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In search of phylogenetic congruence between molecular and morphological data in bryozoans with extreme adult skeletal heteromorphy

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The taxonomy of cyclostome bryozoans, both Recent and fossil, is founded almost entirely on characters of the mineralized skeleton. However, the adequacy of these characters is now being questioned by molecular sequence data. In this study we construct a molecular tree using ssrDNA and lsrDNA sequences and identify a clade of New Zealand cyclostomes containing species exhibiting widely different morphologies. In particular, *Diaperoecia purpurascens* (Hutton), a species assigned to the suborder Tubuliporina on the basis of adult skeletal morphology, is shown to be closely related to New Zealand species assigned to *Heteropora*, including *H. neozelanica* Busk, which has a very different adult skeleton and is traditionally placed in the suborder Cerioporina. A new species resembling the Antarctic genus *Hastingsia*, '*H*'. *whitteni* sp. nov., from North Island, New Zealand, is found to belong to the same clade, despite being placed conventionally in a different family (Hastingsiidae) from both *Diaperoecia* (Diaperoeciidae) and *Heteropora* (Cerioporidae). These results challenge the utility of adult skeletal morphology in cyclostome taxonomy. In contrast to the striking dissimilarity between the adult skeletons of *D. purpurascens* and '*Hastingsia' whitteni* compared to New Zealand species of *Heteropora*, morphological similarities in early colony development, as well possibly as the presence of a gizzard, corroborate the molecular interpretation of their close relationships. Greater attention should be paid in the future to early astogenetic characters in cyclostome taxonomy.

Key words: Bryozoa, Cyclostomata, early astogeny, molecular phylogeny, morphology, New Zealand, taxonomy

Introduction

A recurrent topic of discussion in taxonomy is the reliability of morphology in interpreting phylogenetic relationships and hence in devising 'natural' classifications. Molecular sequence data provide a powerful means of accessing the efficacy of morphology for this purpose. In the ideal scenario there is a high degree of congruence between molecules and morphology, corroborating the taxonomic value of morphology. However, there are numerous instances where molecular sequence data have undermined the taxonomic value of traditional morphological characters by revealing close genetic relationships between morphologically distinct taxa (e.g. Blackwell *et al*., 2003; Sotiaux *et al*., 2009; Pérez, 2011; Bourret *et al*., 2012).

Bryozoa is a phylum of lophotrochozoan invertebrates, distributed globally across many aquatic habitats, and moderately diverse, comprising some 5689 living species (Bock & Gordon, 2013). The two dominant orders of modern bryozoans – Cheilostomata and Cyclostomata – are both marine and have calcareous skeletons that furnish nearly all of the characters used in their taxonomy. Not only are these skeletal characters immediately obvious in preserved material, but exactly the same characters are available to palaeontologists studying fossil cheilostomes and cyclostomes. Indeed, a common procedure in taxonomic studies of cheilostomes and cyclostomes is to soak specimens in dilute bleach to remove all soft tissues, leaving only the calcareous skeleton for identification.

A reasonably large number of skeletal morphological characters are available for cheilostome taxonomy and molecular studies at low taxonomic levels generally show good congruence with morphology (e.g., Hughes *et al*., 2008; Herrera-Cubilla & Jackson, 2014), even though morphological convergence is evident between some higher taxonomic groups (Waeschenbach *et al*., 2012). Cyclostomes, however, have a simpler skeletal morphology and there can be significant incongruence between molecules and morphology, as is apparent from mismatches when traditional suborders founded on skeletal morphology are mapped onto molecular trees (Waeschenbach *et al*., 2009; Taylor *et al*., 2011).

The purpose of this study is to use molecular sequence data to construct a phylogenetic tree for cyclostome bryozoans and to focus particularly on the unexpected relationships found between some species from New Zealand. These species are revised taxonomically, based on traditional skeletal characters, and morphological apomorphies supporting the molecular phylogeny are sought. One of the commonest cyclostome bryozoans found in New Zealand waters is *Diaperoecia purpurascens* (Hutton, 1877) (Fig. 1). Although the generic attribution of this species has varied through time, with others placing it in *Entalophora* or *Pustulopora*, it has always been considered as belonging to suborder Tubuliporina based on skeletal morphology. We here generate ssrDNA and lsrDNA sequences for *Diaperoecia purpurascens* for the first time, showing that the species groups within a clade containing New Zealand material attributed to *Heteropora* (Fig. 2). Traditional cyclostome taxonomy places *Heteropora* in a different suborder – Cerioporina – reflecting the striking differences in the morphology of the zooidal skeletons of *Diaperoecia* and *Heteropora*. However, our molecular findings are corroborated by a study of skeletal characters from early colony development, notably the shape and pattern of the pseudopores on the protoecium, which support a close relationship among *D. purpurascens*, the New Zealand species of *Heteropora* and a previously un-named New Zealand species of '*Hastingsia'* which molecular sequence data group with these other two cyclostomes. Our findings point to the potential taxonomic value of morphological characters seen in the early colony development of cyclostome bryozoans.

Material and methods

Morphology

The material used for this study comprises historical specimens preserved in the collections of the Natural History Museum, London (NHMUK), as well as some more recently collected material from New Zealand which is now divided between the collections of the NHMUK and the National Institute for Water and Atmospheric Research (NIWA) in Wellington, New Zealand.

SEM of skeletal morphology was undertaken using LEO 1455VP and FEI Quanta 650 ESEM scanning electron microscopes at the NHMUK. These instruments allowed the study of uncoated, dried and bleached specimens imaged with back-scattered electrons.

Molecular study

Total genomic DNA was extracted from ethanol-preserved specimens using the DNeasy tissue kit (QIAGEN) following the manufacturer's instructions. lsrDNA was amplified in two fragments using Steno250F + Steno1800R and Steno1800F + Steno3490R (Waeschenbach *et al.,* 2009). ssrDNA was amplified in two fragments using 18e (Hillis & Dixon, 1991) + Stenolae600R (Waeschenbach *et al.* 2009) and Stenolae600F (Waeschenbach *et al.*, 2009) + 18p (Hillis & Dixon, 1991) (for PCR cycling conditions, primer sequences and additional sequencing primer details, see Waeschenbach *et al*., 2009). PCR products were purified using QIAquick PCR purification Kit (QIAGEN). Sequencing was carried out on an Applied Biosystems 3730 DNA Analyser, using Big Dye version 1.1. Sequence identity was checked using the Basic Local Alignment Search Tool (BLAST) (www.ncbi.nih.gov/BLAST/). Contigs were assembled using SEQUENCHER 4.8 (GeneCodes Corporation).

Newly generated lsrDNA and ssrDNA sequences were aligned by eye to an existing alignment, as published in the supplementary data for Waeschenbach *et al.* (2009; see this reference for GenBank accession numbers of published sequences used in the present study). GenBank accession numbers for data generated in this study are as follows: lsrDNA '*Hastingsia' whitteni* sp. nov. (KP331437), *Diaperoecia purpurascens* (KP331438); ssrDNA '*H.' whitteni* sp. nov. (KP331439), *D. purpurascens* (KP331440),. The data were partitioned into three character sets: (1) lsrDNA, (2) ssrDNA, and (3) lsr+ssrDNA. Modeltest (version 3.7macX, Posada and Crandall, 1998) was used to select a model of evolution for the nucleotide data using the Akaike Information Criterion. Phylogenetic trees were constructed using Bayesian inference (BI) (MrBayes, version 3.2.1, Huelsenbeck & Ronquist, 2001). Likelihood settings were set to nst=6, rates=invgamma, ngammacat=4 (equivalent to the GTR+I+G model of evolution). In the combined lsr+ssrDNA analysis, parameters were estimated separately for each gene. Two chains (temp = 0.2) were run for 5,000,000 generations and sampled every 1000 generations. Post-'burnin' was identified when the standard deviation of split frequency reached < 0.01. 2 million and 4.5 million generations were discarded as burnin in the combined lsr+ssrDNA analysis and single gene analyses, respectively. Nodes with < 0.95 posterior probabilities (pp) were collapsed in all the figures.

Results

Taxonomy

Remarks. The three taxa forming the focus of this study are classified below according to conventional morphology-based taxonomy and nomenclature. Changes to this classification implied by the findings of the molecular phylogenetic analysis can be found in the Discussion section at the end of the paper.

Suborder Tubuliporina Milne Edwards, 1838
Family Diaperoeciidae Canu, 1918
Genus **Diaperoecia** Canu, 1918

Type species. *Pustulopora intricaria* Busk, 1875; Recent, Australia.
Remarks. Several genera of tubuliporine cyclostome bryozoans, both living and fossil, have 'vinculariiform' colonies comprising narrow bifurcating branches with autozooids opening evenly around the entire circumference. They include *Entalophora* Lamouroux, 1821, *Pustulopora* Blainville, 1830, *Collapora* Quenstedt, 1881, *Diaperoecia* Canu, 1918, *Mecynoecia* Canu, 1918, *Entalophoroecia* Harmelin, 1976 and *Annectocyma* Hayward & Ryland, 1985. With the exception of *Entalophora*, which is characterized by having an axial lumen (Walter, 1970), characters of the gonozooid provide the main means of distinction between these genera but are not always clear-cut and the taxonomy of these cyclostomes remains unclear.

Canu (1918, p. 329) diagnosed *Diaperoecia* thus: "L'ovicelle est elliptique ou suborbiculaire; elle entoure les péristomes d'un assez grand nombre de tubes qui ne sont pas dérangés dans leurs positions respectives. L'oeciostome isolé et subcentral." (The gonozooid is elliptical or suborbicular; it surrounds the peristomes [of the autozooids] a fairly large number of which are not disturbed in their respective (?) positions. The ooeciostome is isolated and subcentral.)

Brood (1976) redescribed Busk's (1875) type specimens of *Pustulopora intricaria*, noting that the material subsequently placed in this species by Harmer

(1915) from near Sorong in Indonesia was not conspecific. This is unfortunate because Canu (1918) based his concept of *Diaperoecia*, and consequently on the family Diaperoeciidae, on the gonozooids present in Harmer's material, whereas Busk's types are infertile. Key skeletal characters visible in the Australian type material of *D. intricaria* are illustrated in Figs 3–8. Flange-like kenozooidal projections are developed on the sides of some branches (Figs 3, 4). The spacing of apertures across the colony surface is irregular (Figs 3, 4), reflecting a high degree of variability in the lengths of the autozooids. Peristomes are short and some apertures are closed by terminal diaphragms (Fig. 5). Autozooidal frontal walls have closely spaced, subcircular pseudopores (Fig. 6). Transversely fractured branches (Fig. 7) show the presence of small buds near the branch axis and the triple-layered interior walls illustrated in thin section by Brood (1976, fig. 1C). Mural spines are present, some with a shaft and a barbed head (Fig. 8). A similar suite of skeletal characters is evident in *Pustulopora purpurascens* (Hutton, 1877) and this species from New Zealand can therefore be assigned on morphological grounds without reservation to *Diaperoecia*.

Diaperoecia purpurascens (Hutton, 1877)

(Figs 1, 9–20, 47–49, 53–55)

Pustulipora [sic] *purpurascens* Hutton, 1877: 361. *Pustulipora* [sic] *purpurascens*. – Hutton, 1880: 198. *Entalophora purpurascens*. – Hutton, 1891: 107. *Diaperoecia purpurascens*. – Taylor *et al*., 2004: 57, fig. 2A, B. *Diaperoecia purpurascens*. – Taylor *et al*., 2007: 220, fig. 1. *Diaperoecia purpurascens*. – Gordon *et al*., 2009: 293. *Diaperoecia purpurascens*. – Smith & Gordon 2011: 36.

