Bryozoan revelations

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Bryozoans, simple invertebrates living on the sea floor, are emerging as a model system for understanding ecological and evolutionary processes on macroevolutionary scales.

Bryozoans are neglected children of the sea floor. Google corals and you get nearly 4 billion hits, whereas bryozoans get just 4 million. This disparity reflects the enormity and notable beauty of coral reefs and extraordinary diversity of associated species that have long attracted intense scientific research. Yet for all their grandeur, corals occupy less than a tiny fraction of 1% of the global ocean, whereas bryozoans extend from the equator to the poles and intertidal to abyss. Bryozoans are species-rich. As a group, they have at least 10 times more species than corals. They also have a more extensive and continuous fossil record and have been major components of vast seafloor communities for half a billion years (*1*).

So why is bryozoan not a household word? Principally because they are so tiny and morphologically complex that it is difficult to understand their basic functional biology, much less how they interact with other organisms in their environment. Like corals, they are colonial, but their modular skeletonized living chambers called zooids are microscopic with a miniature animal inside called a polypide with a gut and feeding tentacles that protrude through an orifice to feed on plankton and scoots back inside when danger lurks (Fig. 1). Cheilostomes are the most abundant bryozoans today with a rich fossil record extending back 160 million years. Their living chambers vary in degree and complexity of calcification from simple chambers with membranous rooves to spinous rafters to shapes as ornate as gothic cathedrals, flying buttresses, and all. Zooids are also polymorphic to an extent comparable to castes among social insects, but whose functions with the exception of reproduction are barely understood. Add to this a perversely byzantine morphological terminology, and it is no wonder that scientists long fled to more tractable subjects of study.

But not anymore. Cheilostomes are emerging as model systems for understanding ecological and evolutionary processes on macroevolutionary scales. They battle each other for living space with winners overgrowing and smothering losers in ways that depend on specialized mechanisms for budding new zooids and topologies of growth. Patterns of overgrowths preserved in their skeletal remains record complex networks of ecological interactions and adaptations for ecological dominance today and in the fossil record (*2*). Bryozoan colonies also grow in many shapes, ranging from simple encrustations to little mounds to delicate vines and trees (*3*). Like convergence in shape between sharks and dolphins, similar growth forms have repeatedly and independently evolved, providing replicate examples for understanding their ecological significance. Rich anatomy over geological time sheds light on repeated evolutionary innovations of novel forms and their subsequent diversification. For example, cheilostome brood chambers for protection of developing larvae originated from coalescence of modified spines about 100 million years ago (*4*), an innovation hypothesized to have sparked an explosive radiation of brooding species (*5*).

Bryozoan skeletal morphology accurately delimits biological species as confirmed by genetic analysis (*6*), but higher-order systematics are in shambles due to repeated convergent evolution of structures used to define major lineages. In this issue of *Science Advances*, Orr *et al.* (*7*) have at last resolved their evolutionary history through construction of the first comprehensive phylogeny of all bryozoans with detailed relations among cheilostomes.

To construct their phylogeny, the authors sampled genomes from 395 bryozoan specimens and combined this molecular data with 340 already known bryozoan genome sequences. All told, they sampled 40% of cheilostome genera and 10% of species. Remarkable science can be done with phylogenies of this breadth. Nodes represent common ancestors between species and genera at branch tips, and those with known fossil records can be pinned down in time to calibrate molecular clocks. By combining fossil dates with models of mutation rate, clock models yield estimates of ages for all nodes on the tree. Geological ages of fossils are never as old as the origin of a group due to vagaries of sampling, but a time-calibrated tree can reveal evolutionary events absent from the fossil record. For example, until last year (*8*), bryozoan fossils were unknown from the Cambrian period (539 to 485 million years ago), when all other durably skeletonized major phyla first appear. Their recent discovery impressively matches predictions of their Cambrian occurrence based on the phylogeny by Orr *et al.*

Time-calibrated molecular phylogenies are fundamental to resolving questions about origins and rates of change. Taylor (*5*) attributed radiation of advanced cheilostomes to origin of parental brooding of nonfeeding larvae about 110 million years ago. But his hypothesis was untestable because brooding evolved independently within many lineages whose evolutionary relations were unknown. Orr *et al.* have now established those relationships. They find that over 100 million years, about one-fifth of all new species may have independently evolved brooding. Contrary to Taylor's hypothesis, this high transition rate is not matched by more rapid diversification of brooders. But

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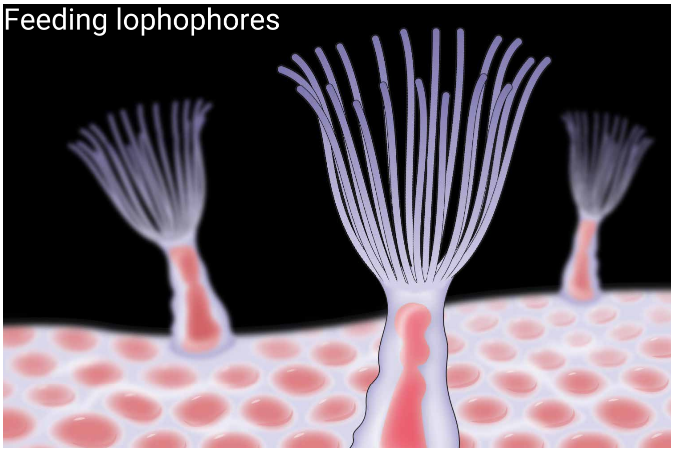

Fig. 1. Bryozoans are tiny, structurally complex organisms that live in colonies made up of modular, skeletonized living chambers called zooids. These microscopic homes allow their inhabitants to pop out to feed on plankton and then retreat if danger threatens. Within a single colony, multiple types of zooids may occur. The research by Orr *et al.* (*7*) offers a way to quantify the rich diversity and evolution of these important sea floor creatures. Credit: Ashley Mastin/*Science Advances*

brooding is associated with a tendency for short distance dispersal that is correlated with heightened diversification. Among other ecologically important traits associated with brooding are the myriad ways that cheilostomes bud new zooids during growth and with polymorphism.

Bryozoan polymorphism refers to occurrence of multiple body types of zooids that may occur within a single colony. Determining the origin and evolution of polymorphism is challenging because zooid budding is clonal so that different polymorphs are genetically identical. As with brooding, it is unknown how many convergent origins of similar appearing polymorphs exist among bryozoans. The number is likely high because relatively few, but distantly related, species take the number of different kinds of polymorphs to extremes (*9*, *10*). The contribution of Orr *et al.* now provides a means to better understand bryozoan polymorphism.

Animal evolution is commonly studied in specialized academic silos with little interaction among researchers working on living representatives, fossils, genomics, anatomy, systematics, and macroevolution. Bryozoan research has always bucked that trend as bryozoan researchers realized early on that we would fail to understand their evolution and diversity without the perspective of their deep history (*1*, *2*, *6*). Orr *et al.* continue this tradition, proving anew that integrative and cross-disciplinary work can succeed at answering old evolutionary questions and setting the stage to ask new ones.

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