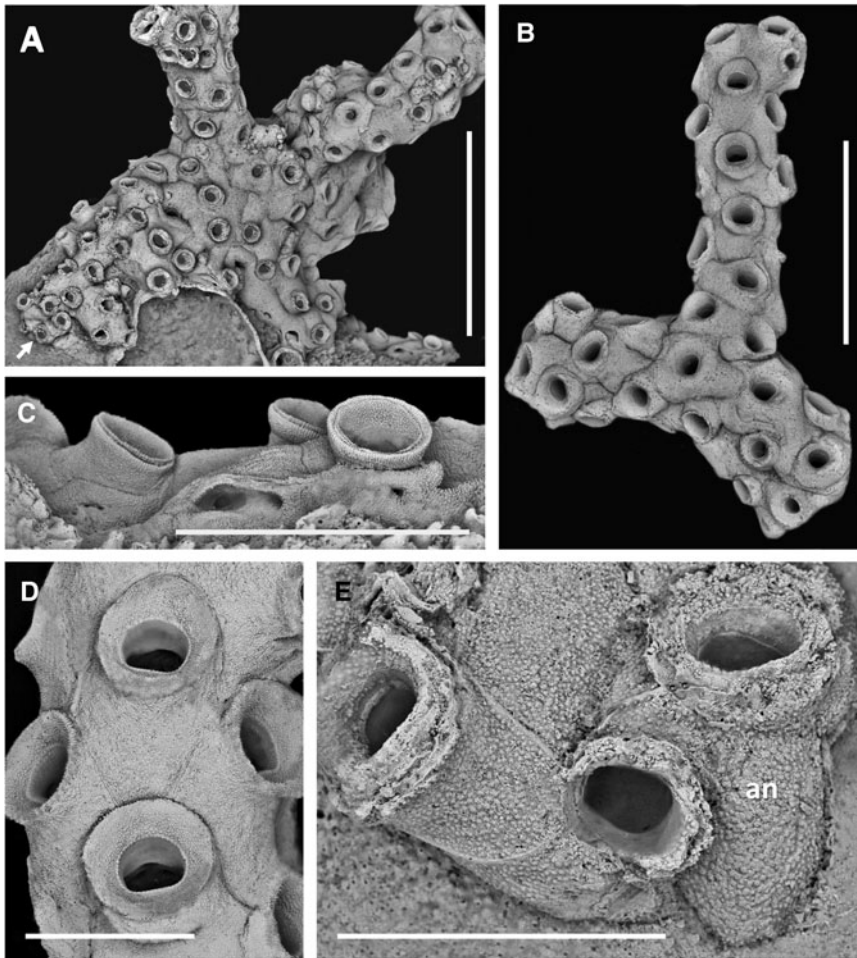


Fig. 15. *Borioplebs norfolkensis* gen. et sp. nov.: (A) NIWA 146138, Station G3, Norfolk Ridge: largest colony fragment, attached to substratum; ancestrula arrowed. (B) NIWA 98172, holotype, Station G3: bifurcation branch. (C) NIWA 146138, lateral view of autozooids and peristomes seen at lower right in A; duplicated peristomes indicated intramural buds. (D) NIWA 98172, part of branch shown in B. (E) NIWA 146138, showing ancestrula (an) and adjacent zooids, peristomes eroded. Scale bars: A, 3 mm; B, 2 mm; C, 1 mm; D, E, 500 μ m.

suggestive of just such a relationship. In the absence of fossil antecedents, ovicells and molecular-sequence data, however, one can only hypothesize on its relationships. Another related family may be Aspidostomatidae, which also has strongly cryptocystal walls, but orifices are never subtubular and there are adventitious avicularia and oecia. Interestingly, Hayward (1995) included the Aspidostomatidae (which can exhibit cryptocyst ridges flanking a sunken area) in Cellarioidea, so there is precedence for including encrusting taxa in the superfamily.

Genus *Borioplebs* gen. nov.

Type Species. *Borioplebs norfolkensis* sp. nov.

