Palaeoecology of Ordovician Bryozoa

By JUNE R. P. ROSS

Most Ordovician ectoproct bryozoans are found in marine carbonate deposits. Evolution in the Early and Middle Ordovician of not only bryozoans but also other calcium carbonate secreting organisms led to marked changes in the organization and species composition of benthic assemblages. In the early stages of establishment of these calcareous assemblages, bryozoans were sediment stabilizers, sediment binders, and framebuilders of structures, which at times formed mounds on the sea floor. Later in the Middle and Late Ordovician increased species diversity and more extensive areas of hard substrate on which benthic assemblages could become established resulted in widely distributed bryozoan assemblages in depositional areas of lagoons, near shore margins, shoals, shelf margins and shallow narrow shelves, more open widespread shelves, and the edges of shallow cratonic basins. Buildups and accumulations of calcareous assemblages, including bryozoans, at some sites formed bioherms. Diversity of bryozoan assemblages in these different facies varied depending on such factors as the initial organisms settling on the substrate (particularly which bryozoan species first became established), organization of tropic levels, rate of influx of clastic material, and other fluctuations, particularly in the physical environment. Distribution patterns of some of the bryozoan species assemblages show migration of species with transgressions and regressions.

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Representatives of ectoproct bryozoans have a long geological history from early in the Ordovician (Tremadoc, about 500 million years ago) to Recent. These colonial benthic animals made up a large part of many epifaunal assemblages in the Ordovician. They were filter feeders.. Many positioned themselves several centimeters or more above the substrate to which they were attached. Some bryozoans, particularly Early Ordovician species, encrusted the substrate and played an important role in stabilizing sediment accumulating on the sea floor. These particular colonies lay close to the water-substrate interface. Most of the bryozoans were passive filter feeders waiting for food to drift to the colonies. The tentacular movements created water currents and the food was caught in these currents and collected for feeding. It appears that the arrangement of zooecial openings across colony surfaces was related to the geometry of tentacle feeding patterns.

Colony forms in Ordovician bryozoans were varied in both shape and size (Fig. 1) and, in addition, encrusting and laminate forms were common. Under different environmental conditions, the colony form of certain species was plastic and varied, e.g., *Batostoma campensis* in Chazyan strata of New York State was encrusting and laminate where it stabilized and bound lime mud and ramose where it was a framebuilder or where it became established on a firm substrate.

Almost all known Ordovician bryozoans belong to the class Stenolaemata which includes the orders Cryptostomata, Trepostomata, Cystoporata, and Cyclostomata. The Cryptostomata, a dominant and highly diverse group in the Ordovician, commonly had bifoliate colonies (Fig. 1A–D) with zooecia opening only on two opposing surfaces. The zooecia diverged from a median lamina. Other Cryptostomata, grouped as Rhabdomesonata (rhabdomesoids), had small stick-like or twig-like colonies. Their tubular zooecia were arranged in distinctive geometric patterns, e.g., *Ulrichostylus, Arthrostylus,* and *Sceptropora.* Another cryptostome

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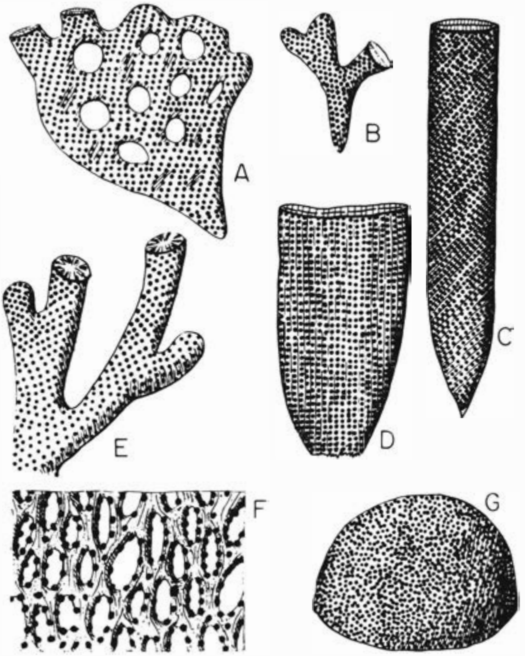


