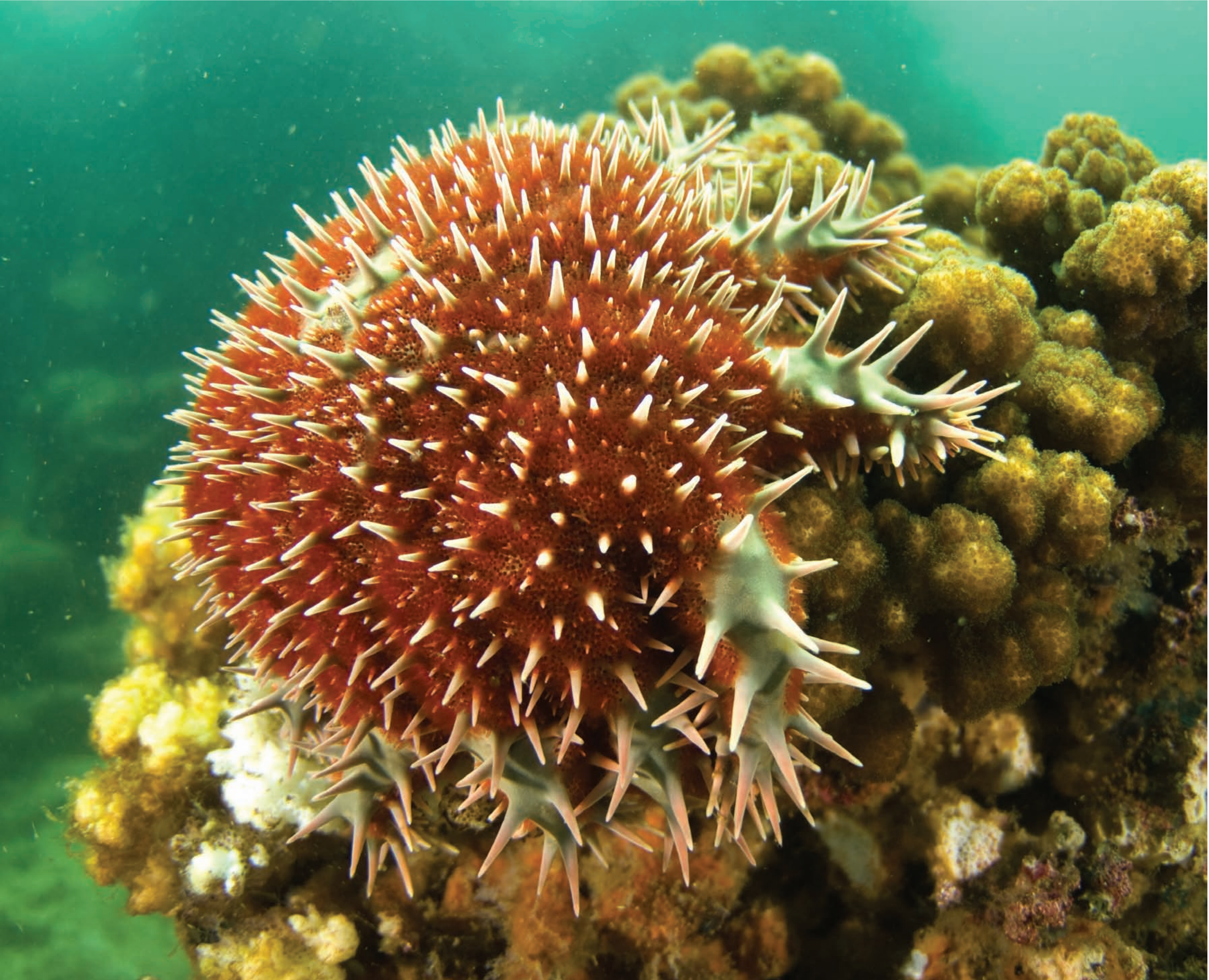


The web of life on the reef

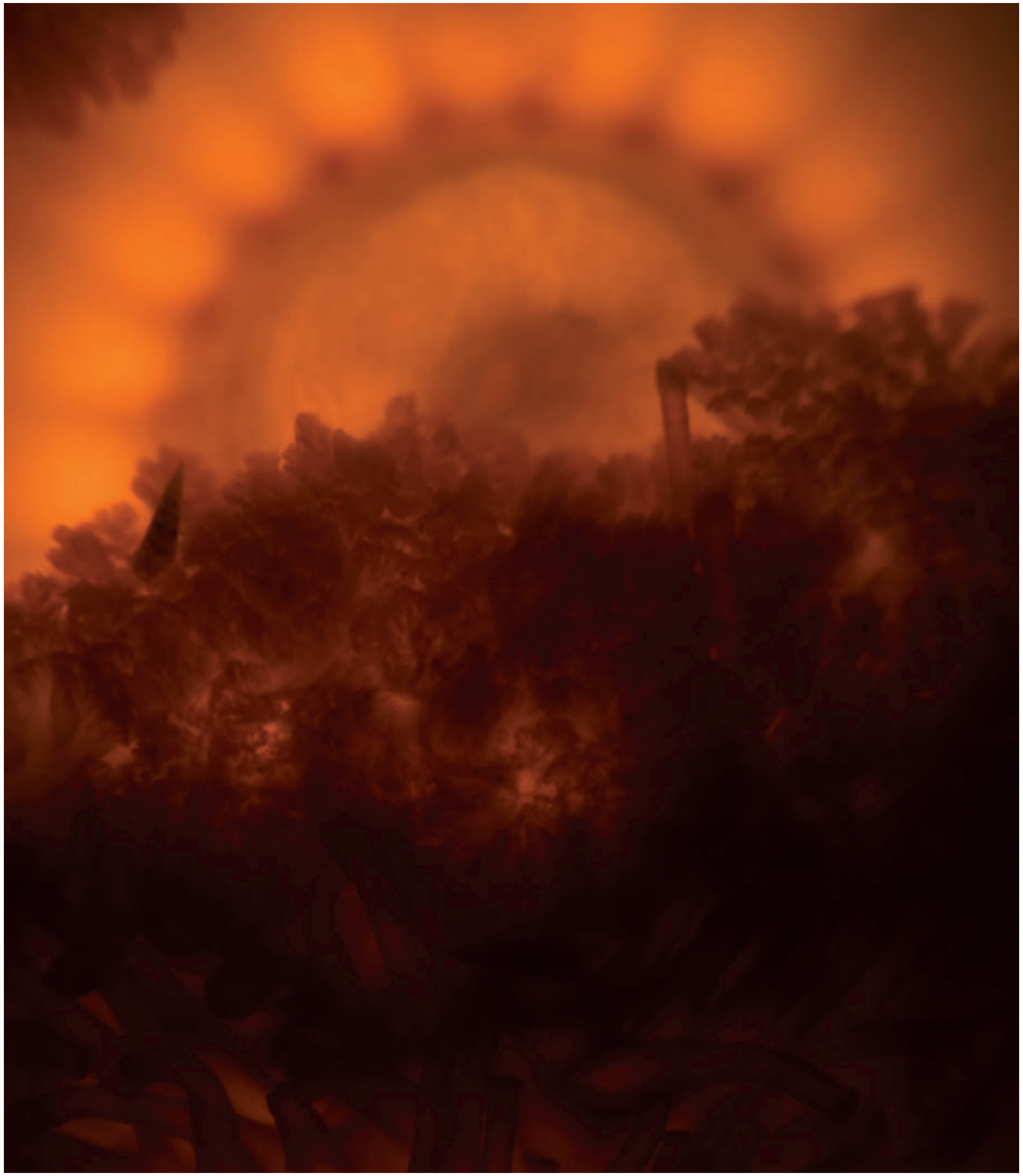
Carlos Sánchez-Ortiz

Seamounts form a cluster of living organisms interacting with one another in an extremely complex network. In the ocean, predation relationships are common and survival is often a matter of competition and supremacy: of killing or being killed, of eating or being eaten. But on the seamounts and reefs positive interactions—those in which two species help each other to in order to survive—are very frequent and can be quite extraordinary. In the reef, life is not only driven by competition and predation but also by symbiosis and joint survival. It is not so much a matter of supremacy as it is one of cooperation.

Positive interactions between species can occur in several ways; the most common ones are: 1. mutualism, where the relationship is obligate and beneficial for both species, as in the anemone and the clownfish, or the microalgae (zooxanthellae) and the polyps of stony corals; 2. commensalism, where one species benefits from its interaction with the host, while the host is largely unaffected, as in manta rays and the suckerfish, or whales and the barnacles attached to their skin; and 3. parasitism, where the guest species survives at the expense of the host, and by doing so affects the host's development, as in the copepod crustaceans that parasitize the swordfish skin, or nematodes that thrive on the skin of many fish.

