

Solar Symbionts

by John E. Parkinson, Ph.D. and Todd C. Lajeunesse, Ph.D.

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EDITOR'S PAGE

Waking up to the dinoflagellates in our reefs



ook deep into nature, Albert Einstein once advised, “and then you will understand everything better.” In that spirit, this issue comes to us thanks to some 140 years of curious biologists looking deeper into the lives of corals and other marine animals that harbor tiny, micro-algae cells known to most of us as zooxanthellae.

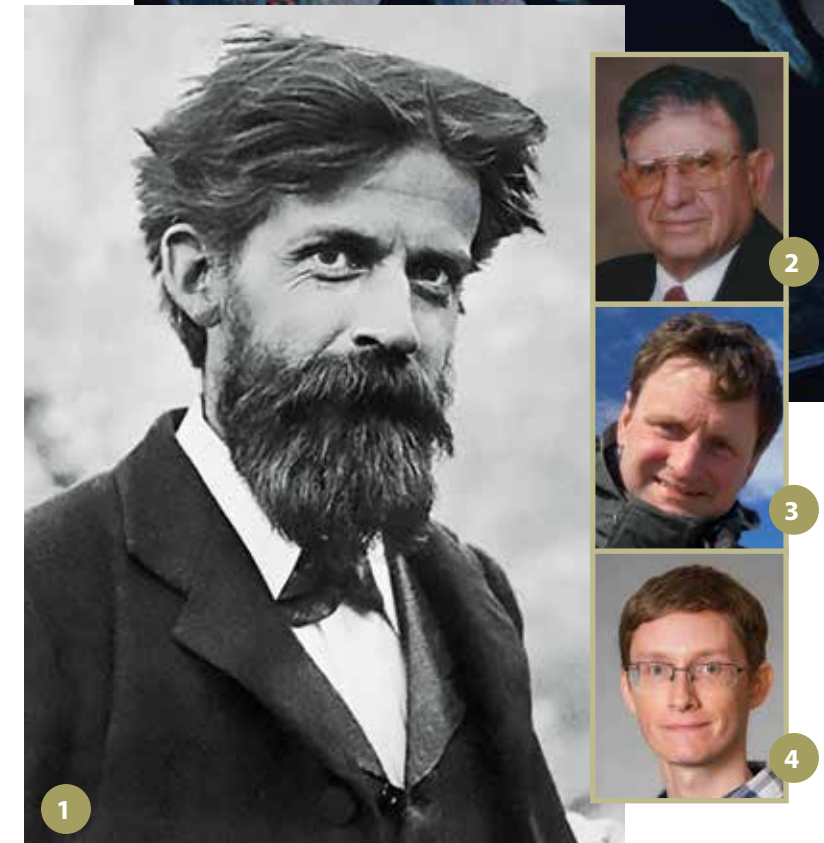
Proper science now refers to them as Symbiodiniaceae, but whatever we call them, these microscopic orbs and their complicated life histories have aroused the curiosity of a long series of brilliant scientists. Dr. Todd LaJeunesse, co-author of this issue’s cover story with Dr. John Parkinson, traces our understanding of zooxanthellae back to the early 1880’s and a Scottish zoologist, Sir Patrick Geddes. According to a recent journal article by Dr. LaJeunesse:

“Geddes’s insight on the mutualistic nature of these yellow cells in animals and protists (*Nature*, 1882) surpassed that of his contemporaries who generally regarded these cells as parasites.... It was Geddes who unequivocally recognized the full significance of the evidence before him. In ascribing the associations as animal lichens, he declared eloquently:

“Such an association is far more complex than that of the fungus and alga in the lichen, and indeed stands unique in the physiology as the highest development, not of parasitism, but of the reciprocity between the animal and vegetable kingdoms.

“Thus, then, for the vegetable cell no more ideal existence can be imagined than that within the body of an animal cell of sufficient active vitality to manure it with carbonic acid (=CO₂) and nitrogen waste, yet of sufficient transparency to allow the free entrance of the necessary light. And conversely, for an animal cell there can be no more ideal existence than to contain a vegetable cell, constantly removing its waste products and supplying it with oxygen and starch....” (*References*, page 46.)

As marine aquarists, we have ringside seats to the ongoing study of this fascinating symbiotic relationship. Many of us fondly remember the renowned and delightful Dr. Hugo Freudenthal, who erected the genus *Symbiodinium* in 1962 and who attended a number



Leaders in Symbiodiniaceae research, 1882–present: (1) Sir Patrick Geddes [1854-1932]; (2) Dr. Hugo D. Freudenthal [1930-2021]; (3) Dr. Todd C. LaJeunesse; (4) Dr. John E. Parkinson.

Top: High-resolution image by Brett Lewis of *Pocillopora* polyps shows masses of *Symbiodinium* sp. endosymbionts (small orange-pink spheres) in the coral’s endodermal tissues.

of Marine Aquarium Conference of North America (MACNA) gatherings prior to his death earlier this year.

We welcome Drs. John Parkinson and Todd LaJeunesse to these pages, and we invite readers to join them in looking more closely at the hidden solar symbionts that lurk by the billions in our reef aquariums and whose health and vitality spells life or death for corals in captive systems and in the wild.

—James Lawrence Shelburne, Vermont

PATRICKGEDDES.CENTRE.ORG.UK; CORAL: BRETT LEWIS/QUEENSLAND UNIVERSITY OF TECHNOLOGY

SOLAR SYMBIONTS

Casting new light on the ancient partnership of reef-building corals and the micro-algae known as zooxanthellae, family Symbiodiniaceae

by John E. Parkinson, Ph.D. and Todd C. LaJeunesse, Ph.D.



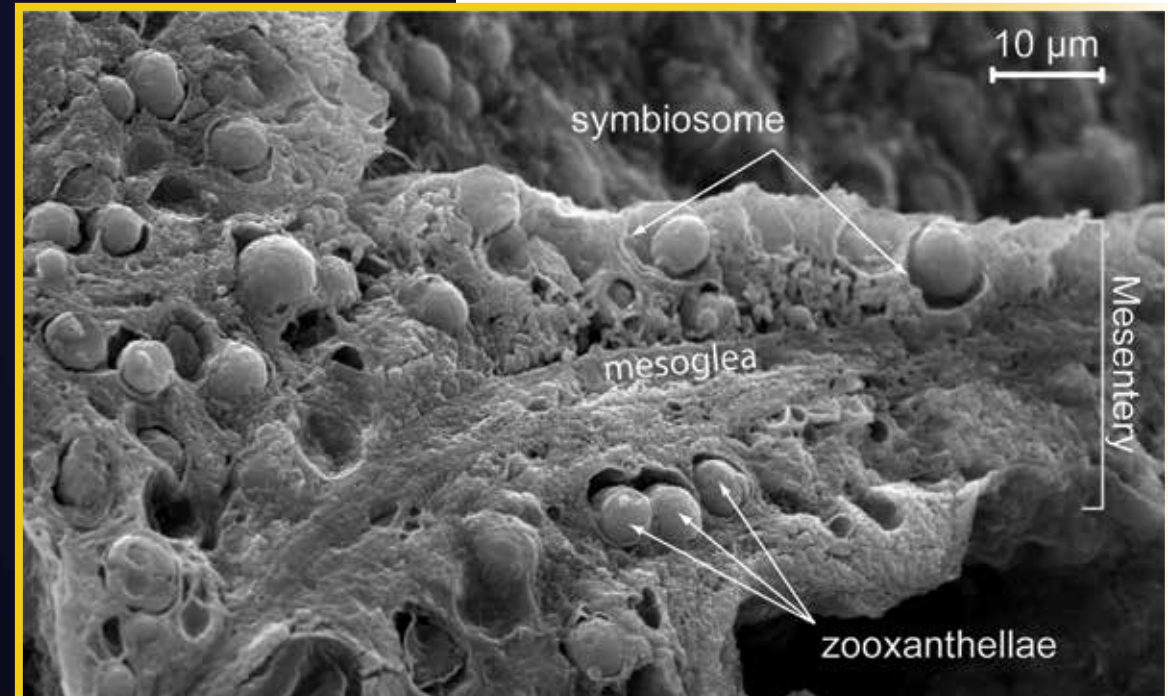
Sir Patrick Geddes, circa 1888, the Scottish zoologist who first described the mutualistic nature of the relationship between microscopic, golden algal cells and the marine invertebrates that host them.