Fig. 1. Forms of bryozoan colonies. An Ordovician genus with the particular colony form is listed. A. Cribrose, Oanduella, X2. B. Strap-shaped, Strictopora, X2. C, Lanceolate, Escharopora, X3. D. Explanate, Phaenopora, X3. E. Ramose, Champlainopora, X2. F. Reticulate, Phylloporina, X10. G. Hemispheric, Prasopora, X2. Colonies in Figs. A to D show bifoliate arrangement of zooecia in cross sectional view. Black dots on colonies represent individual zooecia.

group, the phylloporinids (Fig. 1F) had reticulate colonies with zooecia opening on only one surface. The Cystoporata commonly had dendroid, ramose, laminate, or hemispheric colonies with recrystallized walls forming tubular zooecia. The Trepostomata also had tubular zooecia, many times were polymorphic, and the colonies were hemispherical (Fig. 1G), laminate, ramose (Fig. 1E), or dendroid. The zooecia were commonly crossed by curved or flat platforms. The Cyclostomata, exceedingly rare in the Ordovician, had simple long tubes that were loosely clustered together.

Bryozoans of the order Ctenostomata of the class Gymnolaemata have no skeletons and, therefore, the record of this group is represented by impressions and borings and is very sparse in all parts of the geological record including the Ordovician.

The earliest known bryozoans, represented by rare colonies of Ctenostomata and Cystoporata, are of Early Ordovician (Tremadoc and early Arenig) age. A few fossils from the Cambrian have been erroneously assigned to the Bryozoa. By the middle Arenig, diverse groups of cryptostomes, trepostomes, and cystoporates had broad geographical distributions in carbonate facies on platforms, near shore margins, and open shelves. These groups continued to evolve rapidly in these carbonate facies throughout the Ordovician and they were the dominant group in many assemblages throughout the world, e.g., Middle and Upper Ordovician of the central states of the United States (Ulrich 1890, 1893), of Estonia (Männil 1959), and of the Siberian Platform (Nekhoroshev 1961; Astrova 1965).

Sediment stabilizers, binders, and framebuilders of mounds and bioherms

The evolution in the Early and Middle Ordovician of not only bryozoans but also other calcium carbonate secreting organisms led to significant changes in the structure and species composition of benthic assemblages. Bryozoans were abundant to common in many of these assemblages in the carbonate facies that gradually dveloped. The calcium carbonate secreting organisms, such as pelmatozoans and bryozoans, stabilized, bound, and trapped lime mud, sometimes forming small mounds only a few meters in diameter. Chazyan faunas from upper New York State represent an example of these pioneer assemblages in which bryozoans were widespread in mound and intermound areas (Pitcher 1964; Ross 1981). Other mound deposits with bryozoans as a dominant part of the fauna have been described from Tennessee (Alberstadt *et al.* 1974).

In upper New York State in Chazyan time (Day Point Limestone) (Fig. 2) on the western part of a broad platform near the cratonic margin (Fig. 3), bryozoans, such as ramose colonies of the trepostome *Champlainopora chazyensis*, reticulate colonies of *Phylloporina* sp., and bifoliate strap-shaped blades of the cryptostome *Chazydictya chazyensis*, colonized the shifting sand substrates of the near shore environment. The colonization and establishment of bryozoan assemblages in this unpredictable environment was a chance event and depended on the availability of suitable fragmentary substrate, sometimes pelmatozoan fragments. The bryozoan colonies, fragmented by storm and wave action, made up from 10–20% to 50% by volume of the micritic sediment of mound rock. Some colonies of species such as *Champlainopora chazyensis* also were established in intermound areas where they comprised about 50% by volume of the biosparite. Farther to the east and farther out on the platform, small mounds of 1.5 to 2 m diameter were commonly stabilized and bound by encrustations of the trepostomes *Champlainopora chazyensis* and *Batostoma campensis* and the cystoporate *Ceramoporella* sp. Here the bryozoans made up 20–30% by volume of the micritic rock. Where the mounds were in a nondisrupted environment, *B. campensis* tended to dominate the faunal assemblages.