Etymology. Latin *boreas*, north, and *plebs*, folk, alluding to the provenance of the sole included species near Norfolk ('north folk') Island on the Norfolk Ridge. Gender masculine.

Diagnosis. As for family.

Borioplebs norfolkensis sp. nov.
(Figure 15A–E)

Material Examined. Holotype: NIWA98172, Station G3, northern Norfolk Ridge, 710 m.

Paratype: NIWA 146138, same data as holotype.

Other material: NIWA 98173, same data as holotype.

Etymology. Alluding to the eponymous Norfolk Ridge.

Description. Colony comprising robustly encrusting oligoserial zooid rows shortly ramifying on substratum, giving rise to a few

briefly bifurcating, relatively short, erect cylindrical stems (Figure 15A, B). Maximum breadth of encrusting portion 6.2 mm, maximum height of erect branch/stem 4.9 mm, maximum stem diameter 1.4 mm.

Autozooids (Figure B–D) squatly lageniform and typically overlapping, with subventricose cryptocystal wall rising to elevated funnel-like peristomial rim in which opesia-orifice is set at lower level. Cryptocyst minutely and densely granular. Peristome more or less circular (Figure 15C, D) with short vertical wall and discrete granular rim in youngest zooids, its outer side thickening all around and becoming more oblique as frontal cryptocyst thickens. No gymnocyst evident except where frontal cuticularized walls of adjacent zooids attach along interzooidal boundaries; here, an extremely thin smooth strip of calcification is evident in SEM photos (ZL 565–988 (774 \pm 142), N = 8; ZW 379–527 (454 \pm 51), N = 6).

Inner side of peristomial funnel in older zooids steeper proximal to opesia-orifice, broader and shallower distally, granular (PoL 263–345 (297 \pm 25), N = 11; PoW 261–404 (331 \pm 38), N = 11). Opesia-orifice (Figure 15D) subrounded, with straight proximal rim, its sides descending deeply interiorly below rim (OL 133–189 (155 \pm 19), N = 9; OW 159–197 (186 \pm 14), N = 6). No oral spines. Operculum not clearly in evidence; operculum-like structure in a post-ancestrular zooid of same shape as opesia-orifice. No condyles. Reparative budding evident in a few zooids in which a duplicate peristomial rim is set within the original peristome.

No avicularia or oecia seen. Interzooidal communications via recessed uniporous mural septula.

Ancestrula (Figure 15E) like later autozooids but with smaller dimensions (AnL 504, AnW 266, N = 1). The sole ancestrular area seen shows one distal and one left-distolateral daughter zooids;

additionally, a shorter daughter zooid issues from the left proximalateral side, curving in a proximal direction. The two left-produced daughter zooids abut another zooid that is directed laterally leftwards.

Remarks

The colony form – a relatively small encrusting base from which arise short cylindrical stems – is not common among cheilostomes. The lack of oecia suggests that the sole colony was infertile rather than having internal brooding. Owing to the general overlap of proximal parts of autozooids, especially in erect stems, relatively few lengths and widths could be measured.

Discovery of more material of this morphologically disparate taxon is highly desirable for molecular sequencing and ascertaining its phylogenetic affinities. So far the species is known only from a single locality (NIWA Station G3) on the northern Norfolk Ridge at 710 m depth – the same locality as *Elementella simplex* gen. et sp. nov. and *Radixenia radians* gen. et sp. nov.

Superfamily CRIBRILINOIDEA Hincks, 1879

Family CRIBRILINIDAE Hincks, 1879

Genus *Seabournea* gen. nov.

Type Species. *Seabournea rusti* sp. nov.

Etymology. Honoric for New Zealand paleontologist Dr Seabourne Rust.

Diagnosis. Colony encrusting, unilaminar, multiserial. Costal field occupying most or all of frontal surface. Narrow granular cryptocyst present around opesia. Numerous costae, entire or bifurcating, non-pinnate, with slit-like intercostal lacunae. No lumen pores. Distal arch of autozooid with conspicuous bowl-like ‘apertural plate’. Oral spines present. Avicularia adventitious, lacking pivot bar. Ovicell subimmersed, oecium, with conspicuous transverse ectoecial tabula. Uniporous mural septula present. Ancestrula not seen.

