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# Unexpectedly High Diversity of *Monoporella* (Bryozoa: Cheilostomata) in the Aleutian Islands, Alaska: Taxonomy and Distribution of Six New Species

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**The cheilostome bryozoan genus *Monoporella* is poorly resolved taxonomically; only four Recent species have been formally described, though several undescribed species have been reported in the literature. The literature indicates no more than five species in the genus occurring in any local region of the world, with one to three species in most regions where the genus has been reported. I examined bryozoans from 52 trawl catches in the western and western-central Aleutian Islands, Alaska, and found specimens of *Monoporella* in 12 of these samples. Study of these specimens by scanning electron microscopy (SEM) revealed six new species that are described herein: *M. flexibila*, *M. elongata*, *M. gigantea*, *M. ellefsoni*, *M. seastormi*, and *M. aleutica*. Two of the species have erect colony morphologies, a condition not previously reported in *Monoporella*. The species diversity of *Monoporella* appears to be greater in the Aleutians than in any other part of the world adequately surveyed. I discuss whether this apparent high diversity is an artifact due to insufficient sampling in the deep shelf zone, and present two hypotheses to explain this high diversity should it prove not to be an artifact: 1) the present high local diversity represents a relict of past high diversity occurring broadly around the North Pacific rim; and 2) a local radiation of *Monoporella* occurred in the Aleutian archipelago.**

**Key words:** Alaska, Aleutian Islands, biodiversity, Bryozoa, depth, ecology, local radiation, *Monoporella*, speciation, species diversity, zoogeography

## INTRODUCTION

Species of the cheilostome bryozoan genus *Monoporella* are striking in appearance, due to the large size of their zooids and the often darkly pigmented cuticle and black operculum. *Monoporella* species are also unusual in forming large, spinose ovicells, the ooecium of which is derived from costal spines produced from the frontal wall of the zooid distal to a reproductive zooid. Taylor and McKinney (2002) and Ostrovsky and Taylor (2005) studied the ovicells of several species of *Monoporella* in the context of the evolution of brood chambers in cheilostome bryozoans.

The literature gives the impression of a low worldwide species diversity of *Monoporella*. In addition to several fossil taxa, only four Recent species have been described: *M. nodulifera* (Hincks, 1881); *M. fimbriata* Canu and Bassler, 1927; *M. fimbriata* var. *crassa* Canu and Bassler, 1929, raised to species rank by Tilbrook (2006); and *M. tenuimargo* Canu and Bassler, 1929. The first was originally described from cool-temperate Bass Strait, Australia, and the other three from a tropical region, the Philippines.

The actual Recent diversity is known to be somewhat higher. There are SEM illustrations in the literature (Taylor and McKinney, 2002; Ostrovsky and Taylor, 2005) of two undescribed species, one from Alaska, USA, and the other from the vicinity of Okinawa Island, Japan. Furthermore, since its original description in Australia, the type species, *M. nodulifera*, has been reported from the Mediterranean (Hayward, 1974; Zabala and Maluquer, 1988) and New Zealand (Gordon, 1984). Tilbrook (2006) noted that although the specimens from these latter two localities were similar to one another, they were likely not *M. nodulifera* Hincks. Both Harmer (1926) and Tilbrook (2006) concluded that some of the specimens of *Monoporella* in the collections of the Natural History Museum, London, represent additional, undescribed species.

In July 2004, I made a sizeable collection of bryozoans from shelf areas in the western Aleutian Islands, Alaska; colleagues obtained and sent to me additional specimens in 2006. In all, the collection indicates a high diversity of bryozoans occurring subtidally in the region. Conspicuous in the collection are tan to dark brown-colored colonies with exceptionally large zooids. Scanning electron microscopic examination of these colonies showed that they belong to *Monoporella* and allowed the discrimination of six species. None was previously described, though Ferdinand Canu (unpublished manuscript, Muséum National d'Histoire Naturelle, Paris) previously recognized one of them as a

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novel species. Remarkably, two of these species form erect colonies, a condition not previously reported in the genus.

In this paper, I describe the six species of *Monoporella* found in the Aleutian collection on the basis of external characters of the calcified zooidal skeleton and one cuticular character, color (i.e., characters traditionally used in cheilostome bryozoan taxonomy). The species described are thus morphospecies; however, in a test of the morphospecies concept in cheilostomes, Jackson and Cheetham (1990, 1994) found for several species among three genera that the characters used to delineate morphospecies were heritable and that the morphospecies so defined were genetically distinct — in short, that they represented biological species. In addition to taxonomy, I provide limited ecological and distributional information for the species detected. Finally, I propose and discuss two hypotheses to address the apparent pattern of high species diversity of *Monoporella* in the Aleutians compared to other regions.

## MATERIALS AND METHODS

On the basis of island sizes, width and depth of intervening passes, and extent of surrounding shelf, the Aleutian Islands are considered to comprise the eastern Aleutians (as far west as Samalga Pass), central Aleutians (Samalga Pass to Amchitka Pass), and western Aleutians (westward from Amchitka Pass) (reviewed by Hunt and Stabeno, 2005). From 20 July–2 August 2004, I examined the catches from 63 otter-trawl tows made in the western Aleutian Islands (Fig. 1) at depths of 50–467 m. This work was done aboard F/V *Sea Storm* under charter to the Alaska Fisheries Science Center (AFSC) of the US National Marine Fisheries Service (NMFS). Since the goal of this trawling was to assay bottom-fish stocks in the region, trawling was conducted just above the bottom; however, due to bottom irregularities, the trawl touched bottom at some time during most tows. The catches, which consisted mostly of fishes, thus also often contained substrates suitable for bryozoans, such as pebbles, hydroids, sponges, dead scallop and other bivalve shells, gastropods, and discarded plastic. Bryozoans were sorted from the catch, rinsed with a stream of seawater, dried in trays in the engine room of the vessel, and finally stored in zip-lock bags. Delicate, erect forms were preserved in 95% ethanol. In all, 42 stations in 2004 yielded bryozoan specimens; among these, six stations contained specimens of *Monoporella* (Table 1).

I received bryozoan specimens from 10 trawl samples from the central and western Aleutians, collected by NMFS biologists from July–August 2006, also aboard the F/V *Sea Storm*. These specimens were preserved initially in buffered 10% formalin and later rinsed in water and transferred to 70% ethanol. After receiving this material in ethanol, I rinsed and air-dried it. Six of the 10 samples from 2006 contained specimens of *Monoporella* (Table 1). Fig. 1 shows the locations of the 12 trawl stations (2004 and 2006) where material for this study was collected.

Selected specimens to be used for scanning electron microscopy (SEM) were soaked in a concentrated sodium hypochlorite solution to remove the soft tissues, rinsed in tapwater, air-dried, and coated with Pd-Pt in a Hitachi E-1030 sputter coater. Electronic images were taken with a Hitachi S-2380 scanning electron microscope at 15 kV accelerating voltage and stored as TIFF files at 500 dpi with ImageCatcher software (Denshi Kongaku Kenkyusyo Co., Tokyo). In a few cases, unbleached specimens were coated for SEM, images were taken, and the specimens were then bleached and re-coated, and additional images taken. For each species, zooid measurements were made at 80X magnification with an ocular micrometer on a stereoscopic microscope. Measurements are presented as the range followed by the mean ± SD in parentheses, all in millimeters. Sample sizes 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; OrL, orifice length; OrW, orifice width; OvL, ovicell length; OvW, ovicell width.

Species of the genus *Monoporella* are rather uniform in overall zooidal morphology (see Fig. 2, which also gives relevant terminology). The species descriptions provided here are thus abbreviated,

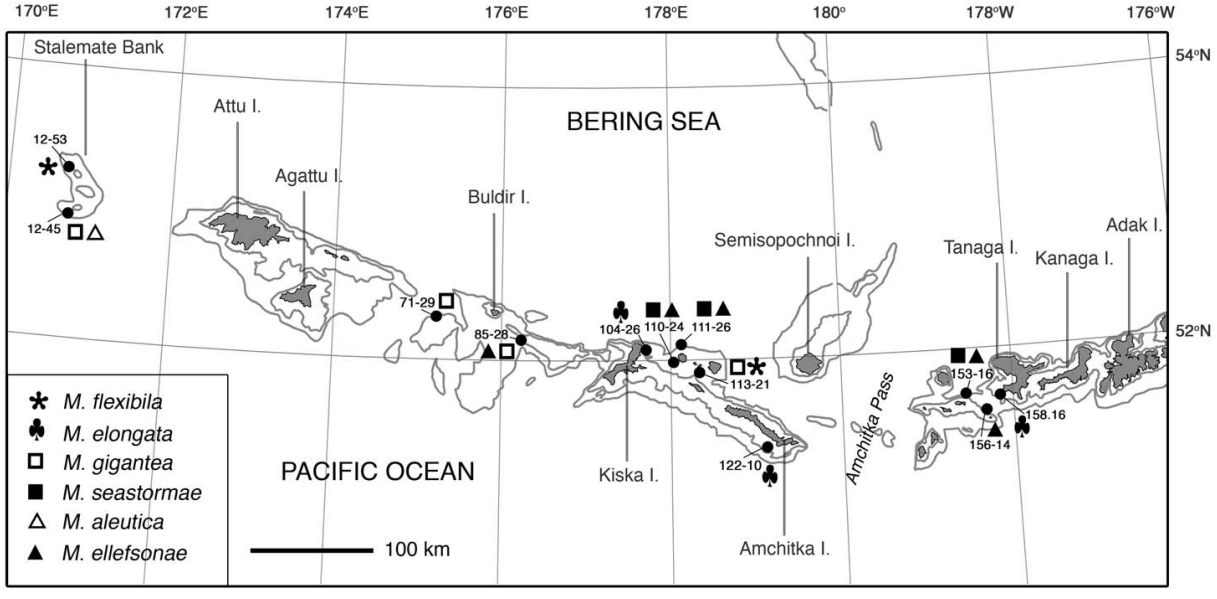


**Fig. 1.** Map showing the western Aleutian Islands (west of Amchitka Pass) and part of the central Aleutian Islands (east of Amchitka Pass). Islands are indicated by dark-gray shading, with the main islands labeled; the 100-m and 500-m depth contours are shown in light gray. Filled circles indicate sampling stations, which are labeled by the station number close to each circle. Other symbols (key, lower left) close to the station markers indicate the *Monoporella* species found at each station.

focusing on diagnostic characters of each species and omitting generic characters that are common to all the species. Species descriptions are based on the specimens listed under TYPE MATERIAL and OTHER MATERIAL at the start of each description. All of the specimens listed have been deposited in the Invertebrate Collection, Yale Peabody Museum (YPM), Yale University, New Haven, Connecticut, USA. To save space, the localities of type specimens are identified by station numbers, for which relevant collecting information can be accessed in Table 1. Unless otherwise noted, specimens were collected by M. H. Dick.