Material. NHMUK 2010.6.25.2 (Fig. 1), 75.1.5.33, 75.1.5.38, 99.7.1.4060–1 (Busk Collection), all from unknown localities in New Zealand. NHMUK 2014.12.17.2 (Figs 9–12, 16), East Ulva Island, Paterson Inlet, Stewart Island, 8/6/1995, D. Foster and A. M. Smith Collection. NHMUK 2017.12.17.3 (Figs 13, 14), 2017.12.17.4 (Fig. 15), craypot at Waitangi, Chatham Island, 4/11/1999, P. D. Taylor Collection. NHMUK 2017.12.17.5 (Figs 17, 18), molecular voucher specimen AW578, 46.93°S; 168.16°E, 39 m, Otago Shelf, New Zealand, A. M. Smith Collection, 25/1/2010. NHMUK 90.10.25.3, Wanganui. National Museum of New Zealand BS 862 (Figs 19, 47–49), outside Whangaroa Harbour, 25 m, 26/1/1981. NHMUK BZ 7733 (Fig. 20), Pleistocene, Nukumaruan, Nukumaru Brown Sand, Nukumaru Beach, 01/2014, P. D. Taylor Collection.

Description. Colony erect, bush-like (Fig. 1), up to 8 cm in diameter, consisting of narrow, bifurcating branches; branch diameter 0.71–2.20 mm, typically 1.0–1.5 mm (see Taylor *et al*., 2007, table 1). Colour in life creamy-brown, purplish-brown post-mortem. All zooidal polymorphs fixed-walled, developing pseudoporous frontal walls away from branch growth tips. Autozooids elongate, frontal walls ranging in length from 0.65–2.24 mm (typically about 1 mm) by in width 0.19–0.48 mm (typically 0.25 mm), crossed by concave growth lines, zooidal boundaries slightly salient (Figs 9, 10); pseudopores teardrop-shaped, pointed distally (Fig. 11); apertures subcircular, about 0.14–0.19 mm in diameter, disposed around entire branch circumference, sometimes almost quincuncially arranged but in other cases unevenly spaced and occasionally clustered into small groups; peristomes short; terminal diaphragms closing older zooids (Fig. 18), sparsely to densely pseudoporous. Kenozooids infrequent. Gonozooids longitudinally elongate (Figs 13–15), >4 mm in total length by 0.6–0.8 mm wide, inconspicuous, the frontal wall only slightly convex, extending distally of ooeciopore typically as lobes in daughter branches following bifurcation, lateral edges indented by neighbouring autozooids but roof seldom pierced by autozooids; pseudopore density higher than in autozooids; ooeciopore subcircular (Fig. 14), slightly smaller than neighbouring autozooidal apertures, about 0.16 mm in diameter, located non-terminally; ooeciostome very short.

Early astogeny observed in two colonies, one recent (Fig. 19), the other an Early Pleistocene fossil (Fig. 20). Fan-like encrusting base giving rise to three erect stems in both cases. Ancestrula (Figs 53–55) curved to the right, 0.83–1.09 mm long, with longitudinally elliptical aperture 0.16–0.19 mm long by 0.14–0.17 mm wide, occluded by a terminal diaphragm in the recent example but open in the fossil. Protoecium large, 0.33–0.37 mm in transverse diameter; pseudopores confined to a crescentic marginal band, closely but irregularly spaced, subcircular, countersunk, external diameter *c*. 12 µm, internal diameter *c*. 6 µm. Non-pseudoporous distal part of protoecium elevated and with chevron-shaped transition to ancestrular tube which has a rugose surface with non-countersunk pseudopores.

Mural spines developed on surfaces of interior walls and internal surfaces of frontal exterior walls, with a moderately long shaft a head covered by sharp barbs, either symmetrically or more often only on the side facing proximally. Distal edges of interior walls exhibiting transversely fibrous ultrastructure.

Remarks. The whereabouts of Hutton's (1877) material of this species is unknown. Although it is known that he sent many of his samples to the then British Museum (Natural History), none could be found appropriately labelled as having originated from F. W. Hutton. Given that there is no controversy about the identity of this species, there is currently no justification for erecting a neotype.

Distribution. Widespread in the seas around New Zealand at the present-day, this species also occurs as a fossil back to at least the Late Pliocene and is especially abundant in the Pleistocene Tainui Shell Bed of Wanganui (PDT, pers obs). Taylor *et al.* (2004, fig. 4C) showed the distribution of *D. purpurascens* based on 137 NZOI station samples, ranging in latitude from 33–54 °S, and in depth from 0–1156 m, although material from the deeper stations may have been transported downslope and 90% of records are shallower than 250 m.

Family Hastingsiidae Borg, 1944

Genus **Hastingsia** Borg, 1944

Type species. *Hastingsia irregularis* Borg, 1944; Recent, Antarctica.

Remarks. Borg (1944) assigned three new species to his new genus *Hastingsia* which he placed in the new monogeneric family Hastingsiidae. He remarked on how the autozooids could open singly or in fascicles on the frontal sides of the branches, with gonozooids located in branch axils. All three of the species assigned to *Hastingsia* were recorded by Borg from Antarctica, although one – *H. gracilis* (MacGillivray, 1883) – was originally described from Victoria, Australia.

'Hastingsia' whitteni sp. nov.

(Figs 21–26, 56–58)

Idmonea giebeliana Stoliczka – Hutton, 1873: 102 [non *Idmonea giebeliana* Stoliczka, 1865]. *Fasciculipora ramosa* d'Orbigny – Gordon, 1967: 63, fig. 45 [non d'Orbigny, 1842]. *Fasciculipora ramosa* – Morton & Miller, 1968: 227, 575, figs 76, 214 [non d'Orbigny, 1842]. *Hastingsia maoriana* Whitten MS 1979: 379, pl. 22, figs 4, 5. *Hastingsia* n. sp. 2 – Gordon *et al*. 2009: 293. *Hastingsia* cf. '*giebeliana*' Stolickza – Gordon *et al*. 2009: 293 [non *Idmonea giebeliana* Stoliczka, 1865].

Etymology. Named for Ronald F. Whitten who first recognised this as a new species and gave description of it in his unpublished PhD thesis (Whitten, 1979).

Material. Holotype: NIWA 98120 (Fig. 23), Auckland, on *Sargassum sinclairii*, 3/1/1996, D. P. Gordon Collection. Paratypes: NIWA 98121 (Figs 24, 56–58), details as for holotype. NHMUK 2017.12.17.6 (Fig. 21), 2017.12.17.7 (Figs 22, 25), 2017.12.17.8 (Fig. 26), NZOI Station KAH1206/69, S39.9857°, E174.1988°, 44 m, 20/4/2012, molecular voucher specimen AW757.

Description. Colony encrusting (Fig. 23), becoming semi-erect (Fig. 26), small, adnate branches bifurcating; pale brownish-cream when alive, purplish-brown post-mortem. All zooidal polymorphs fixed-walled, developing pseudoporous frontal walls away from branch growth tips. Autozooids elongate, frontal walls rugose with moderately developed growth lines (Fig. 25), zooidal boundaries grooved slightly, pseudopores subcircular, density decreasing into peristomes; apertures subcircular to rounded quadrate when connate, about 0.18 mm in diameter, usually clustered into small groups (Figs 21, 23, 25, 26) but sometimes isolated; peristomes long, up to at least 1 mm (Fig. 25); terminal diaphragms not observed. Kenozooids not observed. Gonozooids appearing in early astogeny, longitudinally elongate, at least 1.5 mm in total length by 1.2 mm wide, inconspicuous, the frontal wall only slightly convex, boundaries ill-defined (Fig. 21), enclosing some autozooidal peristomes; pseudopore density slightly higher than in the autozooids; ooeciopore not identified but a small aperture, 0.10 by 0.13 mm, in the roof of one gonozooid may be an ooeciopore.

Ancestrula large (Figs 21, 23, 25, 56–58), only a little smaller than later budded autozooids, 0.79–0.82 mm long, with subcircular aperture 0.16–0.18 mm in diameter. Protoecium large, 0.39–0.44 mm in transverse diameter; pseudopores confined to a crescentic marginal band, irregularly spaced, subcircular, countersunk, external diameter *c*. 12 µm, internal diameter *c*. 6 µm. U-shaped transition to ancestrular tube which has a rugose surface and non-countersunk pseudopores.

Mural spines present in autozooids, including the ancestrula, and gonozooids (Fig. 24); branched (in brood chambers) or unbranched with barbed heads (Fig. 22). Transversely fibrous ultrastructure visible at wall growing edges.

Remarks. This new species differs from the type species of *Hastingsia*, *H. irregularis* Borg, 1944), in having larger autozooids and gonozooids, and in not developing extensive erect growth. The linear fascicles depicted by Bock (http://www.bryozoa.net/cyclostomata/hastingsiidae/hastgra.html) in *H. gracilis* (MacGillivray, 1884) have no equivalent in '*H'. whitteni* sp. nov., and the gonozooid in this Australian species is ovoidal with a strongly compressed ooeciopore, contrasting with the new species. The tiny gonozooid of the erect *H. pygmaea* Borg, 1944, the only other species assigned to *Hastingsia*, contrasts with the voluminous gonozooid of *H. whitteni* sp. nov.

This is the first formally published record of *Hastingsia* in New Zealand, although Whitten (1979) referred an undescribed species to this genus in his unpublished PhD thesis. In addition, three fragments from New Zealand donated to the NHMUK collection by F.W. Hutton (NHMUK 75.1.5.35) and labelled by Hutton *Idmonea giebeliana* Stoliczka, 1865 can be assigned to '*H'. whitteni*. In addition, 'Fasciculate sp. 2' of Boardman (1998, p. 29, fig. 75) from Leigh, and the un-named fasciculate cyclostome also from New Zealand figured by Taylor (2000, fig. 6), are both apparently this species.

Material in the NIWA collections identified tentatively as the type species of *Hastingsia*, *H. irregularis*, includes a broken protoecium which seemingly lacks pseudopores and therefore differs significantly from that of '*H*'. *whitteni*, underscoring the problem of assigning the New Zealand species to a genus.

Distribution. Northeastern North Island, New Zealand, Auckland to Whangarei, including Hauraki Gulf from where Whitten (1979) obtained his material.

Suborder Cerioporina von Hagenow, 1851

Family Cerioporidae Busk, 1859

Genus ***Heteropora*** de Blainville, 1830

Type species. *Ceriopora cryptopora* Goldfuss, 1826; Cretaceous, Maastrichtian, The Netherlands.

Remarks. There are unresolved problems over the concept of the genus *Heteropora* owing to the fact that the Cretaceous type species (see Nye, 1976) differs substantially from the extant species, including *H. neozelanica* Busk, 1879 described below, which have been assigned to the genus. One solution (e.g., Gordon *et al*., 2009) has been to refer these recent species to another cerioporid genus *Tetrocycloecia* Canu, 1917, with a Miocene type species (see Taylor & McKinney, 2006, p. 51) but this too may not be congeneric with the species described below.

‘Heteropora’ neozelanica Busk, 1879

(Figs 2, 27–45, 50–52, 59–61)

Heteropora neozelanica Busk, 1879: 724, pl. 15, figs 1–4. *Heteropora neozelanica*. – Nicholson, 1880: 329, figs 1A–C, 2. *Heteropora pelliculata* Waters. – Hutton, 1891: 107. *Heteropora neozelanica*. – Borg, 1933: 306, text-figs 12–14, pl. 5, figs 1–5, pl. 6, figs 3, 4, pl. 7, figs 1–3, pl. 10, figs 1, 2. *Heteropora neozelanica*. – Borg, 1944: 210, pl. 16, fig. 1. *Tetrocycloecia neozelanica*. – Gordon *et al*., 2009: 293. *Tetrocycloecia* spp. – Smith & Gordon 2011: 31.

Material. Lectotype (chosen here): NHMUK 99.7.1.4281 (Figs 27, 28, 30, 31), New Zealand. It is evident that Busk (1879) had more than one specimen at his disposal when he erected *Heteropora neozelanica* as he remarked that Nicholson had furnished him with some very fine specimens of this species. However, his figures (Busk, 1879, pl. 15, figs 1–4) could conceivably be from a single specimen. Busk’s figure 1, which is reproduced here as Fig. 27, depicts an intact ramose colony. Unfortunately, it is not possible to match this or the any of the higher magnifications views (pl. 15, figs 2–4) with material labelled as ‘type’ in the Busk Collection at the NHMUK and it seems possible that the intact colony is either lost or has been broken-up into the fragments that are now mounted on slides. One of these (Fig. 28, 30, 31) is herein chosen as the lectotype of ‘*H’. neozelanica*. Neither Busk (1879) nor Nicholson (1880) gave any more detailed information than simply New Zealand.