Remarks

A new genus is created for an unusual spinocystal cheilostome that has a skeletal character normally associated with *Arachnopusia* (Arachnopusiidae), viz an ‘apertural plate’. Hayward (1995) reported it in many species, described as occurring under the operculum. In *Seabournea* gen. nov., in which it is exceptionally large, it appears in a frontal position in the distal transverse wall of the autozooid, flanked by the bases of the oral spines. Since the present material lacks any cuticular structures, its relationship to the operculum in life is unknown. Its function is unknown but it would be an ideal place to house a large gland. Inasmuch as it is larger in ovicellate zooids it is possible it may be complementary to protecting embryos (perhaps through biochemical deterrence to micropredation).

Seabournea gen. nov. may not be a cribrilid; the oecium is very reminiscent of that in the calloporid genus *Corbulella* Gordon, 1984 and the presence of a narrow granular cryptocyst bordering the opesia is unexpected in a cribrimorph (though admittedly not normally described in the literature even if present; a very narrow cryptocyst seems evident in Larwood’s (1985) figures of some ‘myagromorph’ cribrilids). If *Seabournea* is a calloporid it would be analogous to the cribrimorph look-alike *Membraniporella* Smitt, 1873, which differs in having a wholly endoecial frontal skeletal surface in the oecium and in lacking an ‘apertural plate’.

Seabournea rusti sp. nov.
(Figure 16A–D)

Material Examined

Holotype: NIWA 146139, Station TAN1503/116, Iceberg Seamount, Andes Seamount complex, south-eastern Chatham Rise, 497–590 m.

Etymology. Eponymous for Dr Seabourne Rust.

Description. Colony encrusting, unilaminar, pluri-multiserial, maximum length 10 mm.

Autozooids (Figure 16A, B) elongate-oval to roundly subhexagonal (ZL 627–1052 (886 ± 158) $N = 7$; ZW 462–600 (533 ± 43), $N = 9$). Costal field occupying most or all of frontal surface. Narrow granular cryptocyst present around opesia. Numerous costae, 17–24, these entire or bifurcating, non-pinnate, with slit-like intercostal lacunae. Generally, the suboral costal, simple, parallel-sided; about two-thirds of succeeding costae bifurcating like a tuning fork, with opposing tips fusing in midline as a raised ridge; remaining costae in proximal third of spinocyst tapering convergently to midline. No lumen pores. Distal arch of autozooid with conspicuous bowl-like ‘apertural plate’ (Figure 16B–D) set between oral-spine bases. Two pairs of oral spines.

Avicularia adventitious, borne proximally or proximalaterally on concealed gymnocyst; elevated, rostrum elongate-triangular (Figure 16C) when tip not broken (AvL 195–267 (228 ± 30), $N = 5$; AvW 107–132 (120 ± 12), $N = 5$). No pivot bar or obvious condyles, combined foramen drop-shaped; proximal cryptocyst steeply sloping, smooth.

Ovicell (Figure 16A) subimmersed; oecium formed by distal kenozooid, with conspicuous transverse ectoecial tabula bordered by raised rim. Ovicell opening arches across distal margin of apertural plate, which is larger and transversely oval in ovicellate zooids (OoL 366, OoW 612, $N = 1$).

Uniporous mural septula present; basal pore-chambers absent. Ancestrula not seen.

Remarks

The sole colony of *Seabournea rusti* gen. nov. et sp. nov. encrusted the surface of a hexactinellid sponge, *Aphrocallistes beatrix*, at the type locality, captured in an upslope dredge tow. It is so far known only from the eastern Chatham Rise, New Zealand, at 497–590 m (end and start depths of tow).

Superfamily LEPRALIELLOIDEA Vigneaux, 1949

Family ROMANCHEINIDAE Jullien, 1888

Genus *Waeschenbachia* gen. nov.

