Photo 1:
Massive coral colonies, like the *Acropora* seen in this photo, are characteristic of photosymbiotic corals. The graininess of the image is caused by high plankton content in the seawater. Black Tip Reef, Daymaniyat Islands National Park, Oman. Depth approx. 12 meters

# Coral Reefs

**They usually are less than a centimeter in diameter, but they can build colonies sometimes running kilometers in length. How do corals manage these massive feats of construction, and what part do single-cell algae play?**

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Of all ecosystems existing on the Earth, coral reefs are considered the most complex. The largest of them occur in the tropics, in shallow and warm waters that are fully saline (above 35‰). The Great Coral Reef along Australia's eastern shoreline runs for more than 2000 km, sometimes reaching more than 200 km in width. It is not a uniform structure, but instead consists of many (more than 3,000) different atolls and reefs. It is the largest biological structure on the Earth.

Corals are the main builders contributing to reefs, although sponges and algae forming calcareous skeletons also play a significant role. The skeletons of corals are likewise made of calcium carbonate. Although some corals live individually, most of them are colony-forming animals, and these are the ones we will be considering in this article.

## Photosynthetic speed

Colonies range in size, sometimes reaching several meters in diameter, but the dimensions of individual coral polyps rarely exceed a centimeter in diameter.

Photo 2:
Flat and bushy coal colonies act like "solar panels," making it significantly easier for their symbiotic algae to photosynthesize, and therefore easier for them to build their skeletons. The Tatawa Besar Reef, Komodo National Park, Indonesia. Depth approx. 3 meters

Photo 3:
Longitudinal section of a tabulate coral fossil. The dark vertical elements represent the skeleton between individual polyps, and the numerous horizontal partitions are known as *tabulae*. The lower density bands and increment above indicates the annual growth, whereas the upper density bands show initial growth in the next year. The scale of the image is about 20 mm top to bottom, and so judging by the pace of growth (10-20 millimeters per year), this type of coral was presumably photosymbiotic. From a glacial erratic boulder near Warsaw, most likely from the Silurian (about 420 million years ago)

Corals secrete an external skeleton which is covered by a thin "skin" of soft tissue. As they deposit successive layers of skeleton underneath their bodies, and the colony slowly grows.

How is it that such small organisms are capable of building such major structures? Coral polyps build their skeletons by "capturing" calcium ions and hydrocarbon ions out of the seawater, which form from the dissociation of carbonic acid. The secret behind why corals are now so dominant in reef-building lies in the symbiotic relationship they have developed with a certain group of algae (a relationship called "photosymbiosis"). In modern corals, these are mainly endosymbiotic dinoflagellates from the genus *Symbiodinium*, known as "zooxanthellae." They reside in the tissues of their host, carrying out photosynthesis when light is present. They absorb carbon dioxide from the microenvironment around the coral, thereby reducing its concentration and also the concentration of carbonic acid. That, in turn, raises the alkalinity of the water immediately surrounding a coral enough to enable the process of building a carbonate skeleton to proceed much faster than without such interspecies cooperation. Skeleton growth in corals without symbiotic algae ("azooxanthellate" corals), such as *Balanophyllia regia*, a coral from the moderate waters of the Atlantic, have been found to grow less than 2 millimeters a year, whereas photosymbiotic corals usually grow at a pace of upwards of 10 or 20 millimeters per year – a tenfold difference in speed. We can therefore say that coral reefs owe their ability to grow quickly to these single-cell algae.

We can take this last assertion even further, as the algae's assistance is not limited to skeleton growth. Studies have shown that the zooxanthellae "share" the organic substances produced in the process of photosynthesis, supplying even as much as 90% of the coral's energy needs. How do the algae benefit from the arrangement? The coral polyp provides shelter and supplies (nearly directly) carbon dioxide from its respiration and the products of its metabolism (mainly nitrates). The gains are therefore mutual.

