

ANNALS OF BRYOZOLOGY 3



EDITED BY
PATRICK N. WYSE JACKSON &
MARY E. SPENCER JONES



Paper in:

Patrick N. Wyse Jackson & Mary E. Spencer Jones (eds) (2011) *Annals of Bryozoology 3: aspects of the history of research on bryozoans*. International Bryozoology Association, Dublin, pp. viii+225.

Bryozoans of the Northeast Coast of the United States: taxonomic history and summary of a new survey

Judith E. Winston¹ and Peter J. Hayward²

¹Virginia Museum of Natural History, Martinsville, VA 24112, USA

²School of Biological Sciences, University of Wales, Swansea, SA2 8PP, Wales, UK

1. Introduction
2. History of Taxonomic Study of Northeast Coast Bryozoans
3. Northeast Coast Bryozoan Diversity
4. Biogeography
5. Conclusions
6. Acknowledgments

1. Introduction

More than a hundred species of bryozoans occur on the northeast coast of the United States from Maine to Virginia. They are found in habitats ranging from the rocky intertidal coast of the northern Gulf of Maine to the sheltered sandy shorelines of the Chesapeake Bay (Figure 1). Considering that this part of the U.S. was explored and settled very early and that the first marine laboratories were established here in the nineteenth century, we could expect the invertebrate fauna to be well known today. For some groups of macrofauna that is true, but it is not yet the case for bryozoans.

A modern guide to their identification and distribution has been long been lacking; the most recent compilations are 60–100 years old. For this reason the authors began a multiyear survey that included both new collections at previously unsampled sites and study of material in museums and in collections made by other researchers. Most new sampling (about 100 stations) was done intertidally, but a number of subtidal sites in the Gulf of Maine were also surveyed. Additional information and collections were obtained from ecologists working on benthic surveys or other research projects in the study area and by examining museum specimens of bryozoans from the Museum of Comparative Zoology (MCZ), Harvard University, the Gray Museum, Marine Biological Laboratory (now belonging to the Peabody Museum, Yale University), the Virginia Institute of Marine Science, and the National Museum of Natural History.



Figure 1a. Range of NE coast habitats. Bryozoan taxonomy class collecting in the rocky intertidal of the mid-Maine coast.



Figure 1b. Range of NE coast habitats. Sandy protected beach near the mouth of the Chesapeake Bay.



Figure 2. Left. A young Edward Desor (Harvard University Archives) Right. Desor's descriptions were not illustrated. This 1909 watercolor study of *Bugula turrita* was done by an AMNH artist for an exhibit of the time.

Here we trace the history of bryozoan taxonomic research in the region and summarize the results of our recently completed survey.

2. History of Taxonomic Study of Northeast Coast Bryozoans

The earliest bryozoan records for the northeastern U.S. coast are those of Edward Desor (1848) (Figure 2). Pierre Jean Edouard Desor (1811–1881) was a Swiss geologist and naturalist, born at Friedrichsdorf, Germany. In 1837, he met Agassiz at a meeting of naturalists in Neuchâtel, Switzerland and began collaborating with him. He followed Agassiz to the United States in 1847 and worked briefly as one of his assistants and as an assistant for the U.S. Coast Survey until he and Agassiz had a major falling out (Lurie 1966). In 1852, he returned to Neuchâtel where he was professor of geology for the duration of his career (Obit. 1882).

At the October 18th meeting of the Boston Society of Natural History, “Mr. Desor gave an account of his recent zoological investigations among the shoals of Nantucket, whilst on board the (U.S. Coast) surveying steamer *Bibb*; Capt. Davis having afforded him every opportunity for dredging in depths varying from three to twenty-five fathoms” (Desor 1848, p. 65). He recorded 20 species of hydroids, echinoderms, sponges, and bryozoans. Of the five species of bryozoans he described, two of the three he described as new species,

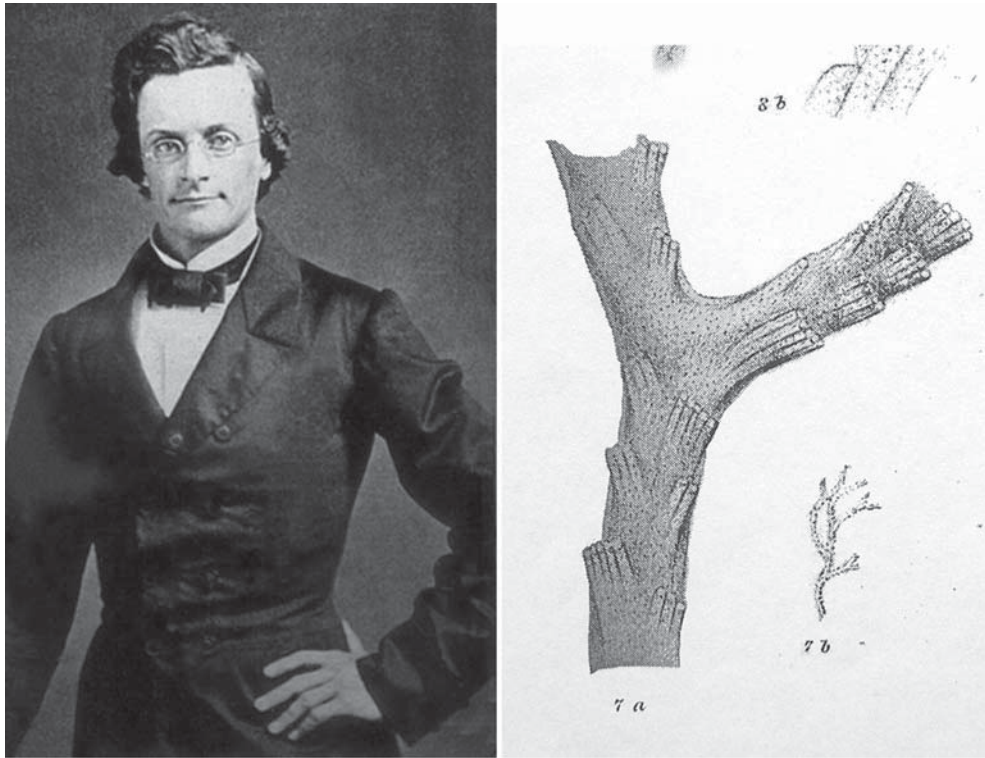


Figure 3. Left. William Stimpson (Smithsonian Archives). Right. *Exidmonea pruinosa* from Stimpson (1853).