Type Species. *Waeschenbachia splendida* sp. nov.

Etymology. Honoric for Dr Andrea Waeschenbach, Natural History Museum, London, in recognition of her contribution to knowledge of bryozoan phylogeny.

Diagnosis. Colony encrusting, unilaminar, almost spot-like. Autozooidal frontal shield umbonuloid, convex suboral umbo conspicuous areolar-septular pores principally in two series. Orifices dimorphic, that of the autozooid longer than wide, poster broadly and deeply rounded. Peristomial rim thick, elevated, bearing a corona of up to 17 long articulated oral spines. No lyrula or peristomial denticle. No avicularia. Ovicellate orifice proportionally wider than in autozooids, and broadest proximally. Ovicell hyperstomial, escharelliform; ectoecium membranous, endoecium imperforate, surface irregular; orifice flanked by 6–7 oral spines on each side. Ancestrula not seen.

Remarks

A new genus is required for a species of Romancheinidae with an exceptionally large number of orificial spines. Although

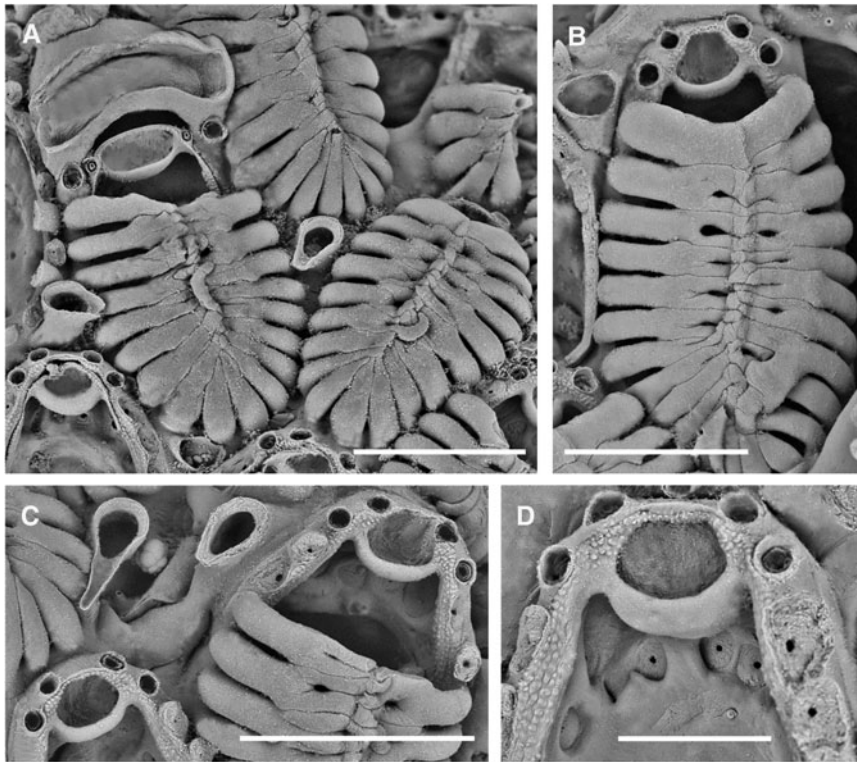


Fig. 16. *Seabourmea rusti* gen. et sp. nov.: NIWA 146139, Station TAN1503/116, Chatham Rise: (A) ovicellate zooid with elongate 'apertural plate', parts of autozooids and adventitious avicularia. (B) autozooid, showing four oral spine bases and 'apertural plate'. (C) avicularium (at left) with unbroken rostrum, and bowl-like 'apertural plates' of two autozooids. (D) close-up of autozooidal 'apertural plate, oral-spine bases, broken costal-spine bases (at right) and uniporous septula. Scale bars: A, C, 500 µm; B, 400 µm; D, 200 µm.

superficially resembling *Escharella* Gray, 1848, there is no median denticle and orifices are dimorphic. The related romancheinid genera *Hippomenella* Canu & Bassler, 1917 and *Hippopleurifera* Canu & Bassler, 1925 have similar orifices but are aviculiferous and never have so many oral spines.

