Cribrimorph and Other Cauloramphus Species (Bryozoa: Cheilostomata) from the Northwestern Pacific

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We provide original descriptions for nine new species in the cheilostome bryozoan genus Cauloramphus (C. gracilis, C. ordinarius, C. amphidisjunctus, C. cheliferoides, C. oshurkovi, C. infensus, C. parvus, C. peltatus, and C. ascofer) and a redescriptions of C. disjunctus Canu and Bassler, 1929. We delineate a group of eight species, here termed the ‘C. disjunctus clade,’ that have the opesial spine joints calcified to a greater or lesser extent in mature zooids; most also have paired, hypertrophied avicularia. This group includes C. amphidisjunctus, C. cheliferoides, C. infensus, C. parvus, C. peltatus, and C. ascofer in the Aleutian Islands, Alaska; C. oshurkovi in the Commander Islands; and C. disjunctus in Japan. High levels of apparent endemism in two unrelated bryozoan genera (Cauloramphus and Monoporella), and geographical population differentiation in C. ascofer indicating ongoing allopatric speciation, suggest high speciation rates for deep benthic bryozoans in the western Aleutians. A phylogenetic hypothesis for the C. disjunctus clade indicates that populations of Cauloramphus dispersed between the Aleutians and Asia on at least three separate occasions, and that the polarity of at least two of these dispersal events was from the Aleutians to Asia.

Key words: Bryozoa, Cauloramphus, Cheilostomata, disjunctus clade, dispersal, diversity, new species, phylogeny, speciation

INTRODUCTION

Anascan-grade cheilostome bryozoans in the large paraphyletic family Calloporidae typically have a well-exposed frontal membrane (non-calcified frontal wall), often have articulated circum-opesial spines surrounding the frontal membrane, and usually have a prominent hyperstomial oviscell. Within Calloporidae, species of Cauloramphus Norman, 1903, are unusual in having, in addition to circum-opesial spines, avicularia attached to the lateral gymnocyst by a flexible cuticular joint, a reduced kenozooidal ooecium (Ostrovsky et al., 2007), and internal brooding.

At the start of this study, 21 valid Recent species of Cauloramphus had been described worldwide. Most species are distributed in cool-temperate waters around the North Pacific rim. Some, however, have circumpolar Arctic (e.g., C. cymbaeformis) or amph-Boreal (e.g., C. spinifer) distributions, and a few range into the Subtropics or Tropics, usually in deeper water, e.g., C. brunea Canu and Bassler, 1930, in the Galapagos and C. opertus Canu and Bassler, 1928, in the Gulf of Mexico.

Dick et al. (2009) illustrated and provided brief morphological descriptions of what they identified as Cauloramphus disjunctus and three other, undescribed Cauloramphus species from the western Aleutian Islands, Alaska; two of these species have a cribrimorph costal shield and provide a remarkable example of the parallel evolution of complex characters. Upon examination of the type series for C. disjunctus, we concluded that none of the Aleutian or the Commander species is C. disjunctus, but that several of them (including the cribrimorph species) having hypertrophied avicularia like those in C. disjunctus comprise a monophyletic group within Cauloramphus, which we term the ‘C. disjunctus clade.’

Here we formally describe eight new species of Cauloramphus from the shelf zone at depths of 80–415 m in the western Aleutian Islands, Alaska (Dick, 2008), including the species briefly described and illustrated in Dick et al. (2009); describe one new species collected subtidally from the Commander Islands to the west; and redescribe C. disjunctus Canu and Bassler, 1929. We also present a hypothesis on the phylogeny of the C. disjunctus clade, based on morphology and previous molecular data.
We first present taxonomic descriptions, which establish the names of the species included in the study. We suggest that the reader interested more in distribution, local diversity, and phylogeny than in taxonomy skim the figures in the taxonomic section for a rough idea of the morphologies involved, and then proceed to the following section, entitled ‘General Results and Discussion.’

MATERIALS AND METHODS

Most of the specimens included in this study were among collections made by M. Dick from 45 otter-trawl tows at 40 sampling stations (two or three tows were made at three of the stations) in the western Aleutian Islands (Fig. 1) at depths of 50–467 m, from 20 July to 2 August 2004. Collecting was conducted aboard F/V Sea Storm, chartered by the Alaska Fisheries Science Center, U.S. National Marine Fisheries Service.

The study area, details of collection, preparation of specimens, and examination by scanning electron microscopy were as described by Dick (2008). In some cases, dried specimens were coated for SEM and images were taken; the same specimens were then bleached, rinsed, dried, and re-coated, and additional SEM images were taken. Collection data are given in Table 1. Type material has been deposited in the Yale Peabody Museum (YPM), Yale University, New Haven, CT, USA, and The Natural History Museum (NHM), London, UK. To conserve space, locality information in the “Material examined” sections for the Aleutian species is indicated only by sampling stations, with information on the stations given in Table 1.

Most measurements were taken at 80X magnification with an ocular micrometer attached to a Nikon SMZ-10 stereoscopic microscope. Measurements from type specimens of C. disjunctus and from the Kamchatka specimen of C. ascofer were made from SEM images by using ImageJ v. 1.42q software (http://rsb.info.nih.gov/ij). Measurements in the text are in millimeters. Sample sizes for measurements and counts are given as numbers of zooids and colonies; for example, (n = 30, 2) indicates 15 zooids per colony measured for each of two colonies. Abbreviations for measurements are: ZL, autozooid length; ZW, autozooid width; OpL, opesia length; OpW, opesia width; OrL, orifice length; OrW, orifice width (the orifice measurements are: OrL, orifice lateral; OrW, orifice width; OpL, opesia lateral; OpW, opesia width); AvL, avicularium length; AvW, avicularium width; AvL/AvD, ratio of avicularium length to depth; AvD/AvL, ratio of avicularium depth to length; OpD, opesia depth; OpL, opesia length; OpW, opesia width; OrD, orifice depth; OrW, orifice width; OrD/OrW, ratio of orifice depth to width.

We documented two other potentially useful characters that have not been employed before in Cauloramphus taxonomy. One is the position of attachment of the avicularia. This is determined from zooids having the modal number of orificial spines for a particular colony or population by counting spines in the proximal direction starting from the most distal single (if the modal number of orificial spines includes an unpaired median spine) or paired spine on one side. An attachment point of ‘3/4’ means attachment on the lateral gymnocyist between the 3rd and 4th spines on either side, counting from the distal end; ‘2’ indicates attachment lateral to the 2nd spine on either side, counting from the distal end. The other character is the length to depth ratio of the avicularium, or AvL/AvD.

Table 1. Information on sampling stations in the western Aleutian Islands, Alaska, USA, at which Cauloramphus specimens were collected.