Cellularia (now *Bugula*) *turrata* and *Membranipora tenuis*, are still among the most common species found in the central part of the study area today. The third “new” species, his *Cellularia densa*, was later identified by Osburn (1912), as *Tricellularia ternata* (Solander, 1786). The collections of the Boston Society of Natural History, in which Desor deposited his specimens, were scattered when the Society was disbanded in 1946 (Johnson 2004), and the bryozoans appear to have been lost.

William Stimpson (1832–1872) studied with Agassiz at Harvard University in 1850. In 1852, he took a position at the recently started Smithsonian Institution in Washington, D.C (Figure 3). In 1866 when Stimpson was appointed director of the Chicago Academy of Sciences, he borrowed most of the Smithsonian’s invertebrate collections to use at the academy. The collections and his research notes and drawings were destroyed in 1871 when the Academy burned in the great Chicago fire. Devastated by the loss, he died of tuberculosis at the age of forty, less than eight months after the fire (SI website 2010).

Stimpson’s 1854 work “Marine Invertebrata of Grand Manan” published in the Smithsonian Contributions to Knowledge, vol. 6 was based on observations of the marine fauna of the island (located about 10 miles off Eastport, Maine and Campobello, New Brunswick) and adjacent waters which he made during three months he spent there in the

summer of 1852. This publication listed 16 species of bryozoans with short descriptions. Of the 11 species he described as new, only seven were illustrated, mostly at too low a magnification to be useful without the specimens on which they were based. Two cyclostomes, *Crisia cribraria* and *Idmonea* (now *Exidmonea*) *pruinosa* (Figure 3) are recognized to occur in the northern part of the Gulf of Maine. The other species were either synonymized by Osburn 1912 or are not recognizable from Stimpson's illustrations.

The next publication on U.S. northeast coast bryozoans was by Joseph Leidy (1855). Joseph Leidy (1823–1891) was an M.D. and a member of the Academy of Natural Sciences of Philadelphia (Figure 4). At the age of 23 Leidy was elected Chairman of the Board of Curators at the Academy of Natural Sciences, a position he kept for the rest of his life, although most of his income came from the teaching positions he held at the University of Pennsylvania and Swarthmore College (Warren 1998). In addition to his research in vertebrate paleontology, Leidy was interested in many groups of living and fossil invertebrates, including a brief foray into bryozoan taxonomy. His 1855 work, "Contributions to the marine invertebrate fauna of the coasts of Rhode Island and New Jersey," was published in the Journal of the Academy, included descriptions of eight bryozoan species. Like most taxonomic work of the time, his collections were based on brief self-funded trips to the shore, "...descriptions of invertebrate animals observed during a visit of two weeks, the last August, to Joseph P. Hazarde, Esq., on Point Judith, at the entrance of Naragansette Bay, Rhode Island; and of other invertebrate animals collected by Samuel Ashmead, Esq., or myself, in short visit to Absecom Beach, in the vicinity of Atlantic City, New Jersey, and to Beesley's Point at the mouth of Great Egg Harbor, New Jersey."

Leidy listed seven species from Rhode Island and New Jersey. Two of the species he described and illustrated from Rhode Island, *Schizoporella variabilis* and *Bowerbankia gracilis* (Figure 4) are still among the most common in the region. He illustrated two other common species, *Electra monostachys* (as *Escharina lineata*) and *Cryptosula pallasiana* (as *Escharina pediostoma*). He also described a new marine entoproct, *Pedicellina americana*.

The next person to record bryozoans from the area was A. S. Packard (1867). Alpheus Spring Packard (1839–1905) eventually became Professor of Zoology at Brown University (Figure 5). As a young man, he studied under Louis Agassiz at Harvard and worked as an assistant at the MCZ, but like most of the young men who worked there, eventually had disagreements with Agassiz that led to his leaving the museum (Cockerell 1920). Packard's first paper on bryozoans, "A list of animals dredged near Caribou Island, Southern Labrador, during July and August 1860," was published in 1863. It resulted from a field trip he made with a group of Williams College students to this island at the extreme northeast end of the Gulf of Saint Lawrence. Packard described 37 species of bryozoans. One of them, *Lepralia* (now *Schizomavella*) *globifera* (Figure 5), was later synonymized by Osburn under the E. Atlantic species *Schizomavella auriculata*, but is a good species and still common offshore in the Gulf of Maine (Winston *et al.* 2000).

His 1867 paper, "Observations on the glacial phenomena of Labrador and Maine; with