“The sun does not shine for a few trees and flowers, but for the wide world’s joy.”

— Henry Ward Beecher



Elkhorn Coral, *Acropora palmata*, spreads its massive branches to collect solar energy on a Caribbean reef. Inset: Microscopic endosymbiont cells, colloquially known as zooxanthellae, family Symbiodiniaceae.



Inset above: Zooxanthellae reach high cell densities through prolific mitotic division in the endodermal tissues of many shallow tropical and sub-tropical cnidarians. This is a SEM (scanning electron microscope) image of a freeze-fractured internal mesentery from a reef coral polyp (*Porites porites*) that shows the distribution and density of symbiont cells. Image: Tye Pettay, University of South Carolina.

Left: Multicolored polyps of a “SBB Half Baked” *Acropora tenuis* colony in the reef aquarium of Shane Backer and photographed by Michael Vargas. The bright blue, purple, bright green, and yellow colors seen in corals result from animal-derived pigments produced by the cnidarian tissues and not derived from the micro-algal symbionts.

Take a look at any of the best coral displays in reef aquaria around the world and you’ll notice a common thread: excellent lighting. With recent improvements in our capacity to manage water quality, flow, and, most importantly, light levels, increasingly diverse coral communities are being cultivated in captivity. While sophisticated, high-intensity lighting systems enhance the look of any reef tank, illumination serves more than just an aesthetic role. Exposure to appropriate wavelengths of light is critical for the welfare of live coral growing in aquarium settings.

Corals—especially Scleractinian or stony corals—have always fascinated seafarers and biologists alike. How do these “simple” soft-bodied animals create such large skeletons? Today, we can zoom in and see that reef-building corals are symbiotic with single-celled algae that live within the host animal’s tissues. These algae are minuscule and rely on light-driven photosynthesis to survive. In turn, the corals farm energy from the algae to

lay down skeletal material and grow. These micro-algae, colloquially known as “zooxanthellae,” or to science as Symbiodiniaceae, are truly remarkable organisms that enable corals to construct the vast reef ecosystems found in shallow, tropical seas across the planet.

The intricate associations between corals and zooxanthellae highlight why mutualistic symbioses are so important to Earth’s biosphere. Rather than look at a coral animal in isolation, biologists are now taking a more all-encompassing view of the coral holobiont—the coral itself and all the associated micro-organisms found on and within it: bacteria, archaea, fungi, viruses, and protists, and most importantly its dinoflagellate symbionts.

Whenever we show off our reef tanks, we have a unique opportunity to share this knowledge with others. Imagine: If you keep stony corals, you can truthfully claim to be culturing billions of dinoflagellates in your living room reef tank. All that expensive lighting is primarily driving symbiont photosynthesis. Science happens to be intensely

interested in Symbiodiniaceae right now, and here we offer a view of what we know and are learning, in hopes that this information will help you better understand the zooxanthellae in your reef aquarium and inspire you to tell this story to those who might not be aware of it.

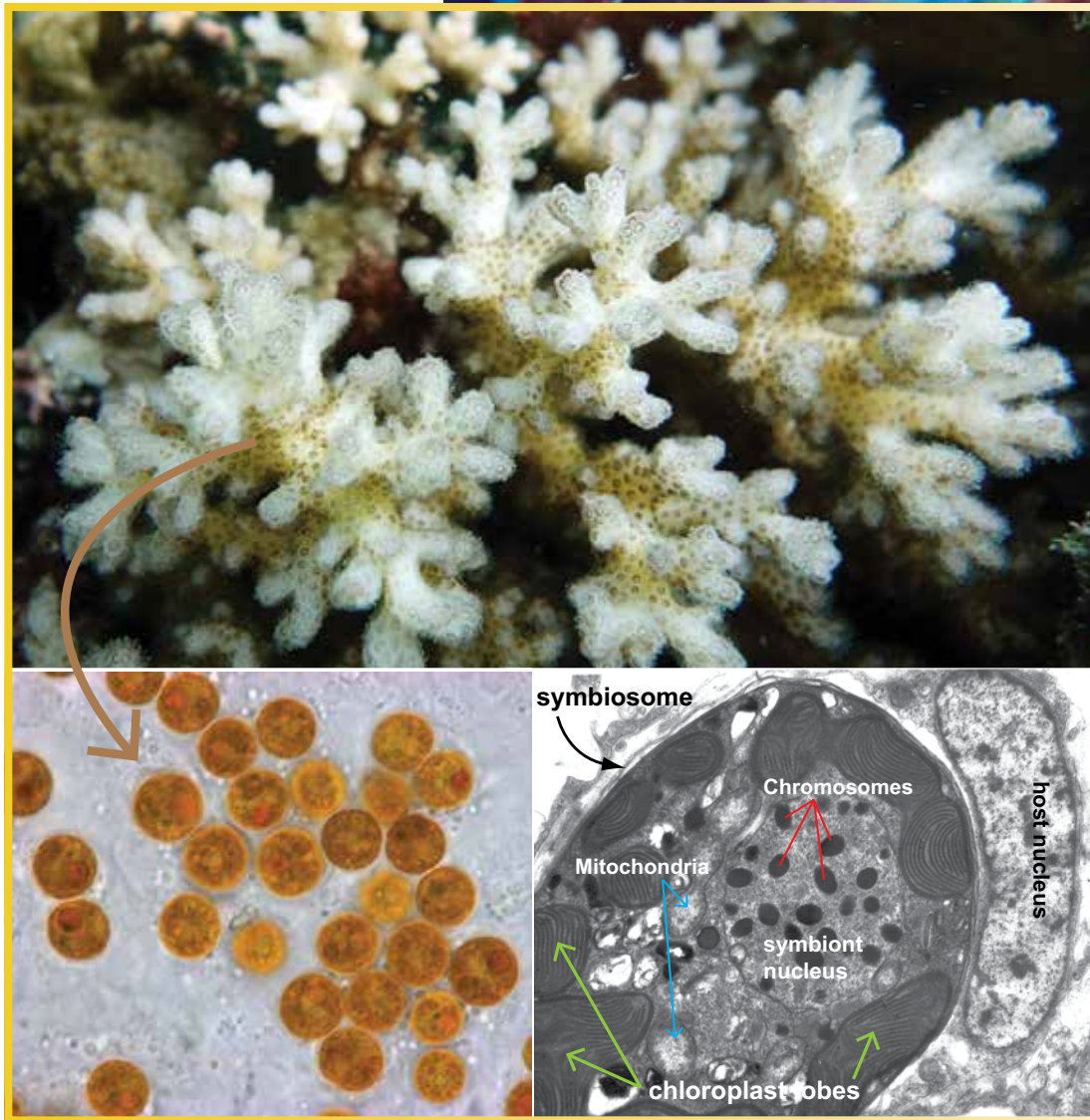
IDENTITY AND LOCATION OF CORAL PHOTOBIONTS

The word zooxanthellae (*zoo-zan-THELL-ee*) is a historical name dating back to the late 1800s. It was applied to any micro-algae with brown pigments, including symbiotic dinoflagellates that associate with corals, as well as diatoms and other photosynthesizing protists that do not typically associate with animal hosts. These days, we don’t use “zooxanthellae” in the scientific literature as often as we used to. From a scientific standpoint, the naming system for zooxanthellae found in most animals has recently undergone major changes. The group is now recognized as a large family

of numerous genera whose origins date back to the time of the dinosaurs. The symbionts that associate with stony corals all belong to the same taxonomic family: Symbiodiniaceae (*sim-bye-oh-din-ee-AY-see-ee*). Technically, all Symbiodiniaceae are zooxanthellae, but not all zooxanthellae are Symbiodiniaceae. Efforts to describe different species with their own unique physiological and ecological attributes are ongoing. These species distinctions are important for scientists so we know exactly which organisms we’re studying and so we can accurately report on discoveries pertaining to each. These taxonomic and systematic distinctions may not be critical for hobbyists. In most instances, it’s fine to use the terms “zooxanthellae” or “Symbiodiniaceae” interchangeably—everyone should know what you mean.

