

A setigerous collar in *Membranipora chesapeakensis* n. sp. (Bryozoa): implications for the evolution of cheilostomes from ctenostomes

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Abstract. *Membranipora chesapeakensis* n. sp. was collected on wood substrate in the Chesapeake Bay, Maryland. Colonies are erect, vermiform or ribbon-shaped to bilaminar, with two back-to-back layers sharing one basal cuticle. There is a minute cryptocyst and a beaded gymnocyst; zoids have 14 tentacles and lack knobs or other decorations in their corners. Closest affinities are with *M. tenuis* Desor, *sensu lato*. A setigerous collar is present, the first reported among membraniporid cheilostomes. Membraniporids are morphologically similar to the earliest fossil cheilostomes and to the encrusting ctenostomes from which most cheilostomes are thought to have evolved. A setigerous collar, probably generally present in ctenostomes, has hitherto been found only in two aberrant cheilostome genera. The presence of a setigerous collar in a species of *Membranipora* suggests that setigerous collars may also have been present in early cheilostomes and therefore supports the hypothesis that most or all cheilostomes evolved from ctenostomes.

Additional key words: Ectoprocta, Polyzoa, Cheilostomata, Ctenostomata, Membraniporidae, Chesapeake, Maryland

The “setigerous collar,” or “pleated collar,” is an acellular secretion present in some bryozoan taxa. In retracted zoids* the collar projects distally from the diaphragm into the vestibule. When the lophophore is extended, the collar projects from the neck of the autozoid like the starch-stiffened formal collars popular in Elizabethan England. We know of no published suggestion as to its function. Setigerous collars have been found to be present in all ctenostome bryozoans in which they have been sought. However, they are known from only two cheilostome genera, *Aetea* and *Scruparia*. The collar of *Aetea* is only a short ring of teeth; *Scruparia* has a relatively short vestibule and proportionally diminished collar. Both genera have erect colonies and are regarded as aberrant cheilostomes (Prenant & Bobin 1966, pp. 78, 94; Jebram 1992). Although they did not rule out convergent evolution of the collar, these authors consider these genera outside the main line of cheilostome evolution and possibly indicative of a polyphyletic origin of cheilostomes. Furthermore, both *Aetea* and *Scruparia* brood