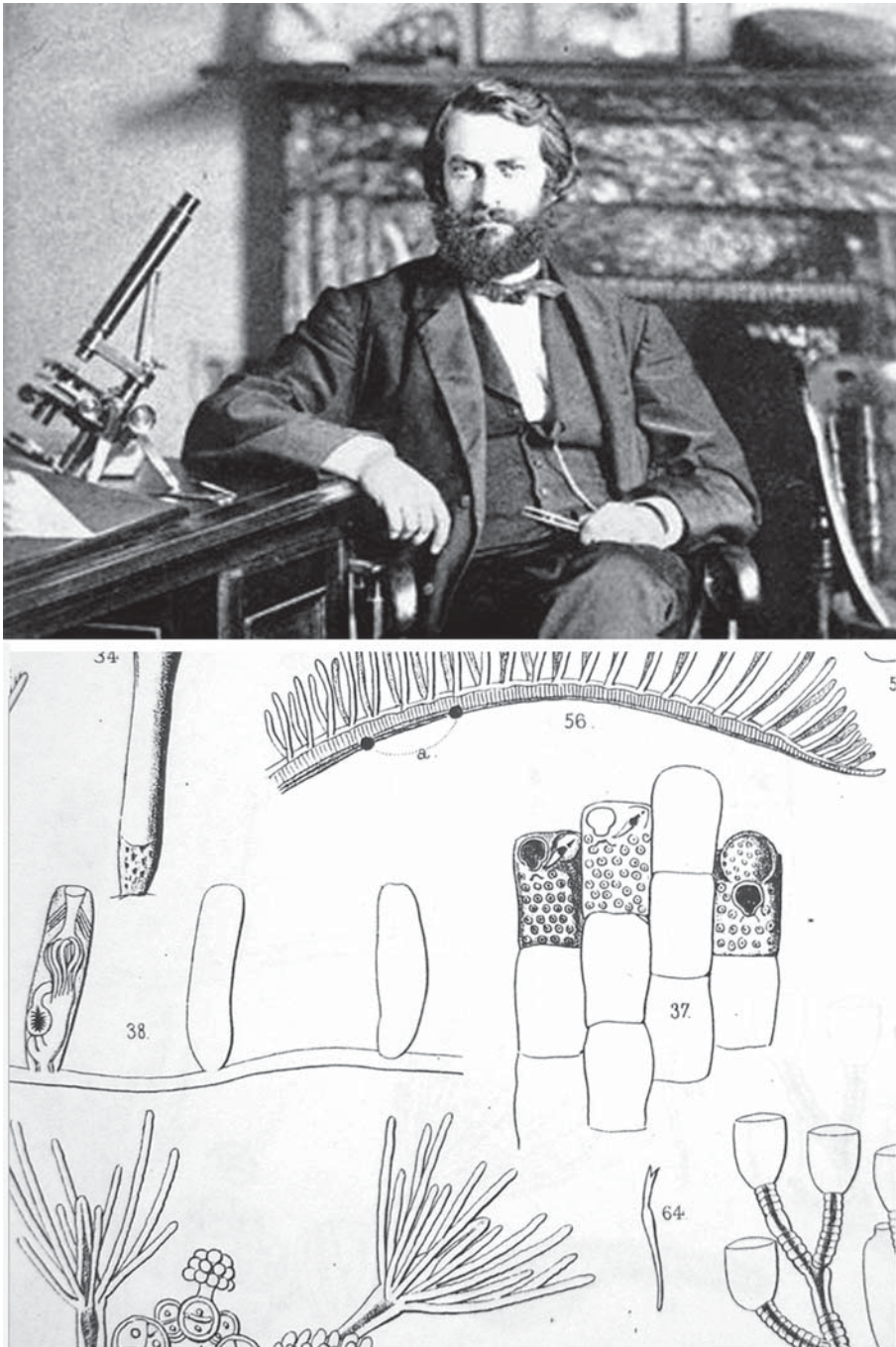


Figure 4. Top. Joseph Leidy at his desk (Academy of Natural Science of Philadelphia archives). Bottom. *Bowerbankia gracilis* (no. 38) and *Schizoporella variabilis* (no. 37). Plate from Leidy (1855).

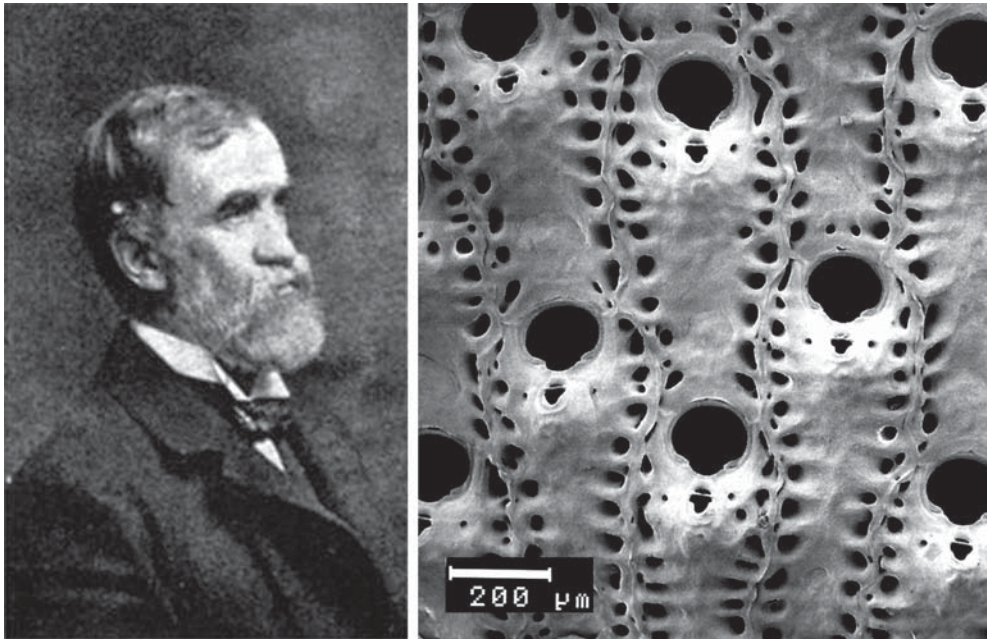


Figure 5. Left. Alpheus S. Packard. Right. *Schizomavella globifera*, a species Packard described in 1863.

a view of the invertebrate fauna of Labrador,” was the result of his being invited to join an expedition to Labrador, organized by New York artist William Bradford, the first American painter to paint Arctic scenes, in the summer of 1864. Packard (1867) listed 44 bryozoan species, including five, none of them new species, mentioned as also occurring in Maine.

