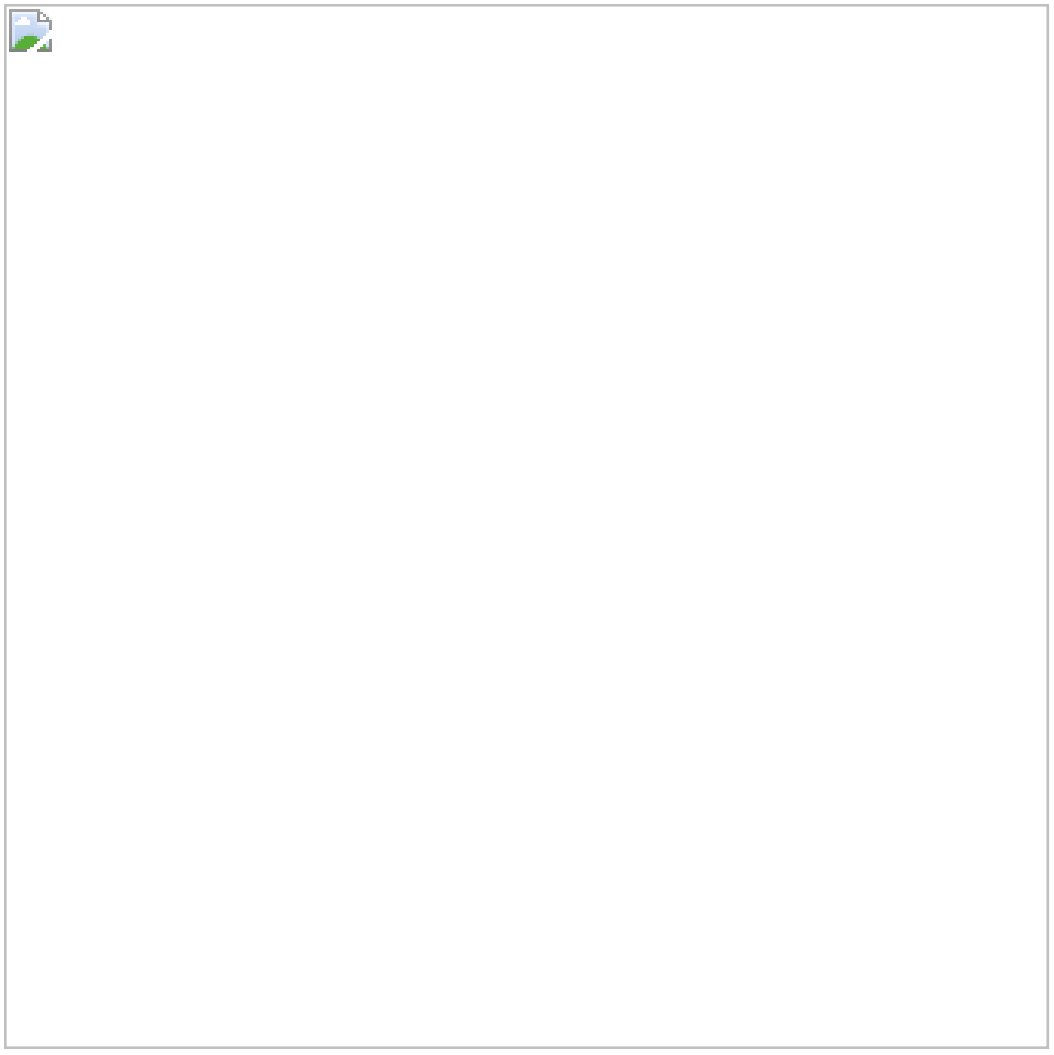

Doryporella smirnovi sp. nov. (Bryozoa: Cheilostomata) and Its Impact on Phylogeny and Classification

Authors: Grischenko, Andrei V., Taylor, Paul D., and Mawatari, Shunsuke F.

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Doryporella smirnovi sp. nov. (Bryozoa: Cheilostomata) and Its Impact on Phylogeny and Classification

Andrei V. Grischenko[1]*, Paul D. Taylor[2] and Shunsuke F. Mawatari[1]

[1]*Laboratory of Systematics and Evolution, Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo 060-0810, Japan*
[2]*Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

ABSTRACT—A new species of *Doryporella*, *D. smirnovi* sp. nov. is described from the area of the Commander Islands. Inclusion of this species in a revised phylogenetic analysis of *Doryporella* and its relatives permits the recognition of a clade comprising *Doryporella* and *Doryporellina*. This clade is accorded family-level status as the Doryporellidae fam. nov., thereby removing *Doryporella* (and *Doryporellina*) from the large and paraphyletic Calloporidae.