Higher in the stratigraphic sequence toward the top of the Day Point Limestone, species diversity increased and biohermal buildups developed. The term bioherm is used to describe a carbonate buildup that has topographic relief and the internal composition and framework of which is largely derived from *in situ* production of organisms (Wilson 1975). The same mix of species was present as noted above but here *Batostoma campensis* lacked encrusting growth and was only ramose. Both *B. campensis* and *Champlainopora chazyensis* functioned as framebuilders in the carbonate buildups. Reticulate colonies of *Phylloporina* extended as horizontal growths among the *Batostoma* branches.

The succeeding Crown Point Limestone was also deposited in a platform facies but in quieter, less agitated water. In the western region, closer to the shoreline, isolated thickets of ramose colonies of *Champlainopora chazyensis* and small patches with colonies of *Chazydictya chazyensis, Stictopora fenestrata, Eopachydictya gregaria, Phylloporina* sp., *Nicholsonella* sp. and *Jordanopora heroensis* became established. These were framebuilders and sediment trappers. The bryozoans comprised 20–40% of the biomicritic sediments.

Stromatoporoids commonly dominated bioherms on the eastern part of the platform which was farther from shore. Several cryptostome bryozoans and a few trepostomes were present in bioherms that reached 8–9 m in height. In different bioherms, the bryozoan species were present in different proportions.

Bryozoan carbonate facies of epeiric seas

Later in the Middle Ordovician and subsequently in the Late Ordovician, calcium carbonate secreting organisms dominated the extraordinarily widespread seas of cratonic shelves and shallow basins. Upper New York State and the vast Midcontinent area of North America were two regions in which carbonate facies were widespread and across which successive marine transgressions and regressions occurred.

The carbonate facies and their associated faunal assemblages in upper New York State provide a framework for analyzing Middle and early Late Ordovician bryozoan paleoecology. Bryozoan assemblages were established in a number of depositional sites such as lagoon, near shore, shoal, shallow shelf, open shelf, shelf margin and shallow cratonic basin (Figs. 3, 4) (Ross 1970, 1972). These depositional areas lay to the west of the Adirondack Arch.

In Black Riveran time (Lowville Formation) in upper New York State, bryozoans were restricted in diversity and abundance as a result of the inhospitable lagoonal facies. Where present, they were established in channels and other areas of the platform where water flow was continuous and where colonies were not overcome by lime mud from stagnant turbid waters. Numerous skeletal fragments that had accumulated on the sea floor provided extensive sites for attachment of benthic organisms. The lack of a hard, stabilized substrate was generally no longer a significant limiting factor as it had been in Early Ordovician times.

The accumulating lime muds were not suitable for most bryozoan settlement and growth. There were few species. The strap-shaped cryptostome *Stictopora labyrinthica* was the most abundant and widespread species and large complete colonies were embedded in the lime mud in growth position. This species commonly attached itself to colonies of the tabulate coral *Tetradium.* Variants of this species found at different sites on the platform represent adaptions to particular environmental conditions. Other bryozoan species became established in less silty and less muddy parts of the