<table>
<thead>
<tr>
<th>Station</th>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth</th>
<th>Bottom temp. (°C)</th>
<th>Collection Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>12-45</td>
<td>Stalemate Bank</td>
<td>52°54.7′N</td>
<td>170°49.0′E</td>
<td>189 m</td>
<td>4.0</td>
<td>30 July 2004</td>
</tr>
<tr>
<td>110-24</td>
<td>Rat Island group</td>
<td>51°58.4′N</td>
<td>178°13.5′E</td>
<td>95 m</td>
<td>4.9</td>
<td>22 July 2004</td>
</tr>
<tr>
<td>111-26</td>
<td>Rat Island group</td>
<td>52°03.7′N</td>
<td>178°17.8′E</td>
<td>355 m</td>
<td>4.0</td>
<td>22 July 2004</td>
</tr>
<tr>
<td>113-21</td>
<td>Rat Island group</td>
<td>51°51.6′N</td>
<td>178°27.8′E</td>
<td>227 m</td>
<td>4.3</td>
<td>23 July 2004</td>
</tr>
<tr>
<td>116-13</td>
<td>S. of Amchitka L.</td>
<td>51°29.5′N</td>
<td>178°40.5′E</td>
<td>156 m</td>
<td>4.5</td>
<td>20 July 2004</td>
</tr>
</tbody>
</table>
ZOOID MEASUREMENTS AND AVICULARIUM RATIO

Table 2. Summary of measurements, other characters, and geographical range for Cauloramphus species treated in this study. Measurements are mean values in millimeters and spine counts are modal values. For sample sizes, and ranges and standard deviations of measurements, refer to the species accounts in the text. For C. ascofer, the two values indicate separate measurements from the Stalemate Bank and Rat Island populations, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Avicularium position</th>
<th>Orificial spines</th>
<th>Intermediate spines</th>
<th>Opesia spines</th>
<th>Total spines</th>
<th>Cryptocyst</th>
<th>Known range</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. gracilis</td>
<td>5/6</td>
<td>8</td>
<td>2</td>
<td>15</td>
<td>25</td>
<td>smooth</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. ordinarius</td>
<td>4/5</td>
<td>5</td>
<td>0</td>
<td>11</td>
<td>16</td>
<td>tubercles</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. disjunctus</td>
<td>4/5</td>
<td>4</td>
<td>2</td>
<td>17</td>
<td>23</td>
<td>smooth</td>
<td>Japan</td>
</tr>
<tr>
<td>C. amphidisjunctus</td>
<td>3/4</td>
<td>2</td>
<td>2</td>
<td>13</td>
<td>18</td>
<td>smooth</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. cheliferoides</td>
<td>3/4</td>
<td>2</td>
<td>2</td>
<td>11, 12</td>
<td>15, 16</td>
<td>smooth</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. oshurkovi</td>
<td>3/4</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>11</td>
<td>smooth</td>
<td>Commander Is.</td>
</tr>
<tr>
<td>C. infensus</td>
<td>4/5</td>
<td>6</td>
<td>0</td>
<td>12</td>
<td>18</td>
<td>tubercles</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. parvus</td>
<td>3/4</td>
<td>2</td>
<td>2</td>
<td>14</td>
<td>18</td>
<td>smooth</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. peltatus</td>
<td>3 or 3/4</td>
<td>2</td>
<td>2</td>
<td>18</td>
<td>22</td>
<td>smooth</td>
<td>W. Aleutians</td>
</tr>
<tr>
<td>C. ascofer</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>10 / 13</td>
<td>14 / 17</td>
<td>absent</td>
<td>W. Aleutians, Kamchatka</td>
</tr>
</tbody>
</table>

TAXONOMY

Class GYMNOLEMATA Allman, 1856
Order CHEILOSTOMATA Busk, 1852
Suborder NEOCHEILOSTOMINA d’Hondt, 1985
Infrafamily FLUSTRINA Smitt, 1868
Superfamily CALLOPOROIDEA Norman, 1903
Family Calloporidae Norman, 1903
Genus Cauloramphus Norman, 1903

DIAGNOSIS. Colony unilaminar, multiserial, encrusting. Gymnocyst reduced or moderately broad; a narrow, sloping cryptocyst usually surrounds the opesia; cryptocyst tuberculate or smooth. Frontal avicularia single, paired, or multiple; with flexible joint at base, often pedunculate. Some species bud sessile (non-jointed) avicularia (fig. 9B in Grischenko et al., 2007; Fig. 2E herein), from marginal pore chambers. Circum-opesial spines present; orificial spines with a flexible joint at base; opesial spines with or without a flexible joint (Dick et al., 2009). Reproductive zooids have a reduced, vestigial kenozooidal ooeicum (e.g., Figs. 2C, 2F, 4D, 5C) with a median ooeical pore; brooding is endozooidal (Ostrovsky et al., 2007). Zooids interconnect by tubular pore chambers (most evident in Figs. 3A, 4A) and uniporous septula (Figs. 2F, 5F).

Cauloramphus gracilis new species

(Fig. 2A–C)

ETYMOLOGY. The species name is from the Latin adjective gracilis (slender, thin), referring to the extremely elongate pedunculate avicularia.

MATERIAL EXAMINED (see Table 1 for station data).
HOLOTYPE: YPM 48068, Stn. 111-26, dried colony on scallop shell; part bleached and coated for SEM. PARATYPES: 1) YPM 48069, Stn. 110-24, colony on rock fragment coated for SEM; 2) YPM 48070, Stn. 113-21, dried colonies on three pebbles; 3) NHM 2010.2.10.17, Stn. 110-24, dried colony on scallop shell; 4) NHM 2010.2.10.18, Stn. 113-21, colonies on rock fragment coated for SEM.

MEASUREMENTS. ZL, 0.77–1.13 (0.94 ± 0.096); ZW, 0.56–0.77 (0.65 ± 0.058); OpL, 0.56–0.76 (0.68 ± 0.054); OpW, 0.35–0.49 (0.41 ± 0.036) (n = 30, 2; YPM 48068, 48069).
AvL, 0.74–0.82 (0.79 ± 0.033); AvD, 0.12–0.13 (0.12 ± 0.007) (n = 5, 1; YPM 48068).

DESCRIPTION. Colony forms irregular patches; largest observed ca. 3 × 1 cm; orange-tan in color. Zooids (Fig. 2A, B) large, closely appressed, delineated by an interzooidal furrow; gymnocyst narrow and steeply sloping around zooid; cryptocyst a narrow, smooth shelf. Basal wall not calcified. Zooids with 19–31 (mode = 25) total spines (n = 30, 2; YPM 48068, 48069). Zooids interconnect by intermediate spines between the orificial and opesial spines; intermediate spines shorter and sharper than orificial spines; longer, straighter, and more erect than opesial spines. Avicularia sparse, lacking on most zooids, single only; with an exceptionally long, thin peduncle (Fig. 2A); total length up to as long as longest distal spines; attached in position 5/6, from near base of most distal opesial spine to as far distally as base of intermediate spine; average AvL/AvD = 6.6. Kenozooidal ooeicum (Fig. 2C) narrow, crescent shaped, rising to a low, chevron-shaped lip at distal end of mural rim.

REMARKS. With its many spines and long-pedunculate avicularia, C. gracilis is similar to C. spectabilis Dick and Ross, 1988, described from Kodiak, Alaska; C. multispinosus Grischenko et al., 2007, described from Akkeshi Bay, Japan; and C. cymbaeformis (Hincks, 1877), a circumpolar, Arctic-boreal species. In C. spectabilis, total spines number 19–
24, with eight or nine long, thick orificial spines and 12–16 arched opesial spines; the cryptocyst is smooth, and the avicularia are long-clavate; however, the zooids are markedly smaller (0.50–0.65 mm long) than in C. gracilis (0.77–1.13 mm); the pair of intermediate spines is lacking, and the avicularian peduncle is not nearly as long and thin (Dick and Ross, 1988). The high overall similarity between C. spectabilis and C. gracilis nonetheless suggests that they are closely related.

In C. multispinosus, the zooids are moderately large (0.55–0.98 mm long), and there are 20–26 total spines arranged as heavy orificial spines and thin, arching opesial spines, as in C. gracilis. The former differs from the latter in having a strongly granulated cryptocyst and only six orificial spines, and avicularia are apparently lacking altogether (Grischenko et al., 2007).

Cauloramphus cymbaeformis is similar to C. gracilis in having moderately large zooids (0.63–0.75 mm), a smooth cryptocyst, and avicularia with a long, thin peduncle. However, zooids have at most around 10 spines, all long, straight, and erect; the spines are irregularly arranged, mostly around the distal half of the mural rim; and the avicularian peduncle tends to be markedly curved (Kluge, 1975).