Key words: Bryozoa, Flustrina, Doryporellidae fam. nov., *Doryporella smirnovi* sp. nov., cladistic phylogenetics

INTRODUCTION

During the compilation of an inventory of the bryozoan fauna of the Commander Islands, Grischenko (1997) recorded two species of the cheilostome bryozoan *Doryporella* – *D. armata* Gontar, 1993 and *D. alcicornis* O'Donoghue and O'Donoghue, 1923 – from the shelf zone of this archipelago. Subsequently a taxonomic revision of the genus *Doryporella* was undertaken (Grischenko *et al*., 2000), utilizing specimens from various regions of the Arctic and North Pacific, including material from the Commander Islands. However, the identity of a specimen previously identified as *D. alcicornis* O'Donoghue and O'Donoghue, 1923 remained doubtful. An SEM investigation of this material indicates that it represents a new species of *Doryporella*. The discovery of this new species affords an opportunity to re-evaluate the phylogeny of *Doryporella* and related taxa, in particular to see the effect of adding this new species to the cladistic analysis of the group.

In contrast to the previous results (Grischenko *et al*., 2000), the revised analysis indicates a close relationship between *Doryporella* and *Doryporellina*, which emerge as a clade. The well-developed, reticulate cryptocystal frontal wall seen in these two genera makes their customary placement within the family Calloporidae questionable. We therefore introduce a new family, the Doryporellidae.

* Corresponding author: Tel. +81-11-706-3524;
FAX. +81-11-746-0862.
E-mail: gat@bio.sci.hokudai.ac.jp

MATERIALS AND METHODS

The single specimen of the new species was obtained during the 14th Cruise of the R.V. *Akademic Oparin* (August–September 1991) in the coastal water of the Commander Islands, Bering Sea. The specimen was initially preserved by drying. It was later bleached in sodium hypochlorite solution, rinsed with tap-water and dried in air prior to examination with a binocular microscope (NIKON: SNZ–10). The dried colony was coated with Pd–Pt using an ion sputter coater (HITACHI: E–1030) and studied with a scanning electron microscope (HITACHI: S–2380N) at 15 kV accelerating voltage.

The specimen described here is deposited in the Zoological Institute of the Russian Academy of Sciences (ZIRAS), St Petersburg.

RESULTS

Systematics

Phylum **Bryozoa** Ehrenberg, 1831
Order **Cheilostomata** Busk, 1852
Suborder **Flustrina** Smitt, 1868
Infraorder **Neocheilostomina** d'Hondt, 1985
Family **Doryporellidae** fam. nov.

Diagnosis: Anascan-grade neocheilostomes with well-developed cryptocystal frontal wall ornamented with a reticulate pattern of polygonal ridges. Gymnocyst greatly reduced. Opesia bell-shaped to oval. Oral spines present, branched or unbranched, one to three pairs adjacent to opesia and sometimes additional spines. Avicularia present, adventitious. Ovicell hyperstomial, ectooecium uncalcified, endooecium reticulated. Pore chambers present. Ancestrula tatiform or modified tatiform.

Type genus: *Doryporella* Norman, 1903; family also includes *Doryporellina* Grischenko, Mawatari and Taylor, 2000.

Remarks: The phylogenetic analysis described below unites *Doryporella* and *Doryporellina* as a clade. The previous inclusion of these two genera within the Calloporidae is unsatisfactory because this family is diverse and paraphyletic. We therefore propose the new family Doryporellidae which can be distinguished from Calloporidae principally by the well-developed polygonal reticulation of the cryptocyst of the autozooids.

Genus **Doryporella** Norman, 1903

Doryporella smirnovi sp. nov.

(Figs 1A–F and 2A–D)

Doryporella alcicornis: Grischenko, 1997: 160; Grischenko *et al.*, 2000: 251 (part).

