Reports

Coral-Bryozoan Mutualism: Structural Innovation and Greater Resource Exploitation

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Shell-encrusting species of the coral *Aulopora* and the bryozoan *Leioclema* changed ecological guilds and escaped limits imposed by substrate size through mutualistic intergrowth during the Early Devonian. Where colonies of these species intergrew, they produced upright, arborescent masses consisting of sparsely branched uniserial *Aulopora* sp. entirely covered, except for calyx openings, by a thin encrustation of *Leioclema* sp. These intergrowths appear to constitute a mutualistic association with benefits including escape from limited space on the substratum into a higher tier of suspension feeders, as well as more modules per colony. Such mutualism between benthic modular competitors may have developed more readily than associations between solitary competitors.

FEW MUTUALISTIC BIOTIC INTERACTIONS have been firmly demonstrated relative to the number of known predator-prey or other interactions, and this is especially so among fossil examples. Symbiotic associations between fossils (for example, bryozoan-boring "worm," bryozoan-hermit crab, coral-stromatoporoid, brachiopod-cornulitid, and bryozoan-nautiloid) are reported commonly, but with the probable exception of zooxanthellae inferred for shallow tropical marine invertebrates (*1*), clear examples of mutualism are rare or lacking from the fossil record. In contrast, predator-prey and competitive interactions among a succession of species within higher level taxa are relatively well known and appear to be evolutionarily "stable" despite species turnover (*2*). This disparity in documented frequency of convincing mutualistic versus predator-prey or other interactions as observed in the fossil record is consistent with ecological models that predict mutualism to be less easily developed and unstable relative to predator-prey and competitive interactions (*3, 4*). We describe an example of facultative mutualism in which colonies of two species encrusting limited substrata evolved the ability to expand their niches cooperatively, thereby changing guilds and escaping the limits imposed by substrate size.

The Lower Devonian Birdsong Shale Member of the Ross Formation in western Tennessee represents a shallow marine shelf accumulation of terrigenous mud containing autochthonous skeletal carbonate debris (*5*). Diverse encrusting organisms for which availability of space was limiting include the tabulate coral *Aulopora* sp. and the trepostome bryozoan *Leioclema* sp., both of which formed encrustations of less than or equal to 2-mm thickness where they occur in isolation. Contact of encrusting linear chains of *Aulopora* sp. and encrusting sheets of *Leioclema* sp. resulted in overgrowth of the coral by the bryozoan so that corallites were completely covered, except the calices which were occupied by coral polyps, similar to encrusting and lobate intergrowths of auloporids and other bryozoans in younger Devonian strata (*6*). However, the coral-bryozoan intergrowths of the Birdsong Shale commonly grew upright, forming arbores-