Invertebrates that depend on photosynthesis for their health and growth harbor high densities of zooxanthellae—in the millions of cells per square centimeter of host tissue. These mutually beneficial partners exchange

TOP: MICHAEL VARGAS; INSET: TYE PETTAY, UNIVERSITY OF SOUTH CAROLINA BEAUFORT



The dinoflagellate symbionts (family Symbiodiniaceae) extracted from a *Pocillopora* colony. The intensity of brown pigmentation spotting the branches indicates where symbiont concentrations are highest. Symbionts range in size from 6 to 11 microns and occur in host tissues at densities of millions per square centimeter (lower left panel). The relationship is an intimate one where the symbiont lives inside the host cell. The transmission electron micrograph (bottom right panel) shows in cross-section a single symbiont cell with numerous chloroplast lobes at the cell's periphery in a host vacuole (symbiosome) appressed next to the host cell nucleus.

inorganic and organic nutrients. The algae transfer their photosynthetic products to the host, which is why corals without proper lighting soon perish. In corals, sea anemones, and jellies, these algal symbionts are located within the cells of the animal's inner tissue layer, referred to as the endodermis or gastrodermis, which is separated from the outer tissue layer (the epidermis) by a gelatinous matrix that glues them together. Only certain host cells contain algae, but when they do, usually one or two symbionts reside within, taking up most of the cell's volume. It's a very tight squeeze.

The densities of these symbionts per unit area vary considerably depending on the location on the colony, species of host, time of year, habitat depth (and thus light levels), and amount of nutrients in the surrounding water. Thin-tissue animals like acroporids or pocilloporids generally contain 1–3 million symbionts per square centimeter, while animals with thicker tissues or complex skeletons may

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contain several times more over the same area. In high-latitude reefs where seasonal fluctuations are greater, symbiont cell densities can fluctuate by about 20–30 percent between the late winter (with higher densities) and late summer (when densities are lowest). The addition of excess nitrogen over time can cause normal symbiont densities to double in experimental colonies, suggesting that the algae are somewhat nitrogen-limited within host cells.

Such biological and environmental factors likely affect symbiont densities in aquarium corals. Having too many or too few symbiont cells does not necessarily mean that a coral will receive fewer or more nutrients from its symbiont population. There is still much we don't know about the flux of nutrients in these mutualisms and how it is regulated. However, characteristics of the animal and the symbiont species, their unique compatibilities, and the environmental conditions all can have a large effect. While possessing far too few symbionts stresses the animal (i.e., coral bleaching), having too many symbionts due to growth caused by too much nitrogen in the water may also disturb the physiological balance important to the long-term stability of these mutualisms.

MICHAEL VARGAS

A rainbow of coloration in a healthy "Matt Orange Envy" *Acropora* colony in the reef aquarium of Shane B. Backer. Golden-brown undertones are provided by their zooxanthellae.



HOW A CORAL'S SKELETON FACILITATES THE CAPTURE OF LIGHT

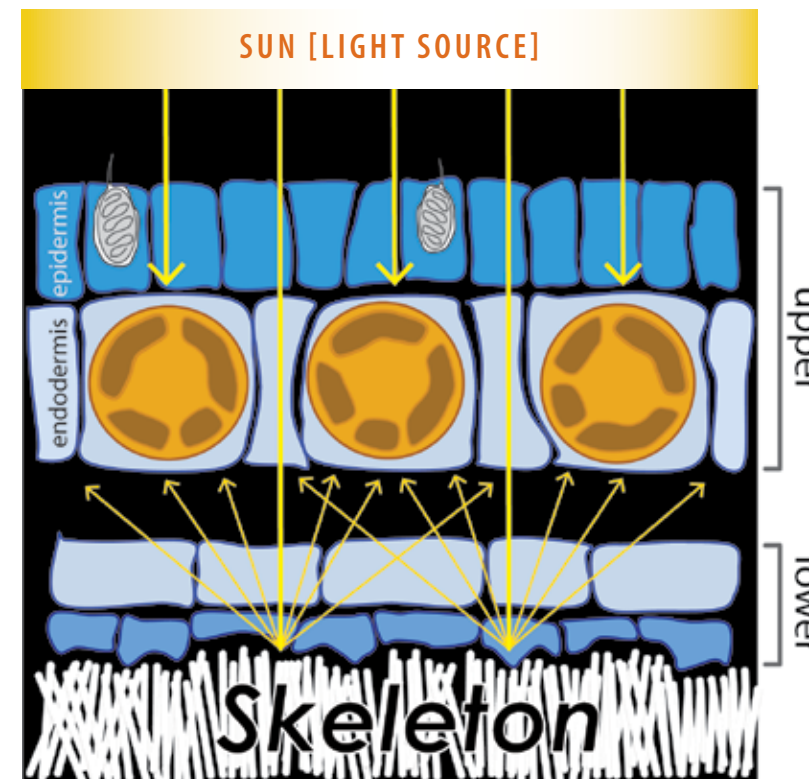
Coral colonies function as sophisticated solar panels. In stony corals, it's the lower epidermal cells at the bottom of the polyp that secrete the skeleton, which consists of calcium carbonate crystals arrayed in complex patterns. Light passes through the clear, thin layer of the upper epidermis to bathe the gastrodermal cells and their resident algae. Any light that penetrates deeper strikes the skeleton and reflects back into the upper gastrodermis, giving the symbionts a second chance at capturing stray photons. Thus, a coral's skeletal architecture enhances the efficiency of its symbionts in collecting solar energy. Indeed, corals are one of the most efficient light collectors in nature; they can absorb similar amounts of

radiation using a tenth of the photosynthetic pigments that land plants use. Modulation of the internal light conditions by the coral's skeleton may have emerged during the long evolutionary history of this mutualism. The trade-off to this impressive efficiency is that corals are easily stressed if there is too much light. Most instances of coral bleaching—which we typically associate with heat stress—are exacerbated by high-light conditions. Optimal lighting for many aquarium corals ranges from 250–400 $\mu\text{mol}/\text{m}^2/\text{sec}$.

THE ORIGINS OF CORAL-ALGAL MUTUALISMS

Modern-day stony corals appear as fossils in the mid-Triassic about 230 million years ago (MYA), but genetic evidence suggests that they might be much older.

BRETT LEWIS, QUEENSLAND UNIVERSITY OF TECHNOLOGY



Above: The simple cell layers of the host cnidarian animal. The upper epi- and endodermis create the top tissue layer that functions in prey capture (cells with nematocysts in the upper epidermis) and photosynthesis (symbiont cells in the phagocyte cells of the upper endodermis). Cells of the lower epidermis secrete proteins and pump calcium that assist in the formation of the skeleton, which acts as a sophisticated reflector that scatters light back up through the tissues, enhancing solar energy capture by the symbionts.

Opposite page: High-resolution image of retracted *Pocillopora verrucosa* polyps shows the distribution and densities of dinoflagellate endosymbionts (numerous small orange-pink spheres) in the coral animal's endodermal tissues. These symbionts have evolved and persisted with this host species for millions of years. Image composition obtained using A1R HD25 confocal fluorescence microscope (Nikon) with excitation wavelengths of 405 nm (DAPI), 488 nm (FITC), 561 nm (TRITC), 640 nm (CY5). Image: Brett Lewis, Queensland University of Technology

LAJEUNESSE AND PARKINSON

Nevertheless, diverse and abundant fossil coral reef communities are not evident until the Mesozoic Era. It would not be until the Middle Jurassic Period (~160 MYA) that coral diversity would undergo a major adaptive radiation in the oceans, when the dinosaurs were doing the same on land. Despite the fact that zooxanthellae do not fossilize, there is indirect evidence indicating that corals were symbiotic at this long-ago time. Because enzymes that drive biochemical reactions tend to favor specific isotopes, and these isotopes are captured in the host skeleton during calcification, it's possible to sample fossilized corals and infer which molecular processes were going on in the past. Analyses of the stable isotopes of oxygen in fossil coral skeletons indicate the presence of photosynthesis, and therefore they must have already evolved a dependency on symbiotic micro-algae.

The diversification and rise to dominance of modern-day corals can be traced back to the evolution of their symbionts and therefore constitutes an exceptionally old and enduring relationship. The major kinds of micro-algae



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that dominate phytoplankton assemblages in present-day oceans emerged about 200 MYA. Among important groups like diatoms and coccolithophores, dinoflagellates underwent an adaptive radiation that gave rise to many of the common dinophyte orders and families. It's perhaps no coincidence that coral-Symbiodiniaceae mutualisms evolved soon after this innovative time. However, the origins of this mutualism may have evolved out of what was initially a parasite-host relationship. Certain other dinoflagellates are parasitic, and this entire micro-algal group is closely related to the apicomplexans—a lineage that comprises only parasitic and pathogenic species, which cause diseases such as toxoplasmosis and malaria.