Paralectotype: NHMUK 99.7.1.4280 (Figs 29, 32), Nicholson Collection.

Other material: NHMUK 2014.12.17.1 (Figs 2, 33, 36, 40–45, 50–52), Otago Shelf, Stn Mu88-29, 87–89 m, 11/5/1988, P. D. Taylor Collection. NHMUK 2014.12.17.9 (Figs 34, 37), molecular voucher specimen AW086, 46.42°S, 167.58°E, 54 m, The Snares, New Zealand, A. M. Smith & J. Porter Collection, February 2008. NIWA 98122 (Figs 59–61), NZOI Stn Z9684, 34°23.55'S, 172°51.72'E, 40 m, 26/1/1999.

Comparative material (*Heteropora* sp.): NHMUK 2014.12.17.10 (Figs 35, 38), molecular voucher specimen NZ064, 47.08°S, 168.12°E, 94 m, The Snares, New Zealand, A. M. Smith & J. Porter Collection, 29/1/2008.

Description. Colony erect, bush-like (Figs 2, 27), 7 cm or more in diameter, consisting of bifurcating branches. Pale yellow to pale brownish-yellow in life, pale creamy brown to purplish-brown post-mortem. Branch diameter variable between colonies, ranging from 0.7~~–2.2 mm, most often 2.0~~–6.0 mm, increasing modestly from distal branch tips to branch bases, mean value variable between colonies. Zooidal polymorphs predominantly free-walled, apart from gonozooids, which have fixed-walled brood chamber roofs (Figs 42, 43), zooids from early astogeny, and old branches and occasional patches of autozooids with short peristomes of exterior wall and kenozooids closed by terminal diaphragms (Figs 39, 40, 43–45). Distinction between autozooids and kenozooids sometimes obscure (Fig. 36). Autozooidal apertures subcircular, about 0.19–0.24 mm in diameter, rim often slightly raised; exterior-walled peristomes rarely developed, sparsely pseudoporous, short, <1 mm high (Figs 40, 44, 45). Basal diaphragms present close to endozone/exozone boundary in some autozooids (Fig. 32). Kenozooids more numerous than the autozooids which they surround entirely, apertures rounded polygonal, typically smaller and more variable in diameter than autozooidal apertures, equidimensional or elongate, about 0.08–0.28 mm wide, thick-walled with sharp zooidal boundaries; some kenozooids closed by terminal diaphragms accreted centripetally, with closely-spaced pseudopores about 10 µm in size, often teardrop-shaped, located slightly to appreciably proximally of apertural rims. Gonozooids subcircular (Fig. 42), variable in size, 1.4–3 mm in diameter, roof bulging very slightly, formed of densely pseudoporous exterior wall accreted centrifugally from the peristomes of autozooids passing through brood chamber, margins becoming overgrown by surrounding zooids; ooeciopore located about midway between centre and distal edge, approximately the same size as an autozooidal aperture, compressed, 0.19 mm long by 0.12 mm wide in the single example studied (Fig. 42); ooeciostome short, slightly flared.

Early astogeny observed in two colonies, both from NZOI Station Z9684 in Spirits Bay, northern New Zealand. Fan-like encrusting base giving rise to a single erect stem. Ancestrula (Figs 59–61) 0.77–1.05 mm long, with subcircular aperture 0.17–0.18 mm long by 0.13–0.18 mm wide, occluded by a terminal diaphragm in one example. Protoecium large, 0.38–0.46 mm in transverse diameter; pseudopores confined to a crescentic marginal band, closely but irregularly spaced, subcircular, countersunk, external diameter *c*. 10 µm, internal diameter *c*. 5 µm. Shallow U-shaped transition to ancestrular tube which has a rugose surface with non-countersunk pseudopores.

Mural spines present in both autozooids and kenozooids, tending to be more numerous and longer in the latter; varies in morphology, many with a smooth shaft bearing a head covered by sharp barbs, longest around circumference of head and downwardly curved; shaft sometimes dividing distally into two or three branches, each with a barbed head; other mural spines with a single long barb directed proximally and resembling the beak on a bird's head. Distal edges of walls exhibit transversely fibrous ultrastructure.

Remarks. Material provisionally assigned to this species varies widely in branch diameter. Busk's syntypes have branches 5–6 mm in diameter, whereas the branches in colonies from the Otago Shelf vary from the same size (see colour photo in Smith & Gordon, p. 31) to about half this size (e.g. Fig. 2). Other aspects of the skeletal morphology, however, seem indistinguishable. In view of the depth-related variability in branch diameters between colonies of *Heteropora pacifica* Borg, 1933 from Washington State described by Schopf *et al.* (1980), the possibility that branch diameter in '*H'. neozelanica* also varies ecophenotypically cannot be excluded. Therefore, '*H'. neozelanica* is here interpreted in a broad sense to encompass most species of '*Heteropora'* from New Zealand waters with widely ranging branch diameters.

The molecular phylogenetic analysis below revealed more than one clade of '*Heteropora*' in New Zealand. Comprehensive research combining morphological and molecular analyses of material from multiple localities around New Zealand will be needed to unravel the complexity of this group of species. This is beyond the scope of the current study.

Neither Busk (1879) nor Nicholson (1880) described the gonozooids of this species. Borg (1933) too was unable to identify them with certainty in the material he had available for study but he believed that some enlarged apertures visible on colony surfaces were possibly ooeciopores of overgrown gonozooids. However, it is clear from his figure (pl. 5, fig. 5) that these supposed ooeciopores are tubes formed by the bryozoan around a symbiont such as a spionid polychaete (cf. Ernst *et al*., 2014). Unequivocal examples of gonozooids are present in material of '*H'. neozelanica* from the Otago Shelf. These show the exterior-walled roof supported by autozooids passing through the brood chamber (Figs 42, 43) and an ooeciopore of about the same size as an autozooidal aperture but laterally compressed.

Distribution. Widely distributed in waters around New Zealand at the present-day, at least from Spirits Bay in the north to Foveaux Strait in the south, as well as The Snares.

Molecular phylogenetics

Figure 46 depicts the molecular phylogeny based on the concatenated dataset of lsr+ssrDNA, in which the newly sequenced taxa '*Hastingsia' whitteni* sp. nov. and *Diaperoecia purpurascens* were analysed in the context of the previously published cyclostome phylogenies of Waeschenbach *et al.* (2009) and Taylor *et al.* (2011). The tubuliporine *Annectocyma tubulosa* forms the sister group to a clade composed of the cerioporines '*Heteropora'* sp. (molecular specimen NZ064), '*Heteropora' neozelanica* (molecular specimen AW086) and the tubuliporines '*Hastingsia' whitteni* sp. nov. (molecular specimen AW757) and *Diaperoecia purpurascens* (molecular specimen AW578), where '*Heteropora'* sp. forms the sister group to an unresolved assemblage of the latter three taxa (Fig. 46). The same topology for this grouping was obtained in analyses using the single gene partitions (Online Supplementary Material), but the node that places '*Heteropora'* sp. as the sister group to '*Hastingsia' whitteni* sp. nov. + '*Heteropora' neozelanica* + *Diaperoecia purpurascens* is only weakly supported in the lsrDNA only analysis (0.72 pp).

Discussion

The results of the molecular phylogenetic analysis, which is the most comprehensive and up-to-date for cyclostomes, are unexpected because they show a close relationship between cyclostome bryozoans previously assigned to different suborders based on morphological criteria. Whereas *Heteropora* is traditionally assigned to the suborder Cerioporina, *Diaperoecia* and *Hastingsia* are placed in the suborder Tubuliporina, although some classifications (e.g., Walter, 1970; Ryland, 1982) would assign the latter genus to a third suborder – Fasciculina – not universally recognised. There have been no previous suggestions in the literature that *Heteropora* might be closely related to *Diaperoecia* and *Hastingsia*, and the only superficial similarity is their pale yellowish to yellowish-brown colour in life and generally purplish-brown post-mortem pigmentation. But can this relationship be supported using morphological characters?

The taxonomy of cyclostome bryozoans has been founded entirely on characters of the mineralized skeleton. Skeletal characters are easily visible without histological preparation, and are conserved in dried material as well as fossils. In contrast, very little is known about the soft part anatomy of cyclostome bryozoans and available data concerns only a small proportion of known species (see Boardman, 1998). Cyclostome suborders have been recognized mainly according to the types of skeletal walls employed by the autozooids and gonozooids.

There are two basic types of skeletal walls in cyclostomes (and other bryozoans): interior and exterior (see Taylor *et al.*, 2014). Interior skeletal walls partition body cavities and are secreted by an epithelium that is present on both sides and wraps around the distal end of the wall. They lack a cuticular outer layer. Exterior skeletal walls are located at the interface between the bryozoan and the environment, and are secreted by an epithelium present on the body cavity side only, the opposite side being covered by a layer of cuticle. When no frontal exterior walls are developed a hypostegal cavity (coelom or pseudocoel) invests the colony, forming a continuous layer that connects the body cavities of the zooids over the outer ends of their interior walls. This skeletal organization was termed ‘double-walled’ by Borg (1926), later renamed ‘free-walled’. In contrast, cyclostomes with frontal exterior walls lack a hypostegal cavity investing the colony, an organization termed ‘single-walled’ by Borg but now known as ‘fixed-walled’.

Two cyclostome suborders (Tubuliporina and Articulata) possess fixed-walled autozooids and gonozooids (i.e., with exterior frontal walls), one order (Cerioporina) has free-walled autozooids but fixed-walled gonozooids, while the other two suborders (Rectangulata and Cancellata) have free-walled autozooids and gonozooids. To Borg (1926) and many later authors, free- vs. fixed-walled skeletal organizations represented fundamental differences of high taxonomic value. Indeed, it has been argued that modern free-walled cyclostomes are more closely related to various orders of free-walled Palaeozoic bryozoans than they are to the fixed-walled cyclostomes (e.g., Boardman, 1984; Viskova, 1992).

The value of skeletal organization in high-level cyclostome taxonomy has been challenged in recent years, firstly by the recognition of taxa showing mixtures of the two organizational types, and subsequently by molecular phylogenetic evidence. Taylor (2000) pointed to examples of mixing free- and fixed-walled organizations in seemingly monophyletic cyclostome taxa (e.g., Eleidae, Cinctiporidae), and even in single colonies (e.g., *Cinctipora elegans*: see Boardman *et al*., 1992). A particularly clear example is *Spiritopora perplexa* Taylor & Gordon, 2003, in which the zooids in the extensive lamellar base of the colony are normally fixed-walled, whereas those forming the erect fronds are predominantly free-walled.

Molecular phylogenetic studies of cyclostomes have recovered trees showing no clear separation between free- and fixed-walled species. Waeschenbach *et al*. (2009) assembled a tree using sequence data from 22 species of cyclostomes, showing poor congruence with traditional classifications based on skeletal organization; transitions between free-and fixed-walled conditions, or vice-versa, have apparently occurred several times during cyclostome evolution. A subsequent molecular study (Taylor *et al*., 2011) showed the dominantly free-walled cyclostome *Tennysonia* to group with the fixed-walled tubuliporine *Idmidronea*, despite the additional difference in the morphology of *Tennysonia*, which has kenozooids as spacers between the autozooidal apertures.

In the light of this accumulating evidence for plasticity in skeletal organization, it is perhaps unsurprising to find the fixed-walled tubuliporines *Diaperoecia purpurascens* and ‘*Hastingsia’ whitteni* in the same molecular clade as the free-walled cerioporine ‘*Heteropora’ neozelanica*. As with the clade containing

Idmidronea and *Tennysonia*, a further difference is apparent in the manner in which the apertures of the autozooids – and hence the lophophores in living colonies – are spaced apart. Areas of the colony surface between the autozooidal apertures of *D. purpurascens* and '*Hastingsia' whitteni* are occupied by the calcified exterior frontal walls of the autozooids (e.g., Fig. 9), whereas in '*Heteropora'* they are filled by kenozooids with open apertures (e.g., Figs 36–38). These kenozooids are best interpreted as 'normal' buds that failed to develop a polypide with a functional lophophore.