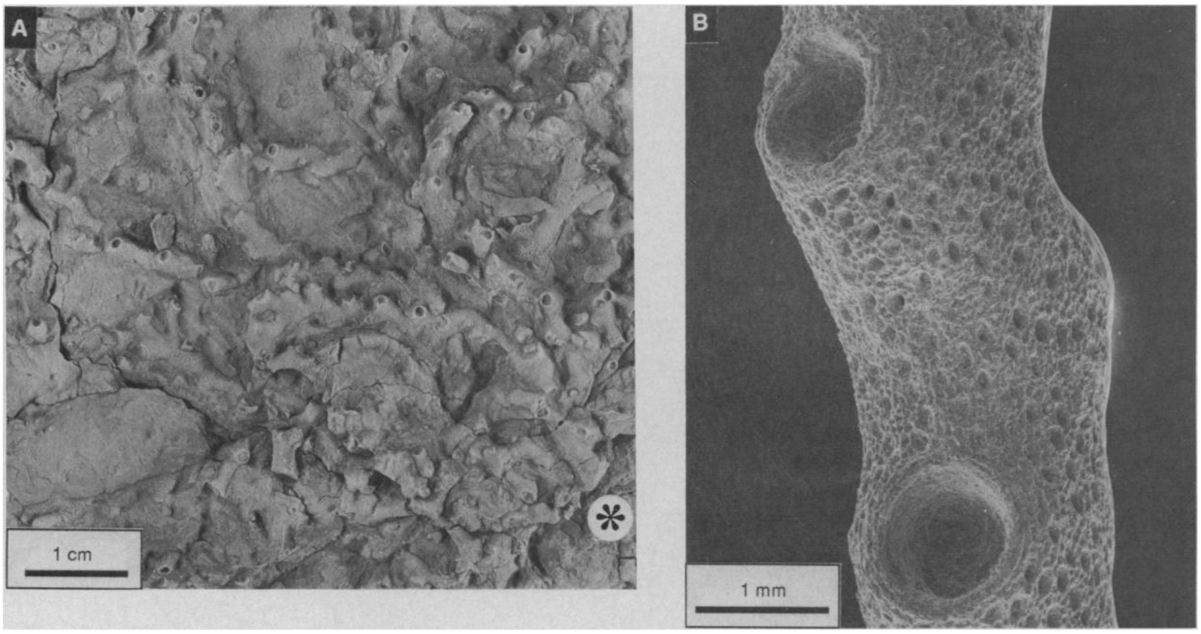

Fig. 1. Arborescent intergrowths of the tabulate coral, *Aulopora* sp. and the trepostome bryozoan *Leioclema* sp. from the Birdsong Shale Member of the Ross Formation (Lower Devonian), Parsons Plant Quarry, Vulcan Materials Corporation, 35°4'N, 88°7'W, Jeanette 7 1/2' Quadrangle, Tennessee. (**A**) Portion of an extensive intergrowth, with branches radiating from the region marked by an asterisk; spaces between branches are filled by a matrix of siliciclastic and lime mud; entire specimen is 13 cm high and 20 cm wide; U.S. National Museum (USNM) 445759; (**B**) detail of a single branch, showing bryzoan overgrowth tapered toward and terminating around coral calices; USNM 445760.

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cent "supercolonies" up to about 20 cm in height and diameter. More than 50 such "supercolonies" have been encountered at a single locality. These intergrowths consisted of branches of uniform width, formed from a single series of *Aulopora* corallites around which grew a continuous cortex of *Leioclema* (Fig. 1). The calices of the coral opened alternately on opposite sides of the branch and were the only parts of the skeletons not engulfed by the bryozoan.

Growth upward into the water column requires the ability to extend vertically and the strength or elasticity to counter shearing forces generated by laterally moving water. The bifurcating uniserial *Aulopora* colonies provided the means of branch extension and multiplication, but where each rigidly calcified, distally expanding corallite budded from its immediate predecessor, its diameter averaged only 0.5 mm (n = 66, SD = 0.20 mm). Encrustation by *Leioclema* sp. increased minimum branch diameter to 2.4 mm (n = 49, SD = 0.73 mm), thereby providing a greatly increased section modulus to the branches. Arborescent growth for either of the two species appears to have occurred only where the bryozoan grew around and strengthened the base of each corallite.

Escape from the substratum by the coral-bryozoan intergrowth provided several benefits to both species. The new growth form elevated the colonies from 2 mm or less elevation to the 10- to 20-cm tier of Middle Paleozoic suspension-feeding guilds (*7*), giving access to nutrients in a part of the water column that was formerly unavailable. In addition, increase in surface area and in rate of increase of surface area of arborescent colonies exceeds that of encrusting colonies of similar diameter beginning at early growth stages (*8*), and the coral-bryozoan intergrowth could grow to a colony diameter that far exceeds (up to an order of magnitude) the diameter of the host shell from which it grew. Furthermore, arborescent growth raises the interacting colonies above the surface of sediment accumulation where the feeding apparatuses could be more readily clogged, and above the solid substrate island where competition for space would have been more intense than within the canopy (*9*).