OCCURRENCE. We found colonies of C. gracilis encrusting dead scallop shells, small sponge-associated pebbles, and highly porous lava stones. It occurred at three stations (Fig. 1) at depths of 95–355 m. The known distribution is limited to the Rat Island group, western Aleutian Islands.

**Cauloramphus ordinarius** new species

(Fig. 2D–F)

CAC (Cauloramphus Aleutian sp. C): Dick et al., 2009, 3142, fig. 1a.

ETYMOLOGY. The species name is from the Latin adjective *ordinarius* (regular, ordinary).

MATERIAL EXAMINED (see Table 1 for station data).

HOLOTYPE: YPM 48068, Stn. 110-24, parts of a single dried colony on shell fragments. PARATYPES, all from Stn. 113-21: 1) YPM 48059, colony fragment on pebble, bleached and coated for SEM; 2) YPM 48060, dried colony on pebble; 3) YPM 48061, two fragments of same colony on pebble, coated for SEM, one part bleached, the other unbleached; 4) NHM 2010.2.10.11, dried colony fragment on shell; 5) NHM 2010.2.10.12, dried colony fragment on shell; 6) NHM 2010.2.10.13, colony fragment on pebble, bleached and coated for SEM.

MEASUREMENTS. ZL, 0.62–0.92 (0.74 ± 0.063); ZW, 0.38–0.64 (0.51 ± 0.051); OpL, 0.33–0.55 (0.49 ± 0.045); OpW 0.23–0.38 (0.26 ± 0.030) (n = 30, 2; YPM 48058, 48061). AvL, 0.13–0.22 (0.17 ± 0.020); AvD, 0.05–0.08 (0.07 ± 0.006) (n = 20, 3; YPM 48058, YPM 48060, YPM 48061).

DESCRIPTION. Colony irregular; light yellowish tan in color; largest observed ca. 1.5 cm in maximum dimension. Zooids (Fig. 2D, E) large, angular at junctions with adjacent zooids in proximal half, semi-oval around distal half; distinct, delineated by deep interzooidal furrow. Basal wall not calcified. Gymnocyst steep, smooth, slightly convex, moderate in width, giving the zooids a slightly tumid appearance; steeper distally. Proximal to orifice, cryptocyst is a narrow, sloping, coarsely tuberculate shelf. Total spines 14–18 (mode = 16); orificial spines 4–6 (mode = 5, frequency 90%); opesial spines 9–13 (mode = 11) (n = 30, 3; YPM 48058, 48061). AvL, 0.13–0.22 (0.17 ± 0.020); AvD, 0.05–0.08 (0.07 ± 0.006) (n = 20, 3; YPM 48058, YPM 48060, YPM 48061).

Cauloramphus cryptorum by Grischenko et al. (2007: p. 1075, fig. 9B).

A. Cymbaeformis (2D–F) Cauloramphus ordinarius n. sp. (C) Vestigial kenozooidal ooeicum at distal end of autozooid (asterisk), bleached. Holotype, YPM 48068. (D–F) Cauloramphus ordinarius n. sp. (D) Autozooids, before bleaching. Paratype 1, YPM 48059. (E) Autozooids, bleached; note marginal avicularia arising from pore chambers (arrowheads). (F) Vestigial kenozooidal ooeicum at distal end of autozooid (arrowhead), bleached. (E, F) Paratype 6, NHM 2010.2.10.13. Scale bars: 0.5 mm (A, B, D, E), 0.1 mm (C), 0.05 mm (F).

Fig. 2. (A–C) Cauloramphus gracilis n. sp. (A) Autozooids; arrowheads indicate long, pedunculate avicularia. Paratype 1, YPM 48069. (B) Autozooids, bleached. Holotype, YPM 48068. (C) Vestigial kenozooidal ooeicum at distal end of autozooid (asterisk), bleached. Holotype, YPM 48068. (D–F) Cauloramphus ordinarius n. sp. (D) Autozooids, before bleaching. Paratype 1, YPM 48059. (E) Autozooids, bleached; note marginal avicularia arising from pore chambers (arrowheads). (F) Vestigial kenozooidal ooeicum at distal end of autozooid (arrowhead), bleached. (E, F) Paratype 6, NHM 2010.2.10.13. Scale bars: 0.5 mm (A, B, D, E), 0.1 mm (C), 0.05 mm (F).
opercular spines not meeting in midline; orificial and opercular spines not well differentiated in form; avicularia fusiform, often attached at or slightly distal to middle of zooid, and usually not longer than the longest opercular spines.

**OCCURRENCE.** We found this species on dead scallop shells and sponge-associated pebbles at two stations (Fig. 1) at depths of 95 and 227 m. The known distribution is limited to the Rat Island group, western Aleutian Islands.

**Cauloramphus disjunctus** Canu and Bassler, 1929

(I) Canu and Bassler, 1929, 109, pl. 8, figs. 4–6 (fig. 5 illustrates the lectotype, USNM 7885; see Material Examined below).

**Cauloramphus disjunctus:** Androsova, 1958, 107, fig. 17 (in part?); Mawatari and Mawatari, 1981, 41, fig. 8; Grischenko, 1997, 163 (in part?).

**MATERIAL EXAMINED.** Type specimens of Canu and Bassler (1929); LECTOTYPE, USNM 7885; PARALECTOTYPES, USNM 539763, 539764, and 539765. Canu and Bassler (1929) did not designate a holotype for this species, but listed four specimens as co-types under USNM 7885. We here designate the specimen in our Fig. 3B–E as lectotype, which retains catalog number USNM 7885, and designate the three remaining specimens paralectotypes, with catalog numbers USNM 539763, 539764, and 539765. Type locality, “Cape Tsiuka, Sea of Japan; 41°36′12″N, 140°36′E” (Canu and Bassler, 1929), which according to the coordinates is actually within Tsugaru Strait, approximately 25 km SSW of Hakodate, Hokkaido. Other material examined: fossil specimen, Pleistocene Setana Formation, Kuromatsunai, Hokkaido, Japan; coll. M. Dick, 24 Aug. 2005; deposited in NHM, London.

**MEASUREMENTS.** ZL, 0.45–0.63 (0.53 ± 0.050); ZW, 0.31–0.51 (0.36 ± 0.039); OpL, 0.30–0.40 (0.35 ± 0.030); OpW, 0.16–0.24 (0.19 ± 0.022) (n = 30, 2; USNM 539763, 539765). AvL, 0.21–0.27 (0.23 ± 0.019); AvD, 0.07–0.11 (0.09 ± 0.012) (n = 13, 2; USNM 7885, USNM 539764).

**DESCRIPTION.** Zooids (Fig. 3A, B, E, F) disjunct, interconnected by tubular chambers separated by around seven uniformly sized lacunae along each lateral margin. Basal wall not calcified. Gymnocyst broad laterally and proximally, sloping, convex. Cryptocyst a narrow, nearly vertical shelf around opesia; smooth. Three or four (mode, 4) relatively short, slender, erect orificial spines distal to orifice; one pair of long, heavy sub-erect intermediate spines lateral to orifice, and 14–20 (mode, 17) tapering, acuminate opercular spines very closely set, with little space between them, angled over the opesia and meeting in midline; total spines 19–26 (mode, 23). Avicularia (Fig. 3B, C, F) predominantly paired, attached in position 4/5, between 1st and 2nd opercular spines; peduncle short, rapidly swelling to body of avicularium; rostrum raised proximally, forming a sharp lip in proximal curvature of avicularium; average AvL/AvD = 2.6. Proximal margin of mature ooeicum (Fig. 3C, D) forms a raised, triangular flange, sometimes very tall and acute. Ancestrula (Fig. 3E) with oval opesia, broad gymnocyct, around 13 spines, giving rise to seven periancestral zooids (one distally, two distolaterally, and four laterally and proximally).