ANCIENT CLADES

Over time, the long evolutionary history of zooxanthellae has given rise to numerous divergent and very old lineages. Most of these have been assigned formal genus names. Currently there are 11 such names, but this number is likely to increase as systematic and taxonomic revisions continue. It is abundantly clear that the diversity of symbiodiniacean zooxanthellae is extremely high and comprises species with many different ecological attributes. For example, there are “specialist” species that are compatible with only one kind of host species. Other zooxanthellae display a much broader host preference and occur in many coral species. Some of these “generalists” occur in corals of the same family, while others are compatible with a variety of distantly related corals.

Most zooxanthellae are obligate (they can't survive long without their host partners), some are facultative (they are equally comfortable within hosts or out on their own), and others are entirely free-living, mostly surviving in bottom habitats like calcium carbonate sands or on the surfaces of seaweeds. Conversely, all reef-building (hermatypic) corals are obligate and thus die if separated from their symbionts, such as during prolonged bleaching events.

Stony corals associate with a subset of symbiodiniacean genera, including *Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium* (formerly Clades A, B, C, and D, respectively). By far, the most common zooxanthellae are members of the genus *Cladocopium* (meaning “of many branches”). This group is prevalent in every ocean and undoubtedly contains the largest number of ecologically distinct species. At the moment, five *Cladocopium* species are formally described, while hundreds remain undescribed. Most corals originating from the broader Indo-Pacific possess this kind of symbiont, and while some are extremely heat-tolerant, others are quite sensitive to hot temperatures. Alternatively, many corals from warm lagoonal habitats in the equatorial Indo-Pacific harbor symbionts from the genus *Durusdinium* (meaning “tough” and “whirling”). Species in this group tend to show remarkable thermal tolerance and animals that host them are less likely to bleach when stressed.

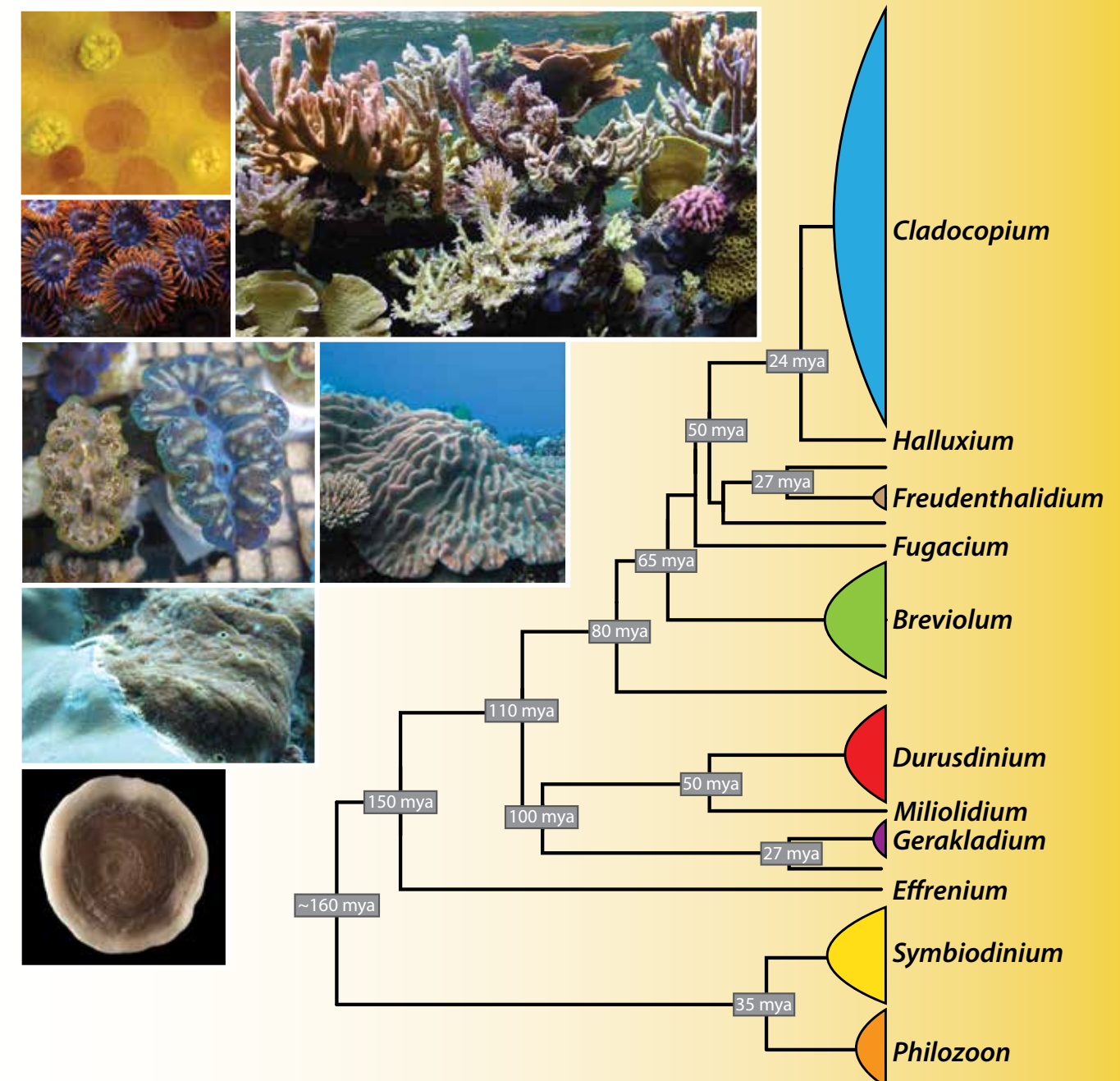
While the Symbiodiniaceae genera are extremely old, the present diversity within them, especially those species associated with cnidarians, is relatively young in

a geological sense. Major pulses of species diversification occurred over the past 5–6 million years. In this recent span of time (encompassing the Pliocene and Pleistocene Epochs), Earth has been at its coldest since the Carboniferous Period, over 300 MYA. This is perhaps why, in recent decades, many reef corals and their symbionts are so sensitive to episodes of unusually warm and rapidly rising temperatures causing mass bleaching and coral mortality around the world.

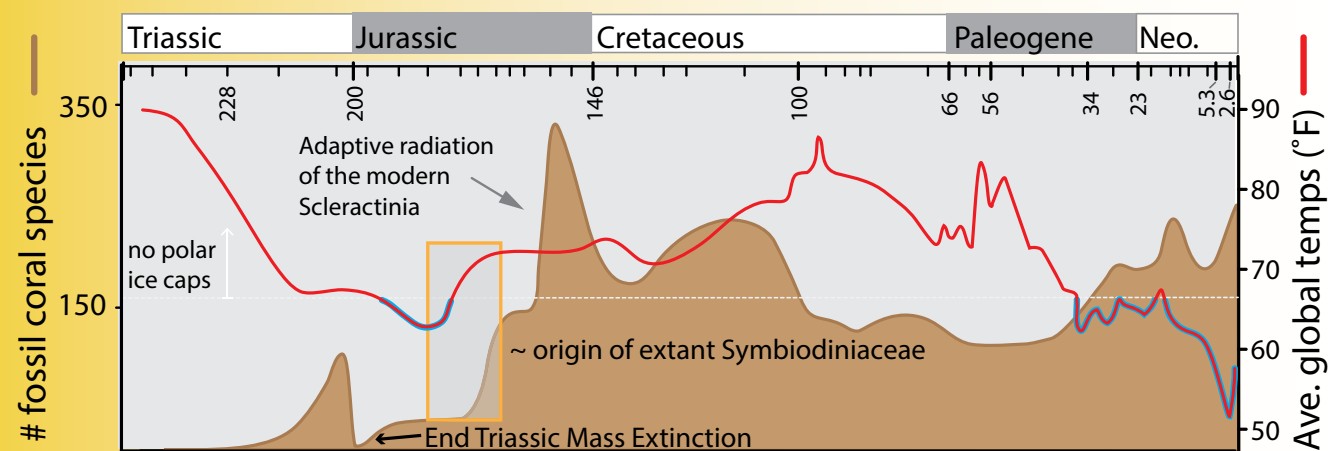
LONG-TERM STABILITY OF THE RELATIONSHIP

Rarely does the symbiont species in an individual coral change. In most cases, once a symbiont has been established in the animal's early life stages, it remains stable for many years, or for the lifetime of the colony, despite episodes of severe stress. Typically, individual reef corals harbor a single dominant symbiodiniacean species. Moreover, the resident symbiont population is often mono-clonal, originating from a single symbiont cell