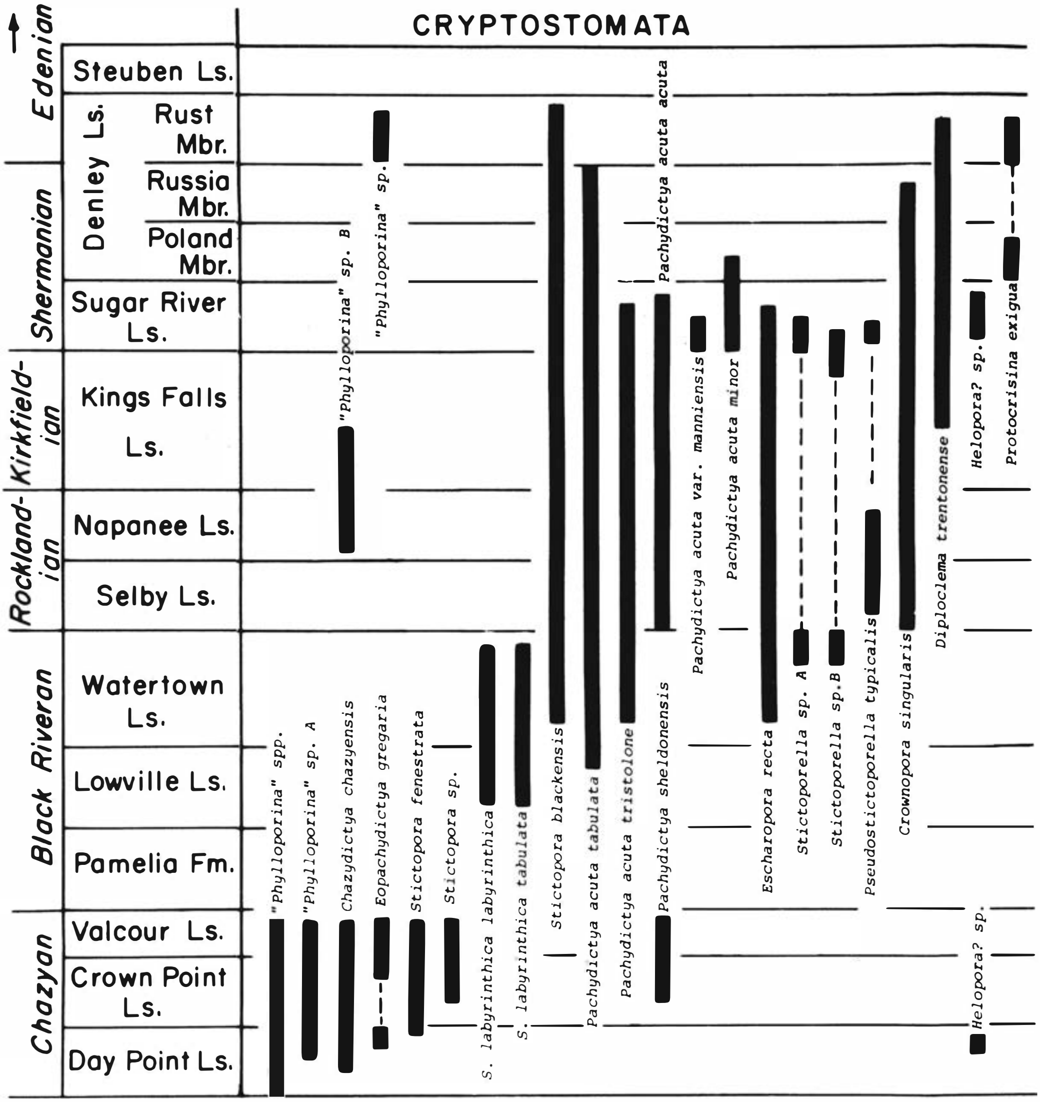
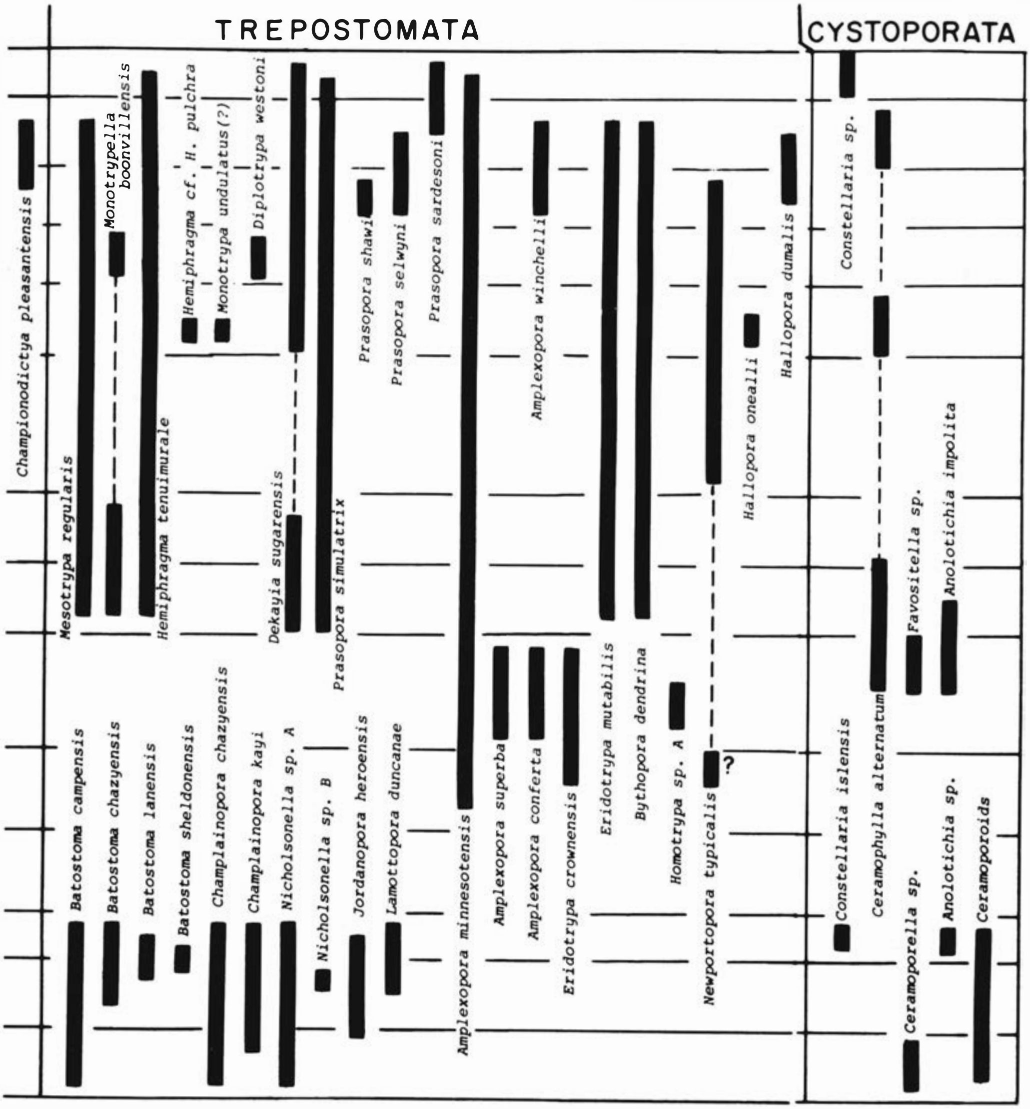