## RESULTS

### Species diversity and distribution

Six species were detected in the study area (Table 2), none of them previously described. Two of these, *M. flexibila*

**Table 1.** Collection data for *Monoporella* species in the Aleutian Islands, Alaska. Stations are listed in order of longitude from west to east; refer to Fig. 1 for their locations relative to islands.

| Stn.[1] | Date | Latitude[2] | Longitude | Depth[3] (m) | Temp.[4] (°C) | Species |
|---|---|---|---|---|---|---|
| 12-45 | 30 July 2004 | 52°54.742'N | 170°48.900'E | 189 | 4.0 | *M. gigantea* |
| | | | | | | *M. aleutica* |
| 12-53 | 31 July 2004 | 53°15.938'N | 170°50.514'E | 181 | 4.0 | *M. flexibila* |
| 71-29 | 25 July 2004 | 52°13.684'N | 175°17.598'E | 179 | 4.3 | *M. gigantea* |
| 85-28 | 24 July 2006 | 52°10.763'N | 176°20.964'E | 93 | 4.8 | *M. gigantea* |
| | | | | | | *M. ellefsoni* |
| 104-26 | 28 July 2006 | 52°05.680'N | 177°42.660'E | 94 | 4.5 | *M. elongata* |
| 110-24 | 22 July 2004 | 51°58.410'N | 178°13.602'E | 95 | 4.9 | *M. ellefsoni* |
| | | | | | | *M. seastormi* |
| 111-26 | 22 July 2004 | 52°03.681'N | 178°17.820'E | 355 | 4.0 | *M. ellefsoni* |
| | | | | | | *M. seastormi* |
| 113-21 | 23 July 2004 | 51°51.609'N | 178°27.869'E | 227 | 4.3 | *M. gigantea* |
| | | | | | | *M. flexibila* |
| 122-10 | 22 July 2006 | 51°22.524'N | 179°06.432'E | 81 | 5.1 | *M. elongata* |
| 153-16 | 21 July 2006 | 51°38.572'N | 178°36.120'W | 123 | 4.9 | *M. ellefsoni* |
| | | | | | | *M. seastormi* |
| 156-14 | 2 Aug. 2006 | 51°33.373'N | 178°21.882'W | 149 | 4.2 | *M. ellefsoni* |
| 158-16 | 2 Aug. 2006 | 51°38.299'N | 178°09.840'W | 91 | 5.1 | *M. elongata* |

[1]National Marine Fisheries Service Aleutian Survey station number. [2]Coordinates are given for the start of each trawl tow. [3]Average bottom depth during trawl tow. [4]Bottom temperature at time of collection.

**Table 2.** Characters of the Aleutian species of *Monoporella* described in this study, along with parallel characters of some previously described species. Numbers in columns ZL to OvW are mean measurements in millimeters; see species descriptions for ranges and sample sizes. No reproductive structures were observed for *M. flexibila*; for this species, measurements of encrusting zooids are followed by those in parentheses for zooids in erect internodes.

| | Growth form[1] | OFZ[2] | Color | Operculum[3] | Distal spines[4] | Crypt. texture[5] | Median crest[6] | ZL[7] | ZW[8] | OrL[9] | OrW[10] | OvL[11] | OvW[12] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *M. flexibila* | ErI | – | very dark chestnut brown | S | 0 | T | A | 1.08 (1.54) | 0.71 (0.49) | 0.13 (0.15) | 0.19 (0.19) | – | – |
| *M. elongata* | ErB | AZ | very dark golden brown | S | 0 | T | W/A | 1.57 | 0.80 | 0.20 | 0.27 | 1.10 | 1.26 |
| *M. gigantea* | EnU | V | light yellowish brown / tan | S | 1–5(2) | G | W/A | 1.62 | 1.11 | 0.18 | 0.23 | 0.88 | 1.31 |
| *M. ellefsoni* | EnU | KZ | dark grayish brown to chestnut brown | S | 0 | G | W/A | 1.09 | 0.84 | 0.13 | 0.19 | 0.79 | 1.06 |
| *M. seastormi* | EnU | AZ | light to medium mustard brown | S | 1–4 | G | W/A | 1.32 | 0.95 | 0.16 | 0.23 | 0.92 | 1.21 |
| *M. aleutica* | EnU | KZ | very dark brown | S | 0 | G | W/A | 1.44 | 1.08 | 0.15 | 0.21 | 0.68 | 0.94 |
| *M. nodulifera*[13] | EnU | AZ | dark brown | P | 3 | G | A | 0.80 | 0.60 | 0.12 | 0.16 | ? | ? |
| *M.* sp. (Chios)[14] | EnU | AZ | pale brown | P? | 6–8(6) | G | S | 0.85 | 0.71 | 0.14 | 0.24 | 0.71 | 0.91 |
| *M. fimbriata*[15] | EnU | AZ | 'light' (= tan?) or rose colored | P? | 5–8 | G | W/A | 0.75 | 0.63 | 0.10 | 0.17 | ? | ? |

[1]Growth form: ErI, erect with internodes; ErB, erect, bilaminar; EnU, encrusting, unilaminar. [2]Ooecium-forming zooids: AZ, autozooidal; V, variable; KZ, kenozooidal. [3]Operculum: S, smooth; P, pitted. [4]Distal spines: range, with modal number in parentheses. [5]Cryptocyst texture: T, tessellated; G, granulated. [6]Median crest: A, absent; W/A, weak or absent; S, strong. [7]Zooid length. [8]Zooid width. [9]Orifice length. [10]Orifice width. [11]Ovicell length. [12]Ovicell width. [13]Data from Tilbrook (2006); values for zooidal measurements are midpoint values of given ranges. [14]Data from Hayward (1974) for material described from the Mediterranean island of Chios as '*M. nodulifera* (Hincks)', but undoubtedly not that species; Hayward (1974) describes the operculum as pitted, whereas Tilbrook (2006) describes the same material as having a smooth operculum. [15]Data from Canu and Bassler (1929); their Pl. 17, Fig. 8 seems to show pitted opercula.

and *M erecta*, have erect colony morphologies, whereas the other four form exclusively unilaminar, encrusting colonies. All but one of the species (*M. elongata*) ranged to ≥181 m in depth (Table 1). Three species (*M. gigantea*, *M. ellefsoni*, *M. seastormi*) showed considerable depth ranges, from minimum depths of 93, 93, and 95 m to maximum depths of 227, 355, and 355 m, respectively. Among the five species with more than one depth record, *M. elongata* had the shallowest and narrowest depth range; it was found at depths of 81–94 m close to islands. All six species occurred in the western Aleutians, that is, west of Amchitka Pass (Fig. 1). *Monoporella gigantea* and *M. flexibila* occurred at Stalemate Bank and at Station 113-21 just west of Amchitka I.; their distributions thus spanned most of the length of the western Aleutians. These two species, along with *M. aleutica*, were restricted to the western Aleutians. Three species (*M. elongata*, *M. ellefsoni*, *M. seastormi*) were found in both the western and central Aleutians, with distributions spanning Amchitka Pass.

## Taxonomy

### Class GYMNOLAEMATA Allman, 1856
### Order CHEILOSTOMATA Busk, 1852
### Suborder NEOCHEILOSTOMINA d'Hondt, 1985
### Infraorder FLUSTRINA Smitt, 1868
### Superfamily MICROPOROIDEA Gray, 1848
### Family Monoporellidae Hincks, 1882
### Genus *Monoporella* Hincks, 1881

(Fig. 2)

*Haploporella* Hincks, 1881: 10 (see REMARKS below).
*Chrossotoechia* Canu and Lecointre, 1925: 6.

TYPE SPECIES. *Hapoloporella nodulifera* Hincks, 1881, selected by Norman (1903: 115).

DIAGNOSIS. Colony encrusting, bilaminar folded erect, or dichotomously branching erect with flexible nodes. Lateral and proximal gymnocyst absent. Frontal surface of autozooid a glistening frontal membrane underlain by a continuous, granulated cryptocyst perforated by small pores; an opesiule lies proximolateral to orifice on each side. Distolateral margins and orifice raised, often delineated from central part of cryptocyst by sharp angular grooves, here termed 'cryptocystal incisions' (Fig. 2). Cryptocyst with or without a median crest. Opesia reduced, entirely covered by operculum. Orifice [defined by Hayward and Ryland (1998: p. 344) as the "opening in the zooid wall through which the lophophore and tentacles are exserted"; in *Monoporella*, the orifice is coincident with the opesia] raised, surrounded by a thick rim; proximal orificial margin with a slight, often denticulate angled shelf (e.g., Fig. 5B). Distal oral spines present or absent. Avicularia lacking. Ovicell large; prominent (approximately half of the brooding cavity is above the colony surface) or subimmersed (less than half of the brooding cavity is above the colony surface); cleithral (closed by zooidal operculum); spinocystal, the ooecium formed from costae (non-articulated spines) elaborated from the frontal wall of the distal zooid; distal part of the ooecium has irregular or slit-like intercostal foraminae; also present are two lateral foraminae, through which larval release occurs (A. Ostrovsky, personal communication). Cormidial brooding complex present (described by Cheetham and Cook [1983: p 166] as a "cluster of polymorphic zooids forming [a] brooding structure"), consisting of a maternal zooid, a distal ooecium-forming zooid, and a bilaterally asymmetrical autozooid on each side having a cryptocystal invagination contributing to a lateral foramen of the ovicell. Zooids interconnect by basal pore chambers.

REMARKS: Hincks (1881) originally named this genus *Haploporella*; however, later in the same paper, in a footnote to the legend of his Plate 1, Fig. 4, Hincks (1881: 135) noted, "This genus stands as *Haploporella* in the text; but Mr. Waters tells me that this name has been applied to a genus of fossil Foraminifera." He then replaced, in the same paper, the homonym *Haploporella* Hincks (1881) with the name *Monoporella*, by using this latter name in the legends of figures for two new species (*M. nodulifera* and *M. lepida*) in the new genus. *Monoporella lepida* was later

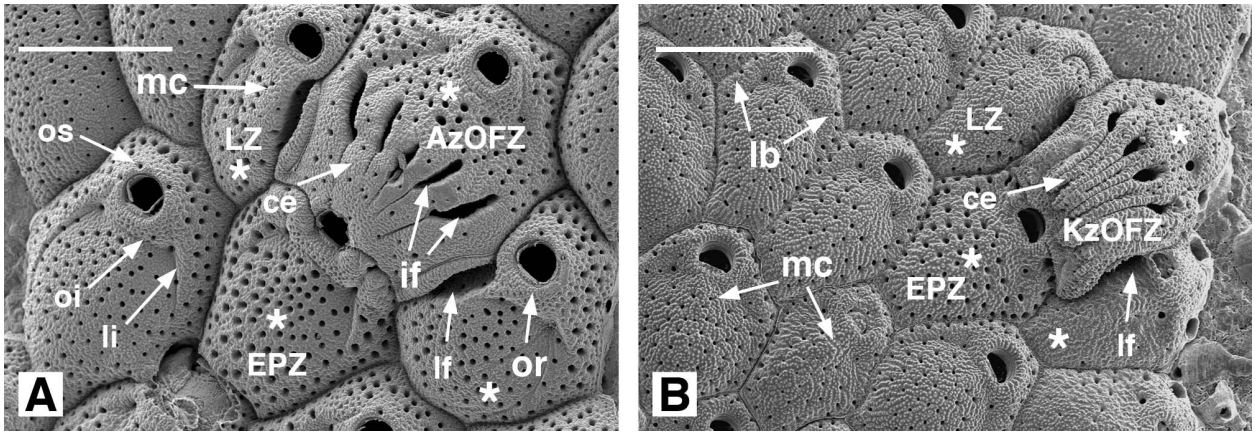


**Fig. 2.** Terminology relevant to *Monoporella* species. Left, *M. gigantea*; right, *M. ellefsoni*; both illustrations to same scale, with scale bars=1 mm. Asterisks indicate the four zooids comprising a cormidial brooding complex, including the egg-producing zooid (**EPZ**), the distal ooecium-forming zooid that may be of autozooidal (**AzOFZ**) or kenozooidal (**KzOFZ**) type, and the two flanking lateral zooids (**LZ**); the lateral zooids are bilaterally asymmetrical due to a cryptocystal invagination on one side that contributes to a lateral foramen (**lf**) of the ovicell. Other abbreviations: **or**, orificial rim; **os**, orificial spines or spine scars; **oi**, orificial cryptocystal incision; **li**, lateral cryptocystal incision; **lb**, lateral buttresses; **mc**, median crest, not well developed in the zooids indicated in (B); **ce**, costal elements; **if**, intercostal foraminae.

removed from *Monoporella* and assigned as the type species of *Opaeophora* Brown, 1948.

The discovery of two different erect colony morphologies in this study necessitated amendment of the generic diagnosis, which had previously included only the encrusting morphology. In addition, all known species of *Monoporella* for which ovicells have been observed have a cormidial brooding complex, as described above, which has not been mentioned in previous generic diagnoses (e.g., Gordon, 1984; Harmer, 1926; Canu and Bassler, 1929). Finally, though previous diagnoses mention distal orificial spines, several species in the present study lack them.