EVOLUTIONARY TIMELINE OF ZOOXANTHELLAE



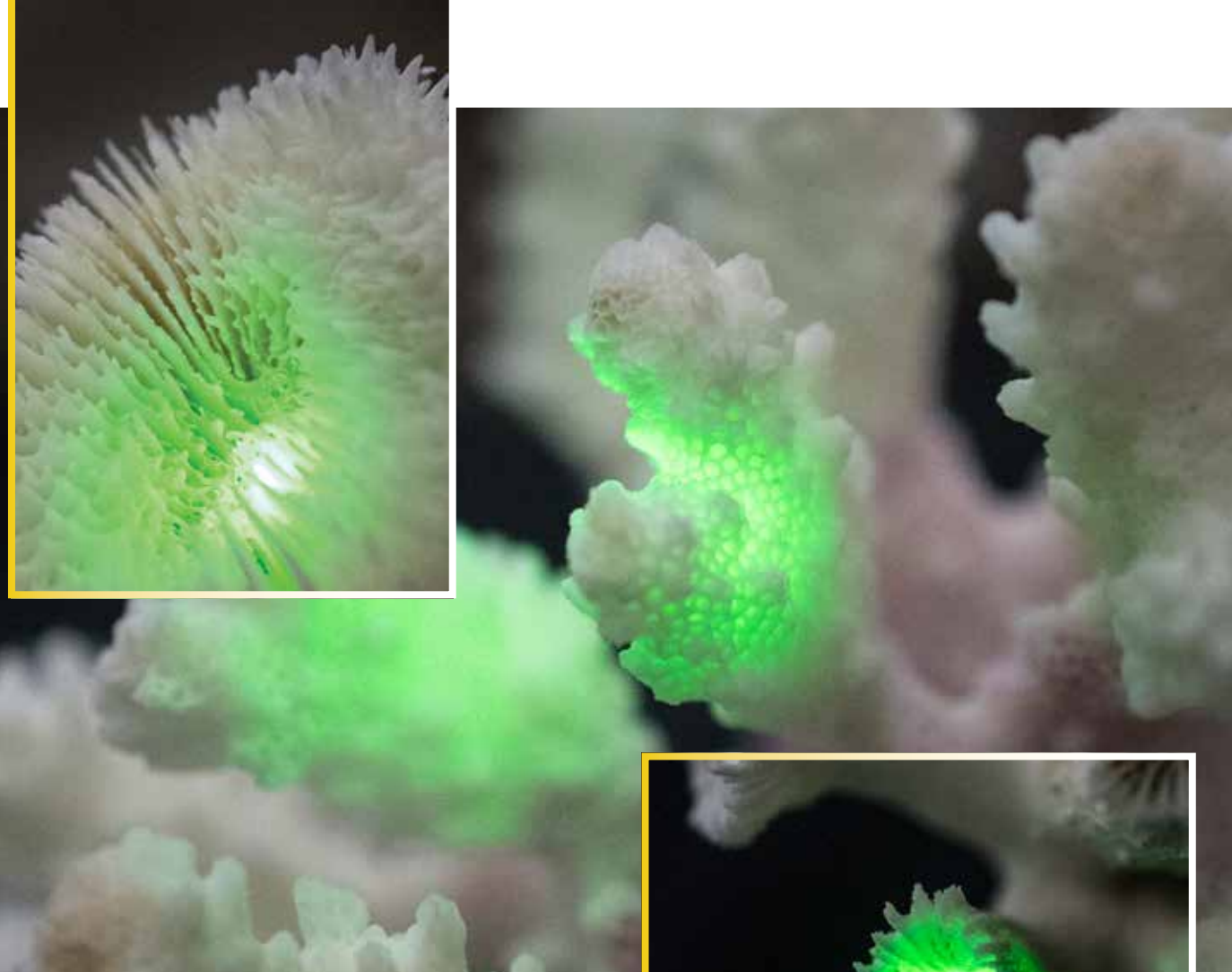
PHYLOGENY: THE ORIGINS OF MODERN STONY CORALS



While the fossil record of modern reef corals starts in the Triassic, the great diversification begins in the Middle Jurassic. This time corresponds to estimated molecular clock-dating of the origin of symbiodiniacean symbionts. This long evolutionary history has given rise to numerous divergent genera featured in the phylogenetic tree (a time-calibrated history of the family Symbiodiniaceae, showing when the different lineages diverged from each other evolutionarily). Many genera are known to associate with invertebrates as well as single-celled protists (discoid foraminifera). The variety of invertebrate hosts includes flatworms, giant clams, sponges, and many kinds of Cnidaria (corals, sea anemones, leather corals, sea fans, jellies, etc).

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LIGHT CAPTURE: Light striking a coral's skeleton is dramatically scattered, as demonstrated with a green laser in these example specimens of glowing coral skeletons. This physical process enhances the collection of solar energy in living animals with symbionts. Symbiont cells in the tissues of corals capture 2–5 times more light than when grown in liquid media. Images: Patrick Mansell, Penn State



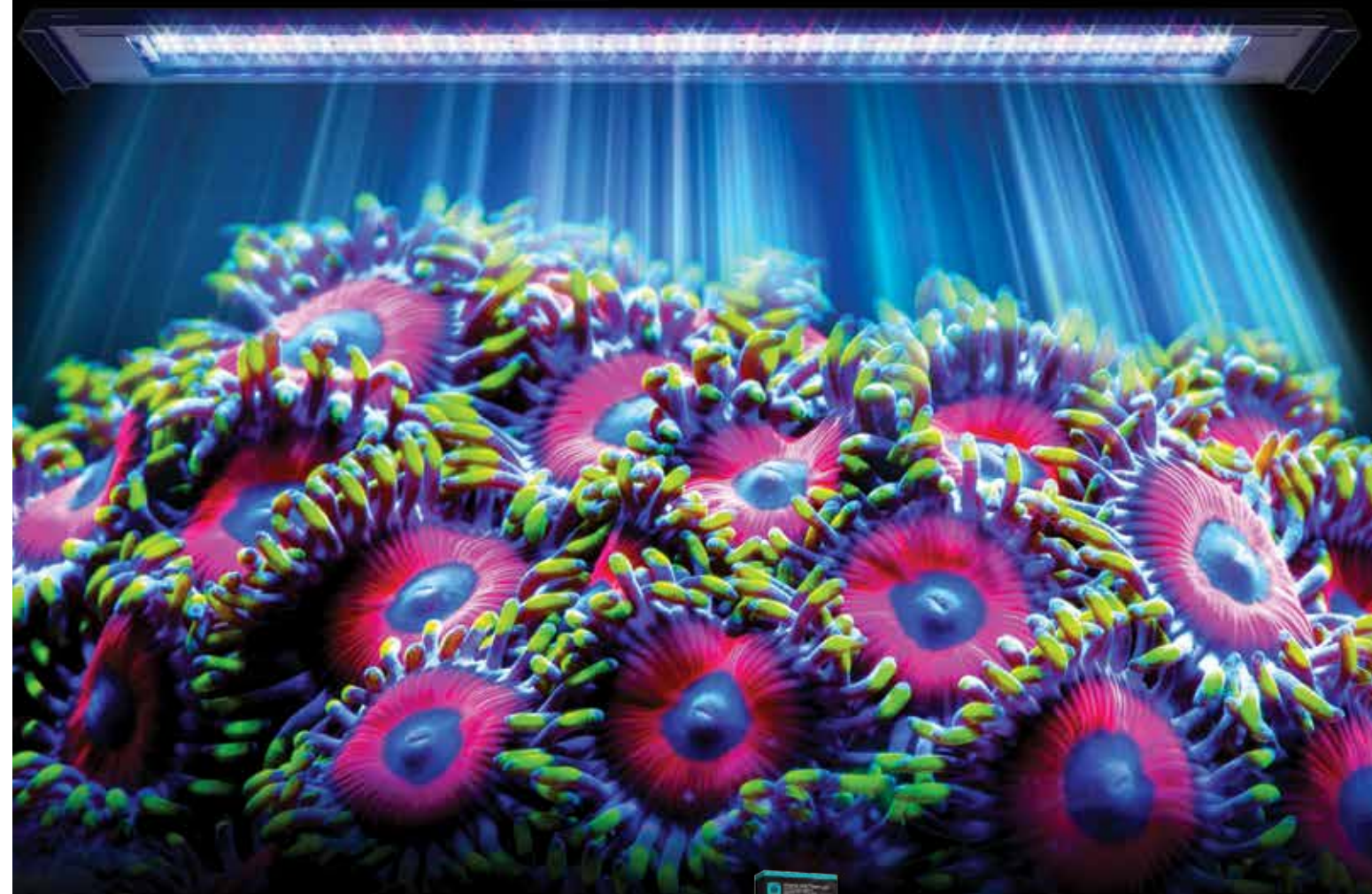
proliferating through cell division to dominate the entire host colony as the animal itself buds polyps and grows larger. In colonies where more than one symbiont is co-abundant, the other dominant symbiont is almost always a member of a different genus. Such insights have been made possible through extensive and repeated field sampling of coral colonies before, during, and after stress events.