Waeschenbachia splendida sp. nov.
(Figure 17A-E)

Material Examined. Holotype: NIWA 132780, Station Z9752, east of Great Island (Manawatāwhi), Three Kings Islands, New Zealand, 190 m.

Etymology. Latin *splendidus*, splendid, alluding to the spectacular corona of orificial spines.

Description. Colony encrusting, unilaminar, loosely pluriserial, attaining 11 mm maximum length.

Autozooids large, subhexagonal, frontal shield umbonuloid, steeply ascending to prominent pointed suboral umbo (Figure 17A) (ZL 1026-1436 (1274 ± 133), $N = 12$; ZW 744-1339 (927 ± 171), $N = 12$). Shield surface centrally imperforate, weakly granular-tubercular, flanked by conspicuous areolar-septular pores (Figure 17B), these principally in two series, but additional pores can occur in lateral wall. Autozooidal orifice (Figure 17C) longer than wide, a little wider distally than proximally, the proximal ends of the anter curved inwards laterally simulating condyles. Poster broadly and deeply rounded (OL 267-275 (271 ± 6), $N = 2$; OW 232-236 (234 ± 3), $N = 2$). Peristomial rim thick, elevated, bearing a spectacular corona of 12-17 basally articulated oral spines up to 970 µm long, some with reparative joints. No lyrula or peristomial denticle.

No avicularia.

Ovicell (Figure 17B, D, E) hyperstomial, opening high above orifice. Ooecium formed by distal autozooid, escharelliform, skeletal surface of endooecium coarsely textured, somewhat irregular and granular-tubercular, continuous with calcified wall of distal zooid; ectooecium wholly cuticular, continuous with membranous frontal wall (359-491 (446 ± 60), $N = 4$; OoW 433-481 (459 ± 23),

$N = 4$). Ovicellate zooids with dimorphic orifice that is proportionally wider than in autozooids (Figure 17E), and broadest proximally, orifice flanked by 6-7 oral spines on each side (FoL 255-337 (297 ± 58), $N = 2$; FoW 240-297 (269 ± 41), $N = 2$).

Ancestrula not seen.

Remarks

The sole colony was growing on an irregular piece of substratum and is also irregular in shape, with zooids orientated in different directions. Interestingly, some oral spines, or parts of spines, were a bit crooked and bent at different angles, with joints, and evidence of repair. Since many zooids had surface debris obscuring their morphology, part of the colony was sacrificed for bleaching and SEM to reveal details of orifices, spine number and oecia. The species is known only from the type locality at 190 m depth.

Discussion

Thirteen new genera, three new families and 16 new species of Zealandian cheilostome Bryozoa are described herein from 26.42° (northern Norfolk Ridge) to 54.02°S latitude (south-east Campbell Plateau) from coastal waters to lower bathyal depths (46-1676 m). One of the new species belongs to the hitherto Eocene-Miocene genus *Vincularia* now recognized in the present-day fauna. Two new combinations and a new non-Zealandian species are also established. Nearly half of the new Zealandian species form spot-like colonies on hard substrata but a range of colony forms is represented, including patch/sheet encrusters, erect rod-like and branching forms and a rooted species of soft sediments that forms the equivalent of planar spots but these are supported by long (>3 mm) rootlets on or above the sediment surface. Rocks are the commonest substratum, followed by scleractinian coral and molluscan shell. Arenaceous foraminiferal tubes are the sole substratum for one soft-sediment species.

