STARFISH

SEE SEA STARS

STAUROMEDUSAE

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Stauromedusae are small jellyfishes that spend their entire life attached to a substrate (usually rock or seaweed) rather than swimming freely up in the water column like most other jellyfish. Because of their attached, benthic lifestyle, they seem in some ways to have more in common with their relatives the hydroids and sea anemones than with the free-swimming, planktonic scyphozoan jellyfish to which, until recently, they have been considered more closely related. Although a few of the larger, often colorful, free-living scyphomedusae could end up stranded in tidepools (as recorded in the fictional *Adventure of the Lions Mane* by Sir Arthur Conan Doyle), most of the jellyfishes likely to be found permanently living along the rocky shore are the little attached jellyfishes known as Stauromedusae, or Staurozoa. There are also some very tiny crawling jellyfishes found along some rocky shores, which are hydromedusae.

BIOGEOGRAPHY, HABITAT, AND LOCOMOTION

Stauromedusae (Fig. 1) are primarily found in the intertidal and shallow subtidal in temperate and boreal (cold) waters, with a few species recorded from tropical or subtropical waters. These animals are found in full-salinity ocean waters along exposed to fairly protected coastlines; some are found in estuaries with slightly lowered salinities. One species of stauromedusa has recently been found living at great depth in hydrothermal vent communities, but most of the 50 or so known species of stauromedusae occur along shallow coastlines; about 40 species occur in the Northern Hemisphere, and about 8 species are known only from the Southern Hemisphere.

Stauromedusae live attached to seaweed, seagrass, gravel, or rock and may be found on exposed rocky shorelines or in tidepools. Although they appear to be static and fixed in place, stauromedusae, like sea anemones, are capable of movement so slow that the movement is not visible, but the acute observer will notice that individuals change their position over time. For instance, stauromedusae living on seagrass will always be found on