An important exception to the usual pattern of symbiont stability can occur when severe stress events disrupt the mutualism, allowing for a temporary increase in the abundance of opportunistic or atypical symbionts. When conditions return to normal, eventually the symbiont community switches back to the original population. Analyses of symbionts in aquarium corals revealed that these animals retained the symbiont that they possessed when they were collected in the wild, despite repeated fragmentation and exposure to

various aquarium environments. Another study of the Elkhorn Coral, *Acropora palmata*, from the Caribbean had similar results. This species is prone to natural fragmentation, which creates large stands dominated by a single animal clone that are many decades or even hundreds of years old. Each physically distinct but genetically identical fragment typically shares the same symbiont clone, pointing to long-term stability with the resident Symbiodiniaceae. Host “flexibility” in nature is limited to a small number of compatible symbiont species whose presence is governed by prevailing external environmental conditions. Partner pairings can sometimes be manipulated by moving colonies to very different environments (e.g., across depths with major light differences) or by experimentally subjecting them to severe thermal stress.

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COLLECTIONS

Our present understanding of the diversity, ecology, and biogeography of zooxanthellae comes from field surveys of coral colonies in locations and reef habitats from around the world. In this example, the upper image is representative of the Rock Island habitats of Palau in the west Pacific Ocean.

Investigations of corals in these inshore environments represent natural experiments to understand how healthy and abundant coral communities cope with living in warm seas with reduced pH and restricted water flow—stressful conditions forecasted for oceans under continued global warming and ocean acidification. Individually tagged colonies are monitored to assess the stability of their mutualisms with specific kinds of zooxanthellae by resampling them months and years later. Image: Allison Lewis, Penn State

WHO HAS CONTROL IN THE RELATIONSHIP?

While it is unclear how the host influences control over its symbionts, and vice versa, both partners share in regulating the mutualism. The critical cellular-biochemical communications between host and symbiont that

govern their interactions are an area of active investigation. These relationships are complicated—far more so than bacterial symbioses—because Symbiodiniaceae cells are eukaryotic, and thus they contain a complex cell architecture (including mitochondria and chloroplasts) and a bizarre genome that is much larger than that found in any bacteria. In fact, the symbiont’s genome is nearly ten times larger than the typical coral’s. Most other endosymbiotic eukaryotes are parasites or pathogens. Of course, corals also host bacterial symbionts, and the concept of the coral plus the micro-algae plus all the other microbes is termed the coral holobiont in recognition that all these players contribute to colony health.

Symbiont cells lack direct access to the outside world because each is “trapped” inside a host cell in a vacuole chamber tightly surrounded by a membrane—the “symbiosome” (see page 32). In this physical sense, the host exerts “control” over the symbiont. The restricted availability of essential nutrients can “regulate” the symbiont’s population densities. Recall that zooxanthellae appear to be nitrogen-limited within host cells. However, more research is needed to better understand the host’s capability to modulate symbiont nutrition. From the other perspective, the symbiont also “regulates” the host to some degree. Dinoflagellates generate a variety of secondary metabolites. The release of these biologically active compounds likely interacts with the host cell’s innate immune system, but details of this molecular interaction are still being worked out. These symbionts, like parasites, likely possess mechanisms for evading cellular digestion and host immune responses.

THE ZOOXANTHELLAE IN AQUARIUM ANIMALS

So, what species of zooxanthellae are you likely to find in symbiosis with corals in a typical reef tank? Unless you have some of their DNA sequenced, you can’t be sure. But, given that the trade obtains the vast majority of animals (e.g., stony corals, soft corals, sea anemones, zoanthids, etc.) from the Indo-Pacific, we can make some educated guesses based on what is already known about the biogeography of these mutualisms. Most coral-algal associations are very consistent. So, if the host and the ocean where

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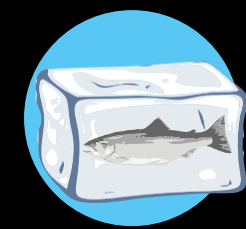
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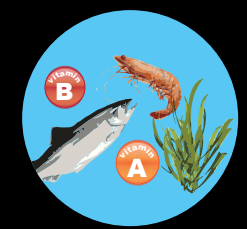
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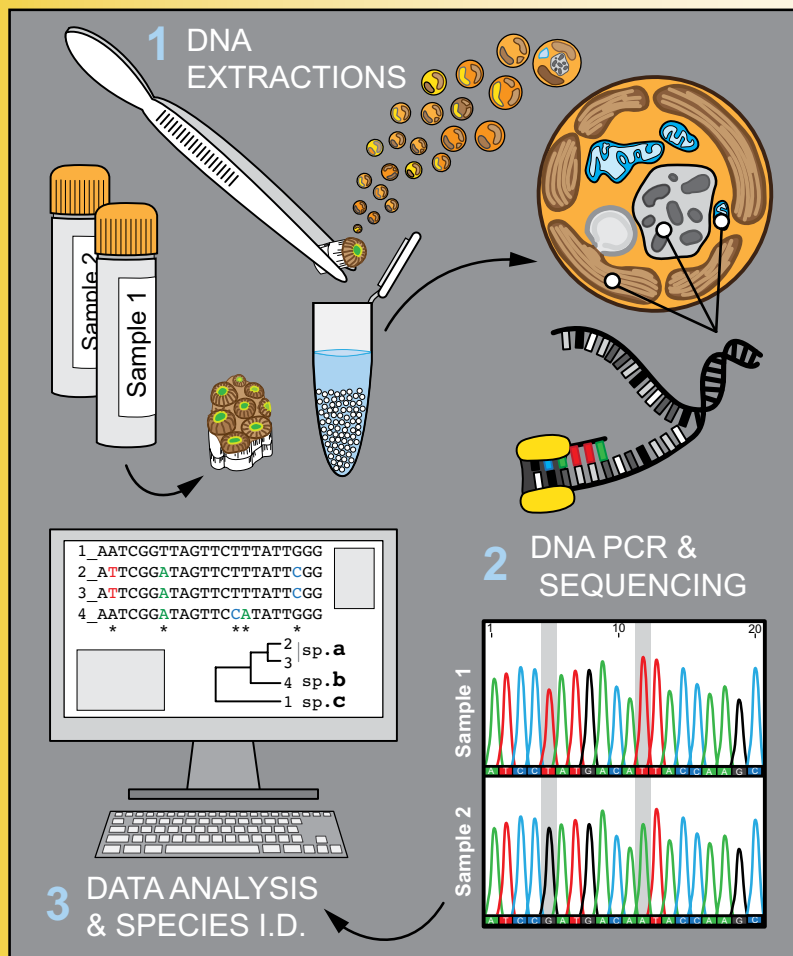
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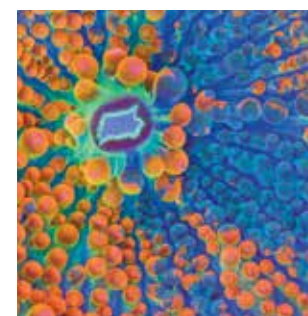
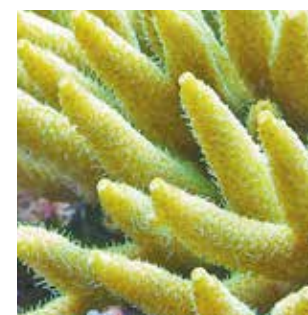
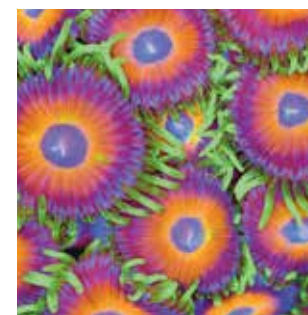
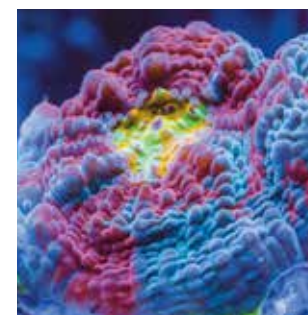
Resolving morphologically similar zooxanthellae requires genetic data—DNA sequences from the symbiont’s genome.