Of the 14 genera described herein, 13 of them new to science and one new to the present-day fauna, five have plesiomorphic and/or transitional skeletal morphologies in their autozooids

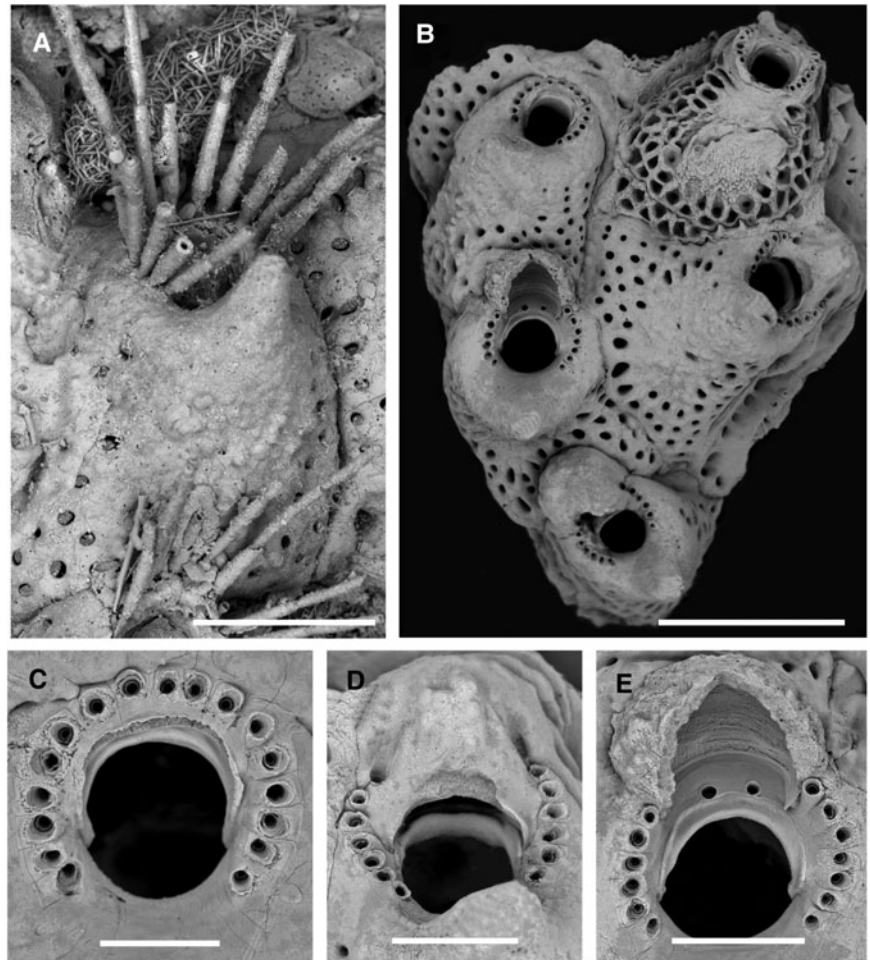


Fig. 17. *Waeschenbachia splendida* gen. et sp. nov., NIWA 132780, holotype, Station Z9752, Three Kings Islands: (A) unbleached autozooid with orificial spines intact. (B) detached bleached fragment showing mostly ovicellate zooids. (C) autozooidal orifice with 17 oral-spine bases. (D, E) ovicellate orifices. Scale bars: A, 500 μ m; B, 1 mm; C, 200 μ m; D, E, 300 μ m.

and/or their ancestrulae. For example, *Elementella* gen. nov. has the simplest skeletal morphology of any known living cheilostome. The autozooidal cystid has no trace of cryptocyst and there are no spines, tubercles, heterozooids or reproductive structures. The two described species essentially have the appearance of simple runner-like ctenostomes that have calcified their lateral walls, resembling the very earliest-known cheilostome, late Jurassic *Pyriporopsis pohowskyi*, which also lacks a cryptocystal margin to the opesia. The ancestrula in *Elementella* is also bipolar, an ancestral character state found in *Pyriporopsis*, *Herpetopora* and some other nominal electrids, as well as a few other basalmost cheilostome families. *Vincularia*, previously known only from the early Eocene to the late Miocene, is represented by a living species. *Radixenia* gen. nov. unusually has multiple zooids (nine) produced from the ancestrula – apparently unique in the Cheilostomata but known in some Ctenostomata. *Borioplebs* gen. nov., with erect cylindrical stems from an encrusting base, has zooids with peristomial orifices that resemble those found in the erect cellariid genus *Syringotrema*.