***Monoporella flexibila*** new species
(Fig. 3)

TYPE MATERIAL. HOLOTYPE: YPM 40867-a, encrusting base of a colony, on a pebble, bleached and coated for SEM (specimen AL-97), and YPM 40867-b, several

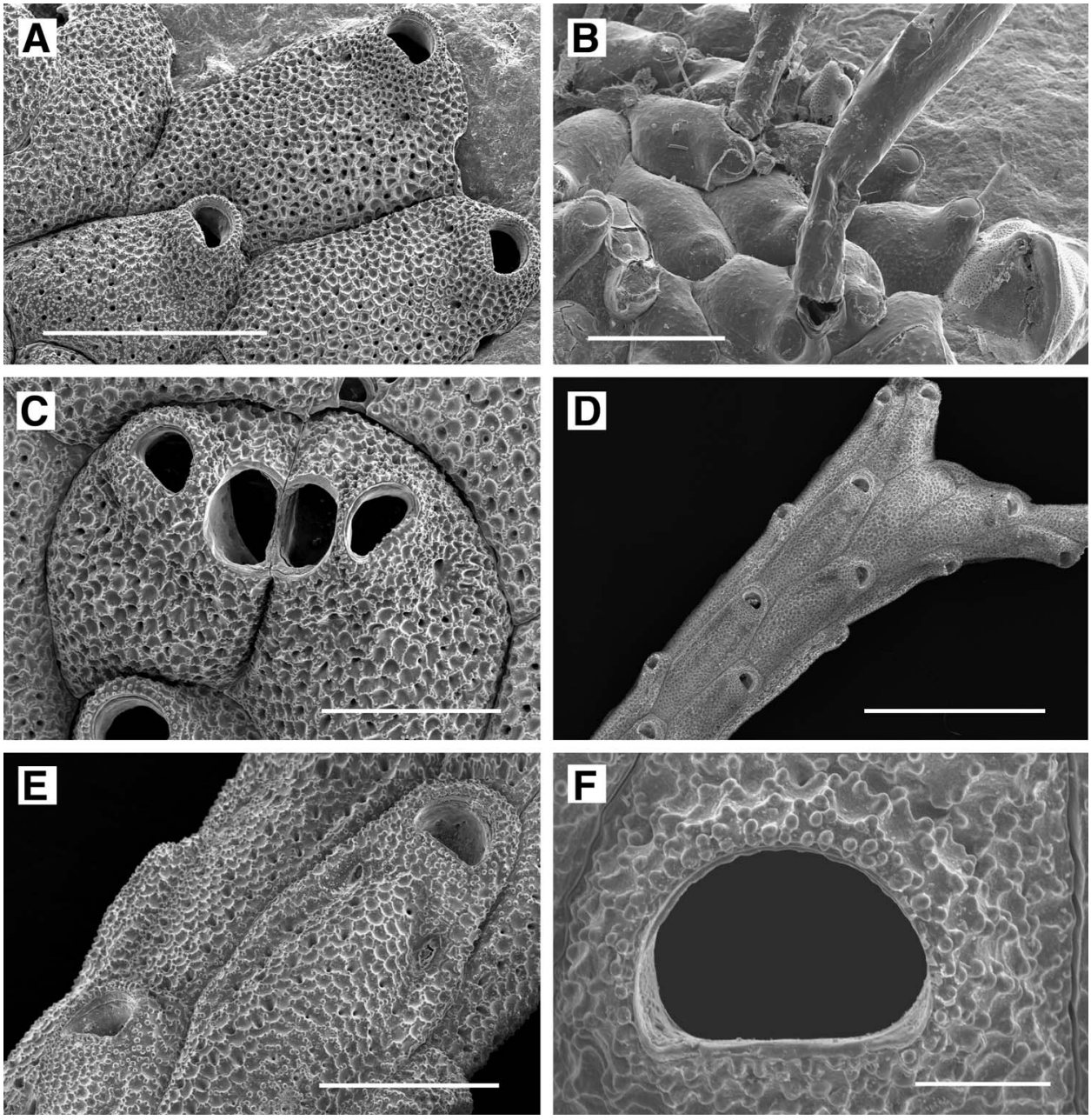


**Fig. 3.** *Monoporella flexibila* n. sp. All panels except (B) show bleached specimens. **(A)** Autozooids in the initial encrusting portion of a colony. **(B)** Encrusting initial portion of a colony showing two vertical stalks arising from paired (lower) and single (upper) stalk-forming zooids. **(C)** A pair of stalk-forming zooids, each member of the pair comprising an autozooid and a distomedially budded kenozooidal interzooid that actually forms half of a stalk. **(D)** Forked distal end of an internode of an erect, flexible branch of a colony. **(E)** Enlargment showing zooidal morphology in an erect internode. **(F)** Orifice of a zooid in an erect internode. Scale bars: 1 mm (A, B); 500 μm (C, E); 2 mm (D); 100 μm (F).

unbleached erect branches from same colony, both from Station 12-53. PARATYPES: YPM 40868, numerous erect branches from one or more colonies, and YPM 40869 (specimen AL-62), several internodes from same lot, bleached and coated for SEM, both from Station 113-21.

ETYMOLOGY. The species name is from the Latin *flexibilis* (flexible), referring to the erect colony morphology with flexible nodes.

MEASUREMENTS. Encrusting zooids (n=15, 1): ZL, 0.82–1.49 (1.079±0.187); ZW, 0.538–0.897 (0.706±0.106); OrL, 0.11–0.15 (0.129±0.012); OrW, 0.18–0.21 (0.192±0.007). Zooids in erect internodes (n=30, 2): ZL, 0.80–2.74 (1.537±0.345); ZW, 0.359–0.590 (0.487±0.057); OrL, 0.13–0.15 (0.142±0.009); OrW, 0.17–0.21 (0.190±0.010).

DESCRIPTION. Colony at first unilaminar, encrusting, forming a small sheet of zooids (Fig. 3A, B). Encrusting zooids convex, inflated, separated by a deep groove; cryptocystal incisions absent or indistinct; opesiules minute. Within an encrusting colony, some zooids in pairs each bud an interzooid medially (Fig. 3B, C), and both members of this pair of adjacent interzooids contribute equally to an erect, jointed stalk with flexible nodes. Zooids in a pair that give rise to stalk-forming interzooids may both have a normal-sized, functional orifice with an operculum; one may have a normal orifice and the other lack an orifice; or both may lack an orifice. Rarely, the single interzooid of an unpaired autozooid produces a stalk (Fig. 3B, upper stalk). The lowest internode of each erect stalk is uncalcified at the base where it emerges from the stalk-forming zooid(s), thus forming a flexible joint. Erect stalks are up to 4 cm tall in the material available, dichotomously branching, internodes Y-shaped, or Y-shaped with the tips of the Y also bifurcated. Internodes (Fig. 3D) subcylindrical in cross section, somewhat flattened in plane of bifurcation; maximum length about 1 cm, maximum width about 3 mm; increasing gradually in width from 4–6 zooids around the circumference at the proximal end to 4–7 zooids across one side just proximal to a bifurcation. Internodal zooids greatly elongate (Fig. 3D, E), with lateral cryptocystal incisions proximal to the opesiules; frontal wall transversely convex; zooids separated by a narrow, shallow groove; opesiules larger and more proximally located than in encrusting zooids. In both zooid types, the orifice is semielliptical (Fig. 3F), markedly broader than long with the proximal angles broadly rounded. The entire frontal surface both zooid types is tessellated (Fig. 3A, C, E) with small depressions delineated by granulated margins (Fig. 3F); frontal pores lie in some of these depressions. The color of dried specimens is dark reddish-brown or chestnut; the operculum is shiny black. Ovicells were not observed in any of the material available.

REMARKS. This is the only species of *Monoporella* known to form flexible, erect branches. It is unknown whether this species can grow in the encrusting form alone, without producing erect branches; in any case, such a colony could easily be identified by zooid morphology, including orifice shape, the lack of well-defined cryptocystal incisions, and the tessellated frontal wall.

OCCURRENCE. This species was found at two stations (Table 1, Fig. 1) at or near opposite ends of the western Aleutians (Stalemate Bank and just west of Amchitka Island), at depths of 181 and 227 m, respectively.

***Monoporella elongata*** new species
(Fig. 4)

"?*Monoporella*" species: Taylor and McKinney, 2002, 311, Fig. 1I, J.

*Monoporella* sp. 2: Ostrovsky and Taylor, 2005, 337, Fig. 10C-F.

TYPE MATERIAL. HOLOTYPE: YPM 40870, broken colony 4 cm high×6 cm wide×9 cm long, dried, unbleached, Station 104-26, coll. Dana Carrison-Stone (NMFS). PARATYPES: YPM 40871 (specimen AL-104), bleached, coated for SEM, and YPM 40872, 14 colony fragments, dried, all from Station 122-10, coll. Paul Von Szalay (NMFS). YPM 40873 (specimen AL-105), bleached, coated for SEM; YPM 40874, large colony fragment, dried, unbleached; both from Station 158-16, coll. unknown (NMFS).

ETYMOLOGY. The species name is derived from Late Latin *elongare* (to make longer). Ferdinand Canu applied the name *M. elongata* to an Alaskan specimen of this species (MNHN 2856-7) in an unpublished manuscript in the Muséum National d'Histoire Naturelle, Paris (Ostrovsky and Taylor, 2005), and I retain Canu's name here.

MEASUREMENTS (n=30, 2). ZL, 1.31–1.92 (1.569 ±0.148). ZW, 0.59–1.12 (0.804±0.147). OrL, 0.18–0.22 (0.195±0.016). OrW, 0.23–0.30 (0.267±0.015). OvL, 0.92–1.33 (1.097±0.117); OvW, 1.03–1.54 (1.261±0.127); ovicell n=27, 2.

DESCRIPTION. Colony can form loosely attached, unilaminar sheets (see Remarks), but most of my specimens are parts of erect, foliaceous, rigid colonies constructed from a highly and irregularly folded, anastomosing, bilaminar sheet (Fig. 4B); dried specimens are a very dark golden-brown color; largest specimen examined is approximately 4 cm high×6 cm wide×9 cm long, though it was larger before being damaged in collection. Zooids vary considerably in shape, from nearly hexagonal to markedly elongate (Fig. 4A); closely appressed; delineated by a thin suture and, in uncleaned material, a narrow line of thickened ectocyst. Orifice (Fig. 4D) large, D-shaped, with rounded proximal angles; operculum brownish black, dull-textured. Cryptocyst gently transversely convex inside slightly raised margins; cryptocystal incisions often indistinct, but clearly evident in some zooids; cryptocystal sculpturing is tessellated with small pits having a smooth or granulated margin. Ovicell (Fig. 4C) prominent, hemispherical; circular, transversely elliptical, or oval in outline; formed from broad, flattened costae; with 3 or 4 (3=28%, 4=72%, n=18) long, narrow intercostal foraminae starting around distal margin and directed toward zooidal orifice; surface finely tessellated. Ooecium-forming zooid of autozooidal type (Fig. 4C). Spines lacking. Autozooids in unilaminar, encrusting sheets were indistinguishable in size and morphology from those in erect, bilaminar sheets.