Material examined: Holotype: ZIRAS 1/50130, mature

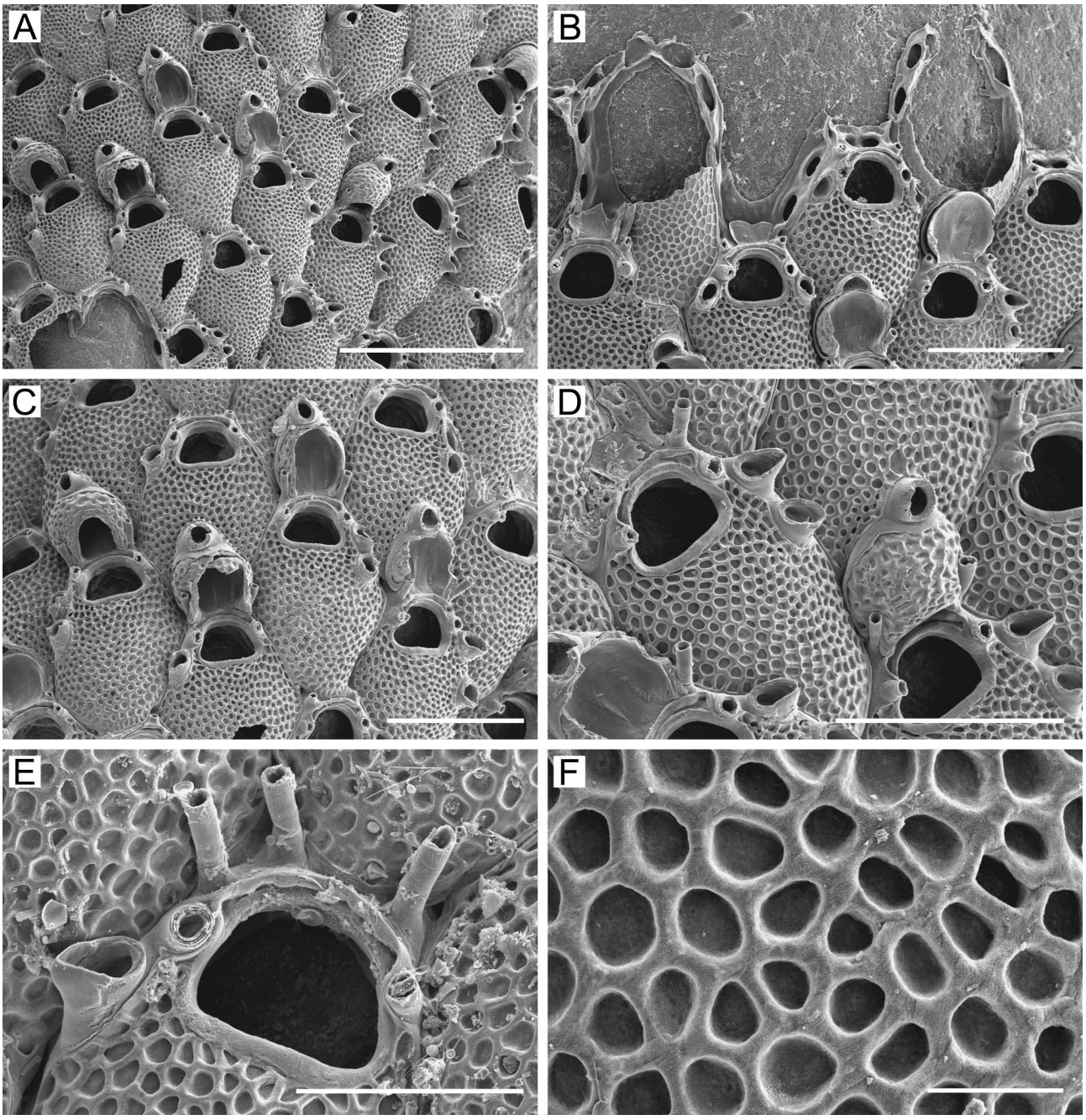

Fig. 1A–F. *Doryporella smirnovi* sp. nov., ZIRAS 1/50130. A, general view of the holotype colony; B, colony growing margin with developing zooids; C, mature zooids with spherical ovicells (some broken) and associated avicularia; D, mature zooids, showing details of ovicells and avicularia; E, immature zooid showing bell-shaped opesia, oral spines and lateral avicularium; F, frontal shield surface ornamented with polygonal reticulation. Scale bars, 1mm (A), 0.5 mm (B, C, D), 0.2 mm (E), 0.05 mm (F).