It is also worth remarking on the various forms of frontal exterior wall calcification that can be found in the predominantly free-walled '*Heteropora' neozelanica*. Aside from the fixed-walled gonozooids, which are found in other cerioporine cyclostomes too, patches of exterior wall calcification are developed elsewhere on colony surfaces. They are particularly common in the proximal parts of branches (Figs 39, 40) but can also be seen in distal branches, for example adjacent to gonozooids (Figs 42–44). The kenozooids in these patches are usually closed by terminal diaphragms, either accreted distally almost as a lamina across the ends of their walls, or more proximally, leaving the distal ends of the vertical kenozooidal walls exposed above the diaphragms (Fig. 40). Autozooids in these patches often develop short exterior-walled peristomes with scattered pseudopores (Fig. 45). Peristomes are also present in the autozooids passing through brood chambers and supporting the roofs of the gonozooids (Figs 42, 43).

Three nominal species of *Heteropora* have been recorded from the Pacific coast of North America. Ross (1973) described the skeletal morphology of *Heteropora* colonies from Washington State, USA, noting the presence of what she termed 'collars' around the aperture of autozooids proximal of the branch growing tips. These collars are clearly exterior-walled peristomes very similar to those seen in New Zealand '*Heteropora*'. Fixed-walled growth, therefore, is more widely distributed taxonomically in Recent species assigned to *Heteropora* than is generally acknowledged.

Gizzard

Despite the paucity of information on cyclostome soft-part anatomy, the molecular tree recovered here (Fig. 46) is corroborated by at least one anatomical feature, the presence of a gizzard. Gizzards are modified sections of stomach cardia with microvillous plates or teeth (Gordon, 1975) and apparently function to allow bryozoans to open diatom frustules (Markham & Ryland, 1987). They have been reported in a relatively small number of bryozoans, including some ctenostome and cheilostome gymnolaemates as well as four species of cyclostomes (Schäfer, 1986). The cyclostome species having gizzards were identified as *Diaperoecia major* (Johnston, 1847) and *D. tubulosa* (Busk, 1875) by Schäfer (1986), and as *Pustulopora purpurascens* Hutton and 'Fasciculate sp. 2' by Boardman (1998). In all of these cyclostomes the gizzard comprises two dental plates that act like jaws. The species identified as *Diaperoecia tubulosa* is now *Annectocyma tubulosa*, a northern hemisphere species recovered as the sister-taxon to the clade of New Zealand cyclostomes described in the current paper. Boardman's (1998) *Pustulopora purpurascens* is *Diaperoecia purpurascens*, and his 'Fasciculate sp. 2', to judge from fig. 75, is probably '*Hastingsia' whitteni* sp. nov. Therefore, the clade including *Annectocyma tubulosa* and all crownward taxa possess a gizzard as an apomorphic character, although no histological data is yet available for New Zealand species of *Heteropora*. The finding of a gizzard in '*Heteropora'* would corroborate this character as a clade-defining apomorphy.

Mural spines

Minute spines of uncertain function grow from the skeletal walls into the zooidal chambers in many cyclostome taxa (Farmer, 1979; Taylor & Weedon, 2000 and references therein). These zooecial or mural spines vary in morphology among species, and also within taxa, both between polymorphs and within the same polymorph.

Mural spines with long shafts supporting barbed heads covered by a few to a moderate number of spinelets occur in the three related species described above, as well as in the type species of *Diaperoecia* (Fig. 8). Most are unbranched (Figs 22, 47–48, 52) but some bifurcate (Fig. 51) and have a barbed head on each branch. The long spines of *Heteropora neozelanica* with globose densely barbed heads are also seen in species of '*Heteropora'* from the Pacific Coast of North America (Farmer, 1979, text-fig. 4; Weedon & Taylor, 1996, fig. 7e) and could be taxonomically diagnostic. However, spines with flattened heads and a small number of spinelets (Figs 8, 47–49) seem to be more taxonomically widespread. They occur, for example, in lichenoporids (Farmer, 1979, pl. 1; Dick *et al*., 2006, fig. 16D) which are distant in molecular trees (Waeschenbach *et al*., 2009, 2012) from the New Zealand cyclostomes described here.

Unfortunately, too little is known about the morphological variants and taxonomic distribution of mural spines for their potential in cyclostome taxonomy to be evaluated. Additionally, they have little utility in fossil cyclostomes as they are too fragile for routine preservation.

Early astogeny

Few taxonomic studies include information on the early astogeny of cyclostome bryozoans. Nevertheless, Jenkins & Taylor (2014) considered early astogeny to be a potentially important source of higher-level taxonomic characters, given that early development may be relatively conserved in evolution and can therefore provide evidence of deep phylogenetic relationships among cyclostomes. Studying early astogenetic stages in species with large erect colonies, including *Diaperoecia purpurascens* and '*Heteropora'*, is difficult as the oldest parts of colonies may be lost or obscured by subsequent growth of the colony or fouling organisms. However, it has been possible to find examples of colonies preserving the ancestrula and other early zooids in both of these species, as well as in the smaller colonies of '*Hastingsia' whitteni.* Contrary to the striking differences seen in the skeletal morphology of later astogenetic stages in these three closely related species, their early astogeny is remarkably similar.

Juvenile colonies of all three species are fan-shaped encrustations comprising fixed-walled autozooids with calcified exterior frontal walls (e.g., Figs 19, 20). One or more erect stems grow upwards from the substrate from this encrusting base. In the case of '*Heteropora'*, the zooids in the erect stems differ from those of the encrusting base in being free-walled, but in *Diaperoecia purpurascens* and '*Hastingsia' whitteni* they have the same fixed-walled skeletal organization.

The greatest similarities are apparent in the ancestrula (Figs 53, 56, 59), and particularly the protoecium, which is large in all three species: 0.33–0.37 mm wide in *D. purpurascens*, 0.39–0.44 mm in '*Hastingsia*' *whitteni*, and 0.38–0.46 mm in '*Heteropora*'. These sizes compare with typical protoecial widths of 0.1–0.2 mm in cyclostomes (e.g., Jenkins & Taylor, 2014).

Cyclostome protoecia exhibit interspecific variability in the number and distribution of pseudopores (Weedon, 1998). All three species from New Zealand are characterized by protoecia with numerous, somewhat irregularly arranged pseudopores distributed in a crescentic band around the proximal and lateral edges of the protoecium (Figs 54, 57, 60). Pseudopores are lacking from more distal parts of the protoecium but reappear on the ancestrular tube.

Not only is the distribution of protoecial pseudopores very distinctive in *Diaperoecia purpurascens*, '*Hastingsia' whitteni* and '*Heteropora'*, but they are very similar in size and shape. In all three species the pseudopores are circular to elliptical and have a characteristic countersunk morphology (Figs 55, 58, 61), with an external diameter of about 10–12 µm and an internal diameter of 5–6 µm. In contrast, pseudopores on the ancestrular tube and later zooids are not countersunk. Weedon (1998) described such pseudopores in a specimen from the Otago Shelf (New Zealand) which he identified as *Diaperoecia* cf. *purpurascens*, noting that the pseudopores are located not only at the boundaries between the strips of calcification forming the protoecium but also, and unusually, within strips.

The ancestrula has not been described in *Annectocyma tubulosa*, the sister-taxon to the New Zealand clade forming the focus of the current study, and attempts to find an example in the collections of the NHMUK have been unsuccessful. A colony of the related *A. major* (Johnston, 1847), however, has a protoecium with a near-marginal band of countersunk pseudopores (Figs 62, 63). The corollary is that this character may be apomorphic for a clade that includes not only the three New Zealand species under study, but also some taxa such as *Annectocyma* from the immediate out-group.

Figure 64~~2~~ summarises diagrammatically how the very similar skeletal organization in the early astogenetic stages of *Diaperoecia purpurascens* and '*Heteropora*' changes in later astogeny. In *D. purpurascens*, the zooids in late astogeny retain the same fixed-walled organization as those from early astogeny. Only the growing tips of the erect branches are covered by hypostegal coelom, and calcified exterior frontal walls of the autozooids form the branch surface between the everted tentacle crowns. In contrast, in '*Heteropora*', the zooids in late astogeny have a free-walled organization, hypostegal coelom extends proximally from the branch growth tips to cover the entire branch surface, and kenozooids function as spacers between the everted tentacle crowns in the absence of calcified exterior frontal walls. Transitions from one state to the other can be construed as heterochronous (see Taylor, 2000).

Implications for cyclostome taxonomy

Our molecular phylogenetic analysis recovers, with strong support, a clade of cyclostomes containing the heteromorphic assemblage of '*Heteropora* spp., '*Hastingsia' whitteni* and *Diaperoecia purpurascens*. While this clade at first seems to have a scant morphological basis, it is apparently corroborated by at least one soft-part character – the presence of a gizzard – and by the skeletal morphology of the ancestrula, with distinctive countersunk pseudopores arranged in a crescent on the protoecium. These are not morphological characters previously applied in cyclostome taxonomy. Therefore, it is unsurprising that the supraspecific classification of the taxa studied here does not mirror their phylogenetic relationships. How then can these taxa be reclassified and named to reflect phylogeny better?

Cyclostome families have been defined largely on characters of the gonozooids since the work on F. Canu and R. S. Bassler in the early 20th century. Indeed, Canu (1918) created Diaperoeciidae on the basis of the supposed morphology of the gonozooid of *Diaperoecia intricaria* (Busk) (but see above), which he described as elliptical or suborbicular, surrounding autozooidal apertures and with a subcentral ooeciopore. While the gonozooids of *Diaperoecia purpurascens*, '*Hastingsia' whitteni* and '*Heteropora*' could just about all be accommodated within this diagnosis, there are major differences in structure of the gonozooids between the first two species and '*Heteropora*'. Gonozooids of *D. purpurascens* and '*H*'. *whitteni* have roofs that calcify in a distal direction, parallel to the frontal walls of the adjacent autozooids. The roofs in '*Heteropora*', however, calcify radially outwards from the autozooids that penetrate the brood chamber.

Notwithstanding the problems posed by the lack of knowledge of gonozooid morphology in the type species of *Diaperoecia*, and the substantial contrast in the growth pattern of the gonozooids described above, the family Diaperoeciidae can be used to accommodate the three species from New Zealand studied here if it is redefined using other morphological characters, viz. the presence of a gizzard, and a protoecium with a marginal band of countersunk pseudopores. As both of these characters are also found in species of *Annectocyma*, this genus can also be included in Diaperoeciidae. The family Annectocymidae Hayward & Ryland, 1985 then becomes a junior synonym of Diaperoeciidae Canu, 1918.

More problematical are the most appropriate generic names for the species here rererred to as '*Hastingsia' whitteni* and '*Heteropora'* spp. While it would be justifiable to place all of these species in *Diaperoecia* given their close phylogenetic affinities to *D. purpurascens,* this would conceal the strong morphological differences between these taxa. On the other hand, the identities of both '*Hastingsia' whitteni* and '*Heteropora'* require clarification through detailed studies of their generic type species, including early astogeny and, in the case of the extant type species of *Hastingsia*, soft-part anatomy to ascertain whether a gizzard is present and sequence data to fix its position on the molecular tree. Pending this research, the generic names *Hastingsia* and *Heteropora* are retained as 'form-genera' for the species described here from New Zealand.

Finally, a serious difficulty is posed by the non-monophyletic status of the species identified here as '*Heteropora*'. Sequenced specimens categorized morphologically as belonging to this genus – taking into account the high degree of variation in skeletal characters evident within colonies (see above) – appear as two branches on the molecular tree (Fig. 46) One branch is part of an unresolved assemblage including *Diaperoecia purpurascens* and '*Hastingsia*' *whitteni*, while the other is sister to the clade containing all these three taxa. There are two possible evolutionary interpretations: (1) the '*Heteropora*' morphotype with its predominantly free-walled skeletal organization evolved twice, or (2) the fixed-walled '*Hastingsia*' *whitteni* and *Diaperoecia purpurascens* evolved from a heteroporid ancestor. The unresolved nature of the node in question means that no inferences can be made about the independent acquisition of the types of skeletal organization, although there is moderate support for a sister-group relationship between '*Heteropora*' *neozelanica* and *Diaperoecia purpurascens* in two of the analyses [lsr+ssrDNA: 0.93 pp (result not shown); ssrDNA: 0.92 pp (Supplementary Fig. 2)], which points to independent acquisitions of either fixed-walled skeletal organization from a free-walled ancestor or vice versa. Sequence data from additional specimens of '*Heteropora*' from New Zealand and elsewhere should help in testing these alternatives.