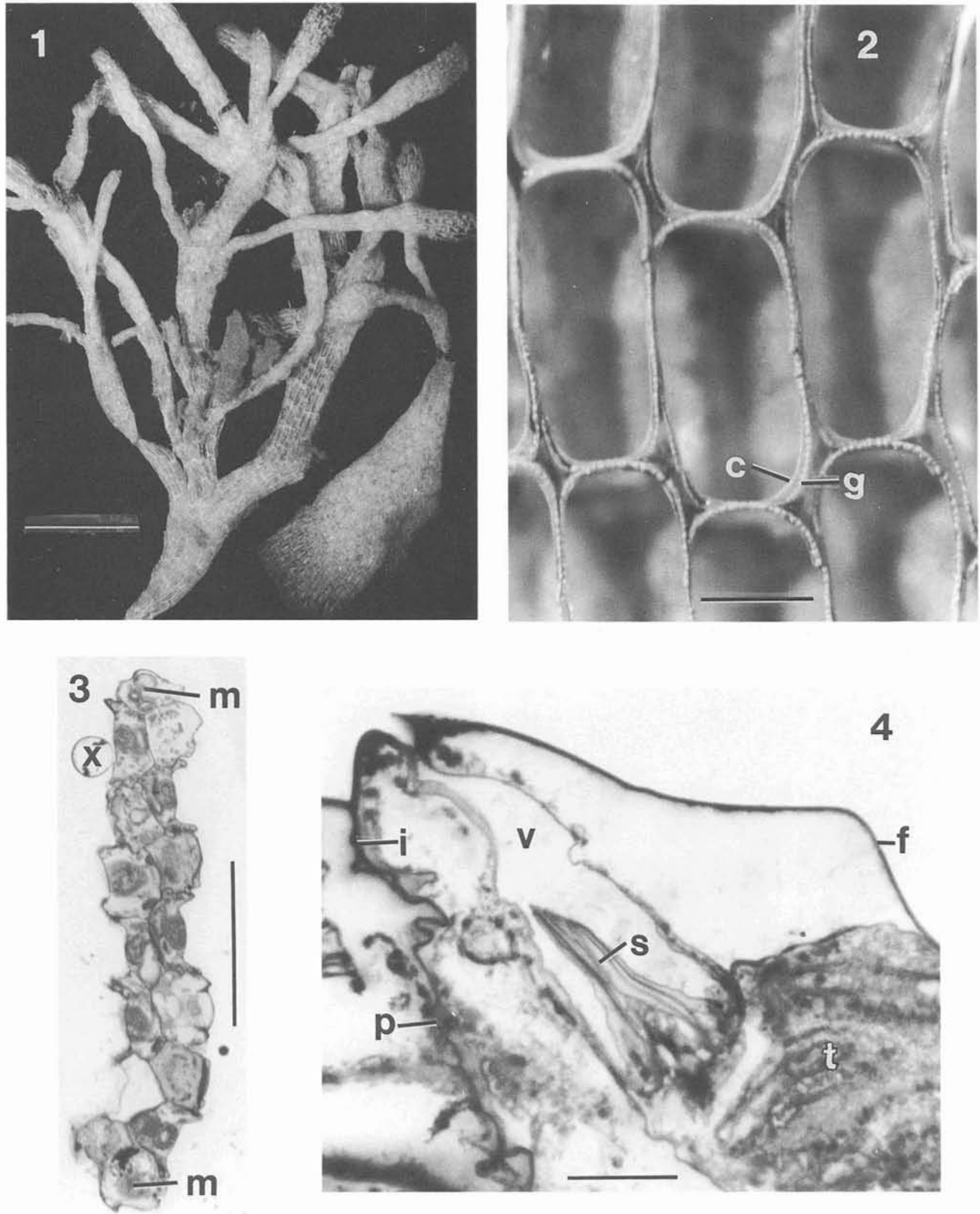
lecithotrophic larvae in specialized organs. Primitive cheilostomes are thought to have possessed planktotrophic cyphonautes larvae because cyphonautes occur among both cheilostomes and ctenostomes (Reed 1991, p. 176), because no brooding has been observed among the earliest fossil cheilostomes (Taylor 1988), and because those early cheilostomes resemble species of *Electra*, *Membranipora*, and *Conopeum*; all of these genera possess at least some members with cyphonautes larvae (Reed 1991, p. 176).

This paper reports the discovery of new species of *Membranipora* with a well-developed setigerous collar. As *Membranipora* holds an undisputed position near the base of the main line of cheilostome evolution, this discovery supports the hypothesis that most or all cheilostomes evolved from a ctenostome ancestor with a setigerous collar (e.g., Banta 1975; Taylor 1988; Jebram 1992).

Methods

Colonies were fixed and stored in 70% ethanol. Some material was stained overnight in alum cochineal, dehydrated through an ethanol series to propylene glycol and vacuum-embedded in Epotuf resin for thin-ground sections containing calcareous tissues in place next to soft tissues (Nye et al. 1972). Other alum cochineal-stained material was glycerinated by placing

* The more common spelling of this word, *zooid*, used by Huxley (1851, p. 579), can be roughly translated “animal-like (thing).” We prefer the shorter alternative spelling *zoid*, derived from “Bryozoid,” (Reichert 1870, p. 248), roughly translated from latinized German, as a “(thing) derived from an animal.”



Figs. 1–4. *Membranipora chesapeakeensis* n. sp. **Fig. 1.** Holotype colony photographed wet in 70% ethanol. Scale bar, 4.0 mm. **Fig. 2.** Paratype. NaOCl-treated autozooids stained in congo red and coated in ammonium chloride; distal at top. Beaded gymnocyst (g); narrow, unadorned cryptocyst (c). Scale bar, 200 μ m. **Fig. 3.** Paratype, Transverse epotuf section of a

specimens in dilute glycerine and allowing the solution to evaporate in a petri dish for several days, then mounted in glycerine jelly. Slides were then ringed in nail polish. Colonies soaked overnight in NaOCl to remove all organic material disintegrated into fragments, which were dyed with 1% aqueous congo red and coated with sublimed ammonium chloride for light photomacrography (Kier et al. 1965).