**REMARKS.** The discovery in the Aleutians and Commander Islands of a clade containing species related to *C. disjunctus* Canu and Bassler raises the possibility that there may be additional, related species along the Asian coast. Androsova’s (1958) drawing of nominal *C. disjunctus* from the northern Sea of Japan appears to indicate some differences from the type material for *C. disjunctus*. Her illustrations show more-elongate avicularia (AvL/AvD up to ca. 4.0) that lack the proximal rostral lip and are attached just distal to the first pair of opercular spines, and the zooids are more disjunct, with longer interzooidal tubes and larger lacunae. Androsova’s drawing is rough, however, and her material needs reexamination.

**Cauloramphus amphidisjunctus** described herein is similar and likely closely related to *C. disjunctus* Canu and Bassler. Differences between the two are noted in Remarks under *C. amphidisjunctus*.

**OCCURRENCE.** This is a subtidal species distributed along both coasts of Japan from central Honshu to southern Hokkaido. Mawatari and Mawatari (1981) listed its range as Matsuishima (Sendai Bay, northeastern Honshu) to Kushiro (south-central Hokkaido) on the Pacific side, and as far south as Toyama Bay (central Honshu) on the Sea of Japan. Androsova (1958) reported nominal *C. disjunctus* from the northern Sea of Japan at depths of 36–93 m. Grischenko (1997) listed this species from depths of 5–46 m on the shelf around the Commander Islands, but his material needs reexamination in light of our discovery of *C. oshurkovi*.
in the Commanders.

*Cauloramphus amphidisjunctus* new species

(Fig. 4)

ETYMOLOGY. The species name is a combination of *disjunctus*, referring to *C. disjunctus*, and the Greek *amphi* (both sides of, apart), indicating morphological and geographical separation from *C. disjunctus*.

MATERIAL EXAMINED (see Table 1 for station data). HOLOTYPE: YPM 48071, Stn. 12-45, dried colony on plastic; parts coated for SEM, bleached and unbleached. PARATYPES: 1) YPM 48072, Stn. 116-13, colonies on fragments of skate egg case; 2) YPM 48073, Stn. 116-13, colony fragments on skate egg case, coated for SEM; 3) NHM 2010.2.10.19, Stn. 12-45, two dried colonies on plastic; 4) NHM 2010.2.10.20, Stn. 12-45, dried colony on pebble.

MEASUREMENTS. ZL, 0.51–0.74 (0.64 ± 0.055); ZW, 0.36–0.51 (0.44 ± 0.040); OpL, 0.30–0.49 (0.38 ± 0.052); OpW, 0.17–0.23 (0.20 ± 0.018); AvL, 0.26–0.35 (0.30 ± 0.024); AvD, 0.11–0.17 (0.13 ± 0.015) (n = 30, 2; YPM 48071, 48072).

DESCRIPTION. Zooids (Fig. 4A–C) separated by a deep furrow, connected by narrow tubular chambers separated by about seven large, irregular lacunae along each lateral margin. Basal wall not calcified. Gymnocyst broad laterally and proximally, nearly vertical. Cryptocyst a narrow, nearly vertical, shelf around opesia; smooth. Two or three short (mode, 2), slender orificial spines distal to orifice, angled distally; one pair of slightly longer, thicker, erect intermediate spines lateral to orifice, and 11–16 (mode, 13) tapering, acuminate opesial spines angled over opesia, occasionally but not usually meeting in midline, separated at base by a distance equal to or somewhat less than maximum spine diameter; total spines 15–21 (mode, 18). In older zooids, bases of intermediate and opesial spines become calcified so that spines remain after bleaching and gentle rinsing. Avicularia (Fig. 4A, B) paired, attached in position 3/4, between 1st and 2nd angled opesial spines; peduncle short, rapidly swelling to body of avicularium; rostrum usually not raised proximally, but continuous with proximal curvature of avicularium; average AvL/AvD = 2.3. Proximal margin of mature ooecium (Fig. 4D) forms a raised, triangular flange; when tall, flange is spatulate rather than very narrow and acute.

REMARKS. Compared to *C. disjunctus* (Table 2), this species has larger zooids and avicularia, though the latter have almost the same length/depth ratio; narrower tubes connecting zooids; larger lacunae that are less regular in size and spacing; and fewer orificial and opesial spines. Most avicularia lack a lip at the proximal end of the rostrum. The most striking difference is in the density of opesial spines, which are much more closely packed in *C. disjunctus* than in *C. amphidisjunctus*.

With markedly disjunct zooids and a similar overall distribution of spines, these two forms are clearly closely related and may be sibling species. We consider them to be distinct species because *C. disjunctus* in northern Japan shows a high degree of morphological continuity from the Lower Pleistocene (Fig. 3F) to the present (Fig. 3B), whereas the geographically separate Aleutian form is divergent in several qualitative and quantitative characters that, taken together, likely indicate significant genetic divergence.

OCCURRENCE. We found this species at stations 116-13 southwest of Amchitka I. and 12-45 on Stalemate Bank, at depths of 156 and 189 m, respectively. The known distribution is limited to the western Aleutian Islands.

*Cauloramphus cheliferoides* new species

(Fig. 5A–C)

“*Cauloramphus disjunctus* Ortman, 1890”: Dick et al., 2009, 3143, fig. 1b. In addition to misspelling ‘Ortmann’, Dick et al. (2009) erroneously cited the original description of *C. disjunctus* as Ortman (1890), when it is actually Canu and Bassler (1929).

ETYMOLOGY. The species name combines the Greek *chéle* (claw), the Latin *fere* (to bear), and the Greek suffix -oides (in the form of) to convey the meaning ‘as though bearing chelae, or claws’, referring to the paired avicularia appearing like paired chelae.

MATERIAL EXAMINED (see Table 1 for station data). HOLOTYPE: YPM 48062, Stn. 111-26, dried colony on scallop shell fragment. PARATYPES: 1) YPM 48063, Stn. 111-26, colony on scallop shell fragment, bleached and coated for SEM; 2) YPM 48064, Stn. 111-26, dried colony on scallop shell fragment; 3) YPM 48065, Stn. 111-26, dried colony on scallop shell fragment; 4) YPM 48066, Stn. 111-26, dried colony on polychaete tube; 5) YPM 48067, Stn. 110-24, two dried colonies on volcanic pebbles; 6) NHM 2010.2.10.14, Stn. 110-24, dried colony on scallop shell fragment; 7) NHM 2010.2.10.15, Stn. 110-24, two dried colonies on volcanic pebbles; 8) NHM 2010.2.10.16, dried colony on scallop shell. OTHER: Colony on shell fragment with colony of *C. ascofer*, on slide labeled “Amchitka I., C.E. O’Clair, 69-RD2-9”; we were unable to obtain exact locality and depth information for this old (probably 1969) collection number.

MEASUREMENTS. ZL, 0.47–0.64 (0.56 ± 0.049); ZW, 0.33–0.46 (0.40 ± 0.033); OpL, 0.23–0.41 (0.33 ± 0.043); OpW, 0.13–0.23 (0.19 ± 0.025) (n = 30, 2; YPM 48062, 48063). AvL, 0.20–0.28 (0.24 ± 0.018); AvD, 0.10–0.17 (0.13 ± 0.018) (n = 30, 2; YPM 48062, YPM 48064).