Conclusions

1. The skeletal morphology is described in three species of cyclostome bryozoans from New Zealand – *Diaperoecia purpurascens* (Hutton, 1877), '*Hastingsia'*

whitteni sp. nov. and '*Heteropora' neozelanica* Busk, 1879 – based on SEM of type and other material.

2. Traditional taxonomy places these species in three separate families (Diaperoeciidae, Hastingsiidae and Cerioporidae (=Heteroporidae)) and two or three suborders, reflecting major differences in their skeletal morphology.
3. A molecular phylogenetic analysis showed, however, that the three heteromorphic species are closely related and form a clade that is sister to *Annectocyma*.
4. Morphological support for this 'diaperoeciid' clade + *Annectocyma* comes from the presence of a gizzard (yet to be proven as present in '*Heteropora' neozelanica*) and the skeletal morphology of the earliest part of the colony, the protoecium. In all of these taxa, the protoecium is large and has a peripheral band of countersunk pseudopores.
5. The occurrence of fixed- and free-walled species in the diaperoeciid clade further underscores the plasticity in skeletal organization exhibited by cyclostome bryozoans.
6. Until more is known about the type species of both *Hastingia* and *Heteropora*, these genus names are best employed as form-genera for '*Hastingsia*' *whitteni*, '*Heteropora*' *neozelanica* and '*Heteropora*' sp.
7. Much work remains to be done on assembling a more complete molecular tree of cyclostomes and in identifying morphological characters supportive of the clades that can be identified on molecular grounds. Only then will it be possible to overhaul the morphological classification of cyclostomes currently in use and replace it with one that is more reflective of phylogeny.

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Figure captions

Figures 1, 2. Dried colonies of two cyclostome bryozoans from New Zealand described here. **1.** *Diaperoecia purpurascens* (Hutton), unknown locality in New Zealand, NHMUK 2010.6.25.2. **2.** '*Heteropora' neozelanica* Busk, Otago Shelf, NHMUK 2014.12.17.1. Scale bars: 10 mm.

Figures 3–8. *Diaperoecia intricaria* (Busk); back-scattered scanning electron micrographs of syntypes of the type species of the genus *Diaperoecia*; NHMUK 75.5.29.35, syntypes, SW Australia, Busk ex Gould Collection. **3.** Bifurcating branches and kenozooidal flange (arrow). **4.** Detail showing irregular distribution of autozooid apertures and a kenozooidal outgrowth (lower right). **5.** Terminal diaphragm. **6.** Autozooids with short peristomes and pseudoporous frontal walls. **7.** Oblique transversely fractured branch. **8.** Mural spine. Scale bars: 3, 4 = 1 mm; 5–7 = 100 µm; 8 = 10 µm.

Figures 9–18. *Diaperoecia purpurascens* (Hutton); back-scattered scanning electron micrographs. **9–12, 16.** East Ulva Island, Paterson Inlet, Stewart Island, New Zealand, D. Foster and A. M. Smith Collection, 8/6/1995, NHMUK 2014.12.17.2; **9.** Bifurcating branch; **10.** Detail showing autozooids; **11.** Pseudopores across a zooidal boundary; **12.** Transversely fractured branch; **16.** Longitudinally sectioned branch showing aperture (upper left), distantly spaced interzooidal pores in interior walls, closely spaced pseudopores in exterior frontal wall (left), and mural spines growing from frontal wall. **13–15.** From craypot at Waitangi, Chatham Island, P. D. Taylor Collection, 4/11/1999; **13, 14.** NHMUK 2017.12.17.3; **13.** Fertile branch showing longitudinally elongate gonozooid. **14.** Detail of gonozooid and ooeciopore. **15.** NHMUK 2017.12.17.4, another fertile branch with gonozooid scarcely visible (possible ooeciopore arrowed). **17, 18.** Molecular sequence voucher specimen, Otago Shelf, A. M. Smith Collection, 25/1/2012, NHMUK 2017.12.17.5; **17.** Broken branch; **18.** Incomplete terminal diaphragm. Scale bars: 9, 13, 15 = 1 mm; 10 = 200 µm; 11 = 50 µm; 12, 17 = 500 µm; 14, 16, 18 = 100 µm.

Figures 19, 20. *Diaperoecia purpurascens* (Hutton); back-scattered scanning electron micrographs of encrusting colony bases with broken ends of erect stems; arrows point to ancestrular protoecia. **19.** Outside Whangaroa Harbour, 26/1/1981, National Museum of New Zealand BS 862. **20.** Pleistocene fossil, Nukumaru Brown Sand, Nukumaru Beach, 01/2014, NHMUK BZ 7733, P. D. Taylor Collection. Scale bars = 1 mm.

Figures 21–26. **'***Hastingsia' whitteni* sp. nov.; back-scattered scanning electron micrographs. **21, 22, 25, 26.** Paratypes (molecular voucher specimens AW757), NZOI Station KAH1206/69, S39.9857°, E174.1988°, 44 m, 20/4/2012. **21.** Fertile colony (possible ooeciopore arrowed) with ancestrula (bottom), paratype, NHMUK 2017.12.17.6. **22, 25.** Paratype, NHMUK 2017.12.17.7; **22.** Mural spine; **25.** Entire colony showing ancestrula (left) with long peristome. **26.** Paratype, semi-erect colony, NHMUK 2017.12.17.8. **23, 24.** Auckland, on *Sargassum sinclairii*, 3/1/1996, D. P. Gordon Collection; **23.** Holotype, NIWA 98120; **24.** Incomplete gonozooid from paratype, NIWA 98121. Scale bars: 21, 23, 25, 26 = 1 mm; 22 = 10 µm; 24 = 500 µm.

Figures 27–32. **'***Heteropora' neozelanica* Busk. **27.** Reproduction of colony illustrated by Busk (1879, fig. 1). **28–32.** Back-scattered scanning electron micrographs of Busk's syntypes. **28, 30, 31.** Lectotype, NHMUK 99.7.1.4281; **28.** Branch fragment; **30.** Autozooid surrounded by slightly smaller and more polygonal kenozooids. **31.** Mural spines visible in kenozooid aperture. **29, 32.** Paralectotype, NHMUK 99.7.1.4280; **29.** Transversely sectioned branch showing axial endozone surrounded by exozone with thick-walled zooids; **32.** Aborally convex ~~terminal~~ basal diaphragm. Scale bars: 27 = 10 mm; 28, 29 = 1 mm; 30 = 200 mm; 31 = 100 µm; 32 = 50 µm.

Figures 33–45. **'***Heteropora'* spp. from New Zealand. **33–34, 36–37, 39–45**, '*H*'. *neozelanica* Busk; back-scattered scanning electron micrographs. **33, 36, 39–45.** NHM 2014.12.17.1, Otago Shelf, Stn Mu88-29, 87–89 m, 11/5/1988, P. D. Taylor Collection; **33.** Bifurcating branch;~~.~~ **36.** Detail of apertures of varying size, lacking a clear distinction between autozooids and kenozooids; **39.** Branch with free-walled zooids distally and fixed-walled proximally; **40.** Detail of fixed-walled part of branch showing autozooids with peristomes (some containing terminal diaphragms) and kenozooids with terminal diaphragms well proximal of wall edges. **41.** Transversely fractured branch showing endozone and exozone; **42.** Gonozooid with ooeciopore arrowed (distal is to the left); **43.** Broken gonozooid surrounded by band of fixed-walled zooids; **44.** Close-up of fixed-walled zooids showing autozooids with peristomes, kenozooids with terminal diaphragms almost flush with the ends of the vertical walls (cf. Fig. 40), and a zooid of a fouling cheilostome (top); **45.** Detail of exterior-walled peristome with pseudopore (arrowed) and base of interior wall calcification. **34, 35, 37, 38.** Molecular voucher specimens; **35, 38.** *Heteropora* sp., NHMUK 2017.12.17.10, voucher NZ064, The Snares, 94 m, A. M. Smith & J. Porter Collection, February 2008; this species was distinguished using molecular evidence but is morphologically almost identical to specimens shown here as ‘*H.*’ *neozelanica*; **35.** Branch surface; **38.** Raised autozooidal apertures surrounded by kenozooids. **34, 37.** ‘*H*’. *neozelanica* Busk~~‘*Heteropora*’ sp.~~, NHMUK 2017.12.17.9, voucher AW086, The Snares, 54 m; The Snares, A. M. Smith & J. Porter Collection, February 2008; ~~this species was distinguished using molecular evidence but is morphologically almost identical to specimens shown here as ‘*H.*’ *neozelanica*;~~ **34.** Branch surface showing free-walled zooids; **37.** Autozooidal and kenozooidal apertures moderately well differentiated; Scale bars: 33–35, 39, 41, 43 = 1 mm; 36–38, 40, 44 = 200 µm; 42 = 500 µm; 45 = 100 µm.

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Figure 46. Bayesian analysis of the concatenated lsrDNA and ssrDNA dataset constructed using MrBayes version 3.2.1 under the GTR+I+G model; 5,000,000 generations, 2,000,000 generations burn-in. All nodes with <0.95 posterior probability have been collapsed. The branch length scale bar indicates number of substitutions per site. Box indicates the clade forming the focus of the current study. Cyclostome suborders based on conventional morphological classifications are given on the right.

Figures 47–52. Mural spines; high-resolution back-scattered electron micrographs. **47–49.** *Diaperoecia purpurascens* (Hutton), National Museum of New Zealand BS 862, outside Whangaroa Harbour; **47.** Group of mural spines on inside of frontal wall; **48.** Detail of barbed mural spine with flat head; **49.** Mural spine on interior wall with spinelets directed proximally. **50–52.** ‘*Heteropora*’ *neozelanica* Busk, NHMUK 2014.12.17.1, Otago Shelf, Stn Mu88-29; **50.** Kenozooid containing numerous mural spines; **51.** Bifid mural spine; **52.** Mural spine with long shaft. Scale bars: 47, 50 = 50 µm; 48, 49, 51, 52 = 5 µm.

Figures 53–61. Comparative morphology of ancestrulae; back-scattered scanning electron micrographs. **53–55.** *Diaperoecia purpurascens* (Hutton), outside Whangaroa Harbour, 26/1/1981, National Museum of New Zealand BS 862; **53.** Ancestrula; **54.** Protoecium; **55.** Protoecial pseudopores. **56–58.** '*Hastingsia' whitteni* sp. nov., Auckland, on *Sargassum sinclairii*, 3/1/1996, D. P. Gordon Collection, paratype NIWA 98121; **56.** Ancestrula; **57.** Protoecium; **58.** Protoecial pseudopores. **59–61.** '*Heteropora' neozelanica* Busk, NZOI Stn Z9684, NIWA 98122; **59.** Ancestrula; **60.** Protoecium; **61.** Protoecial pseudopores. Scale bars: 53, 56, 59 = 200 µm; 54, 57, 60 = 100 µm; 55, 58, 61 = 20 µm.

Figure 62–63. *Annectocyma major* (Johnston, 1847), English Channel, 49°19.9,N 3°22.4'W, 77 m, 3/2/1962. **62**, ancestrula with aperture closed by a terminal diaphragm, and early budded zooids. **63**, damaged protoecium showing countersunk pseudopores. Scale bars: 62 = 500 µm; 63 = 200 µm.