Several of these relationships were observed in macroinvertebrates during our expedition. The epibionts, or guest species, we found belonged mostly in the cnidaria (anemones), crustaceans (shrimp, crabs, hermit crabs, and goose barnacle), mollusks (snails) and polychaetes (sea worms); while the most common hosts were sponges, cnidaria (sea fans, sea pens, stony corals, black corals and hydrocorals), echinoderms (starfish, sea urchins, sea cucumbers

Crown-of-thorns sea star *Acanthaster planci*, preying on the polyps of a stony coral. Photo © Octavio Aburto-Oropeza.



and sea spiders), and mollusks (clams and oysters). We were able to witness the remarkable parasitic relationship of minutely small snails that feed on the mouth tentacles of the sea cucumber (*Isostichopus fuscus*), and photographed the phenomenon for the first time.

Corals and their symbionts

Because they are easily accessible to divers, corals (stony corals, black corals, sea fans) from tropical seas are well known for their rich diversity and beauty. It is a lesser-known fact, however, that corals are also widely distributed in cold or deep ocean waters. These cold water corals offer a rich array of microhabitats and substrate for other species that become intimately associated with them for most or part of their life. The key is the arborescent, or tree-like, morphology of the corals, which allows the colonies of polyps to rise above the substrate's boundary layer, where water flow is higher. It follows then, that any epibiont, or guest species living within the coral branches can maximize the volume of water where they can search for the suspended food that drifts through the coral branches.

Crustaceans as coral epibionts

Many animals like sponges, flat worms, polychaetes, shrimps, crabs, sea spiders, mollusks, and fish live in the corals without causing their hosts any apparent harm under normal circumstances. In most cases the relationship between corals and their associated guest species is casual and non-specific, as the visitor is capable of living independently or associated with different species of corals. The most extraordinary association occurs when the guest species has an obligate association to a particular species of coral and the epibiont, through the processes of evolution and natural selection, has modified its color, morphology, conduct and reproductive cycle to adapt to the host.

At least 120 species of shrimp and crabs have been reported in the Indo-Pacific as obligate epibionts that frequently live between branches or tentacles of larger host organisms. Others, like the coral-gall crab *Hapalocarcinus marsupials*, live in the tips of the corals where

Feeding tentacles and calcareous ring of a sea cucumber *Isostichopus fuscus*. Diminutive parasitic snails *Melanella townsendi* can also be seen feeding around the tentacles. Photo © Carlos Sánchez-Ortiz.

they build a permanent home made up of galleries that cause the coral to grow abnormally. There are also species that can penetrate even further and live in the coral's cavities, like small oysters (*Fungiacava*) or polychaete worms (*Toposyllis*). In the American Pacific region, there have been close to 30 reported species of shrimp and crabs in obligate symbioses with corals, urchins and starfish. These symbionts can feed off the host's mucus, as well as eat small invertebrates, algae, or organic sediment.

The shallow rocky reefs (up to 20 m deep) of the southern Gulf of California harbor 16 species of stony coral of the genera *Pocillopora, Porites, Pavona* and *Psammocora*. Nine species of obligate symbiotic shrimp and crabs have been reported for the species of *Pocillopora* (seven were seen in our expedition), and the majority of these species (both host and symbionts) are widely distributed, having been recorded as far as in the Indo-Pacific and Red Seas. The crabs from the genus *Trapezia* and the snapping shrimp *Alpheus lottini,* are dominant symbionts that hide in the coral branches and feed on the coral's mucus, which is rich in lipids. Both crabs and shrimp actively defend the coral from intruders, even during attacks from their worst predators like the crown of thorns (*Acanthasther ellisii),* snapping them with their claws. This symbiosis increases the vitality of the coral colony, promoting the cleansing of its fragile surface and the safe elongation of its branches.

Crypsis, mimicry, camouflage

In several of the symbiotic crab and shrimp species we observed a striking morphologic similarity of the symbiont with the anatomical parts of its host (morphological mimicry), or a marked convergence in coloring that allows the symbiont to hide from potential predators (camouflage or visual mimicry). Crypsis is an even wider phenomenon than strict mimicry or camouflage, involving the evolution of a set of traits that allow the organism to hide in the surrounding environment. This evolutionary adaptation can produce extraordinary and unique symbiotic forms as a result of the reciprocal influence between host and symbiont.

In our submarine expedition we could observe that seamount environments 20 to 150 m

Porcelain crab *Quadrella nitida* (female with eggs), a symbiont of the sea fan *Muricea fruticosa*. Photo © Lorenzo Rosenzweig.

Male individual of a new species of caridean shrimps, in the subfamily Pontoniinae, that lives in symbiotic association with the sea fan *Ellisella limbaughi*, protecting itself from predators by copying the host's color. Photo © Lorenzo Rosenzweig.