The most prolific 19th century worker on NE coast invertebrates, including bryozoans, was Addison Emery Verrill (1839–1927) (Figure 6), another student of Louis Agassiz at the Lawrence Scientific School at Harvard, and another disgruntled ex-employee of his at the MCZ (Dexter 1965). In 1864 Verrill became the first professor of zoology at Yale University, a position he retained until his retirement in 1907 (Figure 6). He built up a large collection at the Peabody Museum at Yale, of which he was curator for many years. From 1871 until 1887, he was also in charge of the U.S. Commission of Fish and Fisheries in southern New England (Howe 2008). During that time, he produced a number of reports on the region’s invertebrates (Verrill 1872, 1875a, b, 1879a, b, c, 1885)

The first paper of Verrill’s that included bryozoans was published in 1872. One new species, *Alcyonidium ramosum*, was described (Figure 6). This species was later renamed *Alcyonidium verrilli* by Osburn (1912) because the name *A. ramosum* was pre-occupied by a Lamouroux species.

Verrill and Smith’s 1874 “Report on the invertebrate animals of Vineyard Sound and adjacent waters,” published in the United States Commission of Fish and Fisheries. Report on the Condition of the Sea Fisheries of the South Coast of New England in 1871 and 72,

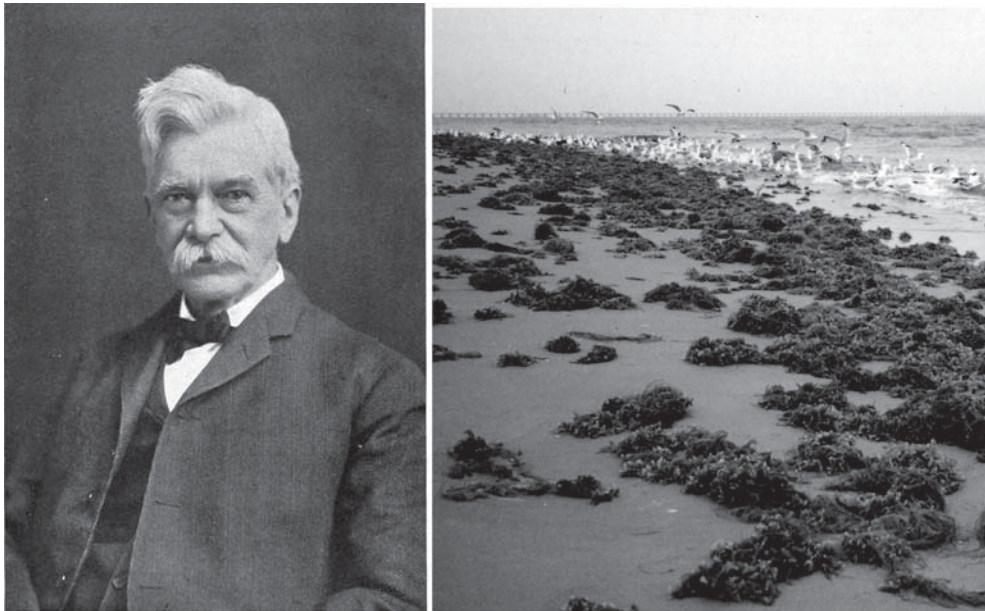


Figure 6. Left. Addison E. Verrill (Yale University). Right. Mounds of *Alcyonidium verrilli* washed up on the beach at Lynnhaven Inlet, Virginia Beach, Virginia.

pp. 295–747, was the first ecological study of marine invertebrates of southern New England and marked a time of transition from the individual collecting done by early workers and the era of larger government or institution sponsored surveys. Bryozoan species were briefly described with distribution information on pp. 711–714; some species were figured in Plates 33 and 34. The species listed were also discussed in the appropriate habitat section, e.g., *Bugula turrita* and *Flustrellidra hispida* under “Animals Inhabiting the Rocky Shores of the Bays and Sounds”, pp 303-334. Two new species, *Vesicularia armata*, now *Aeverrillia armata* and *Vesicularia dichotoma*, now *Amathia dichotoma*, were described in this work.

Aside from the reports of these nineteenth century workers, taxonomic monographs on the bryozoan fauna of the northeast U.S. coast from Maine to Virginia consist of descriptions of the bryozoan fauna from just three localities: Mount Desert Island, Maine, Woods Hole, Massachusetts, and Chesapeake Bay. All three are the work of the same author, Raymond C. Osburn (Figure 7).

Raymond Carroll Osburn (1872–1955) was born in Ohio and home-schooled during his childhood. He had such a good educational background that he was able to earn his B.S. degree at Ohio State University in just three years. He took his M.S. degree at Ohio State also before moving to Columbia University for his Ph.D. (1906). Osburn held various jobs over his career, teaching at several institutions in the northeast and serving as a research scientist for the U.S. Bureau of Fisheries, and associate director of the New York Aquarium. Later he returned to Ohio State University where he was Department