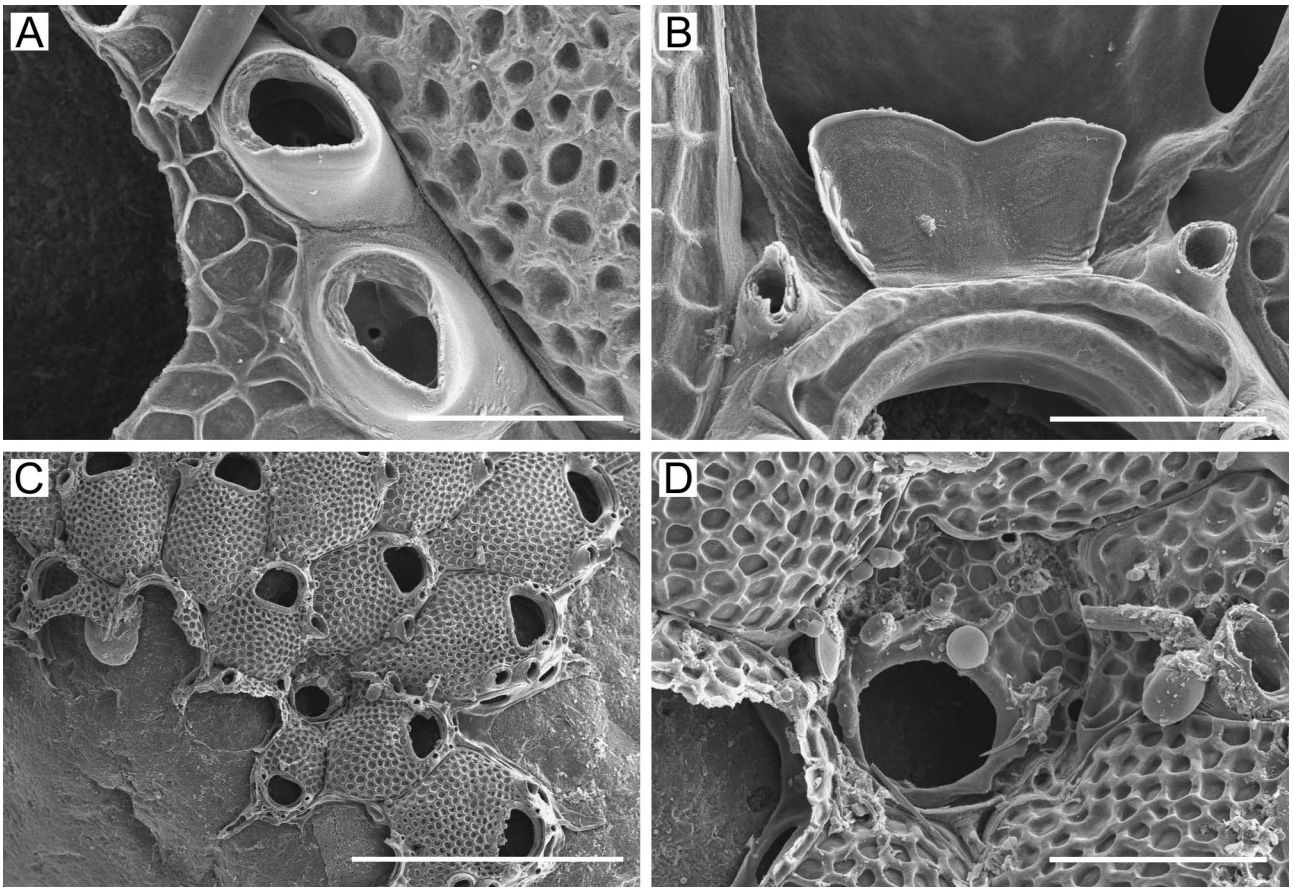

Fig. 2A–D. *Doryporella smirnovi* sp. nov., ZIRAS 1/50130. A, paired lateral avicularia; B, proximal margin of opesia with groove and bicuspate ooecial fold of developing ovicell; C, ancestrular region; D, ancestrula with spines on peripheral gymnocyst and tubercles around opesia (distal end of ancestrula is towards bottom left). Scale bars, 0.1 mm (A, B), 1mm (C), 0.2 mm (D).

colony, about 6×5 mm in size, encrusting a pebble. Pacific Institution of Bio-Organic Chemistry Collection on the R.V. *Akademik Oparin* (14th Expedition), 24 August 1991, Stn 47, Bering Sea, sector to north-west of Bering Island (Commander Islands archipelago), 55°25.2'N, 165°33.8'E, depth 152 m, sand, Trawl Sygsbi; collector A.V. Smirnov.