Taxonomic Account

Family Membraniporidae Busk 1854

Membranipora deBlainville 1830

Membranipora chesapeakeensis new species

Type specimens. Holotype, Smithsonian Institution, U.S. National Museum of Natural History, bryozoan Type USNM 15223, preserved in 70% ethanol, Fig. 1), is a 0.1 g fragment of a mass of paratype USNM 15224 weighing 12.3 g, preserved in 70% ethanol. Paratype specimen USNM 15225 is a dry slide from the same sample. Small colony fragments of paratype, labeled "Specimen 21," are deposited in the invertebrate reference collection at the Smithsonian Environmental Research Center, Edgewater, Maryland; a small amount of paratype, including sectioned material, is retained in the senior author's collection.

Type locality. A 12.4 g mass, from which holotype and paratype specimens were selected, was growing on a small tree taken by otter trawl at 4–6 m from a mud bottom at the mouth of the Rhode River (Maryland) between Cheston Point and Dutchman Point, Chesapeake Bay, in May 1993. Bottom salinity at the time of collection was 4‰. The collector was Timothy C. Steelman of the Smithsonian Environmental Research Center, Edgewater, Maryland.

Diagnosis. Colony tan, erect; branches vermiform, ribbon-shaped, or frondose. Brackish water. Autozooids rectangular, monomorphic, arranged in quincunx, lightly calcified. Cryptocyst narrow and smooth; gymnocyst narrow and finely beaded. No spines, stolons, ovicells, or avicularia; 14 tentacles. A setigerous collar fills most of the vestibule.

Description. Preserved colonies are tan and erect, intermixed with muddy tubes of an errant polychaete, identified tentatively as *Hedista diversicolor*. Each colony branch originates from the distolateral margin of a flattened bilaminar frond as a vermiform cylinder of

four or more zoid rows (Fig. 1). The vermiform portion gradually expands laterally as it elongates, adding new zoid rows and widening gradually into a bilaminar ribbon or elongate frond with 20 or more rows of monomorphic zoids on a side. Sections demonstrate that the lateral colony margins are also occupied by ordinary autozooids (Fig. 3); we saw no specialized kenozooids or other heterozooids. There are no stolons or other obvious provisions for attachment; the erect colony parts presumably grew from an encrusting base that has become lost or obscured. Colonies are lightly calcified and disintegrate into groups of a few zoids when treated in NaOCl.

Autozooids are rectangular, arranged in quincunx, lightly calcified. The basal wall of each autozoid is adherent to that of one or more zoids on the opposite side of the colony. Sections demonstrate that the basal cuticle is shared (Fig. 4); we found no evidence of foreign material or visible line of demarcation in the basal cuticle. Inspection of the growing tip of the colony confirms that the basal wall of each zoid develops simultaneously with its basally opposite partner. This indicates that the basal wall is developmentally and morphologically shared and implies developmental coordination between the zoids on opposite sides of the colony; it cannot be a case of one colony growing haphazardly on the back of another erect frond.

Zoids on opposite sides of the colony are offset so that the lateral wall separating two zoids on one face runs beneath the midline of a row of zoids on the opposite face (Fig. 3). The basal two-thirds of each transverse wall is a simple calcareous partition perforated by communication pores; each pore is occupied by a refractile cincture and at least two specialized cells that send lobes through the cincture from the proximal to the distal side of the pore (Fig. 4, p). These cells are herein named "bobin cells" after their discoverer, the late Dr. Geneviève Bobin. The frontal third of each transverse wall resembles a lateral wall: a layer of cuticle continuous with the frontal membrane of the distal zoid and the vestibular floor of the proximal zoid is sandwiched between two calcified layers (Fig. 4, i). This doubled wall apparently results from incorporation of intercalary cuticle into the transverse wall as the wall grows vertically from the original, simple, anterior transverse wall. Lateral walls of each autozoid are provided with up to four pore plates 25–50 μm in

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frondose branch containing 16 zoids, showing the relative positions of zoids and apparently unmodified marginal autozooids (m). The circle (x) is a grinding artifact. Scale bar, 500 μm . **Fig. 4.** Paratype. Median sagittal thin-ground epotuf section to show the setigerous collar. Frontal membrane (f); intercalary cuticle (i); communication pores (p) with bobin cells; setigerous collar (s); tentacles (t); vestibule (v). Scale bar, 50 μm .

diameter, each with 1 or 2 communication pores and bobin cells. Lateral septulae lack evident proximo-lateral polarity, so that the annular side of lateral septulae may occur at either end of the zoid, seemingly at random.