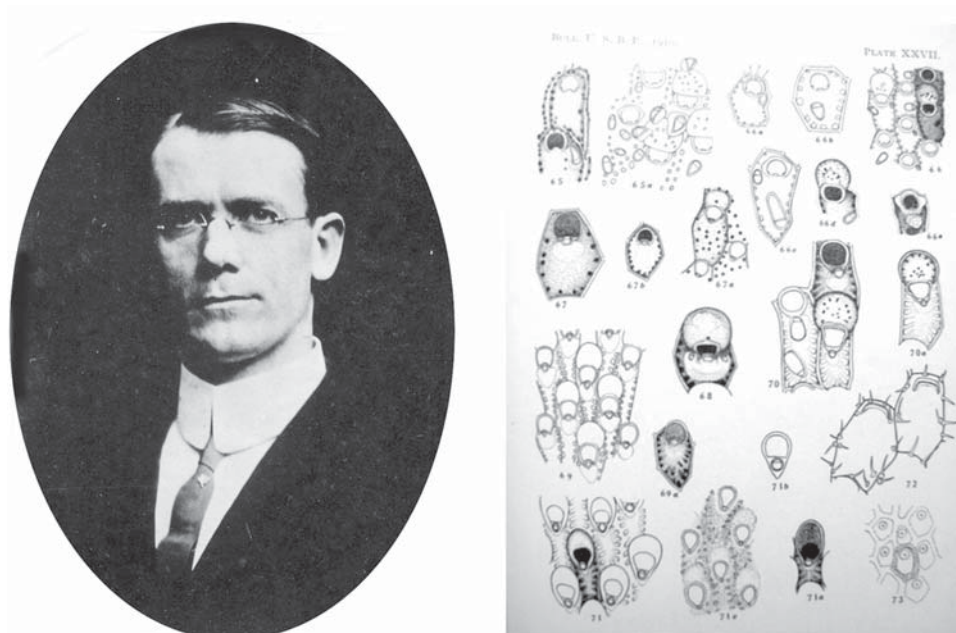


Figure 7. Left. Raymond C. Osburn in 1920 (Smithsonian Archives). Right a plate from his 1912 Woods Hole monograph.

Chairman and directed the activities of the department's freshwater biology station at Put-In-Bay, Ohio. On his retirement, Osburn was called to California to work on the bryozoan collections of the Allan Hancock Foundation. There he published the three volumes on Pacific bryozoans for which he is best known (Miller 1955).

The "Bryozoa of the Woods Hole Region", published in the *Bulletin of the Bureau of Fisheries* in 1912, was based on the results of a six year survey by the US Bureau of Fisheries. The survey covered Buzzard's Bay and Vineyard Sound with 458 dredging stations, as well as shore collections and dock piling scrapings. Some additional samples came from Nantucket and at Crab Ledge, off Chatham (on Cape Cod's "elbow") to the north of Nantucket Sound. This work brought the number of species known from the northeast coast up to 81 (including 5 entoprocts), plus several "varieties". Five species were described as new. Osburn considered most of the others to be widely distributed North Atlantic or cosmopolitan species. Osburn divided the bryozoan fauna into that characteristic of "inner waters", e.g. Vineyard Sound, and "outer waters", e.g. Crab Ledge. However, even his "outer waters" would be considered shallow by current standards as dredging took place only down to 46 metres.

The bryozoan material of "The Bryozoa of the Mount Desert Region" (Osburn 1933) was collected as part of a biological survey of the region around Mount Desert Island, Maine, in the northern part of the Gulf of Maine (44°20' N, 68°20' W). It took place during six summers (1926–1931) under the direction of William Procter, an heir of one of the founders of the Procter and Gamble Company. Procter quit his investment business in

1920 when he was 45 to study entomology at Columbia University, then built his own biology field station on Mount Desert Island, published his research and became recognized as a scientist (H.B.W. 1951). For the marine part of the survey, all available coastal habitats were covered, but the sites were limited in depth to the intertidal or subtidal. The deepest dredge haul was from 100 metres, and no stations were from more than four miles offshore or six miles from Mount Desert Island.

From the specimens collected in the survey Osburn identified 83 species that he considered mostly arctic in distribution. Four new species were described in this report: *Oncousoecia canadensis*, *Diaperoecia harmeri*, *Smittina reduplicata*, and *Smittina novanglia*.

Osburn's first work on Chesapeake Bay bryozoans was a preliminary report published in 1932 that listed 18 species dredged from the deeper waters of the Bay by R. P. Cowles (Osburn 1932). The list also appeared in Cowles' classic, "Biological Study of the Offshore Waters of Chesapeake Bay" (Cowles 1930).

In 1944 Osburn published "A survey of the Bryozoa of Chesapeake Bay" which covered the bryozoans he had collected in the shallower waters of the Bay along most of its length, plus specimens from Chincoteague Bay on the Delmarva Peninsula, a back barrier island sound.

Osburn found 28 species of bryozoans, noting the difference between open ocean and estuarine environments in the proportions of the different bryozoan groups with ctenostomes (11 species) and anascan cheilostomes (9 species), the most abundant.

Osburn's output on bryozoans was monumental, however, the Chesapeake Bay publication was produced more than 60 years ago; his other east coast work is even older (1933 and 1912). The Woods Hole species list is the only one to have been revised. For the *Keys to Marine Invertebrates of the Woods Hole Region* (1964) Rogick reviewed both her own (Rogick 1949, Rogick and Croasdale 1949) and Osburn's previous work in the area. The illustrations and species list provided are still useful, but the classification and nomenclature are now long out of date. Apart from these works, there exist only a few un-illustrated taxonomic checklists: Hutchins (1945), for Long Island Sound, Abbott (1973) for Block Island Sound, Maturo (1968) for the continental shelf from Cape Hatteras to the Hudson Canyon, a more detailed study of a few species described by early workers (Maturo and Schopf 1968).

Although we limited our study to localities from Maine to Virginia, some species described first from Canada also were found in the Gulf of Maine. Dawson (1859, 1865), Hincks (1877, 1888, 1889, and 1892), Whiteaves (1901), and Cornish (1907) were early workers on that region, the northernmost part of the Acadian province. In the 1960s, Neil Powell studied the bryozoan fauna of the Bay of Fundy (Powell and Crowell 1967, Powell 1968).

The studies reported above probably sampled most species at the sites their authors covered, but they do not provide anything like an adequate sample of the northeast coast bryozoan fauna. Hundreds of miles of shoreline received no coverage at all, including all of the Gulf of Maine between Mount Desert Island and the north side of Cape Cod, and

most of the Virginian Province (from southern New England to Cape Hatteras) except Chesapeake Bay. There was no material from the outer shelf or from subtidal habitats such as rock walls that could not be sampled by dredge.

3. Northeast Coast Bryozoan Diversity

The pre-survey species table we compiled from the existing literature at the start of our project contained 20 ctenostomes, 102 cheilostomes and 14 cyclostomes, for a total of 136 species. The list showed a 52% correspondence in species names with those from the British fauna (as reported in Ryland and Hayward 1977, Hayward and Ryland 1979, Hayward 1985, Hayward and Ryland 1985).