Diagnosis: *Doryporella* with bell-shaped opesia; 4–5 oral spines; usually two avicularia along one lateral edge of each zooid; ancestrula modified tatiform with dimpled cryptocyst and tubercles around edge of opesia.

Etymology: The new species is named in honour of Dr Alexei V. Smirnov (Zoological Institution Russian Academy of Science, St Petersburg) who collected the material.

Description: Colony encrusting, multiserial, sheet-like (Fig. 1A), more or less circular, attaining 6 mm maximum width, light-yellow in colour when dry. Autozooids elongate, hexagonal to irregularly oval (0.52–0.93 mm long × 0.42–0.51 mm wide), separated by distinct narrow sutures (Fig. 1C). Vertical gymnocystal walls with a pair of distal and two pairs of distolateral pore chamber windows (Fig. 1B). Frontal wall cryptocystal, convex, non-porous, ornamented by a pattern of polygonal reticulate ridges, most obvious in young zooids, non-granular. Opesia bell-shaped with straight proximal edge, slightly wider than long (0.12–0.18 mm long × 0.15–0.22 mm wide); a shallow crescentic groove extends along the outside of the distal margin, and the frontal wall proximal of the opesia lacking depressions. Operculum shape as opesia but smaller, with hemispherical thickening. Oral spines hollow, up to 0.19 mm long, four to five in number (Fig. 1C–E): two to three spines at the distolateral corners of the opesia; and a pair located a little more proximally. Oral spines orientated upwards and distally. Avicularia adventitious, located along lateral margins of zooids (0.07–0.13 mm long), usually a pair on one side (Fig. 2A), sometimes symmetrically placed near opposite proximolateral corners of the opesia (Fig. 1B). Avicularia occasionally single or absent. Mandible subtriangular, pointed, without calcified pivotal bar, orientated laterally or proximolaterally. Ovicell (Fig. 1A–D) prominent, spherical (0.20–0.25 mm long × 0.20–0.25 mm wide), with surface having same reticulate pattern as frontal wall, as long as broad, ectooecium uncalcified. Additional avicularium associated with ovicells (0.05–0.08 mm long), located along distal gymnocystal margin of ovicell, rostrum directed distally.

Ancestrula (Fig. 2D) modified tatiform, small (0.25 mm long × 0.21 mm wide), with finely dimpled cryptocyst. Six short spines associated with narrow peripheral gymnocyst. Opesia subcircular (0.09 mm long × 0.11 mm wide), with

smooth margin having seven short bulge-like tubercles along lateral and proximolateral border. Two distolateral periancestrular zooids budded from the ancestrula. Periancestrular zooids (Fig. 2C) small (0.33 mm long × 0.21 mm wide), wide, oval, with inflated frontal walls, with or without single avicularium. Three pairs of oral spines present in some zooids from primary zone of astogenetic change.

Remarks: *Doryporella smirnovi* sp. nov. differs from other species of *Doryporella* in the absence of modified suboral or asymmetrically arranged spines. The type species of the genus, *D. spathulifera*, possesses a large flattened suboral spine associated with a median suboral avicularium which is not developed in *D. smirnovi*. Two other species, *D. armata* and *D. alcicornis*, both have large, oval opesiae whereas this structure is smaller and bell-shaped in *D. smirnovi*. Additionally, among species of *Doryporella* only *D. smirnovi* has paired lateral avicularia and a modified tatiform ancestrula with a wrinkled cryptocyst.

Distribution: The new species is presently known only from the area of the Commander Islands (Bering Sea) and can be categorized as a Pacific High-Boreal species.