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Fig. 4. *Cauloramphus amphidisjunctus* n. sp. Holotype, YPM 48071. (A, B) Autozooids and avicularia, unbleached. (C) Autozooids, bleached. (D) Distal end of bleached zooid showing kenozooidal ooecium (asterisk). Scale bars: 0.5 mm (A–C), 0.05 mm (D).
DESCRIPTION. Colony white to light tan in color, forming small irregular or circular patches; largest observed 1 cm in diameter. Zooids (Fig. 5A, B) distinct, delineated by a conspicuous interzooidal furrow, interconnected by seven to ten tubular chambers on each side, with tiny, compressed lacunae between connections. Basal wall not calcified. Gymnocyst smooth, sloping, convex, broad proximally and laterally. Cryptocyst a smooth, nearly vertical rim around distal orifice, acute or rounded. Zooids with two short, thin, erect spines distal to orifice; most distal pair longer and thicker than the rest, slightly curved in distal direction, somewhat flattened (elliptical in cross-section). In older zooids, bases of intermediate and opesial spines become calcified so that spines remain after bleaching and gentle rinsing. Newly formed zooids have two (paired) avicularia, one on each side attached by a tiny pedicle in position 3/4, between first and second most distal opesial spines. Avicularia (Fig. 5A) large, conspicuous, about half as long as zooid, with bulbous chamber and aquiliform rostrum hooked at tip; average AvL/AvD = 1.8. Kenozoidal ooecium (Fig. 5C) a narrow crescent around distal margin, with proximal lip greatly extended (Fig. 5A, C) as a triangular flange, up to as long as distal orificial spines.

REMARKS. Dick et al. (2009) identified this species as C. disjunctus due to the large, paired avicularia and some-
scarcely evident in the former. In C. oshurkovi, both the two thin distal spines and the opesial spines are more widely spaced; Cauloramphus oshurkovi has many fewer opesial and hence total spines (mode = 11, range 10–12) than C. cheliferoides (mode = 15 or 16, range 14–19) (Table 2).

OCCURRENCE. This species is known only from the type locality near Medny Island, Commander Islands.

*Cauloramphus infensus* new species

(Fig. 6A–D)

MATERIAL EXAMINED (see Table 1 for station data).

HOLOTYPE: YPM 48051, Stn. 110-24, large colony on scallop shell, dried. PARATYPES: 1) YPM 48052, Stn. 110-24, dried colony fragment on volcanic pebble; 2) YPM 48053, Stn. 110-24, two dried colony fragments on volcanic pebbles; 3) YPM 48054, Stn. 111-26, dried colonies on scallop shell; 4) YPM 48055, Stn. 111-26, Colony on volcanic rock; 5) YPM 48056, Stn. 110-24, colony on pebble, bleached and coated for SEM; 6) YPM 48057, Stn. 110-24, Colony on volcanic pebble; 7) NHM 2010.2.10.7, Stn. 110-24, dried colony on volcanic rock; 8) NHM 2010.2.10.8, Stn. 110-24, dried colony on volcanic pebble; 9) NHM 2010.2.10.9, Stn. 110-24, dried colony on volcanic pebble; 10) NHM 2010.2.10.10, Stn. 110-24, colony on pebble, bleached and coated for SEM; 11) NHM 2010.2.10.10, Stn. 110-24, colony on pebble, bleached and coated for SEM.

ETYMOLOGY. The species name is from the Latin adjective *infensus* (hostile, aggressive), referring to the large, paired avicularia.

MEASUREMENTS. ZL, 0.49–0.74 (0.61 ± 0.057); ZW, 0.35–0.51 (0.42 ± 0.044); OpL, 0.32–0.51 (0.43 ± 0.052); OpW, 0.18–0.28 (0.24 ± 0.030); AvL, 0.37–0.51 (0.43 ± 0.031); AvD, 0.13–0.21 (0.17 ± 0.017) (n = 30; YPM 48051, 48055).

DESCRIPTION. Colony tan in color; largest observed 2 × 3 cm. Zooids (Fig. 6A–C) close together, separated by a deep furrow; short interzoidal tubular connection and tiny lacunae evident only between some zooids in SEM images. Basal wall not calcified, or with non-calculated central window of variable size. Lateral and proximal gymnocyst usually narrow and nearly vertical, though some zooids have an extensive proximal gymnocyst. Cryptocyst a conspicuous sloping shelf laterally and proximally; covered with low, coarse tubercles that are elliptical in outline. Zooids have 4–7 (mode, 6) long, tapering, acute orificial spines, erect or angled slightly distally, arranged around the orifice distally and laterally; more proximal orificial spines generally as long as or longer than longest opesial spines. Intermediate spines lacking. Angled over opesia are 10–14 (mode, 12) long, straight, tapering, acute opesial spines, meeting in midline; opesial spines separated at base by a distance equal to or less than maximum spine width; not touching one another laterally. Total number of spines 15–20 (mode, 18). In older zooids, bases of the intermediate and opesial spines become calcified so that spines remain after bleaching and gentle rinsing. Avicularia (Fig. 6A) single or paired; elongate (average AvL/AvD = 2.5); approximately as long as zooid width; hooked at tip; attached in 4/5 position. Proximal lip of mature ooecium (Fig. 6D) forms a short to moderately tall, triangular, often acute projection.

REMARKS. With large, often paired avicularia, *C. infensus* resembles *C. disjunctus*, *C. amphidisjunctus*, *C. cheliferoides*, *C. parvus*, and *C. oshurkovi*. It differs from these species in having larger zooids than all except *C. amphidisjunctus*; longer avicularia in both absolute terms and in relation to zooid width; six long, heavy orificial spines, with no differentiation of a pair of intermediate spines; and a tuberculate rather than a smooth cryptocyst.

OCCURRENCE. We found this species only at Stations 110-24 and 111-26, at depths of 95 m and 355 m, respectively. The known distribution is confined to the Rat Island Group, western Aleutian Islands.

*Cauloramphus parvus* new species

(Fig. 6E, F)

MATERIAL EXAMINED (see Table 1 for station data).

HOLOTYPE: YPM 48074, Station 111-26, tiny colony on small volcanic pebble.

ETYMOLOGY. The species name is from the Latin adjective *parvus* (small), referring to the small, precocious colony and small zooids.

MEASUREMENTS. ZL, 0.33–0.51 (0.44 ± 0.052); ZW, 0.26–0.36 (0.30 ± 0.033); OpL, 0.23–0.35 (0.29 ± 0.034); OpW, 0.12–0.18 (0.15 ± 0.019); AvL, 0.21–0.26 (0.24 ± 0.016); AvD, 0.07–0.10 (0.09 ± 0.011) (n = 15, 1; YPM 48074).

DESCRIPTION. Only one tiny colony was observed; tan in color, 2 × 3 mm. Lateral and proximal gymnocyst narrow; cryptocyst a smooth, narrow vertical rim around opesia.
Zooids (Fig. 6E, F) tiny, with two thin, nearly erect orificial spines at distal end; two tall, thick, straight, slightly flattened intermediate spines lateral to orifice, angled medially; and 11–16 (mode, 14) cylindrical, tapering, acuminate opesial spines angled over opesia and meeting in midline; total spines 15–20 (mode, 18). Distal pair of opesial spines very slightly curved toward orifice. Avicularia paired on most zooids, attached in position 3/4; elongate, AvL:AvD = 2.7. Proximal lip of ooecium tall; rounded or acute.

REMARKS. Cauloramphus parvus is very similar in spine number and formula to C. cheliferoides (Table 2); however, C. parvus has the smallest zooids of any species included in this report, while the avicularia are longer relative to zooid size and less bulbous than those of C. cheliferoides. The next most similar species is C. infensus, which has similarly elongate avicularia, but much larger zooids and avicularia (Table 2), a much different spine formula, and a relatively wide, tuberculate cryptocyst. Cauloramphus parvus is a precocious breeder; the colony observed has only 46 zooids, of which at least 25% have mature ooecia, starting in the third generation of zooids from the ancestrula.

OCCURRENCE. The only known locality is Station 111-26 in the Rat Island group, at a depth of 355 m.