REMARKS. *Monoporella elongata* n. sp. and *M. flexibila* n. sp. are the only known erect species of *Monoporella*; they share elongate zooids, dark color, and tessellated cryptocysts, suggesting they may be closely related. In most cases, the attachment substratum of *M. elongata* was unknown, but in one case, portions of several separate colonies occurred as unilaminar, loosely attached sheets (largest was a broken colony 1.8×2.3 cm in extent, ovicells

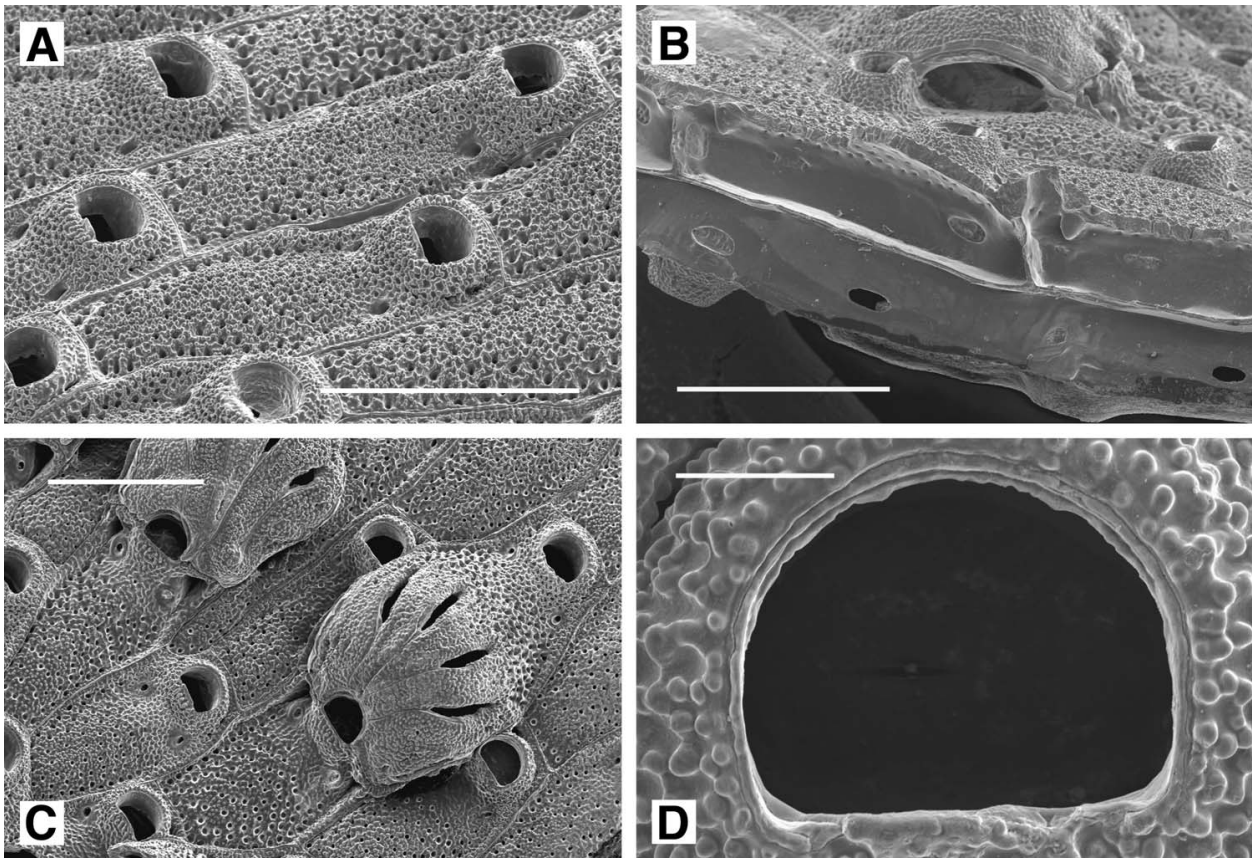


**Fig. 4.** *Monoporella elongata* n. sp. All panels show bleached specimens. **(A)** Autozooids. **(B)** Lateral view of the broken edge of a colony, showing the bilaminar construction; large opening near top center is a lateral foramen of an ovicell. **(C)** Ovicellate zooids, each of which is part of a cormidial brooding complex; the ooecium-forming zooid is of the autozooidal type. **(D)** Zooidal orifice. Scale bars: 1 mm (A–C); 100 μm (D).

lacking) overgrowing parts of a large (11 cm long, 8 cm wide, 7 cm high), rigid, erect, foliaceous colony of *Porella* (*Rhamphostomella*?) *pacifica* O'Donoghue, 1925, collected at Station 158-16. It may be normal for *M. elongata* to start out as a unilaminar sheet, which then gives rise to the erect form.

*Monoporella elongata* might be distributed in Japan in addition to the Aleutians, as Tilbrook (2006) noted that a specimen from deep water, Japan, residing in the Natural History Museum, London (NHM 1928.9.13.74) appeared to be the same species as Canu's Alaskan specimen.

OCCURRENCE. Parts of damaged colonies were found at three sampling stations (Table 1, Fig. 1) in the western and central Aleutians, at depths of 81–94 m near Kiska, Amchitka, and Tanaga Islands.

### ***Monoporella gigantea*** new species
(Fig. 5)

TYPE MATERIAL. HOLOTYPE: YPM 40875 (specimen AL-96), on bivalve shell fragment, bleached and coated for SEM, Station 85-28, coll. Dana Carrison-Stone (NMFS). PARATYPES: YPM 40876 (specimen AL-19), on pebble, Station 113-21; YPM 40877 (specimen AL-95; includes ancestrula), on rock fragment, Station 12-45; YPM 40878 (specimen AL-107), on pebble, Station 71-29; all bleached and coated for SEM. YPM 40879 (specimen AL-113), on plastic, unbleached, coated for SEM, and YPM 40880, on plastic, dried specimen, both from Station 12-45.

ETYMOLOGY. The species name derives from the Latin *giganteus*, meaning 'giant,' referring to the large size of the zooids.

MEASUREMENTS (n=30, 2). ZL, 1.41–2.00 (1.622 ±0.153). ZW, 0.85–1.36 (1.108±0.122). OrL, 0.16–0.20 (0.177±0.011). OrW, 0.22–0.26 (0.234±0.013). OvL, 0.85–0.92 (0.88); OvW, 1.18–1.53 (1.31); ovicell n=3, 2.

DESCRIPTION. Colony unilaminar, encrusting, ramifying in multiserial lobes 2–6 zooids wide, sometimes anastomosing to form broader lobes; largest colony observed 2.5 cm across. Colony color tan, or light yellowish- to chocolate-brown; zooidal operculum dark chestnut brown, contrasting sharply with lighter frontal surface. Zooidal frontal wall convex (Fig. 5A, B), inflated, rising sharply around zooidal margin, giving rise to a deep groove separating zooids; frontal granulation very fine, uniform. Orifice (Fig. 5C) large, D-shaped. Zooids have 1–5 short, sharp, chitinous, chestnut-brown, distal oral spines (frequencies 1=3%, 2=43%, 3=31%, 4=22%, 5=1%; n=104) (Fig. 5A). Cryptocystal incisons sharp (Fig. 5B). Ovicell subimmersed; ooecium (Fig. 5D) much broader than long, the distal margin nearly straight and transverse; with 3–5 (n=5) long, narrow foraminae in distal half; boundary between costal pairs usually indicated by a fine incision. Ooecium-forming zooid variable:

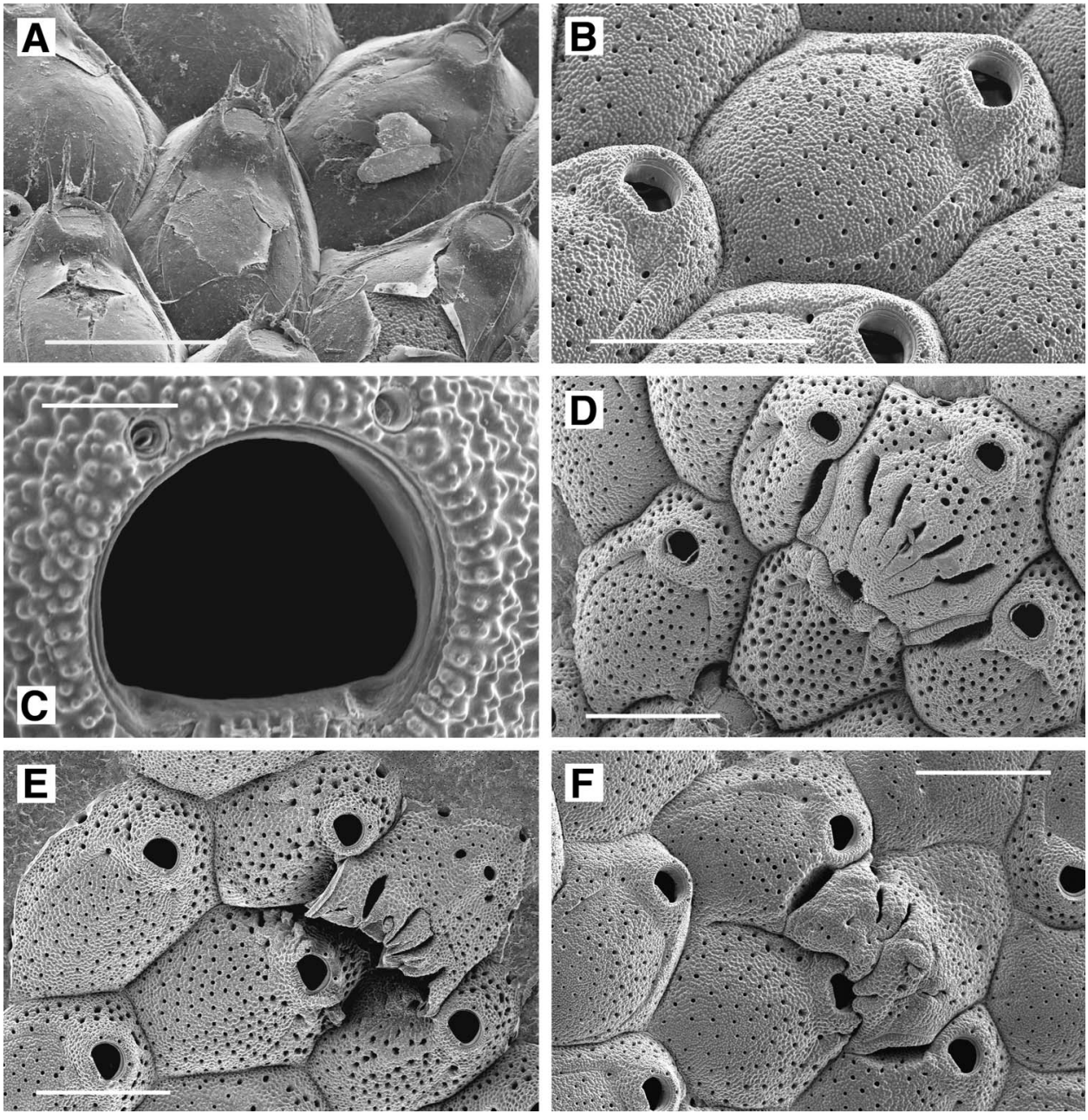


**Fig. 5.** *Monoporella gigantea* n. sp. All panels except (A) show bleached specimens. **(A)** Autozooids, all of which have distal oral spines; dried ectocyst is peeling away from the cryptocyst in some zooids. **(B)** Autozooids; note the scars of distal oral spines. **(C)** Autozooidal orifice. **(D)** Cormidial brooding complex; the ooecium-forming zooid is of the autozooidal type. **(E)** Cormidial brooding complex with the ooecium damaged; the ooecium-forming zooid is of mixed type, comprising a kenozooid that retains a much-reduced orifice and enlarged opesiules. **(F)** Cormidial brooding complex with a kenozooidal ooecium-forming zooid (associated with the damaged or stunted condition of the ooecium?). The complexes in (D–F) are all from the same colony. Scale bars: 1 mm (A, B, D–F); 100 μm (C).

of autozooidal type (Fig. 5D), of intermediate type, with much-reduced orifice and enlarged opesiules (Fig. 5E), or of kenozooidal type (Fig. 5F); all three types were observed in a single colony. Ancestrula large, identical to later autozooids; one observed, 1.28 mm long by 0.85 mm wide, with four oral spines, budding a daughter zooid distolaterally on each side.

REMARKS. Among the Aleutian species described herein, *M. gigantea* is the lightest in color; is the only exclusively encrusting species with average zooid size over 1.5 mm; and is the only species with spines on most zooids.

OCCURRENCE. Found at four sampling stations (Table 1, Fig. 1) spanning the western Aleutians; depth range 93–227 m. Substrates utilized (n=8 colonies) included the interior of a dead bivalve shell (1), a plastic panel in an abandoned crab pot (2), and pebbles (5).