DISCUSSION

Phylogenetic analysis

The discovery of the new species of *Doryporella* described here has forced a re-evaluation of the phylogeny of this genus and its relationship with *Doryporellina*. In an earlier paper (Grischenko *et al*., 2000) revising the then known species of *Doryporella*, a cladistic anlaysis was performed based on skeletal morphological characters. Twenty-one skeletal characters were coded for the four putative species of *Doryporella* along with five out-group species of calloporid cheilostomes chosen because of their morphological and biogeographical similarities to the species of *Doryporella*. After removal of one of the out-group species (*Megapora ringens* (Busk, 1856)) whose position proved to be unstable, a single most parsimonious tree was recovered using the phylogenetics program PAUP 3.1. The tree grouped together three of the four putative species of *Doryporella* as a clade, but excluded from this clade *Doryporella reticulata* Ryland, 1963, showing it instead as being more closely-related to *Amphiblestrum flemingii* (Busk, 1854). These results led to the proposal of the new genus *Doryporellina* for *D. reticulata* in order to maintain the monophyly of *Doryporella*. The reticulated cryptocystal frontal shield present in both *Doryporella* and *Doryporellina* was interpreted by Grischenko *et al.* (2000) to have evolved convergently.

A new phylogenetic analysis incorporating the recently-discovered species *Doryporella smirnovi* was performed to establish the correct generic affinities of this species (*Doryporella* or *Doryporellina*), and to ascertain the effect on the phylogenetic tree of adding this new taxon. The same out-group species were used as those employed by Grischenko *et al*. (2000), with *Megapora ringens* again being excluded from the final analysis. The original 21 characters were all coded and three extra characters were added: presence of an avicularium associated with the ovicell, granulation of the cryptocyst, and reticulation of the ovicell roof (Table 1). The analysis was undertaken using PAUP 4.0 after first confirming that the original results of Grischenko *et al*. (2000) were replicated using the same character matrix in this updated version of the program. Minimum length trees were found using the branch and bound option.

Analysis of the in-group taxa alone yielded an unrooted tree of 24 steps with CI 0.875 (0.700 when uninformative characters are excluded) and RI 0.571. Two clades occur in this tree: *smirnovi* + *reticulata*, and *armata* + *spathulifera*. Bootstrap analysis of 1000 replicates found the first of these clades in 65% of the trees and the second in 64%. The *armata* + *spathulifera* clade was also found in the earlier analysis of Grischenko *et al*. (2000) and the new data cor-

Table 1. Character matrix for species of *Doryporella* and *Doryporellina* and out-group taxa employed in the cladistic analysis. Characters 1–21 are the same as those used by Grischenko *et al*. (2000); characters 22–24 are novel to this new analysis.

		10	20
alcicornis	110120011	1000100100	00001
armata	110110011	0011100100	01101
spathulifera	110221011	0011100100	00101
reticulata	111121100	0100011011	10011
unicornis	000000000	000110??00	11110
flemingii	100121000	000001?000	01010
impressa	100131100	0000000?00	?0010
arctica	100132000	0000000?01	00010
smirnovi	110221011	0000100001	00101

Character list:

1. Extent of cryptocyst: restricted (0); extensive a and shelf-like (1)
2. Reticulation of cryptocyst: absent (0); present (1)
3. Beading of cryptocyst: absent (0); present (1)
4. Distal pore windows: absent (0); 1 (1); 2 (2)
5. Distolateral pore windows: absent (0); 1 (1); 2 (2); more than 2 (3)
6. Opesia shape: ovoidal (0); bell-shaped (1); semielliptical (2)
7. Opesia rim: unbeaded (0); beaded (1)
8. Groove distal of opesia: absent (0); present (1)
9. Branched oral spines: absent (0); present (1)
10. Asymmetrical distribution of oral spines: absent (0); present (1)
11. Separated outer pair of oral spines: absent (0); present (1)
12. Suboral spine/s: absent (0); present (1)
13. Suboral avicularium: absent (0); present (1)
14. Lateral avicuilarium: absent (0); present (1)
15. Proximal avicularium: absent (0); present (1)
16. Calcified pivotal bar of avicularium: absent (0); present (1)
17. Ancestrula: modified or non-tatiform (0); tatiform (1)
18. Closure plates: absent (0); present (1)
19. Opesia proportions: longer than wide (0); wider than long (1)
20. Ovicell proportions: longer than wide (0); wider than long (1)
21. Autozooid proportions: less than 1.5 × longer than wide (0); about 2 × longer than wide (1)
22. Avicularium associated with ovicell: absent (0); present (1)
23. Granulated cryptocyst: absent (0); present (1)
24. Reticulated ovicell: absent (0); present (1)