The interspersed distribution of *Aulopora* calices and *Leioclema* apertures would mutually benefit the two species. Bryozoans generate a flow of water toward their colony surfaces with their ciliated tentacles and feed predominately on the phytoplankton carried in that flow. Large surface areas of bryozoans function most efficiently where there are regularly distributed chimneys, which are localized regions for outflow of filtered water from the colony (*10–14*). The calices of the *Aulopora* are regularly distributed along branches at approximately 3.5 mm (n = 67, SD = 0.60 mm) and average 1.3 mm in diameter (n = 70, SD = 0.15 mm). This spacing and size fall within the range of chimmey spacing and diameter in living bryozoans (*14, 15*) and is also consistent with spacing of maculae, which are surface disruptions in large Paleozoic bryozoan colonies that are thought to represent chimney locations (*10, 13*). The *Aulopora* calices protruded above the surface of the encrusting *Leioclema* and apparently served as chimney sites, saving the bryozoan the cost of secreting skeleton and maintaining the areas of most chimneys.

Corals are carnivorous suspension feeders that do not generate substantial feeding currents. Therefore, the *Aulopora* polyps benefited from the feeding activities of the *Leioclema* because almost all water drawn toward the branches was delivered to the polyps, the bryozoans having removed a largely different part of the plankton than that required by the coral. Some bryozoans with large lophophores have been observed to capture zooplankton (*11, 14, 16, 17*), but spacing between *Leioclema* zooecia suggests that the species was characterized by small lophophores, so feeding competition should have been minimal (*18*). Furthermore, the bryozoan-generated currents would have prevented the accumulation of concentrations of metabolic wastes near coral colonies, even during times of low ambient current flow.

It has been suggested that coevolutionary relationships between species, particularly within a guild where there is competition for shared resources, may be founded rapidly within local populations (*19*), although they might not be expected to survive on a global scale. It has been further suggested that mutualism might be particularly favored in environments where resources are severely limiting (*20*) and if the interacting species are clonal (*21*). The *Aulopora-Leioclema* arborescent intergrowths conform to all three predictions (*22*).

In the living marine fauna, some species of encrusting cnidarians and bryozoans are known to form mutualistic intergrowths (*23*), resulting in competitive advantages for both species, without a fundamental change in growth form. Presence of the hydroid *Zanclea* increases probability that a host bryozoan overgrows competitors while apparently costing the bryozoan only the energy used to build a calcareous tube over the creeping stolon of *Zanclea*. The hydroid benefits by having a protective skeleton constructed for its stolon as well as from the absence of spatial competitors on the bryozoan's feeding surface. Its costs appear only to be the energy required to attack the bryozoan's competitors along the periphery of the host colony with its nematocyst-laden tentacles.

The *Aulopora-Leioclema* intergrowths support the hypothesis (*21*) that, among hard-substrate benthos, interspecific mutualism is more readily attained by colonial or modular organisms than by solitary organisms. The developmental plasticity and indeterminate growth of modular organisms allows them to alter their overall form and behavior upon encounter with competitors (*24*). Mutualistic intergrowth of colonies should be possible or even probable where colony form permits use of the same substrate space, and behavior of each interacting species can be used to the advantage of its counterpart.

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Twinning in $MgSiO_3$ Perovskite

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Crystals of $MgSiO_3$ perovskite synthesized at high pressures and temperatures have orthorhombic symmetry under ambient conditions. Examination by transmission electron microscopy shows that the microstructure of crystals synthesized at 26 gigapascals and 1600°C is dominated by a large number of twin domains that are related by reflection operations with respect to {112} and {110} planes. These twins may be associated with the transformations of $MgSiO_3$ perovskite from the cubic to tetragonal and tetragonal to orthorhombic phases, respectively, upon decreasing pressure and temperature. These observations suggest that under the experimental synthesis conditions, and perhaps in the earth's lower mantle, the stable phase of $MgSiO_3$ might have the cubic perovskite structure.

Many materials with ABX_3 compositions and perovskite-type structures undergo sequences of crystallographic phase transitions (*1*) from high- to low-symmetry forms on decreasing temperature, for example, $SrTiO_3$ (*2*), $CsPbCl_3$ (*3*), $NaMgF_3$ (*4*), and $CaTiO_3$ (*5*). These transitions are commonly associated with dramatic changes in magnetic, electric, thermal, and elastic properties and thus are of great interest in materials science and condensed matter physics. Optical and electron microscopy studies indicate that twinning is the predominant microstructural feature in the lower symmetry polymorphs of these perovskites, and the presence of these twins may have important consequences for the physical properties of these materials (*6*).