***Monoporella ellefsoni*** new species
(Fig. 6)

TYPE MATERIAL. HOLOTYPE: YPM 40881 (specimen AL-103), on bivalve shell fragment, bleached and coated for SEM, Station 111-26. PARATYPES: YPM 40882 (specimen AL-100), Station 153-16, coll. Dana Carrison-Stone (NMFS); YPM 40883 (specimen AL-102), YPM 40884 (specimen AL-109), and YPM 40885 (specimen AL-111), Station 111-26; all bleached and coated for SEM. YPM 40886, four unbleached colonies, each on a separate shell fragment, Station 111-26. YPM 40887, one colony on shell fragment, Station 85-28, coll. Dana Carrison-Stone (NMFS). OTHER MATERIAL: YPM 40888, colony of *M. ellefsoni* contacting colony of *M. seastormi* on shell fragment, Station 111-26.

ETYMOLOGY. The species is named for fisherman Jermond Ellefson, engineer in 2004 aboard the F/V *Sea Storm*, from which this Aleutian collection was made, in appreciation of his generous help in obtaining and drying bryozoans and his interest in all things marine.

MEASUREMENTS (n=45, 3). ZL, 0.90–1.36 (1.089 ±0.103). ZW, 0.64–1.12 (0.840±0.104). OrL, 0.12–0.14 (0.129±0.006). OrW, 0.17–0.21 (0.185±0.009). OvL, 0.69–0.92 (0.791±0.083); OvW, 0.95–1.13 (1.059±0.062); ovicell n=7, 3.

DESCRIPTION. Colony unilaminar, encrusting, forming irregularly shaped coherent sheets; largest observed 2×5 cm in extent; color variable, dark grayish-, reddish- or chestnut-brown. Zooidal boundaries distinct (Fig. 6A), delineated by a very narrow groove and suture; zooidal margins rising sharply. Cryptocyst markedly convex (Fig. 6A), inflated, sometimes with a weak median crest for a short distance proximal to orifice; cryptocystal incisions sharp, well defined, the orificial incision often slightly curved or angled, so that the incisions together seem to form an arc. Orifice (Fig. 6B) markedly broader than long; oral spines lacking. Cryptocyst thick, pores deeply set, with small, circular surface openings; surface granulation often pronounced (Fig. 6A, C). Ovicell subimmersed; ooecium-forming zooid reduced in extent distal to ooecium and always of kenozooidal type (Figs. 6C, D, 9D); in some colonies, these ooecium-forming kenozooids lack opesiules (Fig. 6D), whereas in others they have enlarged opesiules (Fig. 6C, 9D). This difference appears related to variation in degree of calcification of the colony, with the opesiules of the kenozooids filled in more heavily calcified colonies and enlarged in more lightly calcified colonies. This difference in calcification is also reflected in the ooecia. In colonies in which enlarged opesiules are evident in the ooecium-forming kenozooids, the ooecial costae are less heavily calcified, and deep sutural grooves are evident between costal pairs and even between individual

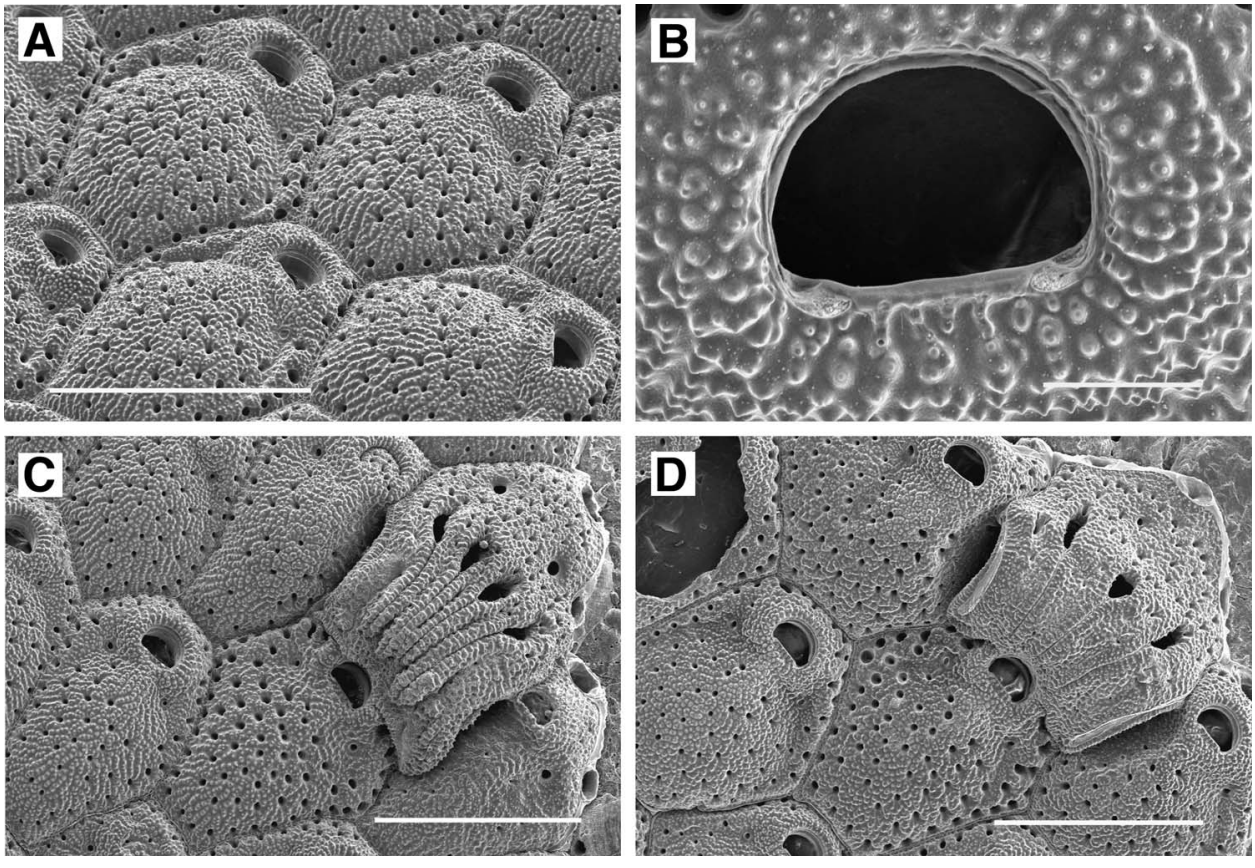


**Fig. 6.** *Monoporella ellefsoni* n. sp. All panels show bleached specimens. **(A)** Autozooids. **(B)** Autozooidal orifice. **(C)** Cormidial brooding complex, with the ooecium having moderately calcified costal elements with deep sutural grooves. **(D)** Cormidial brooding complex, with the ooecium having heavily calcified costal elements with thin sutures. In both (B) and (C), the ooecium-forming zooid is of the kenozooidal type. Scale bars: 1 mm (A, C, D); 100 μm (B).

costae, giving them the appearance of flexible tendrils (Fig. 6C, 9D). In colonies in which the ooecium-forming zooids have the opesiules reduced or lacking, the ooecial costae are more heavily calcified, with costal pairs appearing as broad, flattened straps (Fig. 6D), with a thin suture line between adjacent straps. Ooecia usually broader than long, perforated by 2–4 (2=11%, 3=41%, 4=48%, n=27) short, slitlike foraminae across distal margin. Ancestrula (Fig. 8A) like autozooids, but smaller; two observed, 0.87 mm long×0.56 mm wide and 0.82 mm long×0.69 mm wide; oral spines lacking.

REMARKS. *Monoporella ellefsoni* can be distinguished from the other species treated herein by the following combination of characters: smallest zooids, close to 1 mm in average length; only unilaminar, sheetlike colonies; ooecium-forming zooids of kenozooidal type, with or without enlarged opesiules; oral spines lacking. At first it appeared that the heavily and lightly calcified forms described above might be distinct species. However, the two forms are virtually identical in all mean zooidal measurements. Furthermore, both forms occurred on *Chlamys* shells at Station 111-26, where the species was generally abundant, and in a few colonies, ooecium-forming zooids and ooecia occurred with morphologies intermediate between the two forms.

OCCURRENCE. This species was found at five stations (Table 1, Fig. 1) from the western to central Aleutians, ranging in depth from 93–355 m. It co-occurred with *M. seastormi* at three of the stations. With the exception of a single colony on a rock, it was exclusively found on the inner and outer surfaces of dead shells of *Chlamys* sp.

***Monoporella seastormi*** new species
(Fig. 7)

TYPE MATERIAL. HOLOTYPE: YPM 40889 (specimen AL-108), on shell fragment, bleached and coated for SEM, Station 111-26. PARATYPES: YPM 40890 (specimen AL-101), Station 111-26; YPM 40891 (specimen AL-98), YPM 40892 (specimen AL-99), YPM 40893 (specimen AL-110, ancestrula), Station 110-24; all on bivalve shell fragments, all bleached and coated for SEM. YPM 40894, six dried colonies on shell fragments, Station 111-26. OTHER MATERIAL: YPM 40895, dried colony of *M. seastormi* contacting colony of *M. ellefsoni* on shell fragment, Station 111-26.

ETYMOLOGY. The species name derives from the chartered F/V *Sea Storm*, which has been instrumental in Aleutian and other Alaskan bottom-trawling surveys conducted by the US National Marine Fisheries Service.

MEASUREMENTS (n=75, 5). ZL, 0.82–1.74 (1.321 ±0.154). ZW, 0.667–1.231 (0.952±0.125). OrL, 0.13–0.18 (0.163±0.012). OrW, 0.17–0.25 (0.225±0.013). OvL, 0.87–1.03 (0.923±0.050); OvW, 0.90–1.46 (1.209±0.164); ovicell n=11, 4.

DESCRIPTION. Colony unilaminar, encrusting, forming irregular sheets; largest observed 3×5 cm; light to dark

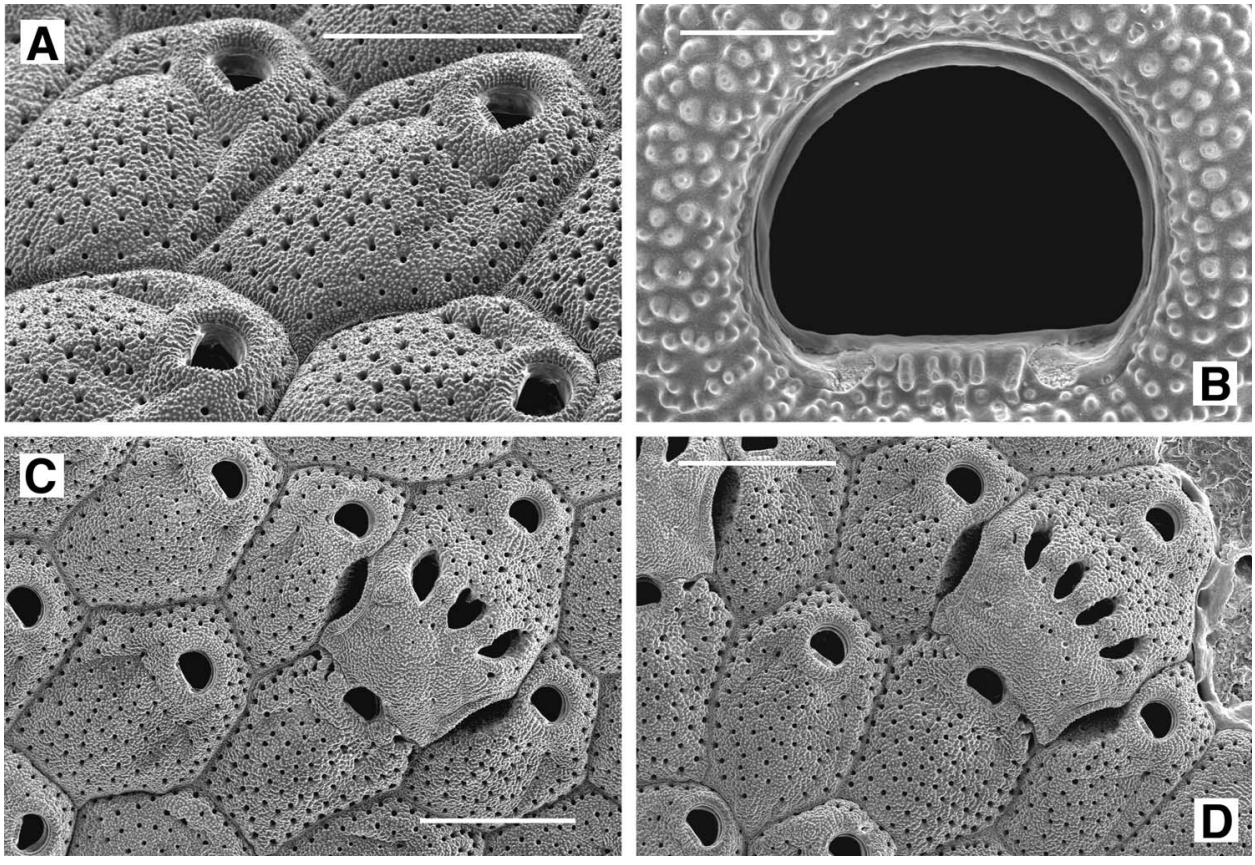


**Fig. 7.** *Microporella seastormi* n. sp. All panels show bleached specimens. **(A)** Autozooids. **(B)** Autozooidal orifice. (**C, D)** Cormidial brooding complexes from the same colony, with ooecium-forming zooids of the autozooidal type. **(D)** Scale bars: 1 mm (A, C, D); 100 μm (B).