1. After preserving small coral fragments collected from nature, both host and symbiont DNA are extracted together using chemical solvents in the laboratory.
2. Diagnostic genes from the symbiont’s genome (found in the nucleus, mitochondria, and chloroplast) are targeted for analysis. After copying certain genes via polymerase chain reaction (PCR), the nucleotide sequence is “read” by an instrument, which outputs color-coded chromatograms representing nucleotide order (differences between Sample 1 and 2 are highlighted here with a gray background).
3. Gene sequences are represented as strings of nucleotide letters (A’s, C’s, T’s, and G’s) and aligned in a computer against other sequences (differences are highlighted here with asterisks). Sequence similarity along with supporting ecological, morphological, and geographic evidence provides the basis for identifying and describing species.

Image: Todd LaJeunesse

it was collected are known, one may predict the resident symbiont species with fairly high accuracy. For example, the aquarium pest *Aiptasia* (the brown or glass sea anemone) almost always hosts *Breviolum minutum*. If you happen to be growing some Caribbean Pillar Coral (which is highly endangered—please don’t trade in this species), you would know the symbiont could only be *Breviolum dendrogyrum*. Indo-Pacific corals are far more likely to possess *Cladocopium* than any other kind of symbiont, while Caribbean corals tend to favor *Breviolum*, especially if they were obtained from depths less than 30 feet. Collected any deeper, and they typically possess specific species of *Cladocopium*. The only published research conducted on corals from public and private aquaria found a good diversity of *Cladocopium* in these captive coral communities. This is probably because corals in

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Acropora spp. corals being propagated by Shane Backer at SBB Corals in Jersey City, New Jersey.



A single polyp of WWC Bizarro *Cyphastrea* photographed at Ocean Avenue Aquatics in Arlington, Texas.

cultivation are sourced from a variety of regions around the West Pacific and have brought with them the symbionts they had when they were retrieved from nature. Pacific coral communities are typically dominated by a few host-generalist symbionts. These generalist species differ in their physiology, so their dominance in a community is dictated by long-standing environmental conditions typical of each region or location. Most Indo-Pacific corals produce larvae that must obtain their symbionts from the environment. Upon larval settlement and metamorphosis, a newly formed polyp is typically colonized and rapidly populated by the generalist symbiont that dominates the corals from the surrounding habitat. Exceptions include corals in the genera *Porites* and *Montipora* and those in the family Pocilloporidae. These corals are unique because they produce eggs containing large numbers of symbionts supplied during their development. This close relationship leads to the evolution of highly unique host-specific symbionts. A reef tank with many of these corals therefore contains a large number of distinct *Cladocopium* species.

CLIMATE CHANGE AND THE FUTURE OF REEF CORALS

The capacity for harboring different symbionts leads to some intriguing possibilities with respect to forecasting the fate of

CAPTIVE SYSTEMS

Aquarium corals and other invertebrates that host micro-algal endosymbionts have been shown to harbor and support populations of *Symbiodinium* species that rival the diversity found in the wild. Indeed, a number of species not previously collected and described from nature have been found lurking in some captive reef systems.

In a study published in 2009, samples from six public and six private aquaria across the continental U.S. and Hawaii were tested to determine what Symbiodiniaceae species were present in representative captive systems; a total of 126 specimens comprising 20 genera of Anthozoans (16 scleractinian corals, two alcyonarians, one corallimorpharian, and one zoanthid). As reported in the study (*Symbiodinium Diversity and Stability in Aquarium Corals*; Smith et al. *Journal of Phycology* 45, 1030–1036 [2009]): “The specimens analyzed had been in captivity for periods ranging from two months to 18 years, with most in cultivation for seven or more years. Only a few colonies were documented to have experienced repeated episodes of bleaching and recovery.... DNA extractions found 26 putative species in the genus *Cladocopium* as well as several in the genus *Durusdinium*.

“Virtually all of these were found to contain a single dominant symbiont population, and in only one case was a mixture of two symbionts detected in a colony. More than half of the diversity detected matched with symbiodiniacean ‘species’ previously identified from surveys of natural host populations, while 10 were determined to be new types (i.e., species).”

The diversity of zooxanthellae, along with the detection of new or undescribed species, was not necessarily unexpected, but the fact that there was no single “aquarium hardy” species present was an important finding. The paper concluded: “The absence of a dominant ‘weedy’ symbiont indicates that symbioses in artificial systems are not stressed and/or do not undergo competitive replacements facilitated by the aquarium environment, and/or are incapable of changing symbionts. Indeed, most coral colonies appear to associate stably with a particular symbiont over timescales ranging from years to decades, regardless of external environmental factors and/or bleaching history.”

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Sign of the times: Bleached scleractinian corals on a reef in Thailand. Loss of *Symbiodinium* spp. symbionts during heat waves has led to a significant loss of stony coral cover globally.

these mutualisms under climate change, as well as for coral reef restoration. Because many Symbiodiniaceae species are physiologically distinct, it may be possible for a coral colony's physiology to change if its symbiont changes (for example, after transplanting to very different environments). If a coral colony experiences a shift to a more heat-tolerant

species, it may survive longer in warming oceans. However, this may come at a cost to the stability and function of the relationship.

Many coral scientists have been pursuing these lines of inquiry, and while manipulation of the dominant resident symbiont is possible under very specific circumstances, it's not yet clear how great a benefit it provides, what the trade-offs are, and how such interventions can be implemented at a scale large enough to have a real impact on reef ecosystems.

This is yet another area of active research, as we desperately seek ways to mitigate the impact of the climate crisis on corals. As we have seen, the coral-algal symbiosis has ancient and complex origins, and modern science is working with increasing urgency to shine a light on the role of *Symbiodinium* in the health

and survival of stony coral reefs. Of course, nothing will be as effective as drastically reducing our greenhouse gas emissions, which are directly contributing to ocean warming and acidification.



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SYMBIODINIACEAE NAMING CONVENTIONS

Originally, all Symbiodiniaceae throughout the world were assumed to belong to one species because they looked similar under the microscope. Once molecular data became available, it was obvious that this was an oversimplification.

The first big split was the recognition of several “Clades,” or major lineages, within the old genus *Symbiodinium*. These “Clades” were given letter designations: first A, B, and C, then later D–J were added. With further study, it became clear that most major “Clades” contained multiple “types,” so further subdivision was required. Alphanumeric designations like A1, C15, and D1a were created. The first letter corresponded to the “Clade,” while the subsequent numbers and letters referred to specific gene sequence variants. The numbering system was somewhat arbitrary, which led to confusion.

Eventually it was established that a combination of molecular, ecological, and morphological data can be used together to delineate species boundaries. Using this system, formal taxonomic names could be assigned to “types.” B1 became *Symbiodinium minutum*, B2 became *Symbiodinium psygmophilum*, and D1a became *Symbiodinium trenchii*.

But these species names didn’t convey the “Clade” information, even though “Clades” were useful concepts

that reflected evolutionary history. The solution was fairly simple: the old genus was broken apart into many genera, each corresponding to one of the “Clades.” Now the entire group is referred to as the family Symbiodiniaceae, and the new genus names typically start with the first letter of the old “Clade” designation (except for “Clade A,” which retained the original name *Symbiodinium*.) “Clade B” became *Breviolum*, “Clade D” became *Durusdinium*, etc. Now it’s easy to tell that *Breviolum minutum* and *Breviolum psygmophilum* are more closely related to each other than they are to *Durusdinium trenchii*.