## Ancient corals tell their story

Coral reefs are structures that emerge over hundreds of thousands, even millions or years. The question arises, therefore, of how long ago the phenomenon of photosymbiosis first arose, in other words how old the special relationship between corals and certain algae is. The first large reefs that corals contributed

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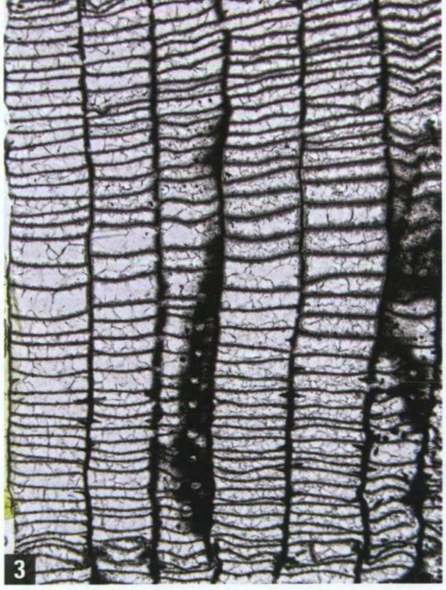


to appeared on the Earth back in the late Ordovician, around 460 million years ago. Unfortunately, the cells of symbiotic algae are not preserved in the fossil record, and so evidence of their presence has to be sought in the fossilized skeletons of their potential hosts.

The oldest reefs differed significantly from those we see today. They were built mainly by microorganisms and sponges, with corals making a smaller contribution than they do to modern reefs. The class of corals is subdivided into three subclasses: Scleractinia, Rugosa, and Tabulata. The former (also known as stony corals), which have built our modern-day reefs, did not become widespread until the Triassic (around 240 million years ago). Their earlier fossil record is unclear, although they are thought to be much older and to have lived in parallel with representatives of the other groups. The corals that built reefs back in the Paleozoic were from the other two suborders, Rugosa and Tabulata. Rugose corals, or "horn" corals, were somewhat similar to those of today, whereas tabulate corals formed horizontal internal partitions (*tabulae*). Both Rugosa and Tabulata went extinct 250 million years ago, making way for Scleractinia as the architects of modern reefs.

If the presence of symbiotic dinoflagellates speeds up calcification, the first clue attesting to their presence in a coral should be rapid skeletal growth. Studies of the cyclical (seasonal) growth increments in tabulate corals have shown that some species were capable of growing by more than 20 millimeters a year, similar to the pace of modern photosymbiotic corals. In certain groups of tabulate corals, however, there were species that only grew in increments of a few millimeters a year, like today's *Balanophyllia*. And so, judging by these growth rates, we can conclude that at least some fossil corals already had symbiotic algae.

## Those clever dinoflagellates

The amazing architectural feats that photosymbiotic corals are capable of are essentially unattainable for azooxanthellate corals, whose colonies rarely exceed 20 centimeters (although individual species are capable of building colonies a few times that size). Palaeozoic corals exhibit a full range of sizes – from small colonies of a few centimeters to large structures over 1 meter. This is one more observation supporting the hypothesis that dinoflagellates were contributing to some of them.

Research by the geochemist Peter Swart (1983), later in collaboration with coral specialist George Stanley, showed that the presence of symbiotic algae leaves behind a trace in the isotope composition of coral skeletons. Naturally-occurring carbon dioxide mainly contains the stable carbon isotope $^{12}C$, with $^{13}C$ also occurring in small amounts. Zooxanthellae "prefer" to use carbon dioxide with the lighter isotope $^{12}CO_2$ for photosynthesis, which causes the environment to become relatively enriched with the heavier isotope ($^{13}CO_2$), available to the coral polyps in building their skeletons. Oxygen isotopes can also provide some information. Zooxanthellate corals occur mainly in tropical waters, where water molecules with the lighter oxygen isotope, $^{16}O$, evaporate more easily, leaving tropical seas with slightly higher concentrations of the heavier isotope, $^{18}O$. Again, coral skeletons become enriched with the heavier isotope.

By studying the isotope composition of fossil coral skeletons, it was first demonstrated that the symbiosis with algae most likely arose at the end of the Triassic, slightly more than 200 million years ago (Stanley and Swart, 1995). Preliminary research of the skeletal geochemistry of Palaeozoic corals and such anatomic traits as their growth increments, colony size and structure (which also differ somewhat when symbionts are present) have enabled the present author to show that many of them also must have hosted single-cell algae (Zapalski 2014). And so, the reef-building mechanism based on cooperation between corals and algae most likely arose 430 million years ago.

But what types of algae were contributing to building those Paleozoic reefs? Molecular research on zooxanthellae has shown that dinoflagellates from the genus *Symbiodinium* most likely appeared in the early Eocene (around 55 million years ago), and so the symbiotic algae that were involved in building older reefs must have been different. The natural candidates are other dinoflagellates, although single-cell green algae also occur in some organisms (including anemones, close relatives to the corals). Studying the organic matter present in fossil skeletons offers some chance of resolving this as-yet unsolved mystery.

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