The caridean shrimps *Sandyella tricornuta*, symbionts of the black coral *Antipathes galapagensis*, mimic their host not only by copying its color but also by imitating the form of its polyps. Photo © Carlos Sánchez-Ortiz.

deep are dominated by high densities of sea fans (*Muricea, Leptogorgia, Eugorgia, Pacifigorgia* and *Ellisella*), and black corals (*Antipathes*), forming true "forests" of high biological diversity. Knowledge on the fauna associated with these corals, especially those from deep waters, is mainly anecdotal. In particular, we witnessed a remarkable association between a sea fan *Muricea fruticosa* and its symbiotic crab *Quadrella nitida*. This crab, which lives among the branches of the sea fan, is successfully camouflaged by mimicking with its porcelain-white body the white bases of the coral branches, while its red claws mimic the fiery red the tips of the branches.

Other extraordinary cases were found: Numerous species of small shrimps live in association with sea fans and black corals, showing a high specificity in their host-guest relationship. Little is known on the species that conform these biotic interactions in the Gulf of California, but endemic genera of symbiotic shrimp (i.e., *Chacella, Veleronia* and *Pseudoveleronia*) have been reported in the colder waters of the American Pacific coast. In our expedition we found at least two new species of small symbiotic shrimps from the subfamily Pontoniinae associated with sea fans. One of them (Pontoniinae sp. 1) lives in association with the sea fan *Leptogorgia* sp. (also a new species), and has a transparent body with several white blotches that imitate the color and form of the fan's white polyps. The other one (Pontoniinae sp. 2) was found living with the sea fan *Ellisella limbaughi*. The bright orange color of the shrimp helps them to blend perfectly with the sea fan, which has the exact same color in its polyps. The four species were photographed for the first time during our expedition.

The shrimp *Chacella tricornuta*, a symbiont of the black coral *Antipathes galapagensis*, mimics the fluorescent greenish yellow color of the coral's polyps. The most extraordinary thing is that only the females (which are twice as large as the males with maximum size 1cm) possess noticeable dorsal spines that mimic the coral's polyps.

In another species of black coral (*Miyriopathes* cf. *ulex*) we were able to see another striking case of convergent morphologies: its symbiont, the stalked barnacle (*Oxynaspis* cf. *rossi*) has developed small spines in its body that look like the spines in the coral's skeleton (these two last cases were also photographed for the first time during our expedition).

Another extraordinary association observed is that of the hermit crab *Manucomplanus varians* with its epibiont, the hydrocoral *Janaria mirabilis*. This seems to be a mutualistic relationship as the hydrocoral grows over the shell where the hermit crab lives and acts as a camouflage for the crab's "house"; on the other hand, the hermit crab has developed a flat claw (hence the scientific name) that acts as a cover that prevents the incursion of or predators into its dwelling.

Coloration

The evolution of mimicry in epibiotic species is driven by the differential survival from predators of the mimetic symbionts, a trait that depends critically on an almost perfect similarity with the colors of their host. Thus, the evolution of color is of great ecological importance. Color, and especially pattern, are important diagnostic characteristics in the classification of symbiotic shrimp and crab. The extraordinary mimicry observed in several species of crustaceans, mollusks and annelids makes it difficult to detect the epibiont from the host. The perfect imitation of the host's color is achieved through different ways or through a combination of them. One of them is homochromic coloration driven by the food source, as in the case of the snail *Epidendrium billeeanum* that forages on the cup coral *Tubastrea coccinea* and acquires the orange color of its prey. In these cases the color of the body is a direct consequence of the intensity of pigmentation of the food source. Another evolutionary pathway is through hormonal control in the epibiont, which determines the pattern, and pigment density in the chromatophores, a specialized type of cells that can produce specific hues and tonalities, through the metabolic synthesis of different classes of pigments (xanthophylls) and their combination.

Many of these organisms frequently show, besides color, another form of mimicry through the imitation of the host's external structure. This is the case of the sea spider *Ophionereis annulata* and its associated polychaete epibionts, where camouflage is so remarkable that it makes it difficult to see the polychaete with the naked eye, or the crabs associated with sea fans and imitate the color and structure of the host's polyp.

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Mutualistic association between the hermit crab *Manucomplanus varians* and the staghorn hydrocoral *Janaria mirabilis*. The colonial hydrocoral encrusts the gastropod shell that houses the hermit crab, and starts to grow over it. The hermit crab trims the opening as the hydrocoral grows over the entrance, eventually replacing the shell completely in an amazing association between two species. Photo © Octavio Aburto-Oropeza.