Fig. 2. Stratigraphic range of ectoproct bryozoans in Chazyan through to early Edenian from New York State.

near shore lagoonal area and included the ramose trepostomes *Amplexopora minnesotensis* and *Eridotrypa crownensis* and cryptostomes *Pachydicta acuta* and *Escharopora* sp. Later in Black Riveran time (Watertown Limestone), the lagoonal lime muds had many skeletal fragments and bryozoans had a greater diversity than those in the Lowville Formation. Several cryptostomes and trepostomes were abundant. Cystosporates were sparse.

In succeeding Rocklandian, Kirkfieldian, and early Shermanian times, a major marine transgression from west to east enroached on to the Adirondack Arch. During Shermanian time the Adirondack Arch was submerged and the rising Taconic Highlands to the east of the arch created an influx of clastic sediments onto the shelf and basin to the west, as well as changing the



water circulation patterns. In Rocklandian time (Selby and Napanee Limestones) bryozoan assemblages were established in quiet, near shore environments of the transgressing sea. They formed extensive beds on the sea floor of large unfragmented colonies with a number of species including ramose and dendroid colonies of trepostomes *Monotrypella boonvillensis* and *Bythopora dendrina*, the cryptostomes *Escharopora recta* and *Pachydictya acuta tabulata*, and cystoporates *Ceramophylla alternatum* and the massive ramose *Anolotichia impolita*. A consistent and recurring assemblage included *Bythopora dendrina, Eridotrypa mutabilis, Dekayia sugarensis*, and *Crownopora singularis*.