On the basis of the northeastern material we examined (from new and museum collections) much of the apparent trans-Atlantic conspecificity was an artifact of the procedures and philosophy underlying the early studies. Early workers had only European studies on which to base their identifications, but no access to European specimens. They made their identifications based on published descriptions and illustrations alone.

In addition, the most prolific writer on the region's bryozoans, R.C. Osburn, was eager to create a synthesis of previous work. Osburn believed that bryozoan species were extremely variable morphologically, and he synonymized most of the new species described by earlier workers with widespread European species.

Thanks to the level of skeletal detail available for analysis with the scanning electron microscope, the greater sample size and the more careful measurements utilized in recent studies (e.g., Cheetham and Hayek, 1988, Jackson and Cheetham 1990), and to better understanding of bryozoan genetics (e.g., Maturo 1973, Jackson and Cheetham 1990), bryozoan taxonomists have become "splitters". We recognize that slight differences in skeletal morphology are significant at the species level, and we can resolve many problems of inter-colony variation through increased use of measurements and statistics. A number of the species we studied show such differences. They are similar, but not identical to the European species with which they have been identified, and properly described as related but separate species.

We found 114 species in our study, of which 22 were ctenostomes (19.3%), 82 were cheilostomes (71.9%) and 10 were cyclostomes (8.8%). Only 44 (15%) of the species in the British fauna are shared with the US east coast, far less than the literature had indicated.

Thirteen species were new or had to be given new names, having been misidentified or synonymized in the past, including some very common intertidal and subtidal species, e.g., *Cribrilina macropunctata* and *Microporella rogickae* (Winston *et al.* 2000).

We considered 41 species to be either endemic (described from the region and not known beyond it) or native (described from the region, but with current distributions reaching beyond it). This included 11 ctenostomes, 24–26 cheilostomes and 4 cyclostomes, or almost 36% of the fauna.

The ctenostome genera *Alcyonidium* and *Bowerbankia* include some of the most commonly encountered intertidal species in the study area. Only one (*Bowerbankia*

imbricata) appears identical with known European species, although others were previously called by European names). Morphological differences can be used to identify the species we collected and described, but there are likely to be other yet unidentified species that can be identified by morphological or molecular means.

4. Biogeography

The study area covers about half of US Atlantic coast, a length of 1605 km (997 miles) of coast, but allowing for peninsulas, bays, estuaries, islands, etc. it includes 27,877 km (17,322 miles) of shoreline. It encompasses most of two biogeographic regions or provinces (Figure 8). The Acadian Biogeographic Province (also called the Acadian Sub-province of the Northeast Temperate Province) extends from Cape Cod north to Nova Scotia. The Virginian Province (or Virginian Sub-province of the Warm Temperate Province) extends from the south side of Cape Cod to Cape Hatteras (Cook and Auster 2007; Hale 2010). Coastal surveys of different groups of organisms have identified faunal subdivisions within the provinces. For the Acadian there are 3 sub-areas, the northern Gulf

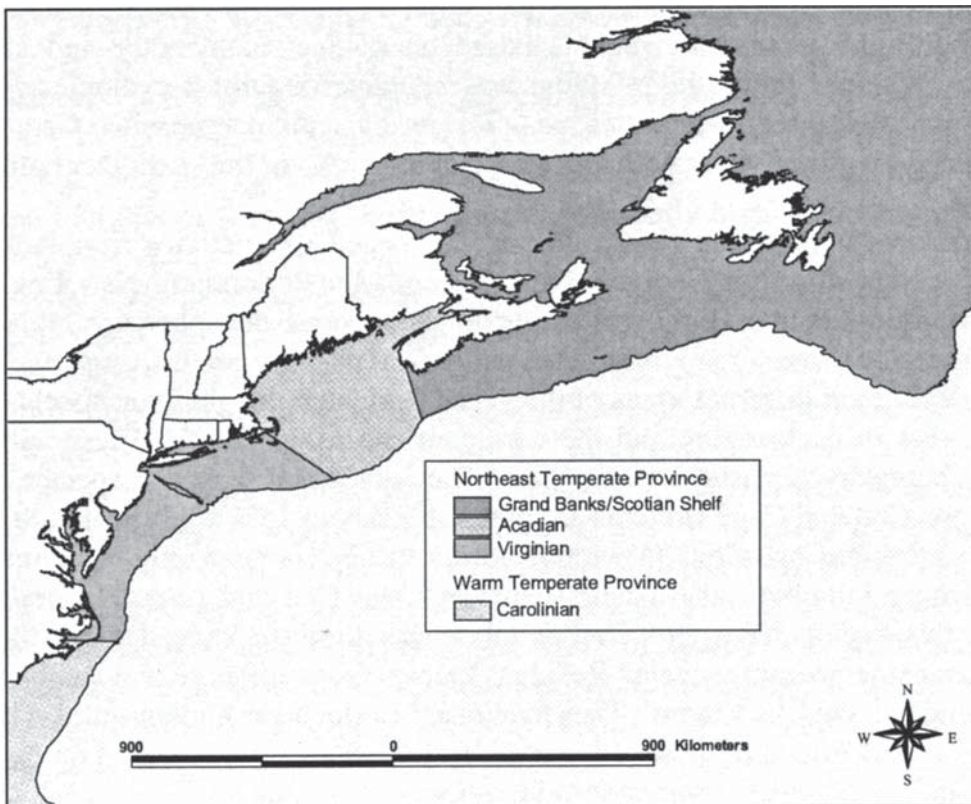


Figure 8. Map showing biogeographic provinces of the northwestern Atlantic continental shelf. From Cook and Auster (2007).

of Maine (from about Cape Elizabeth, Maine to Passamaquoddy Bay), the southern Gulf of Maine (Cape Elizabeth, Maine to Cape Ann, and Massachusetts, and Massachusetts and Cape Cod Bay to Provincetown, Mass. The Virginian province shows two subdivisions: one extending from the south side of Cape Cod to the New York Bight, and a second extending south from the New York Bight to Cape Hatteras (Hale 2010). Estuaries along the coast vary in faunal distributions chiefly by salinity: mesohaline and oligohaline (Hale 2010), although their entrances may contain additional euryhaline species from that province.