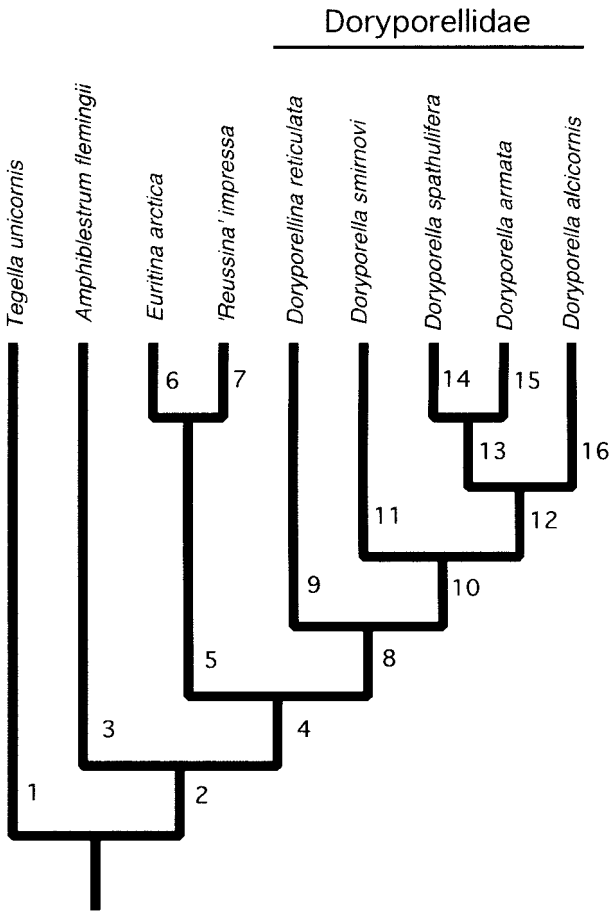

Fig. 3. Favoured tree, one of four equally parsimonious trees of 41 steps, rooted on *Tegella unicornis*, showing the inferred relationships between species of *Doryporella*, *Doryporellina* and out-group taxa. Note that the new species *Doryporella smirnovi* forms the sister group of the three established species of *Doryporella*, and that *Doryporellina reticulata* is the sister group to the four species of *Doryporella*. The new family Doryporellidae comprises the clade *Doryporella* + *Doryporellina*. Tree statistics: CI = 0.683 (0.629 when uninformative characters are excluded); RI = 0.649. Apomorphies, with character numbers in brackets, are as follows: Branch 1: (13) suboral avicularium, (14) lateral avicularium; Branch 2: (1) extensive, shelf-like cryptocyst, (4) one distal pore chamber, (5) two distolateral pore chambers, (6) bell-shaped opesia, (20) ovicell longer than wide; (22) no avicularium associated with ovicell; Branch 3: (15) proximal avicularium; Branch 4: (19) opesia wider than long, (21) autozooid less than 1.5 × longer than wide; Branch 5: (5) more than 2 distolateral pore windows; Branch 6: (6) semielliptical opesia; Branch 7: (7) beaded opesia rim; (19) opesia longer than wide; Branch 8: (2) reticulation of cryptocyst, (24) reticulated ovicell; Branch 9: (3) beaded cryptocyst, (7) beaded opesia rim, (11) separated outer pair of oral spines, (15) proximal avicularium, (16) calcified pivotal bar of avicularium, (18) closure plates, (20) ovicell wider than long; Branch 10: (8) groove distal of opesia, (9) branched oral spines, (14) lateral avicularium, (22) avicularium associated with ovicell, (23) ungranulated cryptocyst; Branch 11: (4) two distal pore windows; Branch 12: (6) ovoidal opesia, (17) tatiform ancestrula, (19) opesia longer than wide; Branch 13: (12) suboral spine/s, (13) suboral avicularium; Branch 14: (4) two distal pore windows, (6) bell-shaped opesia; Branch 15: (5) one distolateral pore window, (21) autozooids about 2 × longer than wide; Branch 16: (10) asymmetrical distribution of oral spines, (22) no avicularium associated with ovicell.