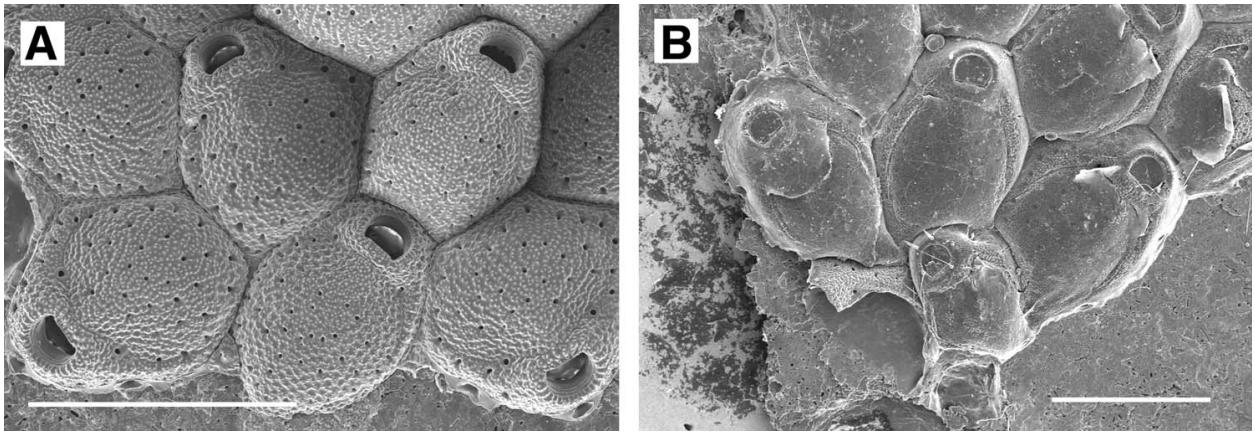


**Fig. 8.** Ancestrulae and periancestrular zooids of two species. **(A)** *Monoporella ellefsoni* n. sp., bleached specimen; ancestrula (bottom center) and periancestrular zooids all lack oral spines. **(B)** *Monoporella seastormi* n. sp., unbleached specimen; ancestrula (bottom center) has a pair of distal oral spines, and the three complete periancestrular zooids each have two or three oral spines or spine scars. Scale bars: 1 mm.

yellowish brown (mustard brown) in color. Zooids (Fig. 7A) well delineated by a sharp groove, zooidal margins low. Cryptocyst convex and inflated inside slightly raised margins; cryptocystal incisions sharp. Orifice (Fig. 7B) variable in shape within a colony, sometimes D-shaped, sometimes markedly broader than long; operculum shiny black. Orificial spines uncommon; most colonies lack them, but some have a few, scattered zooids with 1–4 short, sharp, chestnut-brown chitinous spines, possibly restricted to the zone of astogenetic change. Ovicell subimmersed; ooecium-forming zooid is of autozooidal type (Fig. 7C, D). Ooecium broader than long, or vice-versa; roof of ooecium proximal to foraminae evenly and finely granulated, without sutures evident (Fig. 7C, D) or with very fine sutural incisions between costal pairs; ooecium perforated by 2–6 (2=7%, 3=32%, 4=46%, 5=11%, 6=4%, n=28) intercostal foraminae along distal margin that are about one-third the length of the ooecium. Ancestrula (Fig. 8B) like autozooids, but smaller; one observed, 0.90 mm long×0.60 mm wide; with a pair of distal oral spines; zooids in first periancestrular generation have 2 or 3 oral spines.

REMARKS. Among the encrusting species treated herein, *M. seastormi* is most similar to *M. gigantea*. Spines were observed only in these two species, although they are rare on zooids of the former and usually present on zooids of the latter. Both species have ooecium-forming zooids of the autozooidal type; however, this was the only type observed in *M. seastormi*, whereas in *M. gigantea*, autozooidal, kenozooidal, and intermediate types were observed, sometimes all in the same colony. *Monoporella seastormi* further differs from *M. gigantea* in having smaller zooids (average ZL×ZW=1.32×0.95 mm, compared to 1.62×1.11 mm), and in the form of the ovicell. In *M. seastormi*, there is usually no evidence of intercostal sutures (Fig. 7C, D); in *M. gigantea*, sutural incisions are typically evident between costae (Fig. 5D), and the foraminae tend to be longer in proportion to ovicell length.

OCCURRENCE. *Monoporella seastormi* was recorded at three stations in the western and central Aleutians, at depths of 95–355 m, where it always co-occurred with *M. ellefsoni* (Table 1, Fig. 1); it was found only on the inner and outer surfaces of dead valves of *Chlamys* sp.

### ***Monoporella aleutica*** new species
(Fig. 9)

TYPE MATERIAL. HOLOTYPE: YPM 40896 (specimen AL-106), colony on pebble, bleached and coated for SEM, Station 12-45. PARATYPES: YPM 40897 (specimen AL-112), colony on pebble, unbleached, coated for SEM; YPM 40898, dried colony on shell fragment; both from Station 12-45.

ETYMOLOGY. The species name refers to the Aleutian archipelago, in turn named for the aboriginal inhabitants, the Aleuts.

MEASUREMENTS (n=30, 2). ZL, 1.28–1.62 (1.444 ±0.096). ZW, 0.92–1.35 (1.083±0.094). OrL, 0.13–0.17 (0.147±0.011). OrW, 0.18-0.23 (0.210±0.013). OvL, 0.67–0.69 (0.679); OvW, 0.92–0.95 (0.936); ovicell n=2, 2.

DESCRIPTION. Colony unilaminar, encrusting, consisting of irregular sheets or biserial or narrowly multiserial rami; color a very dark coffee-brown. Zooids (Fig. 9A) well-separated by a wide, sharp groove due to sharply rising zooidal margins; higher distally than proximally. Cryptocyst moderately convex; most zooids with rounded or sharp median crest (Fig. 9A) evident for a short distance proximal to orificial rim; cryptocystal incisions sharp, conspicuous. Orifice (Fig. 9B) small relative to zooid size; conspicuously broader than long. Ovicell subimmersed; ooecium broader than long (Fig. 9C); three and four intercostal foraminae present in the two ovicells observed; foraminae are long slits tapering at one or both ends, extending for about half of ovicell length; suture lines between costae. Ooecium-forming zooid is kenozooidal (Fig. 9C). Oral spines lacking.

REMARKS. *Monoporella aleutica* has the darkest coloration among the encrusting species examined in this study. It is similar to *M. ellefsoni* in entirely lacking oral spines and in having ooecium-forming zooids only of the kenozooidal type; however, its zooids are much larger (mean L×W=1.44×1.08 mm) than those of *M. ellefsoni* (mean L×W=1.09×0.84 mm) (compare Fig. 9C with Fig. 9D). Both the ovicell and the orifice of *M. aleutica* are smaller relative to zooid size, compared to *M. ellefsoni*.

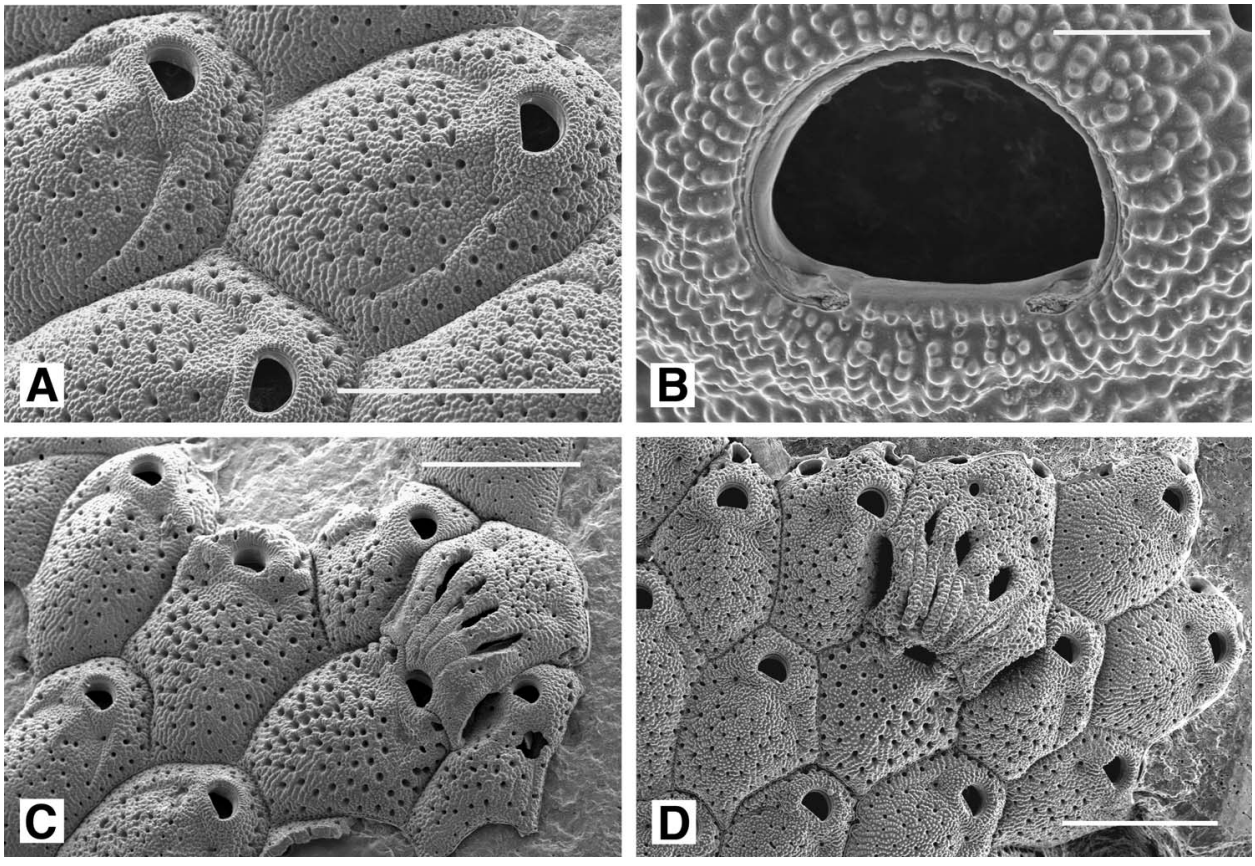


**Fig. 9.** **(A–C)** *Monoporella aleutica* n. sp. **(A)** Autozooids. **(B)** Autozooidal orifice. **(C)** Cormidial brooding complex, with the ooecium-forming zooid of kenozooidal type; note pair of nodules lateral to orifice on zooid to left of center, which will become the maternal zooid in a brooding complex. **(D)** *Monoporella ellefsoni* n. sp., shown at the same scale as (C) for comparison. This species also has ooecium-forming zooids of kenozooidal type, but the zooids are much smaller. All panels show bleached specimens. Scale bars: 1 mm (A, C, D); 100 μm (B).