In the Acadian province, the unique areas in terms of bryozoan fauna are the spatially isolated “lobster holes” in 60-120 feet depths in the Boothbay-Damariscotta, Maine region. In the Gulf of Maine, rocky intertidal and subtidal areas attracted the richest bryozoan communities both in numbers of species and abundance.

The Virginian province is reputed to be taxonomically depauperate compared with other temperate provinces. Its impoverishment has been linked with low nutrient supply and little habitat diversity and habitat degradation (Hale 2010). Although about 80% of our new collection locations were from Cape Cod south, our results confirmed the conclusions made by workers on other groups, that the Virginian Province was lower in species than other temperate regions. In collections from Cape Cod to Virginia We found 15 ctenostomes, 23 cheilostomes, and 2 cyclostomes, 40 species in all, or 35% of total number of species. However, within this region, the sounds behind barrier islands, with their associated oyster bars, were the source of richer, more diverse bryozoan communities than occurred on the open coast and shelf.

One ctenostome species, *Alcyonidium verrilli*, found in subtidal channels in the lower Chesapeake Bay, and also recorded from Delaware Bay and Buzzard’s Bay probably has the greatest biomass of any species in the study area. In Chesapeake Bay, its colonies wash up on the beaches literally by the ton, and the organisms inhabiting them (e.g., small amphipods and polychaetes) provide food for fish and shorebirds (Figure 4).

5. Conclusions

The 150-year history of taxonomic study of the bryozoans of the Northeast coast of the U.S. covers the transition between the era of small-scale collections by naturalists to the professionalization of science and the advent of national and institutional marine surveys. Most of the early work was by young men inspired by the example of their professor, Louis Agassiz. Later taxonomic work was almost all carried out by a single professional scientist, Raymond C. Osburn. The authors of this history recently completed a guidebook to NE coast bryozoans based on a long-term distributional and taxonomic study of this portion of the U.S. Atlantic coastline. In it, we describe new and previously misidentified species, bring the systematics of known species and higher taxa up to date, provide illustrations (SEM images or photographs of living specimens), and information on the biology and distribution of each species to create a comprehensive resource for the identification of shallow water bryozoans from the region.

6. Acknowledgments

Fieldwork at new sites was supported by NSF Grant No. BS-R9024746. 1991 to J.E. Winston “Inventory of the marine bryozoans of the Northeastern United States”. We are grateful for that assistance. We were also able to collect in 1993 as part of a course on bryozoan taxonomy held at the University of Maine’s Darling Marine Center, we are also grateful for that opportunity and for further visits made by one of us in later years to photograph and measure living colonies of common species. We thank also the staff at the museums holding northeast coast specimens and the colleagues who donated or loaned specimens from their own research for the project.

References

- Abbott, M.B. 1973. Seasonal diversity and density in bryozoan populations of Block Island Sound (New York, U.S.A), pp. 37–55. *In* Larwood, G.P. (ed.) *Living and Fossil Bryozoa*. London, Academic Press.
- Cheetham, A.H. and Hayek, L.C. 1988. Phylogeny reconstruction in the Neogene bryozoan *Metrarabdotos*: A paleontologic evaluation of methodology. *Historical Biology* **1**, 65–83.
- Cockerell, T.D.A. 1920. Biographical memoir of Alpheus Spring Packard, 1839-1905. *National Academy of Sciences of the United States of America. Biographical Memoirs* **9**, 181–236.
- Cook, R.R. and Auster, P.J. 2007. A bioregional classification for the continental shelf of northeastern North America for conservation analysis and planning based on representation. *Marine Sanctuaries Conservation Series NMSP-07-03*. US. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD. 14 pp.
- Cornish, G.A. 1907. Report on the marine Polyzoa of Canso, Nova Scotia. *Marine Fisheries Report. Canada. Sessional Paper* **22**, 75–80.
- Cowles, R.P. 1930. A biological study of the offshore waters of Chesapeake Bay. *U. S. Bureau of Fisheries Bulletin* **46**(1091), 277–381.
- Crowell, G. D. and Powell, N.A. 1968. Studies on Bryozoa (Polyzoa) of the Bay of Fundy region. II. Bryozoa from fifty fathoms, Bay of Funday. (1). *Cahiers de Biologie Marine* **9**, 247–259.
- Dawson, J.W. 1859. Polyzoa. *Geological Survey of Canada, Report of Progress for the year 1858*, 255–257.
- Dawson, J.W. 1865. Note on a species of *Gemellaria* from Sable Island. *Proceedings of the Nova Scotian Institute for Natural Science* **1**(3), 3.
- Desor, E. 1848. Recent zoological investigations among the shoals of Nantucket. *Proceedings of the Boston Society of Natural History* **3**, 65–68.
- Desor (obituary). 1882. Edward Desor. *Proceedings of the American Academy of Arts and Sciences* **17**, 422–424.