High-pressure, high-temperature experiments suggest that $(Mg,Fe)SiO_3$ perovskite is the dominant phase of the earth's lower mantle [pressures above 23 gigapascals (GPa) and depths of 670 to 2900 km (*7*)] and, therefore, probably the most abundant mineral of our planet. X-ray diffraction studies of specimens recovered from the experiments have revealed that at ambient conditions the crystal structure is orthorhombic (space group *Pbnm*) and isostructural with the $GdFeO_3$ structure (*8*); these specimens have also been studied by vibrational spectroscopy (*9*), x-ray absorption spectroscopy (*10*), electron diffraction (*11*), and high-resolution electron microscopy (*12*). Most of these analyses have been performed under conditions at which $MgSiO_3$ perovskite is thermodynamically metastable. Under laser irradiation (*9*) or heating above 150°C (*13*) at 1 bar, single crystals have been observed to twin and then rapidly to amorphize. Application of nonhydrostatic stress also can cause twinning in single crystals (*14*). In this report, we characterize the observed twin laws in $MgSiO_3$ perovskite by transmission electron microscopy (TEM) and discuss the implications of twinning for the physical behavior and possible polymorphism of perovskite in the mantle.

We synthesized polycrystalline specimens of $MgSiO_3$ perovskite (0.9 mm in diameter and 1.5 mm in length) from enstatite powder starting material in a 2000-ton uniaxial split-sphere apparatus (USSA-2000) (*15*) following cell designs and techniques developed by Ito and Weidner (*16*) but without adding water to the capsule. Samples were elevated to 26 GPa and 1600°C for 0.5 to 2 hours and either quenched immediately or cooled to 1200°C at a rate of 30°C per minute before quenching. Thin foils were prepared by Ar ion-milling of thin sections (*17*) for observation in a JEOL 200CX transmission electron microscope that was operated at 200 kV. Electron diffraction confirmed that the recovered $MgSiO_3$ perovskite is isostructural with $GdFeO_3$ (space group *Pbnm*). The lattice dimensions are

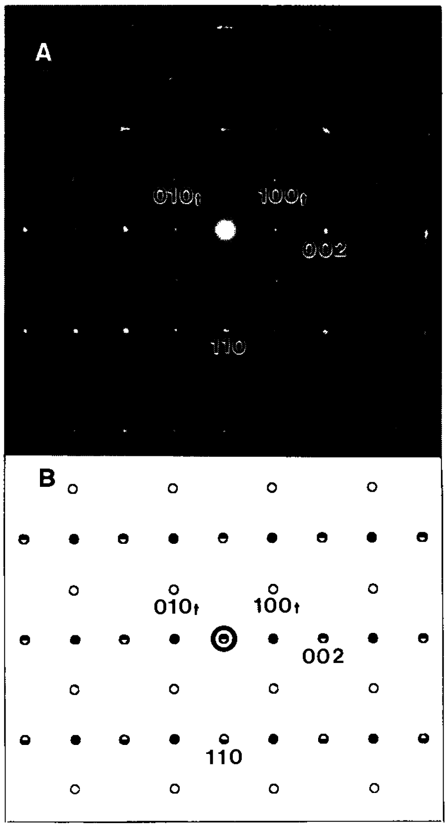

Fig. 1. (**A**) Selected-area electron diffraction (SAED) pattern of $MgSiO_3$ perovskite showing $(\bar{1}12)$ twinning. Diffraction spots (100_t and 010_t) corresponding to the twinned (t) crystal are indicated. (**B**) Schematic of diffraction pattern in (A). Solid circles are diffraction spots from a single crystal domain; open circles are spots attributed to $(\bar{1}12)$ twinning. Patterns viewed along the $[1\bar{1}0]$ zone axis of the matrix (solid spots). Half-filled symbols represent overlapping spots.

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