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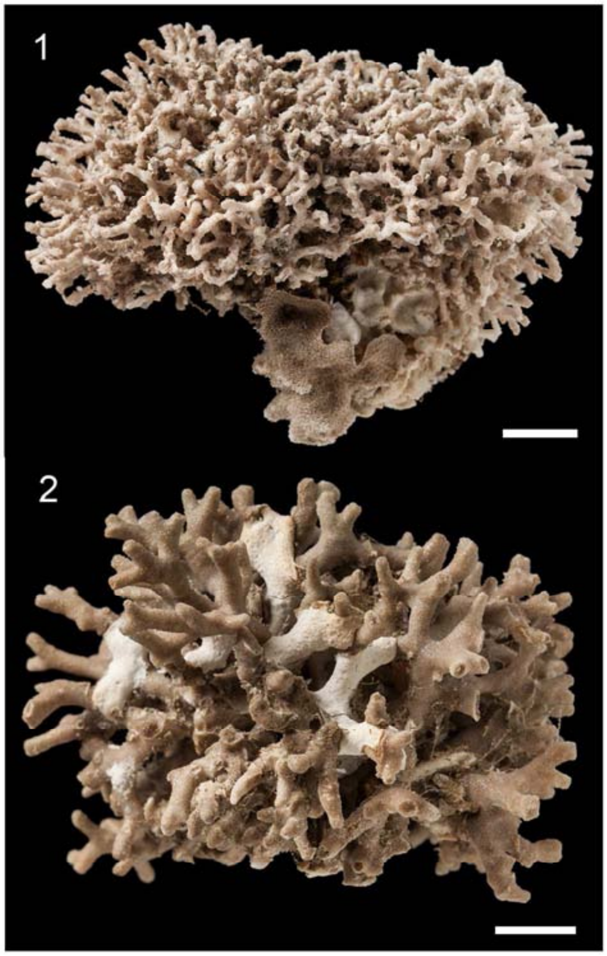
Figure 64~~2~~. Simplified vertical sections through young colonies of *Diaperoecia purpurascens* and '*Heteropora*' showing skeletal organization similarity during early astogenetic stages compared with its dissimilarity in later stages when erect growth develops (see text for full explanation). Solid black lines indicate calcified skeletal walls; dashed lines uncalcified outer body walls enclosing hypostegal coelom. Everted tentacle crowns of autozooids are shown diagrammatically; open apertures between the autozooids in '*Heteropora*' are kenozooids.

Supplementary Material

Supplementary Figure 1. Bayesian analysis of the lsrDNA dataset constructed using MrBayes version 3.2.1 under the GTR+I+G model; 5,000,000 generations, 4,500,000 generations burn-in. The branch length scale bar indicates number of substitutions per site.

Supplementary Figure 2. Bayesian analysis of the ssrDNA dataset constructed using MrBayes version 3.2.1 under the GTR+I+G model; 5,000,000 generations, 4,500,000 generations burn-in. The branch length scale bar indicates number of substitutions per site.



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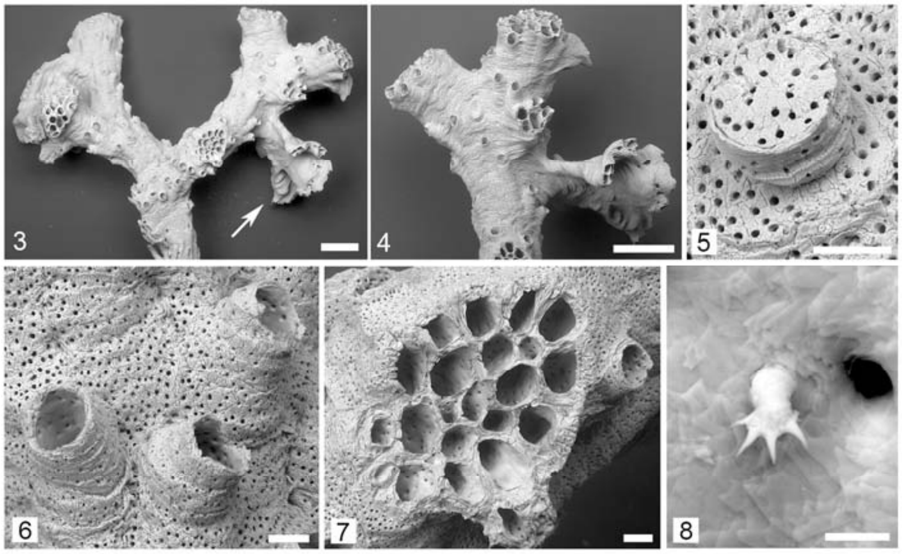

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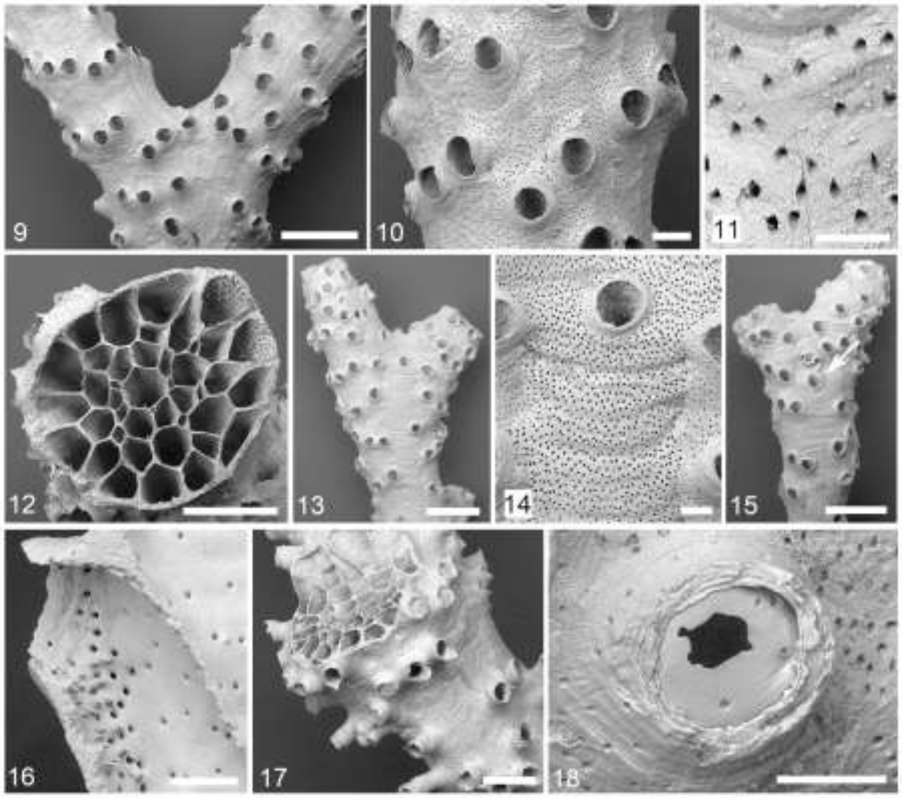

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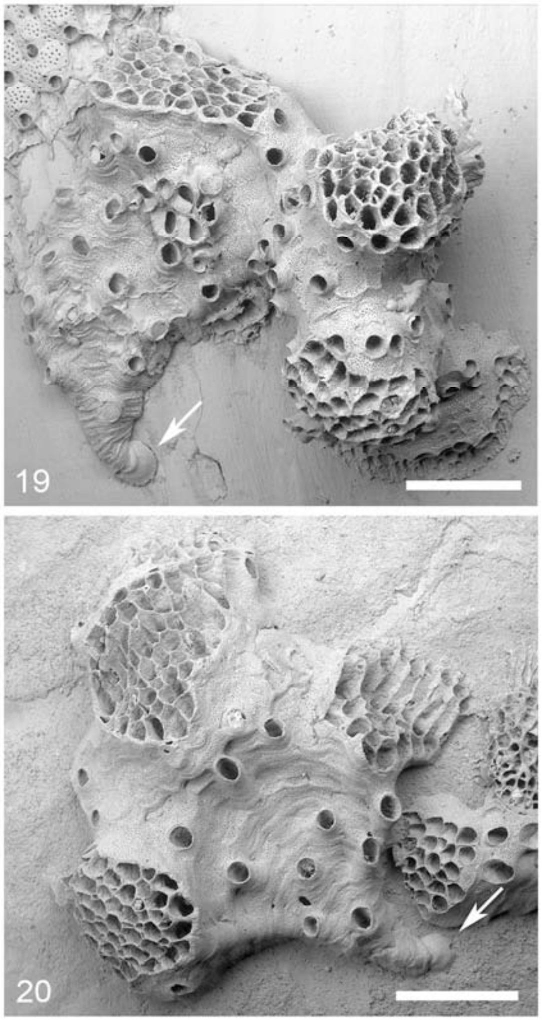

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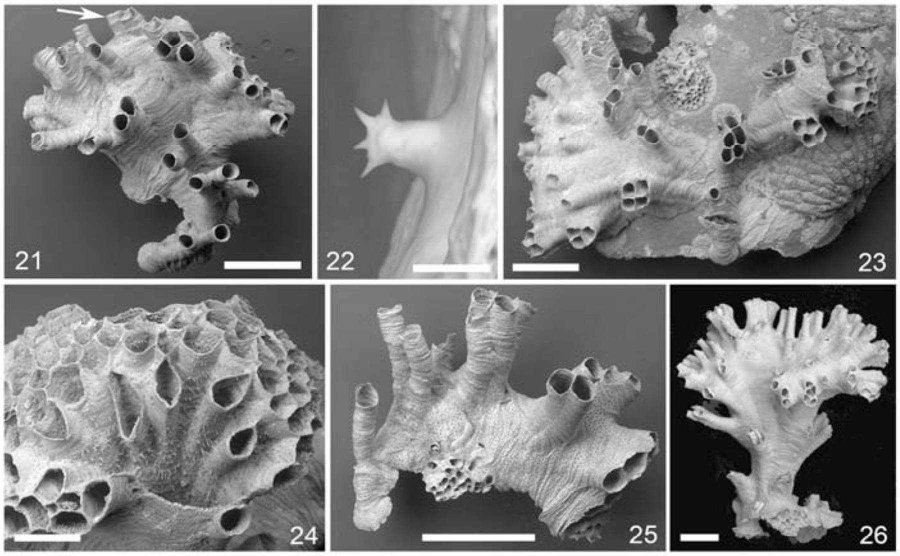

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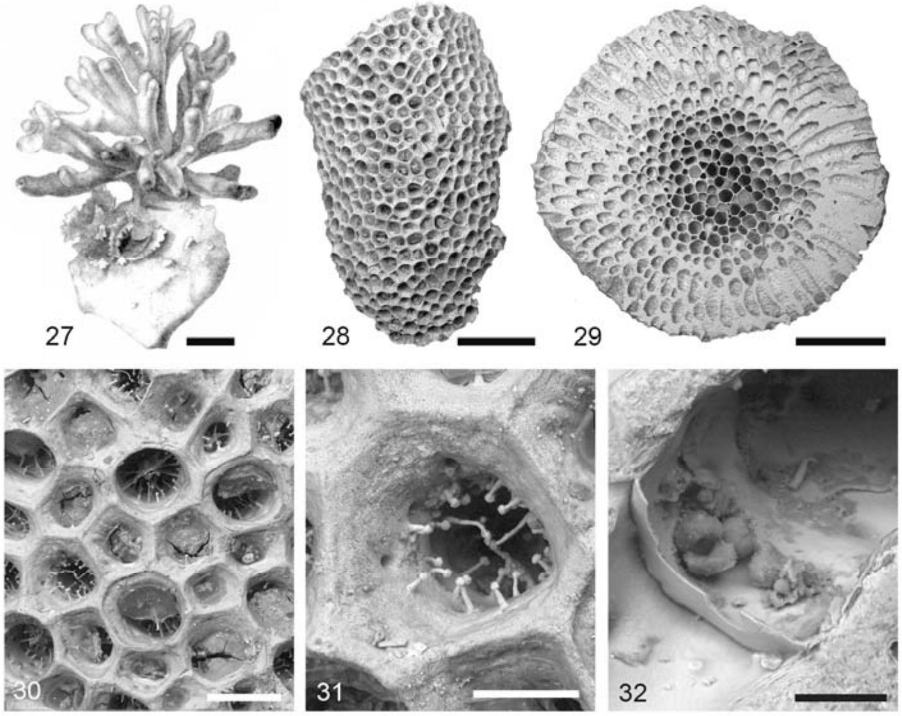