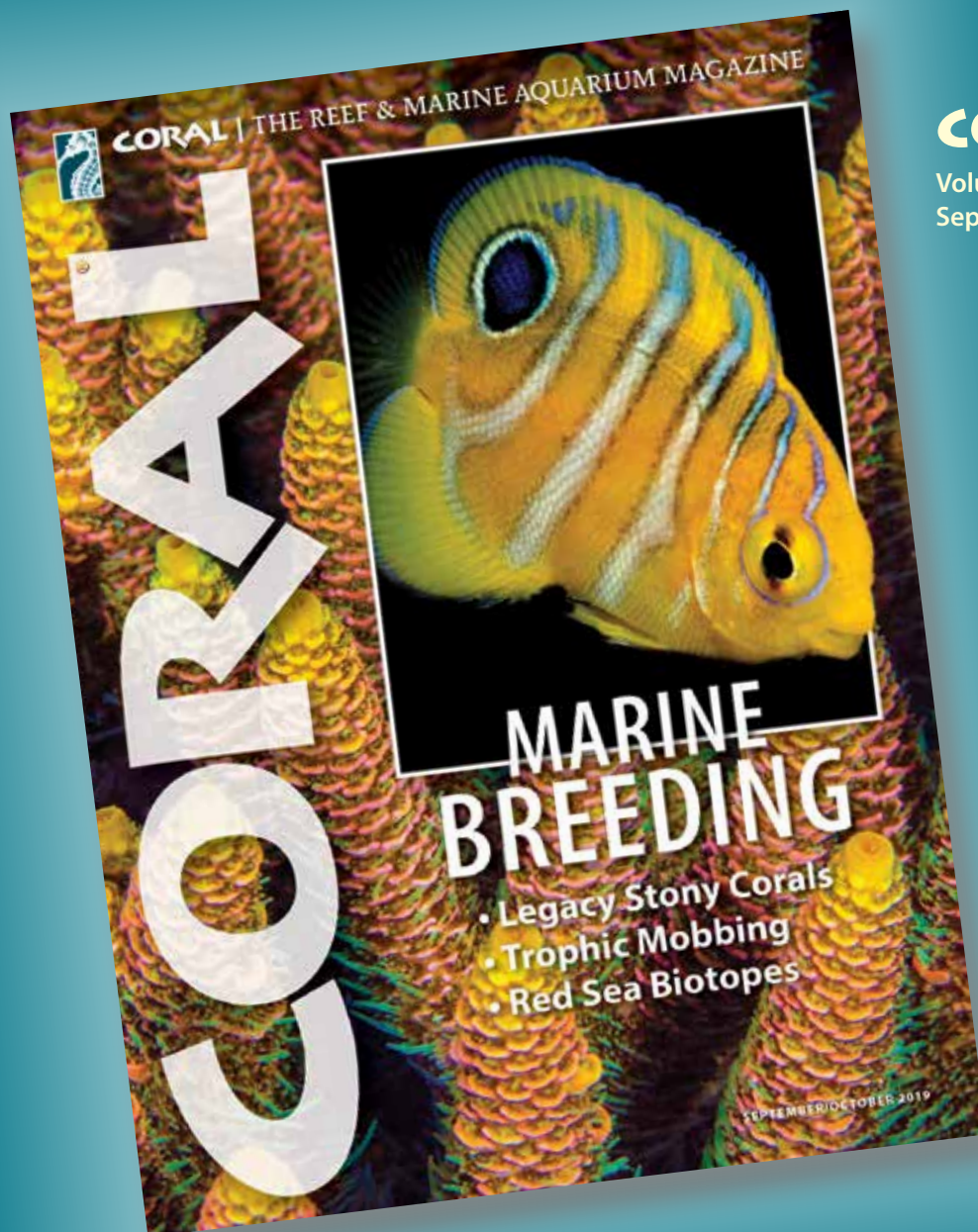
There are hundreds of undescribed Symbiodiniaceae still out there. Unfortunately, naming new species is a very slow process (it takes around a year to compile data and publish) compared to gene sequencing (which takes about a day if you’re set up for it), so for the foreseeable future it will be necessary to rely on some of the older nomenclature.

Below, we have compiled a list of all the most-current genus and species names, along with their previous designations in the old system. Hopefully these guides will prove useful if you are trying to figure out which Symbiodiniaceae might be found in your aquarium corals based on earlier literature.

NEW VALID NAMES	OLD CLADE NAMES	OLDER INVALID NAMES
FAMILY-LEVEL		
Symbiodiniaceae	—	—
GENUS-LEVEL		
<i>Symbiodinium</i>	“Clade A”	—
<i>Philozoon</i>	“Temperate Clade A”	“Temperate-A,” “Mediterranean A,” “A-prime,” “A”
<i>Breviolum</i>	“Clade B”	—
<i>Cladocopium</i>	“Clade C”	—
<i>Durusdinium</i>	“Clade D”	—
<i>Miliolidium</i>	“Foraminifera Clade D”	—
<i>Effrenium</i>	“Clade E”	—
<i>Freudenthalidium</i>	“Clade F” (Fr3)	—
<i>Fugacium</i>	“Clade F” (Fr5)	—
“<i>Symbiodinium</i>” Clade Fr2	“Clade F” (Fr2)	—
“<i>Symbiodinium</i>” Clade Fr4	“Clade F” (Fr4)	—
<i>Gerakladium</i>	“Clade G”	—
“<i>Symbiodinium</i>” Clade G	“Foraminifera Clade G”	—
<i>Hallaxium</i>	“Clade H”	—
“<i>Symbiodinium</i>” Clade I	“Clade I”	—
“<i>Symbiodinium</i>” Clade J	“Clade J”	—

NEW VALID NAMES	OLD ITS2 NAMES	OLDER INVALID NAMES
SPECIES-LEVEL		
<i>S. microadriaticum</i>	A1	“ <i>S. microadriaticum</i> subsp. <i>microadriaticum</i> ”
<i>S. natans</i>	—	—
<i>S. necroappetens</i>	A13, A1.1	“ <i>S. cariborum</i> ,” “ <i>S. microadriaticum</i> subsp. <i>condylactis</i> ”
<i>S. pilosum</i>	A2	“ <i>S. corculorum</i> ,” “ <i>S. meandrinae</i> ”
<i>S. tridacnidorum</i>	A3-Pacific, A3*, A3a, A3x, A6	—
—	A3-Caribbean	“ <i>S. fitti</i> ”
—	A4	“ <i>S. linucheae</i> ”
<i>P. actinarium</i>	A19	—
<i>P. adriaticum</i>	—	—
<i>P. anthopleurum</i>	—	—
<i>P. balanophyllum</i>	—	—
<i>P. colossus</i>	—	—
<i>P. geddesianum</i>	—	—
<i>P. medusarum</i>	—	—
<i>P. paranemonium</i>	—	—
<i>B. aenigmaticum</i>	—	—
<i>B. antillogorgium</i>	B1	—
<i>B. dendrogyrum</i>	B1k	—
<i>B. endomadracis</i>	B7	—
<i>B. faviinorum</i>	B1, B14, B14a	—
<i>B. meandrinium</i>	B1, B20	—
<i>B. minutum</i>	B1, B1-1	“ <i>S. pulchrorum</i> ”
<i>B. pseudominutum</i>	B1	“ <i>S. bermudense</i> ”
<i>B. psygmophilum</i>	B2	—
—	B4	“ <i>S. muscatinei</i> ”
<i>C. goreau</i>	C1	—
<i>C. infistulum</i>	C2	—
<i>C. latusorum</i>	C1c, C1b-c, C42, C42a, C42b, C1c-ff, C1c-42-ff	—
<i>C. pacificum</i>	C1d, C1d-t	—
<i>C. thermophilum</i>	C3-Gulf	—
<i>D. boreum</i>	D15	—
<i>D. eurythalpos</i>	D8, D8-12, D12-13, D13	—
<i>D. glynni</i>	D1	—
<i>D. trenchii</i>	D1a, D1-4	—
<i>M. leei</i>	—	—
<i>E. voratum</i>	E1	“ <i>S. californium</i> ”
<i>Fr. endolithicum</i>	—	—
<i>Fr. heronense</i>	F3.7, Fr3.7	—
<i>Fu. kawagutii</i>	F3.8, Fr5	—
<i>G. endoclionum</i>	—	—
<i>G. spongiolum</i>	—	—
<i>H. pauxillum</i>	H7	—

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