OCCURRENCE. This species was found only on Stalemate Bank, where it co-occurred with *M. gigantea* at Station 12-45 at a depth of 189 m (Table 1, Fig. 1). Three of four colonies were on pebbles attached to sponges, and one colony was on a bivalve shell fragment.

## DISCUSSION

### Taxonomic characters

After examining specimens of *Monoporella* from around the world deposited in the Natural History Museum, London, Tilbrook (2006) listed the characters he concluded were taxonomically informative in distinguishing among species. These characters include number of oral spines; smooth versus pitted operculum; orifice shape; denticulate versus smooth distal border of orifice; presence versus absence of lateral oral nodules; presence versus absence of median frontal crest; number of pores in frontal shield; and possibly number of grooves and fenestrae (foraminae) at distal edge of ovicell.

The two Aleutian species that form different types of erect colonies are unambiguously distinguishable on this basis, although other characters also differ. In contrast, the four species that form unilaminar, encrusting colonies are quite similar to one another in zooid form. Nonetheless, each is distinguishable by a consistent suite of characters (Table 2). Considering all six species, taxonomically useful characters other than colony growth form include zooid size; orifice size and shape; colony color; frontal-wall sculpturing (tessellated or uniformly granulated); presence or absence of oral spines; type of ooecium-forming zooid (autozooidal versus kenozooidal); and characters of the ovicell (size, form, nature of the sutures between costal elements, surface sculpturing, and size and shape of intercostal foraminae). I soon abandoned attempts to count frontal pores. While pore number might prove informative, counting pores on enough zooids to get a range and mean is unbearably tedious; pore number may be correlated with zooid size, which is much easier to measure; and, since counts are practically impossible without SEM images, they are of little use for routine identification with the light microscope.

### Ecology

The Aleutian *Monoporella*s in this study were found at depths of 81–355 m (Table 1, Fig. 10). This range may not accurately reflect the actual depth distributions. In the segment of the 2004 Aleutian Survey during which I collected specimens from trawl catches, 63 trawl tows were made, ranging from 50–467 m in depth. However, among these, only two tows (3% of total) were at depths <80 m (50 and 51 m), and only 12 tows (19%) were at depths <100 m.

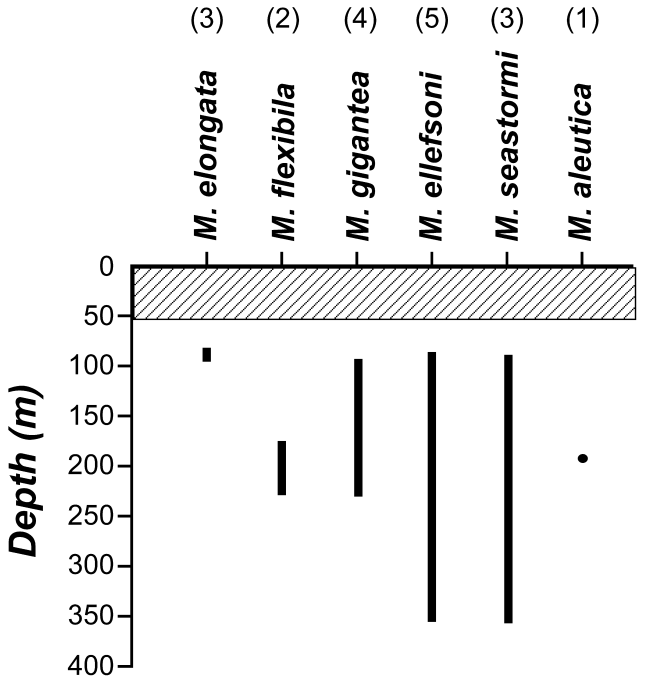


**Fig. 10.** Depth distributions of Aleutian *Monoporella* species inferred from available sampling data. Number in parentheses above each species name indicates the number of stations at which the species was detected. Hatched area indicates that no sampling was conducted between 0 and 50 m depth.

Thus, the distributions of *Monoporella* species were inadequately surveyed at depths of 50–100 m, and not at all at depths <50 m. Similar considerations apply to the specimens obtained in 2006. *Monoporella* species have been detected at depths <50 m in other parts of the world: '*M. nodulifera*' from New Zealand from as shallow as approximately 20 m (Gordon, 1984); '*M. nodulifera*' from the Mediterranean from as shallow as 3–15 m (Hayward, 1974); and *M. fimbriata* from 4–5 m depth in Port Vila Harbor, Efate, Vanuatu (Tilbrook *et al.*, 2001; Tilbrook, 2006).

The Aleutian species of *Monoporella* have large zooids compared to many previously recorded specimens (which include several undescribed species; see Introduction). Zooid lengths for nominal *Monoporella* species reported in the literature include 0.90 mm (maximum, *M. nodulifera* holotype; Tilbrook, 2006); 0.90 mm (maximum, *M. fimbriata*; Tilbrook, 2006); 0.85 mm (mean, '*M. nodulifera*'; Hayward, 1974); 0.90 mm (maximum, *M. fimbriata*; Canu and Bassler, 1929); and 0.75 mm (maximum, '*M. nodulifera*'; Gordon, 1984) (also see Table 2). The Aleutian species have mean zooid lengths ranging from 1.09 to 1.60 mm, with maximum lengths ranging from 1.36 to 2.00 mm.

The large size of the zooids may be related to depth. Tilbrook (2006: pp. 68–69) noted that an undescribed new species from "deep water, Japan" (NHM 1928.9.13.74) had "the largest zooids and orifices of all specimens [he] examined", and Canu and Bassler (1929) reported a zooid length of 1.25 mm for *M. tenuimargo* described from a depth of 340 fathoms (622 m) in the Philippines. Large zooid size in deep-water species relative to other members of a clade may be related to the consistently cold temperatures in deep water. Late-summer (July to early August) bottom temperatures at the Aleutian stations where species of *Monoporella* occurred ranged from 4.0–5.1°C. In evolutionary terms, a correlation between consistently cold water temperatures in a species' habitat (and/or range) and large zooid size could be related to the ecophenotypic response by which cheilostome bryozoan species in general produce larger zooids at colder temperatures (O'Dea and Okamura, 1999, 2000).

The four exclusively encrusting species all appear to be slow reproducers. Ovicells were not seen in young, relatively small colonies 1–2 cm in extent (depending on zooid size), and they are uncommon in larger colonies, which rarely have more than two or three ovicells per colony. The highest ovicell density observed among the encrusting species was a colony of *M. seastormi* 4.5×2 cm in extent with 13 ovicells. Curiously, no ovicells at all were observed for *M. flexibila*. In contrast, all the folded-erect colonies of *M. elongata* examined have high densities of ovicells in parts of the colonies; the largest specimen (4×6×9 cm) has at least 50 ovicells.

Reproduction may be energetically costly in species of *Monoporella*, in which each ovicell involves the four zooids in a brooding complex, with significant external morphological modifications to three of these zooids. However, this cost may be somewhat offset by multiple brooding; A. Ostrovsky (personal communication) observed three embryos in a single ovicell of '*M. nodulifera*' from Chios, Greece, the same material examined by Ostrovsky and Tayor (2005).

**Apparent high diversity of Aleutian *Monoporella* species**

*Monoporella* appears to be more speciose in the Aleutians than anywhere else. While the sampling effort in the Aleutians has been considerable, certainly no more material was examined in this study than has been examined in deep-water collections from some other parts of the world. Gordon's (1984) study of bryozoans from the Kermadec Ridge, New Zealand, incorporating specimens from 57 stations at depths of 10–1,156 m, detected only one species of *Monoporella*. Canu and Bassler (1929) examined material from 52 stations mostly from the vicinity of the Philippines, ranging in depth from 19–1,181 fathoms (35–2,160 m); they reported only two nominal species of *Monoporella* (a third species, *M. waipukurensis*, belongs in another family, perhaps Pacificincolidae). For *Monoporella fimbriata*, they described two new varieties, one of which Tilbrook (2006) raised to species rank as *M. crassa*. If the other variety, *M. fimbriata* var. *carinifera*, also represents a distinct species, there is evidence for as many as five species occurring in the Philippine region, including Scholz's (1991) report of an ancestrula with a tessellated cryptocyst. As far as I can determine, this is the highest previous estimate of species diversity of *Monoporella* from any part of the world (also see Tilbrook, 2006). At least three species of *Monoporella* occur around Japan, which, however, is about 3,000 km long and extends from the cold-temperate (~45°N) to the subtropical (~25°N) zones. These species include putative *M. elongata* (see Remarks for that species); another species that Tilbrook (2006) discussed as similar to *M. nodulifera*; and *Monoporella* sp. 1 from Okinawa illustrated by Ostrovsky and Taylor (2005).

It is possible that the apparent high species diversity of

*Monoporella* in the western Aleutians is an artifact, simply reflecting presently high diversity all across the North Pacific Rim that has gone undetected outside the Aleutians due to insufficient sampling. However, if *Monoporella* species were as diverse and occurred as abundantly in adjacent regions as in the Aleutians, one might expect better representation in previous collections. Despite considerable taxonomic work in the northeastern Pacific (e.g., Osburn, 1950 and references therein; Soule *et al*., 1995) that has included examination of some deep-water samples, there is only one previous report of a *Monoporella* species from Alaska (Canu's unpublished Alaskan record of *M. elongata* described herein) and no records from British Columbia to California. Likewise, despite considerable taxonomic effort in the northwestern Pacific and Bering Sea (e.g., Ortmann, 1890; Kluge, 1975; Grischenko, 2002), there are reports of only three Recent *Monoporella* species from the entire 3,000-km length of Japan, and no records from the northwestern Pacific north of Japan, the Sea of Okhotsk, or the Bering Sea. Nonetheless, that the apparently high Aleutian diversity is a sampling artifact cannot be ruled out, for in fact very little intensive sampling of bryozoans in the deep shelf zone has been conducted around the North Pacific rim.

**Hypotheses to explain the apparent high species diversity of *Monoporella* in the western Aleutians**

I will consider in turn two hypotheses to explain the apparent pattern of relatively high species diversity of *Monoporella* in the western Aleutians, compared to other parts of the world, if this pattern is not an artifact; for convenience, these are referred to here as the 'relict' and 'local-radiation' hypotheses. This discussion is couched in terms of the western Aleutians, though it might apply to a greater extent of the archipelago. Implicit in these hypotheses is that gene flow is restricted between populations of cheilostome bryozoans inhabiting the shelf zone of the western Aleutians and populations inhabiting other parts of the North Pacific Rim, so I will first briefly address cheilostome dispersal ability and potential barriers to gene flow.

*Monoporella*, like virtually all other neocheilostome bryozoans, is undoubtedly a poor disperser. In general, neocheilostome larvae settle within a few minutes to a few hours after release from the brood chamber, and at best have a dispersal range of a few kilometers. In modern populations, this poor dispersal ability has been observed to result in signification population divergences even in disjunct populations that are a few kilometers apart but not separated by any barrier to gene flow other than distance (Ryland, 1976; McKinney and Jackson, 1989).

Potential barriers to cheilostome gene flow, both bounding and within the Aleutian Archipelago, involve considerably more than the separation of populations by a few kilometers. Along its length, the Aleutian archipelago is bounded to the north by the broad Bering Sea Basin (3,000 m deep), and to the south by the Aleutian trench (7,000 m deep) and the entire Pacific Ocean beyond. To the west, Near Strait between Stalemate Bank west of Attu Island and the Commander Island shelf on the Asian side is not so wide (190 km), but this strait reaches a depth of 2,000 m. With respect to western-Aleutian shelf-dwelling cheilostome populations, which have poorly dispersing larvae and presumably limited depth ranges, any genetic exchange with external populations likely traverses the length of the archipelago from the direction of the Alaskan mainland. Even along the archipelago, there are potential barriers. For example, there are three passes ≥430 m in depth between Aleutian island groups (Lindroth, 1963; Hunt and Stabeno, 2005) that might restrict larval dispersal, depending on the depth range of a species. Amchitka Pass, the boundary between the central and Western Aleutians, is both moderately broad (95 km) and exceptionally deep (1,155 m).