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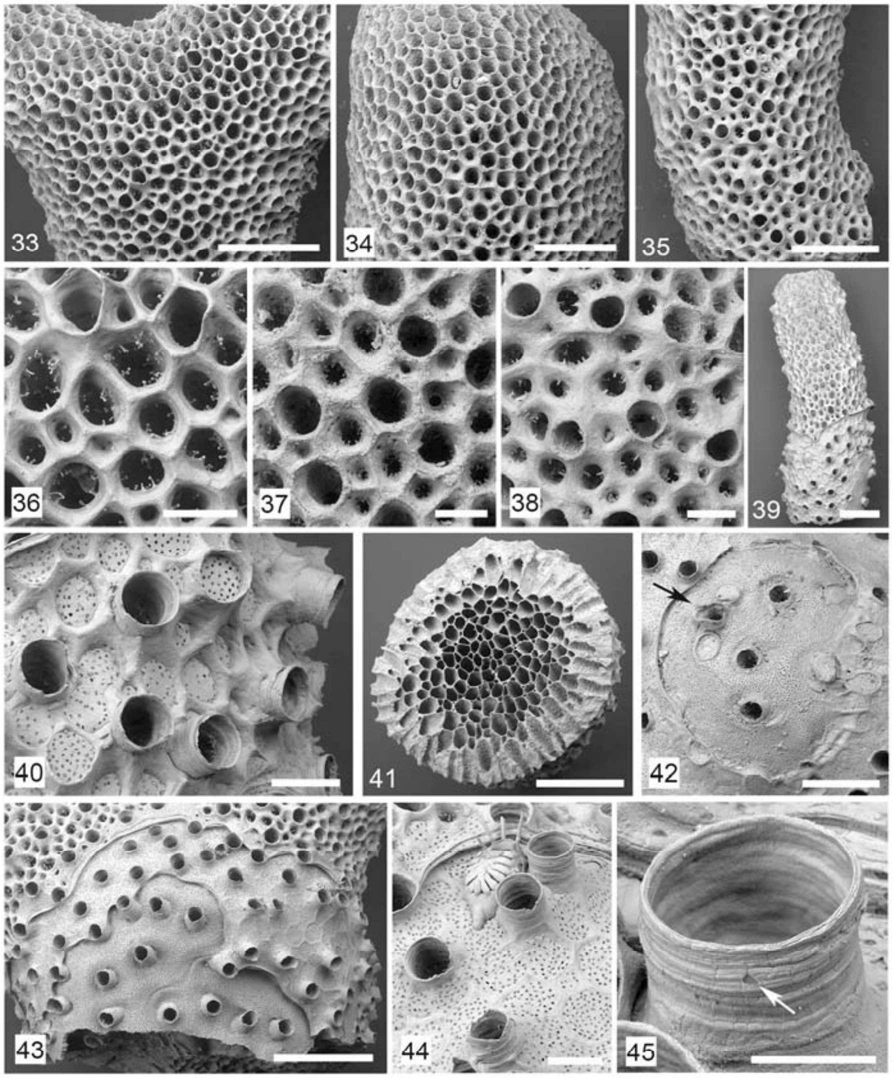

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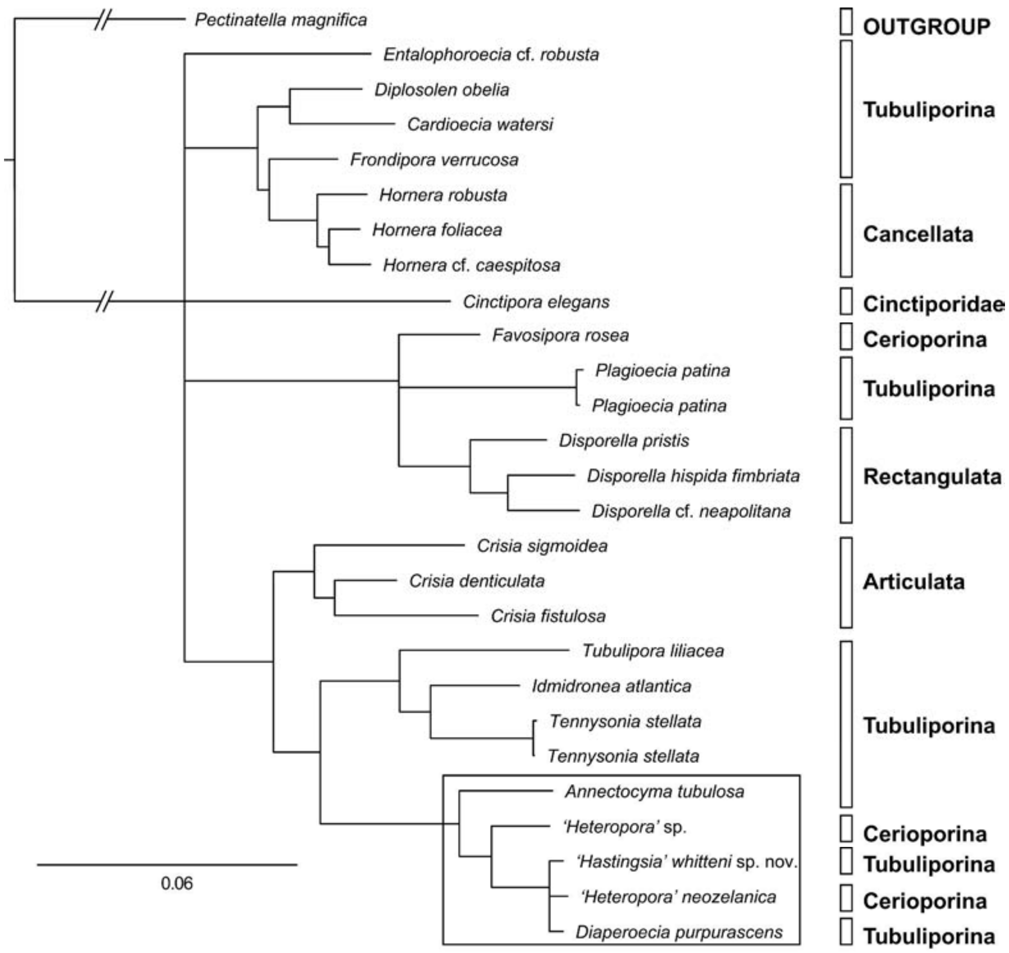

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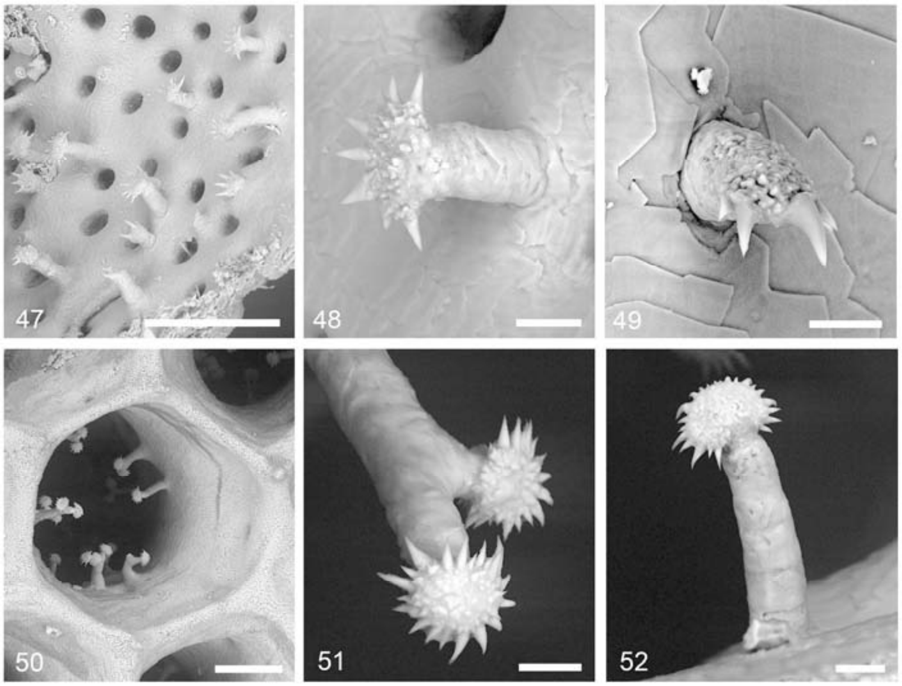

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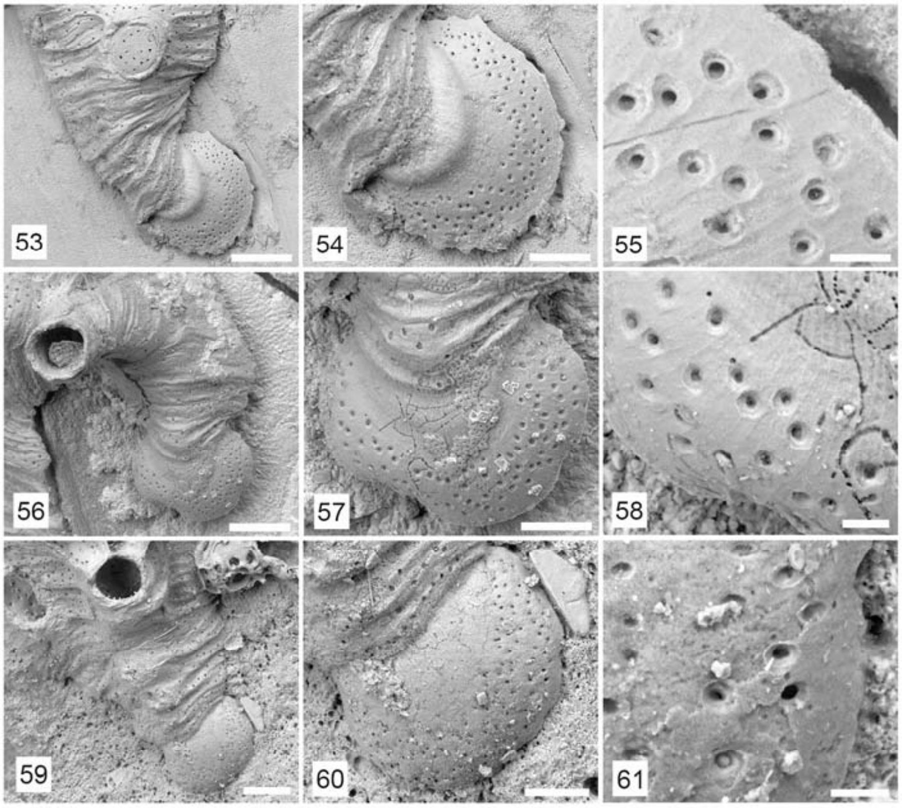
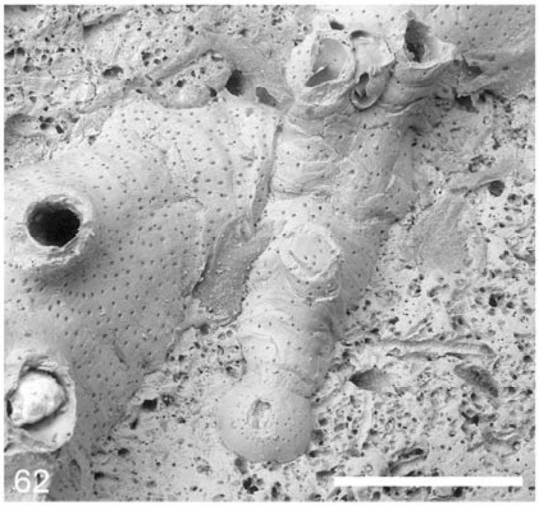
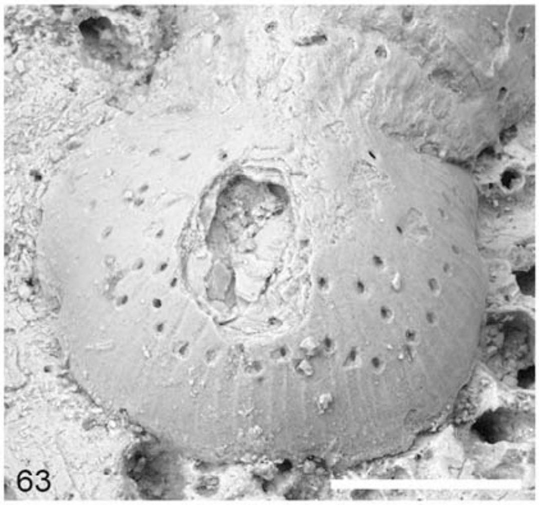