There is a delicately beaded, narrow gymnocyst, widest in zoidal corners, and a minute, smooth cryptocyst, almost hidden beneath the gymnocyst (Fig. 2). Corners of zoids are simple, without knobs or kenozoids. There are no spines, ovicells, or avicularia; the polypide has 14 tentacles. A setigerous collar is present, occupying most of the retracted vestibule. Numerous sperms in various stages of development were found laterally and proximally in the perigastric cavity of all but a few zoids. A few small oocytes were seen in two zoids; we saw no obvious intertentacular organ. No ancestrulae were found.

Measurements. Measurements are given in micrometers (μm) as mean \pm 1 standard deviation (minimum–maximum): autozoid length ($n = 45$) 604 ± 87 (494–798); autozoid width ($n = 45$) 212 ± 24 (152–266); operculum length ($n = 30$), 104 ± 16 (64–144); operculum width ($n = 30$) 85 ± 9 (72–104).

Discussion

Generic assignment

Horowitz (1992) lists 252 Recent species names attributed to the genus *Membranipora*; of these, 118 species are currently accepted under the modern interpretation of the genus. If fossils are included, there are “more than 600 described species,” (Bassler 1953, p. G155).

The type species of *Membranipora*, *Flustra membranacea* (Linnaeus 1758), encrusts algae in unilaminar sheets. Partly frondose, erect bilaminar colonies are formed in many cheilostome genera, including some species of *Membranipora* and species of the closely-related genus *Conopeum* (see, for example, Prenant & Bobin 1966, pp. 118, 127). In some cases, one layer grows on back of the other, resulting in a frond with little or no morphological coordination between the two layers; the layers may even incorporate members of separate species (Nielsen 1981, p. 93). In *Membranipora chesapeakeensis* the erect form has progressed beyond this low level of colonial integration by synchronizing the budding of the two layers at the growing tip. The result is the fusion of the basal cuticle of the two sides and the morphological correspondence between the zoids comprising the two layers.

Coordinated development of zoids to form a bifoliate colony implies major changes in the selective pressures operating on the colony (McKinney & Jackson 1989, p. 55). The ability to form well-coordinated

erect bilaminar colonies may be a plausible criterion for separating bilaminar species of *Membranipora* into the genus *Acanthodesia* Canu & Bassler (1920, p. 99); the type species of *Acanthodesia* is *Flustra savartii* (Audouin 1826, p. 240), a widely-distributed warm-water species that frequently forms bilaminar colonies. Viewed in this light, *M. chesapeakeensis* would probably belong in *Acanthodesia*. Although virtually all modern authors follow Osburn (1950, p. 19) in synonymizing *Acanthodesia* with *Membranipora* on the grounds that morphological intermediates are common between *A. savartii* and various species of *Membranipora*, only zoidal morphology is intermediate, not colony form. In species of *Acanthodesia*, including *A. savartii*, zoids possess a broad, heavily-calcified cryptocyst, whereas in species of *Membranipora*, including *M. membranacea* and *M. chesapeakeensis* n. sp., zoids are lightly calcified and have a narrow cryptocyst. We retain *M. chesapeakeensis* in *Membranipora* because it is unclear how many times the erect habit has evolved among membraniporines and because its zoidal morphology is so different from that of *A. savartii*.