- Dexter, R.W. 1965. The “Salem Secession” of Agassiz zoologists. *Essex Institute Historical Collections* **101**, 1–13.
- H.B.W. 1951. William Procter, 1872–1951. *Journal of the New York Entomological Society* **59**(4), 217–219.
- Hale, S. S. 2010. Biogeographical patterns of marine benthic macroinvertebrates along the Atlantic coast of the northeastern USA. *Estuaries and Coasts* **33**, 1039–1053.
- Hayward, P.J. 1985. *Ctenostome Bryozoans*. Synopses of the British Fauna, new series 33. London & Leiden, E.J. Brill.
- Hayward, P.J. and Ryland, J.S. 1985. *Cyclostome Bryozoans*. Synopses of the British Fauna, n.s., 34. London & Leiden, E.J. Brill.
- Hincks T.H. 1877. On Polyzoa from Iceland and Labrador. *Annals and Magazine of Natural History*, ser. 4, **19**: 97–112.
- Hincks, T.H. 1888. The Polyzoa of the St. Lawrence: a study of arctic forms. *Annals and Magazine of Natural History*, series 6, **1**, 214–227.
- Hincks, T.H. 1889. The Polyzoa of the St. Lawrence, pt. 2. *Annals and Magazine of Natural History*, series 6, **3**, 424–433.
- Hincks, T.H. 1892. The Polyzoa of the St. Lawrence, pt. 3. *Annals and Magazine of Natural History*, series 6, **9**, 149–157.
- Hutchins, L.W. 1945. An annotated check-list of the salt-water Bryozoa of Long Island Sound. *Transactions of the Connecticut Academy of Arts and Sciences* **36**, 533–551.
- Jackson, J.B.C. and Cheetham, A.H. 1990. Evolutionary significance of morphospecies: a test with cheilostome Bryozoa. *Science* **248**, 579–583.
- Johnson, R.I. 2004. The rise and fall of the Boston Society of Natural History. *Northeastern Naturalist* **11**(1), 81–108.
- Lurie, E. 1966. *Louis Agassiz: a life in science*. Abridged edition. Chicago, University of Chicago Press.
- Maturo, F.J.S. 1968. The distributional pattern of the Bryozoa of the east coast of the United States exclusive of New England. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **108**, 261–284.
- Maturo, F.J.S. 1973. Offspring variation from known maternal stocks of *Parasmittina nitida* (Verrill) pp. 577–584. In Larwood, G.P. (ed.) *Living and Fossil Bryozoa*. London, Academic Press.
- Maturo, F.J.S., Jr. and Schopf, T.J.M. 1968. Ectoproct and entoproct type material: re-examination of species from New England and Bermuda named by A. E. Verrill, J. W. Dawson and E. Desor. *Postilla* **120**, 1–95.
- Miller, D.F. 1955. Raymond Carroll Osburn, 1872–1955. *Annals of the Entomological Society of America*, **48**, 422.
- Osburn, R.C. 1912. The Bryozoa of the Woods Hole region. *Bulletin of the Bureau of Fisheries*, **30**, 205–266.
- Osburn, R.C. 1932. Bryozoa from Chesapeake Bay. *Ohio Journal of Science*, **32**, 441–446.
- Osburn, R.C. 1933. Bryozoa of the Mt. Desert region. *Biological Survey of the Mount*

- Desert Island Region*, **5**, 291–385.
- Osburn, R.C. 1944. *A survey of the Bryozoa of Chesapeake Bay*. Maryland Department of Research and Education, Publication no. 63, 1–59.
- Packard, A.S. 1863. A list of animals dredged near Caribou Island, southern Labrador, during July and August, 1860. *Canadian Naturalist and Geologist* **8**, 401–429.
- Packard, A.S. 1867. Observations on the glacial phenomena of Labrador and Maine; with a view of the recent invertebrate fauna of Labrador. *Memoirs of the Boston Society of Natural History* **1**, 210–303.
- Powell, N.A. and Crowell, G.D. 1967. Studies on Bryozoa (Polyzoa) of the Bay of Fundy region. I. Bryozoa from the intertidal zone of Minas Basin and Bay of Fundy. *Cahiers de Biologie Marine* **8**, 331–347.
- Ryland, J.S. and Hayward, P.J. 1977. *British Anascan Bryozoans*. Synopses of the British Fauna, new series 10. London, Academic Press.
- Stimpson, W. 1853. Synopsis of the Marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge* **6**, 1–66.
- Verrill, A.E. 1872. Brief contribution to zoology from the Museum of Yale College, no. XIX, Recent additions to the molluscan fauna of New England and adjacent waters, with notes on other species. *American Journal of Science* **3**, bryozoans, p. 212, pl. 8.
- Verrill, A.E. 1875a. Brief contribution to zoology from the Museum of Yale College, no. XXXII. *American Journal of Science* **9**, bryozoans, p. 414, pl. 7.
- Verrill, A.E. 1875b. Brief contribution to zoology from the Museum of Yale College, no. XXXIII. *American Journal of Science* **10**, bryozoans, p. 42–43, pl. 3.
- Verrill, A.E. 1879a. Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. Part I. *Proceedings of the United States National Museum* **2**, 65–205.
- Verrill, A.E. 1879b. *Preliminary check-list of the marine Invertebrata of the Atlantic Coast from Cape Cod to the Gulf of St. Lawrence*. New Haven, Privately published [Bryozoa, pp. 28–31].
- Verrill, A.E. 1879c. Brief contributions to zoology from the museum of Yale College. No. XLIII. Notice of recent additions to the marine fauna of the eastern coast of North America. No. 6. Polyzoa, Echinodermata, Anthozoa. *American Journal of Science*, series 3, **18**, 52–54.
- Verrill, A. E. 1885. Results of explorations by the steamer Albatross off the east coast of the United States in 1883. *Annual Report of the Commissioner of Fish and Fisheries, 1883*. Bryozoa, p. 530.
- Verrill, A. E. and Smith, S. I. 1874. Report on the invertebrate animals of Vineyard Sound and adjacent waters. In *Report, U.S. Fish Commission, 1871-72*, pt. **8**, 296–747.
- Warren, L.G. 1998. *Joseph Leidy: The Last Man Who Knew Everything*. New Haven, Yale University Press.
- Whiteaves, J.F. 1901. *Catalogue of the Marine Invertebrata of Eastern Canada*.

- Geological Survey of Canada, Ottawa [Polyzoa, p. 91–114].
- Winston, J.E., Hayward, P.J. and Craig, S.F. 2000. Marine bryozoans of the northeast coast of the United States: new and problem species. *Proceedings of the 11th International Bryozoology Conference*, 2000: 412–420.