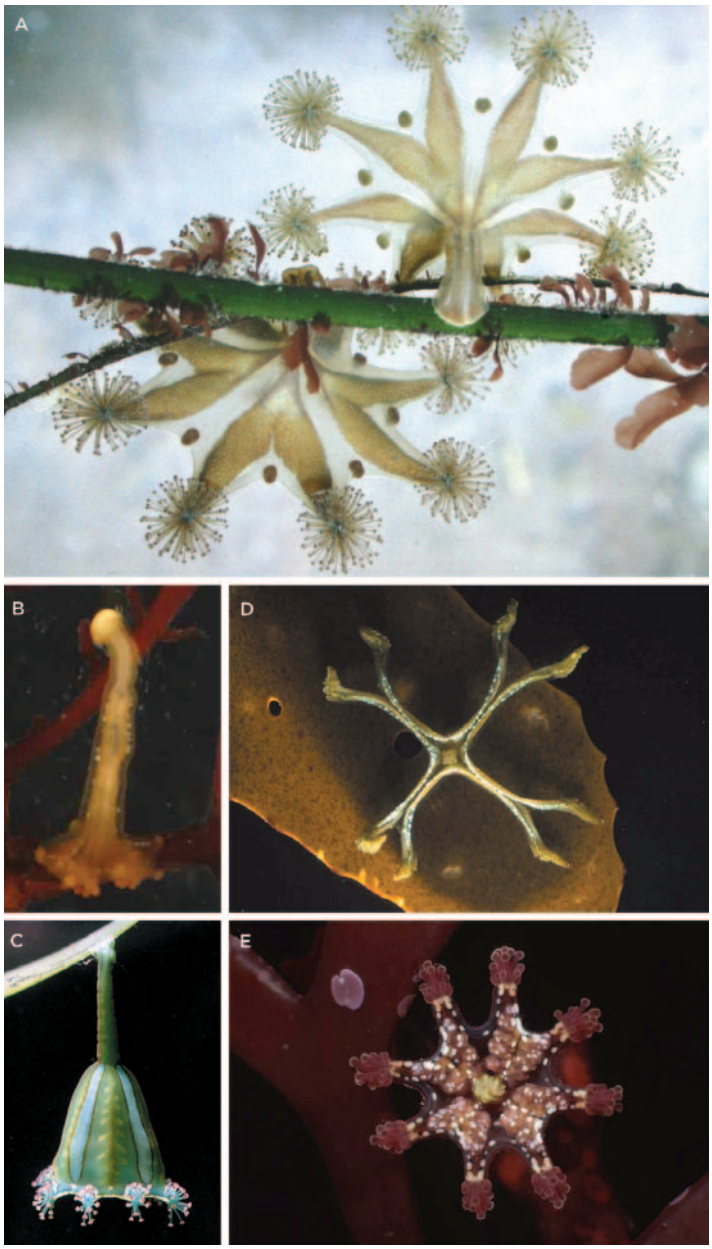

FIGURE 1 Five species of Stauromedusae. (A) Two *Haliclystus* sp. attached to eelgrass (San Juan Island, Washington), tentacle spread approximately 25 mm. (B) *Stenoscyphus inabai* attached to red alga (Misaki, Sagami Bay, Japan), height including stalk 6 mm. (C) *Manania handi*, attached to eelgrass (San Juan Island, Washington), height including stalk approximately 35 mm. (D) *Kishinouyea nagatensis* attached to kelp (Kominato, Boso Peninsula, Japan), tentacle spread approximately 30 mm. (E). Oral view of *Lucernariopsis cruxmelitensis* (Wembury, Plymouth, UK), tentacle spread 8 mm. Photographs A and C by Claudia E. Mills; B, D, E by Yayoi M. Hirano.

the healthy younger parts of the blade, gradually moving down towards the basal new growth as the end of the blade becomes frayed with age. Some stauromedusae can also move rapidly by contracting or twisting the stalk and by bending the calyx or arms, with sometimes a "somersault" kind of motion. On rare occasions, stauromedusae are seen floating freely in the water, perhaps occasionally just letting go, upon which they are carried to a new location where they reattach.

MORPHOLOGY AND LIFE HISTORY

Stauromedusae (see Fig. 1) are composed of a flower-like calyx (cup), edged with clusters of tentacles in most species, on a stalk that attaches to some benthic substrate with an adhesive basal disk. There is a mouth opening on the inside center of the calyx, where food is taken in and indigestible waste is later released. Stauromedusae have four-part symmetry, usually with eight marginal arms at the top edge of the calyx. In most species, each arm is crowned with a cluster of small hollow tentacles, each with a terminal knob covered with cnidocysts—the "stinging cells" that cnidarians use to capture prey. Gonads are usually arranged radially from the base of the calyx towards the marginal arms; in some genera, gonads fill the arms between the terminal tentacles and the central mouth, in others the gonads are located only near the mouth, and in a few the gonads are restricted to the basal part of the stalk.

In general, stauromedusae are colored to match their surroundings and may be so cryptic as to be difficult to see. Some species show slight differences in color between males and females, which are otherwise of similar size and morphology and cannot be sexed without a microscope, if at all, prior to spawning.

Most, if not all, stauromedusae live less than one year. A few species may go through two generations per year, but it seems that most have an annual life cycle. Many species of stauromedusae are most abundant from summer to fall; young specimens less than 1 millimeter long emerge in the spring or early summer (although other species peak in the winter months with a shift in appearance of the young stages to the autumn) and are usually found on seaweed. Stauromedusae reach adult sizes, typically about 1 to 4 centimeters in length or calyx diameter, within several weeks. Like most other medusae, they seem to put most energy into growth until they reach near-adult size, at which point energy is allocated primarily to the production of eggs and sperm for sexual reproduction.

The sexes are separate, and, given enough to eat, most stauromedusae apparently spawn daily for a month or more, until conditions deteriorate and they die. As in many Cnidaria, at least some species of stauromedusae spawn eggs and sperm in response to a light cue after a period of darkness. Laboratory studies indicate that the eggs are sticky and probably remain on the bottom very near the parent stauromedusae. The externally-fertilized embryos develop into microscopic, wormlike, unciliated, planula larvae, which in the laboratory creep along the substrate before encysting to a resting stage that resembles a sticky flattened ball less than 1 millimeter in diameter. Field studies confirm that most species of stauromedusae disappear for several months before their young stages reappear, so encystment of the larvae seems likely also to occur in the field.