*Relict hypothesis*

This hypothesis postulates that the western Aleutians represent a refugium in which high present-day species diversity of *Monoporella* remains as a relict of historically higher-than-present diversity of the genus all across the North Pacific-rim region. Implicit in this hypothesis is that cheilostome populations in the western Aleutians have remained relatively insulated from immigration and emigration for a considerable period, and that some aspect of the environment in the western Aleutians has remained stable relative to the rest of the North Pacific region, maintaining *Monoporella* diversity there but not elsewhere. It is unclear how a western-Aleutian refugium, if it exists, originated or has been maintained. The relict hypothesis will be supported if further sampling on modern shelves to the east and west of the Aleutians fails to detect high species diversities of *Monoporella*, and yet comparably high diversities, including some of the same species as in the Aleutians, are found in Neogene fossil deposits in the North Pacific region.

Some relevant paleontological data exist, though not enough to be conclusive. Several authors have reported nominal *M. fimbriata* from Miocene to Pleistocene deposits in Japan (reviewed by Sakagami *et al*., 1980); possibly more than one species is involved. In addition, Kataoka (1961) described a new species, *M. sulcoecia*, from a Pleistocene deposit in southern Japan. Finally, an unidentified encrusting species of *Monoporella* occurs in the Pleistocene Upper Setana Formation at Kuromatsunai, Hokkaido, Japan (M. Dick, unpublished data). This species lacks spines and a well-developed median crest, and has moderately large zooids (average length, 1.12 mm; n=15), and thus appears to be related to the Aleutian encrusting species.

*Local-radiation hypothesis*

This hypothesis postulates that *Monoporella* underwent a local radiation in the Aleutians. By 'local radiation,' I mean a relatively high level of speciation within a clade in a particular region, compared to that clade in other regions. I purposely avoid the term 'adaptive radiation', which was defined by Schluter (2000: p. 10) as "the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage … the differentiation of a single ancestor into an array of species that inhabit a variety of environments and that differ in the morphological and physiological traits used to exploit those environments." The Aleutian *Monoporella*s did not all arise from a single founding ancestor (see below). Furthermore, it is not clear that the speciation leading to the four encrusting species was accompanied by significant ecological differentiation (that is, was adaptive), as some of the species co-occur side-by-side on the same substrata at

the same depths.

Solid evidence for an Aleutian radiation of *Monoporella* must ultimately come from global taxonomic, zoogeographic, phylogenetic, and phylogeographic analyses of the group. However, two arguments indirectly support this hypothesis. The first is that the Aleutian *Monoporella* species appear to show phylogenetically shallow diversity. They clearly fall into two distinct groups. One group comprises *M. elongata* and *M. flexibila*, both of which lack oral spines and have erect growth forms, a tesselated cryptocyst, and elongate zooids. The other group comprises the four exclusively encrusting species, which are all very similar in autozooidal morphology. The existence of the two species groups suggests that the Aleutian *Monoporella*s could have diversified from as few as two ancestral species, each giving rise to one of the groups.

The shortest cladogram from a maximum-parsimony analysis of six morphological characters and conducted with PAUP* (Swofford, 2000) is shown in Fig. 11. The cladogram includes the six Aleutian species, as well as three previously described species of *Monoporella* for which sufficient information was available in the literature. The tree is unrooted, as the outgroup appropriate for *Monoporella* was unclear, but is displayed so that the three species from other parts of the world form the outgroup to the Aleutian species. There are problems with this analysis that make it unreliable as a global phylogenetic hypothesis. For example, it is not absolutely certain from the literature that *M. fimbriata* and *M*. sp. (Chios) have a pitted operculum (see footnote to Table 2). In addition, increased zooid length, loss of distal spines, and reduction of an autozooidal (AZ) to a kenozooidal (KZ) ooecium-forming zooid seem to be character states that could easily arise convergently. Nonetheless, the cladogram does show the character-state changes that could have occurred in the evolution of the four encrusting species of *Monoporella* in the Aleutians from an ancestral species having the suite of characters, implicitly treated as plesiomorphic in the cladogram, that are common to the three previously described species.

The cladogram also shows the two erect species with a tessellated cryptocyst (*M. flexibila*+*M. elongata*) embedded within a clade containing encrusting species with a granulated cryptoctyst. It is quite plausible that the erect forms are related to one another and comprise a clade embedded within a paraphyletic clade containing encrusting *Monoporella* species. However, the sister-group relationship between the erect species and the *M. ellefsoni*-*M. aleutica* clade, based only on the absence of distal spines, is probably artifactual. There is an intriguing record of a species of *Monoporella* having a tessellated cryptocyst (dubiously identified as *M. nodulifera* and reported only as an ancestrula) from the Philippines (Scholz, 1991). This strongly suggests that the clade represented by *M. flexibila*+*M. elongata* did not originate in the Aleutians, but probably elsewhere and perhaps

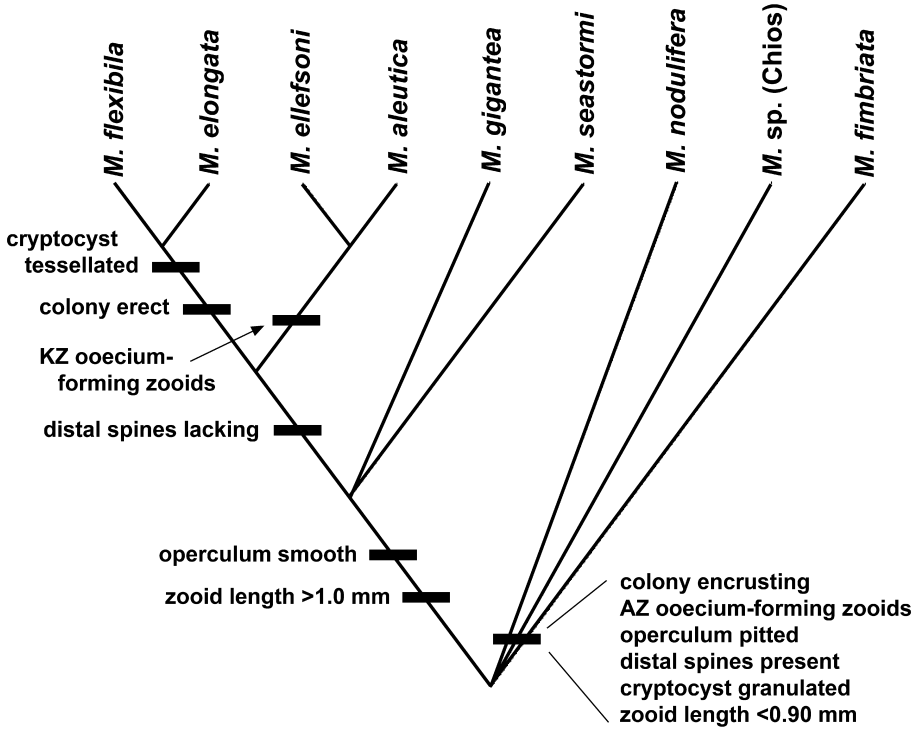


**Fig. 11.** Shortest cladogram showing the relationships among the six Aleutian *Monoporella* species and three species from other parts of the world. This unrooted maximum-parsimony tree, inferred from six morphological characters and generated by PAUP*, is six steps long. The tree is displayed so that the non-Aleutian species (three to the right) form the outgroup to the Aleutian species (six to the left). The six characters involved are indicated in the list (lower right) of character states common to the three non-Aleutian species. Changes in these character states are indicated by the six horizontal bars leading to and within the group of Aleutian species. Autapomorphic characters, such as the nodules lateral to the orifice in *M. nodulifera*, were not included in the analysis. See Discussion for further details.

early on in the *Monoporella* lineage.

The second argument is that isolated island archipelagos are well known for local radiations; an example from marine bryozoans is the putative radiation of *Parasmittina* in the Hawaiian Archipelago (Soule and Soule, 1973). The Aleutian Archipelago, which is older than the Hawaiian Archipelago (Ziegler, 2002), originated in the middle Tertiary (Eocene-Oligocene) Period, and its Neogene history involved significant volcanic activity, episodes of extensive glaciation, and several cycles of sea-level change (Gates *et al*., 1954; Thorson and Hamilton, 1986). Hunt and Stabeno (2005: p. 300) noted that at present there is "significant spatial variation in the physical and biological properties of marine ecosystems along the Aleutian Archipelago" and described this variation in considerable detail. Environmental variation along the 1,700 km extent of the Aleutian Archipelago throughout the Neogene, similar to that occurring today, coupled with restrictions to gene flow between populations by distance or by geographical barriers (e.g., deep sea passes, zones of unsuitable habitat, or strong currents between islands or island groups) could well have driven a radiation of *Monoporella* species, adaptive or otherwise.

The results of Vermeij and Palmer (1990), who analyzed the distributions of 109 species of shallow-water, shell-bearing molluscs across the Aleutian-Commander arc, are relevant to this discussion. These authors found no molluscan species endemic to the Aleutians; that is, they found no species in the Aleutians that did not also occur on either the Alaskan or the Asian mainland. Of the species they examined, 71% were distributed across the North Pacific from mainland Alaska to mainland Asia; 23% were eastern-Pacific species with the western limit of their range in the Aleutians; and 5.5% were Asian species with the eastern limit of their range in the Aleutians. These results mean that, for 28.5% of the species examined, some part of the Aleutians constituted a barrier to eastward or westward dispersal. Interestingly, Vermeij and Palmer found that the dispersal barriers between Aleutian islands were nearly as effective for gastropod species dispersing planktonically as for those lacking a planktonic dispersal stage. The lack of Aleutian endemic shallow-water molluscs appears to weaken the case for a local radiation of *Monoporella.* On the other hand, the molluscan results also demonstrate that apparently strong dispersal barriers are rather common along the Aleutian chain, a necessary condition for the local-radiation hypothesis. Vermeij and Palmer (1990: p. 352) note that these barriers "have been more or less effective for millions of years", indicated by the many eastern-Pacific genera, many extending back to the Oligocene, that lack fossil or living representatives on the Asian side.

Unfortunately, no analysis of the deep-water molluscs, which would be more relevant to *Monoporella*, has been done parallel to that for the shallow-water species in the Aleutians. The dispersal dynamics of deep-water species may be quite different; for example, depth-restricted deep-water species may be much less prone to long-distance dispersal by rafting (attached to floating logs, pumice, seaweeds, etc.) than species inhabiting intertidal and shallow-subtidal habitats. Thus there could be a significant number of Aleutian endemics in deep water. Supporting this contention is another group of benthic marine invertebrates that tends to occur in deeper water (most abundant from 100–200 m depth) (Stone, 2006) and that shows relatively high diversity analogous to that of *Monoporella* in the Aleutians. The species diversity of a diverse assemblage of skeleton-forming benthic cnidarians (the so-called "cold-water corals," including stylasterines, gorgonaceans, stoloniferans, pennatulaceans, alcyonaceans, and scleractinians) increases sharply west of Samalga pass (~169°W) (Heifetz *et al*., 2005). Several of these taxa have apparently undergone high levels of speciation in the Aleutians, resulting in a high number of endemics (Heifetz *et al*., 2005).

My study included specimens from stations covering a little less than half (~800 km) the length of the Aleutian archipelago. Examination of collections from the western central Aleutians to the eastern end of the Archipelago may well detect additional species of *Monoporella*. Molecular-genetic and paleontological studies, and additional sampling in the deep-water shelf zone around the Pacific rim, will be necessary to determine whether the species diversity of *Monoporella* actually is exceptionally high in the Aleutians, and if so, which hypothesis correctly explains this high diversity.

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