Cauloramphus peltatus new species
(Fig. 7)
ALA (Aleutian sp. A): Dick et al., 2009, 3142, fig. 1d.
MATERIAL EXAMINED (see Table 1 for station data).
All material was collected at Station 113-21. HOLOTYPE: YPM 48048, dried colony on pebble. PARATYPES: 1) YPM 48049, dried colonies on two pebbles, coated for SEM; DNA voucher for GenBank EU835947; 2) YPM 48050, dried colony on pebble, coated for SEM. 3) NHM 2010.2.10.4, colonies on two pebbles, coated for SEM; 4) NHM 2010.2.10.5, dried colonies on three pebbles.
ETYMOLOGY. The species name is from the Latin adjective peltatus (armed with a shield).
MEASUREMENTS. ZL, 0.38–0.56 (0.49 ± 0.049); ZW, 0.28–0.44 (0.36 ± 0.037) (n = 30, 3; YPM 48046; YPM 48049, two colonies); AvL, 0.17–0.22 (0.19 ± 0.012); AvD, 0.06–0.10 (0.08 ± 0.010) (n = 20, 3; NHM 2010.2.10.5; YPM 48049, two colonies).
DESCRIPTION. Colony forms small, off-white, irregular patches; largest observed (holotype) 12 × 7 mm in extent; all specimens occurred on small pebbles (largest 1.8 × 1.5 cm; holotype) attached to the bases of sponges. Zooids (Fig. 7A, B) distinct, separated by a broad, deep furrow; closely set, with short interconnecting tubes and slit-like lacunae barely evident in SEM images. Basal wall not calcified. Proximal and lateral gymnocyst extensive; wide and moderately steep. Cryptocyst a smooth, vertical flange surrounding opesia; completely obscured by spines (costae) in intact zooids; evident only from internal view (Fig. 7C). Zooids with two short, moderately stout, erect orificial spines distal to orifice, close to midline; a pair of heavy, erect, somewhat flattened intermediate spines lateral to orifice, and 15–19 (mode, 18) flattened opesial spines, slightly curved and angled over opesia; ends of opesial spines broad. Opesial spines tightly appressed to one another, forming a frontal shield over unmodified frontal membrane.
Opesial spines have lost the basal articulation, which has become calcified, and thus comprise costae, by definition (Gordon, 2000); costae are held weakly together laterally by tiny struts of calcification (Fig. 7D) and medially by terminal interlocking projections (Fig. 7E), and can be forced apart laterally and medially (Fig. 7E) with a probe. Avicularia (Fig. 7A) typically paired, attached in position 3 or 3/4, lateral to most distal (first) pair of opesial spines or on lateral gymnocyst between first and second pairs of opesial spines; elongate (average AvL:AvW = 2.4). Ooecium (Fig. 7F) chevron shaped; proximal margin raised as low, rounded flange; distal margin with deep transverse furrow.
REMARKS. This is the only known Cauloramphus species having a costal shield composed of tightly appressed, weakly fused costae overlying a relatively unmodified opesia and frontal membrane.
OCCURRENCE. Presently known only from Stn. 113-21 in the Rat Island group, western Aleutian Islands, Alaska (see Table 1).

Cauloramphus ascofer new species
(Fig. 8)
CLC (cribrimorph-like Cauloramphus): Dick et al., 2009, 3143, fig. 1e–i.
MATERIAL EXAMINED (see Table 1 for station data).
HOLOTYPE: YPM 48042, Stn. 12-45, dried colony on plastic. PARATYPES: 1) YPM 48043, two dried colonies on scallop shell; 2) YPM 48044, two colonies.
DESCRIPTION. Colonies form irregular white patches on hard substrata, up to 5 cm or more in extent. Zooids (Fig. 8A, B) hyaline and translucent when young, chalky white when older. Boundaries between zooids distinct; short tubular connections alternating with tiny lacunae are evident between zooids in SEM images. Basal wall not calcified. Lateral and proximal gymnocyst broad, sloping, smooth. Opesial spines have lost the non-calcified basal joint, becoming costae; see Table 3 for counts of number of costae. Costae are fused to one another laterally and medially; tips interlocking in the midline, forming rigid shield over opesia (Fig. 8C); a tiny lacuna remains at base between each pair of adjacent costae. Opesia greatly reduced (Fig. 8D), completely covered by costal shield except distally, where it remains as a skeletally-defined ascophoran-type primary orifice tightly closed by a thickened operculum (Fig. 8A, B); see Table 3 for orifice measurements. Internally, there is an ascus (Fig. 1h in Dick et al., 2009). Around distal margin of orifice are four or five (97% and 3%, respectively; n = 60, 2) short, thick, erect orificial spines. Most zooids (88%; n = 60, 2) have a pair of short, clavate avicularia (Fig. 8A, B), one on each side in position 2 or 2/3, lateral or proximolateral to proximal pair of orificial spines; some zooids (12%) have only a single avicularium on either side; avicularian mandible long-triangular, acute, pointing distally. Kenozooloidal ooecium (Fig. 8E) a narrow crescent around distal curvature of orifice; proximal margin of ooecium forms a thin, slightly raised lip. Ancestrula (Fig. 8F) similar to astogenetically mature zooids, but with fewer costae in frontal shield; budding pattern is spiral, with first daughter zooid arising distally and each subsequent zooid arising from angle between the preceding zooid and ancestrula.

REMARKS. Dick et al. (2009: 3143, fig. 1e–i) briefly described and illustrated the functional morphology of this species, which has attained ascophoran-grade morphology. Externally, Cauloramphus ascofer is distinct from all other known species of Cauloramphus in having a reduced frontal shield composed of tightly fused, interlocking costae; a skeletally defined ascophoran-like orifice closed by the operculum; and an ascus.

Specimens from three geographically separate areas were found to differ in zooidal measurements and number of costae (Table 3). Compared to specimens from Stalemate Bank (Stn. 12-45) west of Attu Island, specimens from the Rat Islands (Stns. 111-26, 110-24), roughly 500 km to the east (Fig. 1), have somewhat smaller zooids; a markedly smaller orifice; a different orifice shape (slightly wider than long, rather than equal in length and width as on Stalemate Bank); more costae; and longer avicularia (Table 3). The specimen from Kamchatka is more similar to the Stalemate Bank specimens in zooid size and number of costae, but is more similar to the Rat Island specimens in having an orifice that is wider than long. These differences appear to represent geographical variation between disjunct populations rather than ecophenotypic variation related to depth, because specimens from the Rat Island group were consistent in morphology at depths of 95 and 355 m, which span the 189 m and 176 m depths of the specimens from Stalemate Bank and Kamchatka, respectively.

OCCURRENCE. We found C. ascofer at three stations...
near the center of the Rat Island group (~178°E), at one station on Stalemate Bank to the west (~171°E) (Fig. 1), and in Avacha Gulf, eastern Kamchatka; we also have a specimen labeled “Amchitka I.,” without exact locality information. The known range is the western Aleutian Islands and Avacha Gulf, Kamchatka.

**GENERAL RESULTS AND DISCUSSION**

Diversity and distribution of the Aleutian *Cauloramphus* species

Eight species of *Cauloramphus* were detected in the sampling area (Fig. 1), which extended along the Aleutian shelf from south of Amchitka Island to Stalemate Bank west of Attu Island. Although bryozoans were collected at 40 sampling stations, specimens of *Cauloramphus* were found at only five stations: three relatively close together in the Rat Island group, one roughly 60 km to the southeast near Amchitka I., and one far to the west on Stalemate Bank (Fig. 1; Table 1).