roborates a sister group relationship between these two species of *Doryporella*. Addition of the out-group taxa yielded 4 equally parsimonious trees of length 41 steps and having a CI of 0.683 (0.629 when uninformative characters are excluded), and RI of 0.649. In an exhaustive search of 135135 random trees generated from the data set, mean tree length was found to be 57.07 (SD 4.27), g1= 0.476552 and g2 = –0.185902. Among these random trees 37 were only one step longer than the most parsimonius trees, 158 two steps longer, 334 three steps longer and 550 four steps longer. A majority rule concensus tree computed from the four equally parsimonius trees corresponded to the topology of tree number 2. This favoured tree is shown in Fig. 3. Once again there is a clade comprising *armata* + *spathulifera* but the *smirnovi* + *reticulata* clade found in the in-group analysis is absent. All four equally parsimonious trees place *smirnovi* as the sister taxon to the three established species of *Doryporella*, while three of the four trees have *Doryporellina reticulata* as the sister taxon to this *Doryporella* clade, the other tree grouping *D. reticulata* with *Amphiblestrum flemingii* as in the original analysis of Grischenko *et al*. (2000).

Comparison of this new cladistic analysis with that of Grischenko *et al*. (2000) underscores the volatility of cheilostome phylogenies based on a relatively small number of skeletal morphological characters. It is clear that analyses incorporating soft part anatomy, and more particularly using molecular phylogenies, are strongly needed in cheilostomes.

Taxonomic implications

Initial uncertainty regarding the generic attribution of the new species described in this paper is dispelled by the phylogenetic analysis which shows that it is a sister taxon to the three species forming the *Doryporella* clade. Therefore, assignment of the new species to *Doryporella* is supported by the analysis.

In contrast to the findings of Grischenko *et al*. (2000), the new analysis supports a close relationship between *Doryporella* and *Doryporellina*. Three of the four most equally parsimonious trees place *Doryporellina* in a sister group relationship with *Doryporella*. The original argument for erecting the genus *Doryporellina* is undermined by these new results because inclusion of the species *reticulata* in *Doryporella* no longer renders the genus polyphyletic. Instead, the reticulate frontal shield that was doubtless the reason why Ryland (1963) attributed his species *reticulata* to *Doryporella* is, according to the new analysis, an apomorphy that evolved only once in this group of Arctic-Boreal calloporid species. (Note that evidence still remains for the independent acquisition of similar reticulate frontal shields in other cheilostome bryozoans, *e.g.*, *Biflustra reticulata* Tilbrook *et al.*, 2001). While it would now be possible to place *Doryporellina* in synonymy with *Doryporella*, this is not mandatory because *Doryporellina* lies outside the clade formed by the other species of *Doryporella* and therefore its exist-

ence does not render *Doryporella* paraphyletic. The morphological distinctiveness of *Doryporellina* argues for the retention of the genus. Among the characters of *Doryporellina* permitting its distinction from *Doryporella* are the beads on the opesial rim and on the ridges forming the reticulations of the cryptocyst, the separated outer pair of oral spines, and the occasional occurrence of proximal adventitious avicularia with calcified pivotal bars and of closure plates occluding the opesia.

The Calloporidae as currently understood is a very large family of cheilostomes – Gordon (unpublished) lists 74 genera in this family. Among the Neocheilostomatida (*i.e.*, those cheilostomes having brooded coronate larvae), the Calloporidae are both primitive and paraphyletic (Gordon, 2000). The oldest neocheilostome is the calloporid *Wilbertopora* Cheetham, 1954 from the mid-Cretaceous of the USA, and it is likely that most or all other neocheilostome families nest within the Calloporidae. Clearly, the Calloporidae requires splitting if it is to become a taxon of phylogenetic value. One way of achieving this is by eliminating from the family any well-characterised monophyletic group comprising two or more genera. *Doryporella* is a highly distinctive genus and its classification as an anascan belonging to the Calloporidae has been questioned in the past (Levinsen, 1916) and also by D.P. Gordon in his unpublished listing of cheilostome genera for the *Treatise on Invertebrate Paleontology*. With the recognition of a clade comprising *Doryporella* + *Doryporellina* there are grounds for a new family-level taxon, the Doryporellidae as diagnosed above and distinguished principally by the extensive, reticulated cryptocyst.

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