Interestingly, these four genera can be found at just two NIWA stations. Station G3, north of Norfolk Island on the northern Norfolk Ridge, yielded *Elementella simplex* sp. nov., *Radixenia radians* sp. nov. and *Borioplebs norfolkensis* sp. nov. and station U582 on the Three Kings Ridge yielded *Vincularia regia* sp. nov. The distinctive morphologies of these likely relict cheilostomes recall some other taxon discoveries during the past 40 years of exploration of the northern Norfolk Ridge and waters around New Caledonia. A sphinctozoan sponge (Vacelet *et al.*, 1992), pleurotomariid gastropods (Bouchet & Métivier, 1982), a craniid brachiopod (Laurin, 1992) and primitive pedunculate crinoids (Améziane-Cominardi *et al.*, 1987) were interpreted by

Richer de Forges *et al.* (2000) as ‘relicts of groups earlier believed to have disappeared in the Mesozoic’. Among the Bryozoa, Gordon (1989) and Gordon & d’Hondt (1991) respectively discovered living species of *Plagiopora* MacGillivray, 1895 and *Chelidozoum* Stach, 1935 alive on the Norfolk Ridge, genera that were previously known only from the Australian Miocene. In the popular literature, these and other examples from New Caledonia (northernmost Zealandia), such as the occurrence of the cephalopod *Nautilus macromphalus* and the hemichordate *Cephalodiscus graptolitoides* Dilly, 1993 (which revealed how graptolite coenecial spines are formed) led to the northern Norfolk Ridge being referred to as ‘un nid de fossiles vivants’ (e.g. Richer de Forges *et al.*, 1998). Terrestrial equivalents like the most basal living angiosperm genus (*Amborella*) in New Caledonia and the tuatara and leiopelmatid frogs (inter alia) in New Zealand underscore the apparent archaic elements of the Zealandian biota (Gibbs, 2006).

The Three Kings Ridge lies well to the east of the Norfolk Ridge. Whereas both ridges are volcanic, only the Norfolk Ridge is underlain by continental crust (Mortimer & Campbell, 2014). Though separated from the Norfolk Ridge by the Norfolk Basin, the Three Kings Ridge, which continues south towards the North Island, is a volcanic-arc ridge associated with the eastern Zealandian continental margin. *Vincularia* as a relict bryozoan on the Three Kings Ridge is consistent with the Norfolk Ridge discoveries.

Grandcolas *et al.* (2014) have argued that relict taxa imply regional extinctions, which is true, and that they therefore cannot simultaneously provide evidence of local biota permanence. Molecular evidence suggests that more than 90% of the land biota is derived from Australian, not Gondwanan or Zealandian

ancestors, and probably all within the last 20 million years following a postulated total submergence of Zealandia during the Oligocene marine transgression ~25–23 mya (Mortimer & Campbell, 2014). The marine realm, however, apart from coastal zones, need not have been similarly affected, and, indeed, Mortimer & Campbell (2014) note that New Zealand's rich Cenozoic biota, well-studied for 150 years, would benefit from being reinterpreted from a Zealandian perspective. Analysing phylogeographic literature, Wallis & Jorge (2018) reviewed divergence times between New Zealand lineages and their closest overseas sister groups from a range of environments. They concluded that there is no evidence for a deficit of pre-Oligocene lineages, nor an excess of ones arriving just afterwards. In short, phylogeographic data provide no evidence for complete inundation of New Zealand during the Oligocene. One implication is that archaic Gondwanan or Zealandian elements are not precluded, especially in the marine environment.