This seemingly disjunct sampling distribution is almost certainly an effect of the habitats sampled and sample sizes, rather than reflecting the actual distributions or abundances of the species involved. The samples from Stations 110-24, 111-26, and 113-21 in the Rat Island group were among the largest taken; two of them (110-24 and 111-26) comprised large numbers of dead scallop shells, with one (110-24) also containing many highly porous volcanic stones; both the shells and stones were encrusted by a diversity of *Cauloramphus* species (four or five species at each of these two stations). The sample from Station 113-21 was also exceptionally large and comprised pebbles attached to sponges; these pebbles likewise contained a high diversity (five species) of *Cauloramphus*. In all, eight *Cauloramphus* species were detected in the Rat Island group (islands between Amchitka Pass and Kiska Pass). The two *Cauloramphus* species found at Station 12-45 on Stalemate Bank were both encrusting heavy plastic panels lining the entrance to an abandoned crab pot. *Cauloramphus amphidisjunctus* was found only on smooth, flat substrates: the plastic panels at Station 12-45 and skate egg cases at Station 116-13.

The otter trawl used for sampling was intended to sample near-bottom fishes rather than sessile benthic animals, and only occasionally and haphazardly touched the bottom due to irregular topology. Dedicated bottom trawling in shelly and rocky habitats would likely find all eight of the *Cauloramphus* species over much broader geographical and vertical (Fig. 9) ranges than those detected in this study.

**Phylogeny of the *C. disjunctus* clade**

Dick et al. (2009) previously reported one of the Aleutian species described herein (*C. cheliferoides*) as *C. disjunctus*. At the time, *C. disjunctus* was the only *Cauloramphus* known with hypertrophied, paired avicularia, a frontal basket of closely set spines, and disjunct zooids. *Cauloramphus cheliferoides* is similar in these characters, but differs from *C. disjunctus* in total spine number; number of orificial spines; length/width ratio, form, and point of attachment of the avicularia; and degree of separation of zooids (Table 2). This study has identified a clade containing a number of species with similarities to *C. disjunctus*. A synapomorphy for this clade is the presence of hypertrophied, usually paired avicularia, although *C. ascofer* lacks this character. The cryptocyst in most of the species is smooth, but that in...
C. infensus is tuberculate. Only two of the species, C. disjunctus (Figs. 3A, 4A) and C. amphisdisjunctus (Fig. 4B, C) have overtly disjunct zooids with obvious tubular connections and relatively conspicuous interzoooidal lacunae; the other species exhibit short tubular connections and small lacunae.

Dick et al. (2009) presented a COI molecular phylogeny that included a clade comprising C. ordinarius ("CAC") and a sister group containing C. cheliferoides ("DIS"), C. peltatus ("ALK"), and C. ascofer ("CLC"). Nodal support for both this clade and internal nodes was weak, except for the sister-group relationship between C. peltatus and C. ascofer. Despite the lack of nodal support, the topology made sense, as among all species included in the analysis, C. cheliferoides and C. peltatus uniquely had hypertrophied avicularia in common, and C. peltatus and C. ascofer uniquely had a tight costal shield in common. In addition, a synapomorphy for this clade was calcified opesial spine joints in ontogenetically mature zooids. Alternative optimal topologies required two independent evolutionary events involving calcification of these spine joints, or a gain and a loss (Dick et al., 2009).

In Fig. 10, we present a tree representing a hypothesis of phylogenetic relationships for the eight species in the C. disjunctus clade. This hypothesis retains the topology of clade F, fig. 2 in Dick et al. (2009), indicated with a thick line in our Fig. 10. Cauloramphus ordinarius exhibits a suite of plesiomorphic characters common to many stereotypical Cauloramphus species, including only cuticular (flexible) spine joints, a tuberculate cryptocyst, no differentiation of intermediate spines, and more than two orificial spines. All species in the C. disjunctus clade (clade A, Fig. 10) show calcification of the opesial spine bases in ontogenetically mature zooids. This character can be observed as a tendency for zooids to retain the opesial spines after bleaching and gentle rinsing, or (in the case of C. disjunctus) by retention of the opesial spines in fossilized specimens (Fig. 3F).

Spine retention in bleached specimens is evident in Fig. 4C (C. amphisdisjunctus), Fig. 5B (C. cheliferoides), Fig. 5E (C. oshurkovi), Fig. 6C (C. infensus), Fig. 7C (C. peltatus), and Fig. 8D (C. ascofer); C. parvus and C. disjunctus were not subjected to bleaching.

Within clade A (Fig. 10), C. infensus is basal, retaining the plesiomorphic characters of a tuberculate cryptocyst, lack of well-differentiated intermediate spines, and more than two orificial spines; members of Clade B (Fig. 10) have intermediate spines and a smooth cryptocyst. Within Clade B, species in Clade D (C. disjunctus and C. amphisdisjunctus) are united by the synapomorphy of markedly disjunct zooids. Most species in Clade C share the character of two orificial spines (the presence of two orificial spines equally parsimoniously supports clades A and C as a synapomorphy, with two subsequent autapomorphic changes in orificial spine number in either case). Species in Clade E (C. ascofer + C. peltatus) are united in having a tight costal shield, and molecular data strongly supported this clade (Dick et al., 2009). Similarity in all characters except spine number supports Clade G (C. oshurkovi + C. cheliferoides). Although C. parvus is shown in Fig. 10 as the sister group to Clade G within Clade C, it could as well be the sister group to (Clade E + Clade G).

Cauloramphus ascofer shows several autapomorphies distinguishing it from C. peltatus and other members of Clade C. These include having four orificial spines, loss of intermediate spines, reduction in avicularium size, and a distal shift in the position of the avicularia, from the 3/4 to the 1/2 position. Achieving a fused costal shield and ascophoran-grade morphology apparently freed C. ascofer from whatever selective forces maintained the set of characters common to the other species.
Speciation and dispersal
Dick (2008) detected high species diversity in the bryo-
zoan genus *Monoporella* in the western Aleutian Islands
and noted that this diversity could have arisen through a
local species radiation. The *C. disjunctus* clade shows a
similar pattern, with a diverse group of closely related spe-
cies in the western Aleutians, but apparently with markedly
lower diversity on the Asian side. For the two genera com-
bined, apparent endemism in the western Aleutians is 80%
(12 of the 15 new species described by Dick [2008] and in
this study). That two distantly related genera show similarly
high apparent endemism in the western Aleutians leads us
to speculate that the deep benthic bryozoans in this region
have experienced high rates of speciation.

The western Aleutians have several characteristics that
should be conducive to the isolation and divergence of pop-
ulations, leading to allopatric speciation. This region has
long been isolated from Asia by Near Strait and from main-
land Alaska by distance (Gates et al., 1954; Thorson and
Hamilton, 1986); the Aleutian passes comprise putative dis-
persal barriers for deep benthic animals (Dick, 2008); and
there is (and has long been) considerable variation in envi-
ronment along the archipelago (Hunt and Stabeno, 2005).
We interpret the two geographically separate, morphologi-
cally distinct populations of *C. ascofer* in the western
Aleutians as incipient species, and as evidence of ongoing
allopatric speciation.

The tree in Fig. 10 indicates two separate sister-species
pairs (*C. oshurkovi* and *C. cheliferoides*; *C. disjunctus*
and *C. amphidisjunctus*) with one member each on the Asian
and Aleutian sides. The tree suggests that the population
ancestral to *C. oshurkovi* and *C. cheliferoides* dispersed
from the Aleutians to Asia, as *C. oshurkovi* is embedded in
clad F, with the other two species in the clade restricted to
the Aleutians. The polarity of dispersal is ambiguous for *C.
disjunctus* and *C. amphidisjunctus*, but the basal member
(*C. infensus*) and over half the other species in clade A are
restricted to the Aleutians, favoring dispersal from the
Aleutians to Asia for the population ancestral to clade D.
*Cauloramphus ascofer* has populations on both the Aleutian
and Asian sides. The sister-group relationship between *C.
ascofer* and *C. peltatus* (the latter known only from the
Aleutians) suggests that the common ancestor of these two
species was distributed in the Aleutians, and that *C. ascofer*
originated in the Aleutians and dispersed to Asia. The
Stalemate Bank population is more similar in morphology to
the Asian population than is the Rat Island population farther
eastward; this makes sense, as the Stalemate Bank popu-
lation is at the western end of the Aleutian Archipelago and
is the likely source population for dispersal to Asia.