New young stauromedusae emerge the next season, which may begin, depending on the species, in spring, summer, fall, or even winter, to repeat the seasonal life cycle. We do not know exactly the environmental cues that synchronize these annual events, but there is not much variation in timing from year to year within any given species at each location. Each species operates on a clock slightly different from the others, and species of stauromedusae that co-occur on the same shore may emerge, grow up and finally disappear at substantially different times of the year.

ECOLOGY

Field studies indicate that stauromedusae eat mostly small crustaceans—primarily harpacticoid copepods, gammarid amphipods, chironomid fly larvae, and ostracods, with some species also feeding on small polychaetes (worms) and snails. Stauromedusae are able to capture prey from the plankton as well as on the bottom.

Few predators of stauromedusae are known. Like cnidarian hydroids that live along the rocky shore and are often eaten by nudibranchs, which are found on the hydroid colonies, stauromedusae have also occasionally been reported to be preyed upon by aeolid nudibranchs. Because stauromedusae in the field are often seen to be regenerating portions of their margins, such grazing-predation must be more common than has been reported. A fish has been reported to feed on stauromedusae attached to the undersides of low-intertidal boulders in the Antarctic, which were found whole in the fish's stomach.

Stauromedusa populations are occasionally very dense and monospecific, as has been seen at deep-sea hydrothermal vent sites; individuals so abundant as to be touching are also described for an intertidal species in Antarctica. More often, however, stauromedusae are relatively far apart along low-intertidal and shallow subtidal rocky shores, their cryptic coloration perhaps making them seem even rarer, and they are probably not generally among the species that drive the ecology of most rocky intertidal ecosystems.

PHYLOGENY

Within the phylum Cnidaria, stauromedusae have long been considered an order in the class Scyphozoa, but recent genetic studies (Collins and Daly 2005) point toward elevating these attached, benthic-living jellyfishes to class Staurozoa, at a rank equal to Scyphozoa, Cubozoa, Anthozoa, and Hydrozoa.

SEE ALSO THE FOLLOWING ARTICLES

Amphipods, Isopods, and Other Small Crustaceans / Cnidaria / Hydroids / Hydromedusae / Nudibranchs and Related Species / Sea Anemones

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STEINBECK

SEE RICKETTS, STEINBECK, AND INTERTIDAL ECOLOGY

STONE BORERS

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In soft sedimentary deposits such as mud or sand there are many marine animals that burrow into the sediment seeking food or shelter. There is also a great diversity of marine invertebrates that bore into solid rock along the shore and in subtidal rocky reefs. These animals derive no nutritional benefit from the material they excavate, but the burrows in which they spend their lives protect them from predators or from being dislodged by surf or surge action. Stone-boring marine animals include sponges, annelid worms, sea urchins, and a variety of bivalve molluscs. In their snug burrows, all must maintain contact with the outside seawater for respiratory purposes and to flush out wastes, and all release gametes or larvae into the seawater during reproduction. In addition, most depend on plankton in the water for food.

The rocks penetrated vary in hardness from soft mudstone and shale to sandstone, limestone, and hard, flintlike siliceous chert. Some even bore into poor-quality concrete or the shells of living and dead molluscs and barnacles. None can penetrate granite.

SPONGES

Sponges are primitive animals and are common in the sea attached to rocks and other solid substrates. One worldwide group, the genus *Cliona*, can bore into soft calcareous stone and into the shells of molluscs such as abalone, moon snails, and oysters, and the wall plates of barnacles (Figs. 1, 2). When on a suitable surface for boring, the only exposed parts of the sponge are yellow papillae protruding from small holes (1–3 mm diameter) in the substrate. Most of the sponge's body occupies tunnels below the surface. These excavations honeycomb the surface and

FIGURE 1 Boring sponge *(Cliona)* in rock oyster shell. Photograph by the author.