In succeeding Kirkfieldian time (King Falls Limestone), bryozoans continued to be dominant in the near shore environment but they

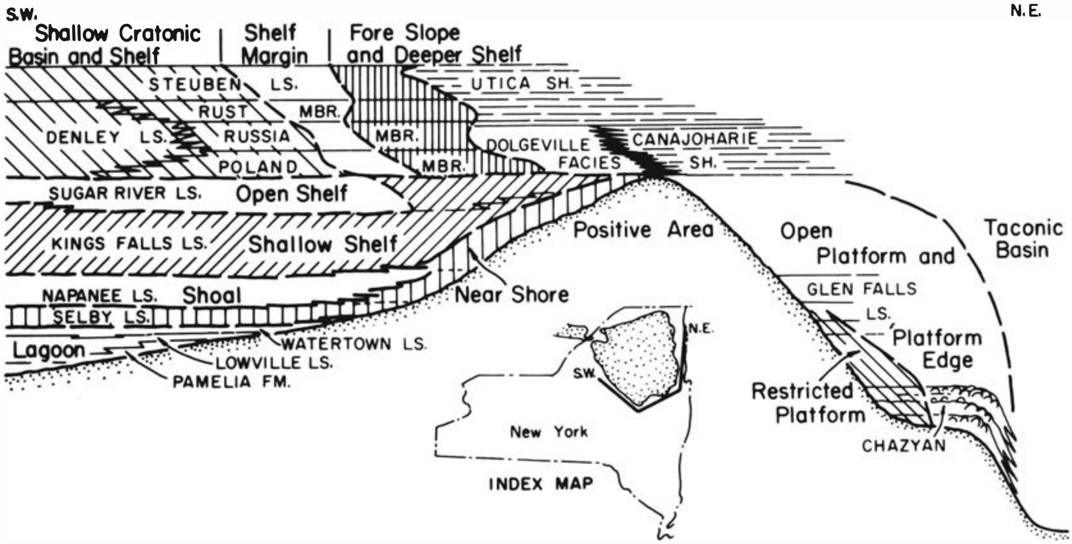


Fig. 3. Stratigraphic cross section along line indicated on index map showing facies relations in Middle Ordovician and early Upper Ordovician in New York State. The index map shows line of section between points marked SW and NE which passes across Adirondack Arch (positive area). Stippled area is Precambrian outcrop of Adirondack Arch.