These conclusions depend 1) on the accuracy of the
topology in Fig. 10, and 2) whether the species apparently
endemic to the Aleutians are actually endemics, or simply
through lack of sufficient sampling effort have not yet been
detected on the Asian side. The conclusions are thus tenta-
tive, and we consider them to represent hypotheses that can
be tested, e.g., by testing the tree topology with additional
DNA data; reexamining specimens from the Asian side that
were previously identified as *C. disjunctus*; and conducting
additional sampling on the Asian side.

On the classification of the cribrimorph *Cauloramphus*

species
In a morphology-based classification, and in the
absence of other definitive characters, the costal shields of
*C. peltatus* and *C. ascofer* would warrant taxonomic
placement of these species in *Cribriilinidae* (Infrorder
Asciophorina, Superfamily Cribriilinoidea) rather than in
*Calloporidae* (Infrorder Flustrina, Superfamily Calloporoidea).
Fortuitously, *Cauloramphus* is an unusually well defined,
polythletic (Boardman et al., 1969) genus in *Calloporidae*,
uniquely delineated by a suite of characters including
circle-oespal spines, uniporous septula, basally jointed
avicularia, and vestigial kenozooidal ooeicia. *Cauloramphus
ascofer* and *C. peltatus* are clearly allied with this genus, but
are so divergent in appearance from other *Cauloramphus*
species and indeed from one another (they represent two
morphological grades distinct from stereotypical anascan-
grade *Cauloramphus* species), that without molecular phy-
logenetic data, morphology-based taxonomic practice would
have warranted either 1) the classification of each in a sep-
arate, monospecific genus related to *Cauloramphus*, or 2)
subdivision of *Cauloramphus* into several subgenera to
accommodate the observed morphological disparity.

A limited molecular phylogeny (Dick et al., 2009) dem-
onstrated that *C. ascofer* and *C. peltatus* are simply highly
derived sister species well embedded in a clade comprising
*Cauloramphus*. There is thus no logical justification for
erecting new genus- or subgenus-level taxa to accommo-
date either or both of these species. *Cauloramphus* provides
a case in point underscoring the need for increased efforts
to reconstruct cheilostome phylogeny with DNA sequences,
not only at higher levels but also at the levels of genus and
family. The current cheilostome classification includes many
monospecific genera. For example, the database *Indexes to
Bryozoan Taxa* (http://www.bryozoa.net/indexes.html; accessed January 2010) lists 90 Recent and fossil genera
in Family Calloporidae, among which 35 (39%) are mono-
specific (13 Recent genera, 14.4%; 22 genera known only
as fossils, 24.4%). Many of these orphan species might, like
the cribrimorph *Cauloramphus* species, represent highly
morphologically divergent representatives of more speciose
genera.

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REFERENCES
Allman GJ (1856) A Monograph of the Freshwater Polyzoa, Includ-
ing All the Known Species, both British and Foreign. The Ray
Society, London
Androssova EI (1958) Bryozoa of the order Cheilostomata from
the northern part of the Sea of Japan. Issledovaniya Dal’nevostoch-
ykh Morei SSSR 5: 90–204 (in Russian)
Boardman RC, Cheetham AH, Cook PL (1969) Intracolony variation
and the genus concept in Bryozoa. Proc N Am Paleont Conv
1969C: 294–320
Busk G (1852) An account of the Polyzoa, and sertularian zoo-
phytes, collected in the voyage of the Rattlesnake, on the coast
of Australia and the Louisiade Archipelago. In "Narrative of
the Voyage of the H.M.S. Rattlesnake, Vol 1" Ed by J MacGil-
Canu F, Bassler RS (1928) Fossil and Recent Bryozoa of the Gulf of
Mexico region. US Natl Mus Proc 72: 1–199
Canu F, Bassler RS (1929) Bryozoa of the Philippine region. US
Natl Mus Bull 100(9): i–xi, 1–685, Plates 1–94
Canu F, Bassler RS (1930) The bryozoan fauna of the Galapagos
Islands. US Natl Mus Proc 78: 1–78
d’Hondt J-L (1985) Contribution à la systématique des Bryozoaires
Nat Zool Paris (Ser 13) 7: 1–12
Dick MH (2008) Unexpectedly high diversity of Monoporella
(Bryozoa: Cheilostomata) in the Aleutian Islands, Alaska: tax-
Dick MH, Ross JRP (1988) Intertidal Bryozoa (Cheilostomata) of the
Kodiak vicinity, Alaska. Cent Pac Northwest Stud Occ Pap 23:
1–133
ascophoran bryozoans was historically contingent but likely.
Proc R Soc B 276: 3141–3148
Gates O, Fraser GD, Snyder GL (1954) Preliminary report on the
geology of the Aleutian Islands, Science 119: 446–447
Gordon D (2000) Towards a phylogeny of the cheilostomes - mor-
phological models of frontal wall/shield evolution. In "Proceed-
ings of the 11th International Bryozoology Association
Conference" Ed by A Herrera Cubilla, JBC Jackson, Smithsonian
Tropical Research Institute, Balboa, pp 17–37
Grischenko AV (1997) Bryozoans (Ctenostomida, Cheilostomida) of
the Commander Islands shelf zone. In "Benthic Flora and
Fauna of the Shelf Zone of the Commander Islands" Ed by AV
Rzhavsky, Dalnauka Press, Vladivostok, pp 153–192 (in
Russian)
Grischenko AV, Dick MH, Mawatari SF (2007) Diversity and taxon-
omy of intertidal Bryozoa (Cheilostomata) at Akkeshi Bay,
Hokkaido, Japan. J Nat Hist 41: 1047–1161
Hincks T (1877) On some Polyzoa from Iceland (Greenland) and
Labrador. Ann Mag Nat Hist (Ser 4) 19: 97–112
Hunt GL Jr, Stabeno PJ (2005) Oceanography and ecology of the
Aleutian archipelago: spatial and temporal variation. Fish
Oceanogr 14 (Suppl 1): 292–306
Kluge GA (1975) Bryozoa of the Northern Seas of the USSR.
Amerind Publishing, New Delhi (English translation of 1962
Russian volume)
Sch Med Nihon Univ 9: 23–61
Norman AM (1903) Notes on the natural history of East Finmark —
Polyzoa. Ann Mag Nat Hist (Ser 7) 11: 567–598
Ortmann A (1890) Die Japanische Bryozenfauna. (Bericht über die
von Herrn Dr. L. Döderlein in Jahre 1880–81 gemachten
Sammlungen). Arch Naturgesch 56: 1–74, pls 1–4
apparatus in the bryozoan genus Cauloramphus (Cheilosto-
matata: Calloporidae) and its inferred homology to ovicells. Zool
Sci 24: 1187–1196
Smitt FA (1868) Bryozoa marina in regionibus arcticis et borealis
vivente recensuit. Ofvers K Vetenskapskad Forh Stockholm
24: 443–467
Thorson RM, Hamilton TD (1986) Glacial geology of the Aleutian
Islands based on the contributions of Robert F. Black. In "Glaci-
ation in Alaska: The Geologic Record" Ed by KM Hamilton, KM
Reed, RM Thorson, Alaska Geological Society, Anchorage,
pp 171–191

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