Figures 53–61. Comparative morphology of ancestrulae; back-scattered scanning electron micrographs. 53–55. Diaperoecia purpurascens (Hutton), outside Whangaroa Harbour, 26/1/1981, National Museum of New Zealand BS 862; 53. Ancestrula; 54. Protoecium; 55. Protoecial pseudopores. 56–58. 'Hastingsia' whitteni sp. nov., Auckland, on Sargassum sinclairii, 3/1/1996, D. P. Gordon Collection, paratype NIWA 98121; 56. Ancestrula; 57. Protoecium; 58. Protoecial pseudopores. 59–61. 'Heteropora' neozelanica Busk, NZOI Stn Z9684, NIWA 98122; 59. Ancestrula; 60. Protoecium; 61. Protoecial pseudopores. Scale bars: 53, 56, 59 = 200 µm; 54, 57, 60 = 100 µm; 55, 58, 61 = 20 µm.
189x189mm (300 x 300 DPI)





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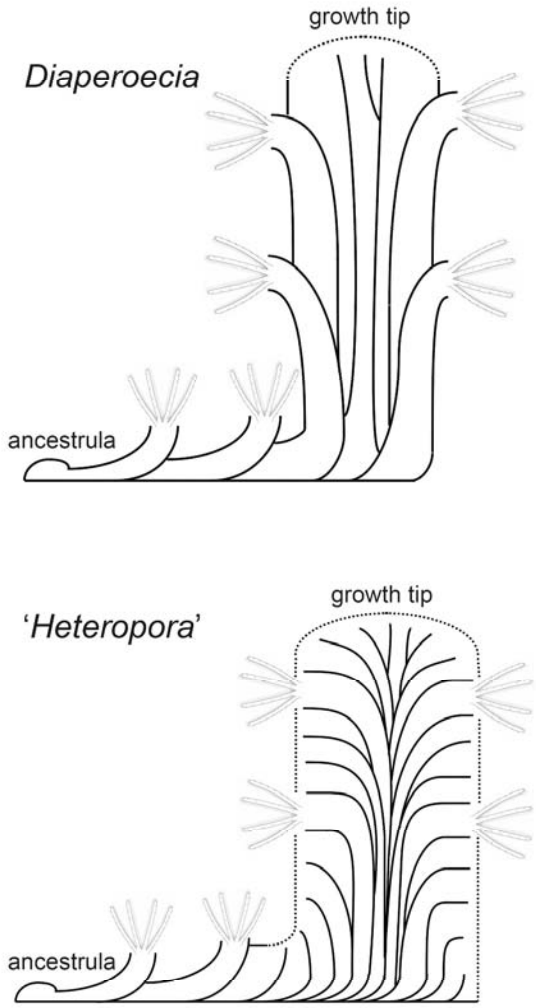

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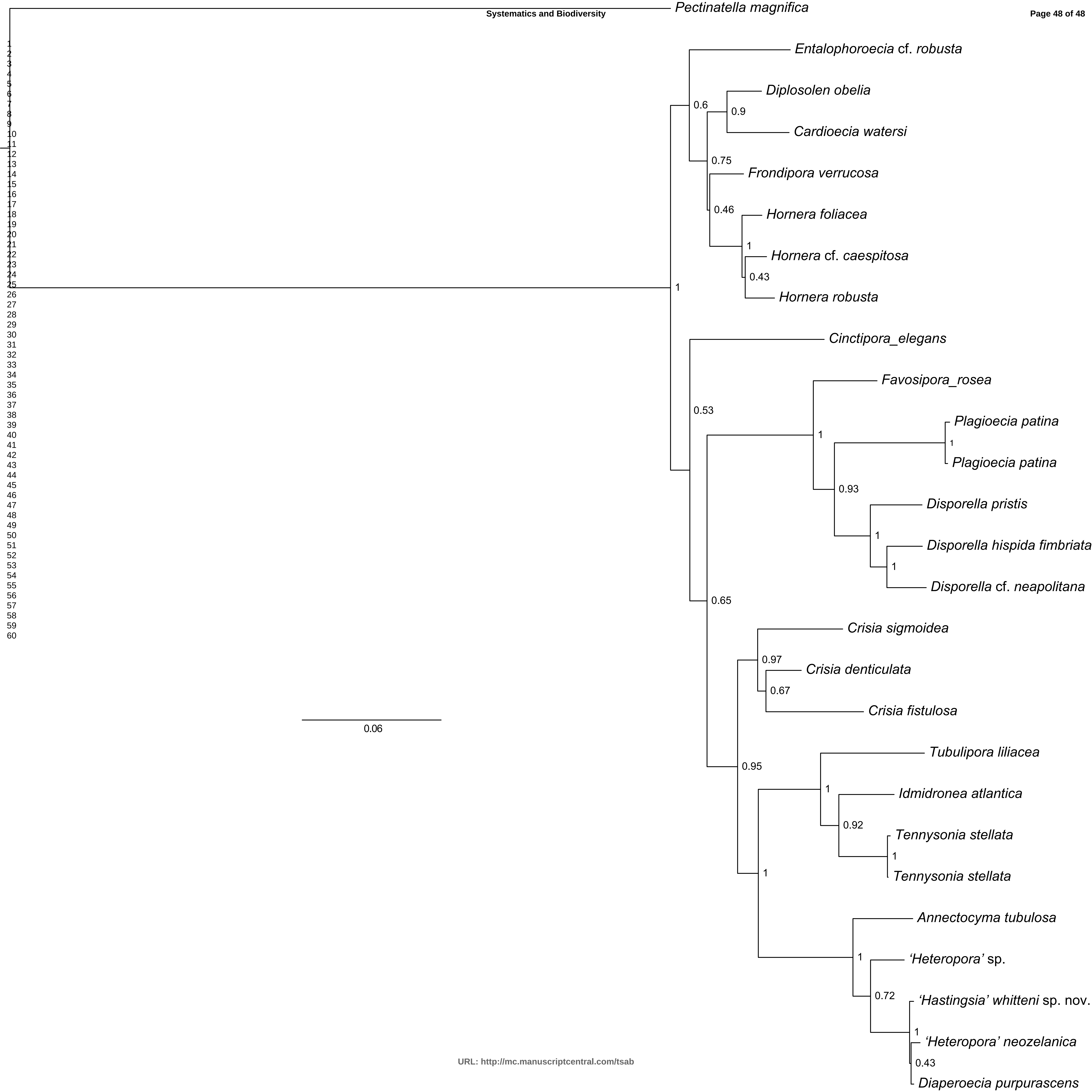
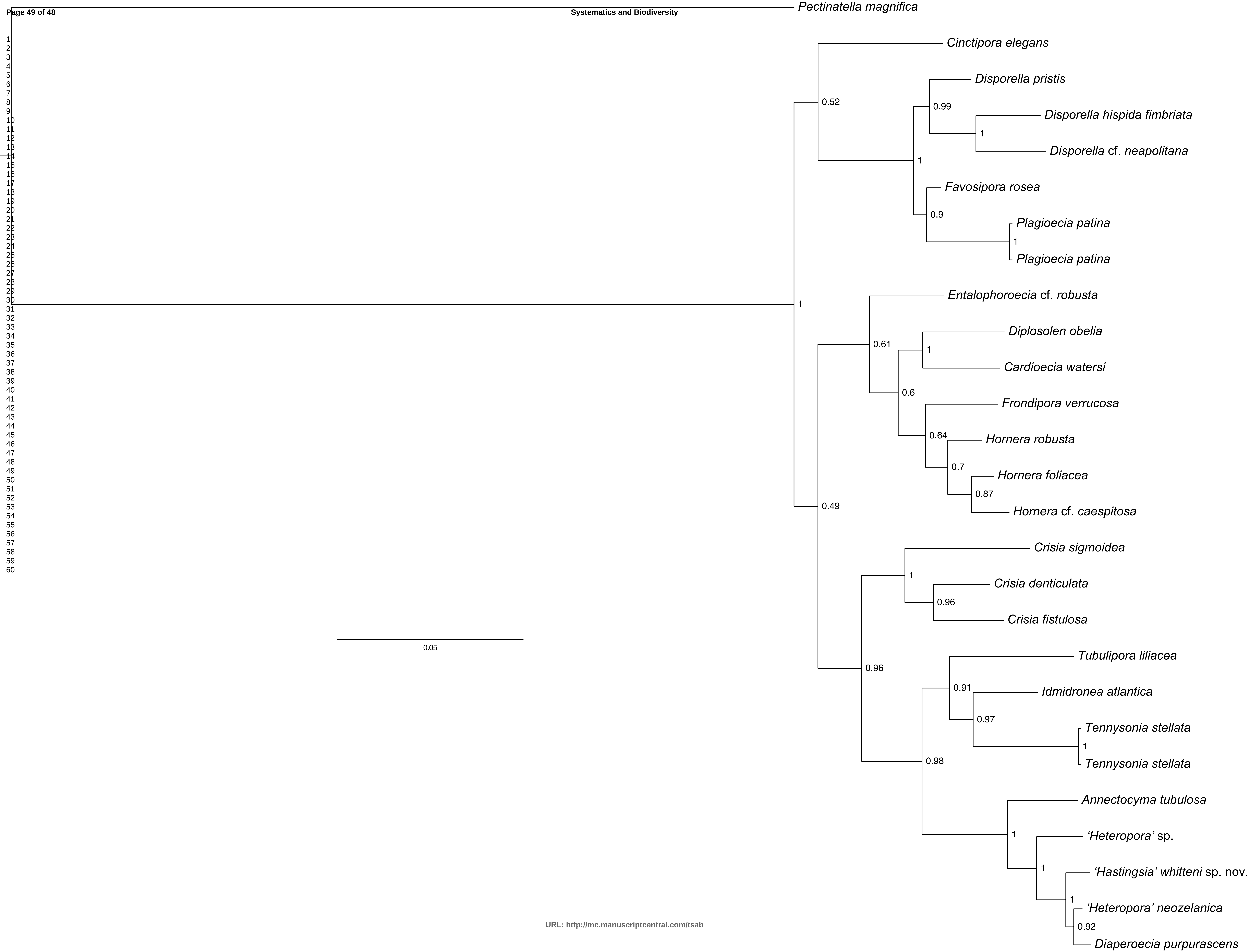

Pectinatella magnifica
Entalophoroecia cf. *robusta*
0.6
Diplosolen obelia
0.9
Cardioecia watersi
0.75
Frondipora verrucosa
0.46
Hornera foliacea
1
Hornera cf. *caespitosa*
0.43
Hornera robusta
1
Cinctipora_elegans
0.53
Favosipora_rosea
1
Plagioecia patina
1
Plagioecia patina
0.93
Disporella pristis
1
Disporella hispida fimbriata
1
Disporella cf. *neapolitana*
0.65
Crisia sigmoidea
0.97
Crisia denticulata
0.67
Crisia fistulosa
0.06
Tubulipora liliacea
0.95
1
Idmidronea atlantica
0.92
Tennysonia stellata
1
Tennysonia stellata
1
Annectocyma tubulosa
1
'Heteropora' sp.
0.72
'Hastingsia' whitteni sp. nov.
1
'Heteropora' neozelanica
0.43
Diaperoecia purpurascens


Pectinatella magnifica
Cinctipora elegans
0.52
Disporella pristis
0.99
Disporella hispida fimbriata
1
Disporella cf. neapolitana
1
Favosipora rosea
0.9
Plagioecia patina
1
Plagioecia patina
1
Entalophoroecia cf. robusta
0.61
Diplosolen obelia
1
Cardioecia watersi
0.6
Frondipora verrucosa
0.64
Hornera robusta
0.7
Hornera foliacea
0.87
Hornera cf. caespitosa
0.49
Crisia sigmoidea
1
Crisia denticulata
0.96
Crisia fistulosa
0.05
Tubulipora liliacea
0.96
0.91
Idmidronea atlantica
0.97
Tennysonia stellata
1
Tennysonia stellata
0.98
Annectocyma tubulosa
1
'Heteropora' sp.
1
'Hastingsia' whitteni sp. nov.
1
'Heteropora' neozelanica
0.92
Diaperoecia purpurascens