One other area of notable bryozoan diversity in the New Zealand region is the Three Kings Shelf, especially the well-studied southern part off Spirits Bay abutting the New Zealand mainland. An intensive survey conducted in 1999 found a remarkable diversity of suspension feeders in the area, especially bryozoans and sponges, richness being highest between 30–80 m depth (Cryer *et al.*, 2000). A total of 298 bryozoan species occurred in the area, a diversity, relative to area sampled, unmatched elsewhere in New Zealand, with a high average taxonomic distinctness (Rowden *et al.*, 2004). At least 60 species of Bryozoa are endemic to the Three Kings Shelf region (e.g. Powell, 1967; Taylor & Gordon, 2003), now also including *Carolanna schackae* gen. et sp. nov. and *Waeschbachia splendida* gen. et sp. nov.

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APPENDIX

Station data

NIWA (NZOI) stations pre-2000
B455, 40.6667°S 172.2167°E, 54 m, 1 June 1961
E416, 45.3500°S 171.9500°E, 1225 m, 13 October 1965
E417, 45.2000°S 171.8167°E, 860 m, 13 October 1965
E796, 45.3333°S 166.7583°E, 251 m, 20 October 1967
G3, 26.4167°S 167.2500°E, 710 m, 27 September 1966
K795, 33.0433°S 179.5767°W, 350 m, 18 July 1974
K826, 28.7999°S 177.8000°W, 142–490 m, 25 July 1974
K855, 30.5533°S 178.5267°W, 115–125 m, 30 July 1974
S45, 54.0250°S 171.0750°E, 1262 m, 21 September 1978
S148, 44.6833°S 174.3483°E, 859 m, 24 October 1979
S150, 45.7667°S 174.4083°E, 1640 m, 26 October 1979
S151, 45.7633°S 174.5083°E, 1586 m, 26 October 1979
S152, 45.8717°S 174.0817°E, 1676 m, 26 October 1979
S153, 45.3517°S 173.5967°E, 1386 m, 27 October 1979
U581, 31.8550°S 172.1467°E, 1170 m, 5 February 1988
U582, 31.8617°S 172.4333°E, 790 m, 5 February 1988
U595, 30.3583°S 173.1450°E, 1474 m, 7 February 1988
Z9671, 34.3600°S 172.7938°E, 55 m, 25 January 1999
Z9680, 34.3600°S 172.6968°E, 46 m, 26 January 1999
Z9692, 34.3782°S 172.8842°E, 52 m, 27 January 1999
Z9701, 34.2983°S 172.7925°E, 76 m, 28 January 1999
Z9752, 34.1672°S 172.1847°E, 190 m, 2 April 1999
Z11008, 33.9167°S 167.9167°E, 920–940, 21 February 2002
NIWA stations post-2000
RV 'Kaharoa'
KAH1706/108, 34.3648°S 172.8000°E, 54 m, 4 June 2017
KAH0204/8, 34.1140–1152°S 174.1432–1450°E, 610–640 m, 14 April 2002
KAH0204/15, 34.0997–1035°S 174.1138–1153°E, 470–480 m, 15 April 2002
KAH0204/28, 34.0927–0963°S 174.1148–1175°E, 490–515 m, 16 April 2002
KAH0204/30, 34.1465–1573°S 173.9632–9635°E, 800–825 m, 17 April 2002
KAH0204/32, 34.1620–1682°S 173.9618–9663°E, 780–810 m, 17 April 2002
KAH0204/47, 34.0425–0492°S 174.8170–8118°E, 792–880 m, 19 April 2002
RV 'Tangaroa'
TAN0205/19, 33.7331°S 179.8347°E, 420–471 m, 14 April 2002
TAN0413/171, 37.4525°S 176.9040°E, 310–410 m, 16 November 2004
TAN0604/116, 42.7698–7938°S 179.9863–9865°E, 950–1045 m, 7 June 2006
TAN1301/CARAVEL FF2, 45.6°S 171.5°E, 1117 m, 28 September 2013
TAN1501/CARAVEL FF4, 45.3°S 171.3°E, 1126 m, 12 January 2015
TAN1501/ANADARKO REF 6, 45.3°S 171.2°E, 1024 m, 13 January 2015
TAN1503/116, 44.1597–1612°S 174.5548–5560°W, 497–590 m, 11 April 2015