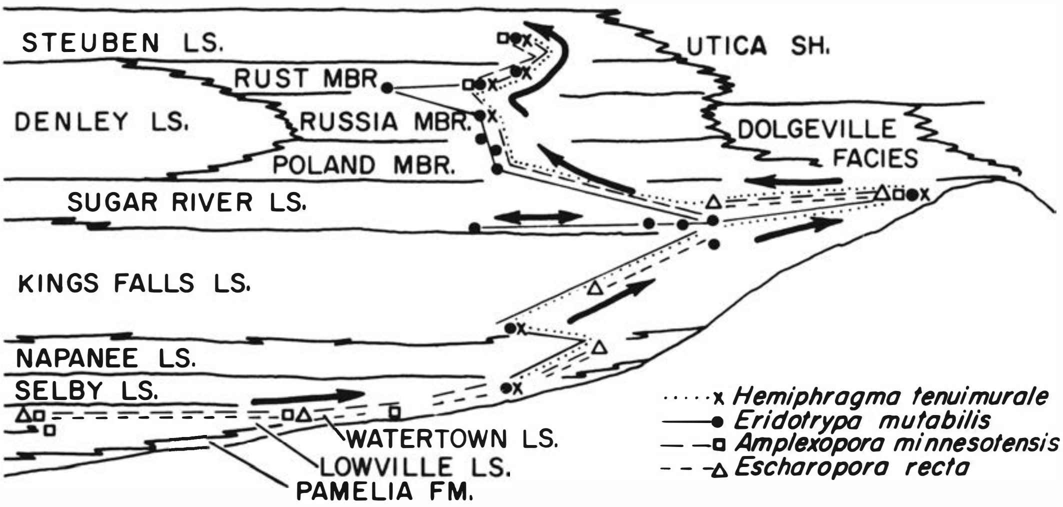


Fig. 4. Stratigraphic cross section showing distribution and migration with facies of four bryozoan species in Middle Ordovician and early Upper Ordovician New York State.

also extended westward across part of the shallow shelf. The benthic faunas continued to form extensive beds on the sea floor.

In early Shermanian time (Sugar River Limestone) as the seas continued to transgress eastward on to the Adirondack Arch, the bryozoan species also continued to migrate eastward (Fig. 4) becoming established in habitats in the near shore, the shallow shelf, and extending out to the open shelf (Fig. 4). However, the continuing influx of clastic material from the rising Taconic Highlands to the east and accompanying modifications in water circulation patterns resulted in a marked change in the bryozoan assemblages. The lanceolate cryptostome *Escharopora recta* and several other cryptostomes disappeared from the assemblages.

Later in Shermanian time (Denley Limestone), other bryozoan species show adaptations to the changing sedimentary patterns. *Prasopora simulatrix* showed marked variability in size and in morphological structures, such as degree of development of acanthopores. In addition, several other species of this genus, namely *P. shawi, P. selwynii,* and *P. sardesoni* appeared. In the later part of Shermanian time (Denley Limestone) a regression took place. This change in the depositional pattern led to a much reduced number of bryozoan species as well as a reduction in the actual number of bryozoans. Another effect on some bryozoans was a reduction in colony size, e.g., *Prasopora shawi* is only a small hemispheric button-like colony.

By the Edenian at the beginning of Late Ordovician time, bryozoans had established themselves as important, and commonly the dominant, substrate colonizers of most carbonate near shore shelf ecosystems. Bryozoans were able to adapt to the wide variety of shelf facies. These evolutionary radiations of bryozoans which are recorded in upper New York State during the Early, Middle, and early Late Ordovician continued into the Late Ordovician epeiric seas. The general community organization that had evolved by the end of the Middle Ordovician remained throughout the rest of the Ordovician. This organization involved a limited number of trophic levels, guild assemblages, niche partitions, and higher taxomonic groups in the ecosystem. Bryozoans are extremely abundant fossils in these strata and many species were of relatively large size so that their proportion of the biomass in many assemblages was relatively high (see Jaanusson 1979).

Summary

During the Ordovician, bryozoans evolved rapidly. They diversified from small, loose or open aggregates of individuals in colonies that encrusted the surfaces of other organisms or fine fragments in lime mud and lime sand into a wide variety of colony forms. The diverse colony forms were adapted to ecological niches that included colonizing of both soft and hard substrate, binding sediment, and forming a framework in and around which other organisms lived. As successful filter feeders, bryozoans adapted by increasing their colony surface and by increasing the kinds of communities in which they were participants.

These invasions into different communities were first strongly evident in the early Middle Ordovician (Chazyan). Several of these adaptions were extremely successful if the abundance of bryozoan fossils is used as an index. Some of the Chazyan communities did not survive into younger parts of the Middle Ordovician. However, new additional communities appeared and into these additional bryozoan radiations gradually became established. The bryozoans were important and dominant participants in most shallow marine carbonate shelves and platforms. In addition to playing an important role as the principal filter feeders in many of these communities, bryozoans became strong competitors for substrate space and some evolved so as to modify substrates by effectively stabilizing and binding sediment.

By the end of Middle Ordovician time, most of the trophic positions for bryozoans had become established. The taxonomic lineages within the bryozoans and the geometry of their zooecial arrangements in colonies had reached the broad limits of their main adaptive diversifications which persisted for the remainder of the Paleozoic.

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