Similar species

Specimens usually identified as *Acanthodesia tenuis* or *Membranipora tenuis* (Desor 1848) from the Chesapeake Bay have autozoids similar to those of *Membranipora chesapeakeensis*, but zoids of *M. tenuis* possess occasional tubercles or knobs in the zoecial corners and form unilaminar encrusting colonies that may rise into broad bilaminar frills (Osburn 1944, p. 35). Osburn's (1912, p. 231) topotype specimens of *M. tenuis* from Massachusetts are similar to his encrusting Chesapeake specimens, but possess a more extensive cryptocyst. Prenant & Bobin (1966, p. 120) and others embraced a broad concept of *M. tenuis*, synonymizing at least six nominal species under this name, including some bilaminar specimens with heavily calcified zoecia and extensive, dentate cryptocysts. Under this concept, the range is euryhaline, eurybathic, virtually circumglobal in temperate to tropical latitudes, and extremely variable in zoecial and colony form. The concept of Cook (1968, p. 118, 127), based largely on west African material, was restricted to encrusting specimens with small to moderate cryptocysts and well-developed cryptocystal denticles. The concept of *M. tenuis* on the east coast of N. America has been encrusting, euryhaline, typically with broad cryptocysts, but sometimes with narrow ones (Osburn 1940, p. 353; Maturo 1957, p. 36). Zoids of *M. tenuis* from North Carolina possess “about 10” tentacles (Maturo 1957, p. 36). It is likely that several variable species

are confused under the name *M. tenuis*, but even under the broadest interpretation of this species, there is no described material with the combination of features that characterize *M. chesapeakeensis*: delicate bilaminar colonies, lightly calcified zoecium with a narrow, beaded gymnocyst and an even narrower, unadorned cryptocyst, no corner knobs, 14 tentacles, and a brackish water habitat. The beaded gymnocyst is an unusual feature; the cryptocyst often is reported as beaded, but to our knowledge, never the gymnocyst. Most species of *Membranipora* are too poorly known to record the presence or absence of setigerous collars, although they are known to be absent in *M. membranacea* (see Lutaud 1961).

M. chesapeakeensis is probably identical to specimens examined by Dudley (1973, p. 282) and attributed by her to an undescribed species of *Membranipora*. She believed her material to be identical to at least some of the specimens identified by Osburn (1944) as *M. membranacea* (Linnaeus 1758). Her specimens, from the mouths of the James and Potomac Rivers in the Chesapeake Bay were from estuarine waters; the colonies were sometimes erect, and the zooids bore "13 to 14 rather stiffly-held tentacles." Zooids of her specimens were slightly smaller than ours (mean zoidal length 515 μm , width 193 μm).

Setigerous collar

Although no function for a setigerous collar is known, its widespread presence throughout ctenostome taxa suggests that it is preserved there by natural selection. Its apparent absence among higher cheilostomes suggests that some change took place early in cheilostome evolution which involved the function of the setigerous collar. However, cheilostomes are seldom sectioned and setigerous collars are sometimes difficult to see and recognize, so it is possible that collars are present in other cheilostome taxa, but have been overlooked.

Membranipora is widely recognized as a relatively primitive cheilostome genus in that its members possess: an extensive frontal membrane without extensive frontal wall development, a simple operculum similar to that of some ctenostomes, a planktotrophic bivalved cyphonautes larva developed after eggs or zygotes were released into the water, no avicularia or ovicells, a regular quincunxal budding pattern similar to that of most higher cheilostomes and readily derived from that of early fossil cheilostomes and some Recent and fossil ctenostomes (Banta 1975; Cheetham & Cook 1983; Taylor 1988).

The finding of a setigerous collar in a species of *Membranipora* indicates that collars are more wide-

spread among cheilostomes than previously believed and that, since *Membranipora* is at least morphologically similar to early fossil cheilostomes, *Aetea* and *Scruparia* may not be so aberrant in this regard.

Reproduction

The species of *Membranipora* that have been adequately studied release unfertilized eggs or zygotes into the water through an extension of the female gonopore, called the intertentacular organ. The zygote develops into a bivalved planktotrophic larva, the cyphonautes, which eventually settles to form a twinned ancestrula, the first pair of autozooids in a new colony. We found no indication of an intertentacular organ in *Membranipora chesapeakeensis*, but because nearly all the zooids examined were males with functional testes, because the intertentacular organ is not developed until oogenesis (Hageman 1981), and because it is difficult to see in most preparation of retracted zooids, its apparent absence from our specimens is not surprising. No ovicells were found in our specimens; most cheilostome ovicells are elaborate structures that necessarily develop at or near the time the zooids are budded, rather than at the time of sexual maturity, so their absence from a sizable colony makes it unlikely that ovicells are ever present. We conclude that *M. chesapeakeensis* is a non-brooding protandrous hermaphrodite, probably with a planktotrophic cyphonautes larva.

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