HYDROMEDUSAE

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Hydromedusae are jellyfishes in the phylum Cnidaria (class Hydrozoa), most of which are born from bottom-living hydroids and are then set free for a relatively short existence in the plankton during which they feed and reproduce sexually. A few hydromedusae, after being released from their hydroids, are adapted to remain attached to the bottom by their tentacles, which they use to crawl slowly around on seaweeds or other substrates along rocky shores, even in places of moderate wave action. These are very tiny species, the largest of which is no more than a few millimeters across the flattened central disk. They are sometimes known as the crawling or creeping hydromedusae and belong to the genera *Staurocladia* and *Eleutheria*. In the rocky intertidal, crawling hydromedusae are perhaps most often encountered in tidepools, but some may also be found by the careful observer to be hanging on tightly to rock or seaweeds along some open rocky shores.

HABITAT, BIOGEOGRAPHY, AND PHYSIOLOGY

Crawling (or creeping) hydromedusae are quite widely distributed globally, although they are not often seen because of their very small size. In some locations these little jellyfishes can be quite common. Seaweeds may require inspection by using a low-power microscope to discover these tiny jellyfish crawling on the surface, and individual blades of algae may bear numbers of these minute animals upon their upper or lower surfaces, even in areas of substantial wave action. These little jellyfish tend to be present in summer through late fall; their parent hydroids are likely present for a longer season, but may be even more cryptic and difficult to find in the field.

There are approximately 15 species of *Staurocladia* (Fig. 1A, B) known so far—from Japan, Hawaii, New Zealand, Australia, Papua New Guinea, Seychelles, Kerguelen Island in the southern Indian Ocean, several locations in Antarctica, South Georgia, South Africa, Chile, Brazil, Falkland Islands, Bermuda, and the Mediterranean. *Eleutheria* is generally considered to have two species that are known from the shores of the European North Atlantic, the Mediterranean, the Black Sea, and perhaps also a single sighting from the Caribbean. *Eleutheria* has recently also been found in Australia, where a morphological and molecular analysis indicates that it has been introduced from the North Atlantic or Mediterranean (Fraser *et al.* 2006).

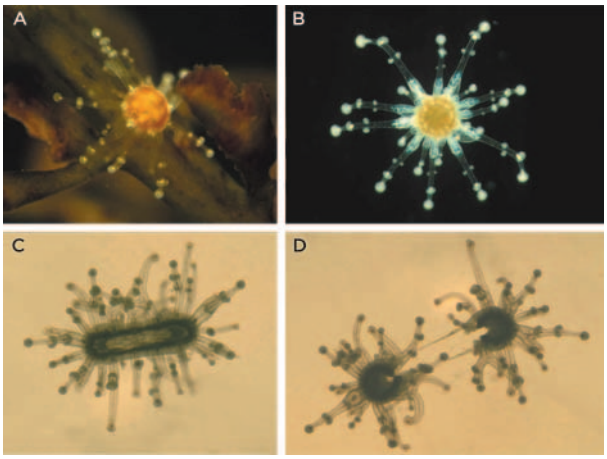

FIGURE 1 (A) *Staurocladia oahuensis* on seaweed. (B) *Staurocladia bilateralis*, isolated from seaweed. (C and D) *Staurocladia oahuensis* medusa undergoing asexual reproduction by binary fission: time series showing initial elongation of medusa followed by pulling apart to form two medusae, nearing completion. All photographs by Yayoi M. Hirano of medusae in Kominato, Boso Peninsula, Japan; central disk diameters approximately 0.5 mm. C and D reproduced with permission from *Scientia Marina*.

Species in both genera seem exceptionally well adapted to living in tidepools, and some of the temperate and warm-water species show wide ranges of temperature tolerance from the teens to more than 30 °C.

MORPHOLOGY AND LIFE HISTORY

The various species of crawling hydromedusae have 5 to 60 tentacles extending out from the central disk. There is a red eyespot facing upward at the base of each tentacle. The tentacles are bifurcated, with one branch terminating in a small adhesive sucker that attaches to the substrate and the other branch terminating with a knob of stinging cells known as "cnidocysts", which are used to capture prey. The distribution, or pattern, of additional cnidocyst clusters along the tentacles is one of the important features for distinguishing species. The mouth opens on the center of the bottom side of the central disk, toward the substratum.

These crawling hydromedusae reproduce both sexually and asexually. Asexual reproduction by species of *Staurocladia* is generally accomplished by a process known as fission (also used by many sea anemones that live on the rocky shore), dividing their small bodies in half by adhering with their tentacles to the bottom and then pulling themselves apart into two approximately equal halves (Fig. 1C, D). *Eleutheria* reproduces asexually by budding tiny new jellyfish from the edges of the central disk between existing tentacles, or over the canals within the subumbrella; at least two species of *Staurocladia* are also capable of asexual budding from the edges of the bell margin.

Both *Staurocladia* and *Eleutheria* medusae can also reproduce sexually, which usually occurs after a period of asexual reproduction by each individual. Each jellyfish can produce eggs or sperm; where sexual reproduction is known, sexes are separate in *Staurocladia* medusae, meaning that each jellyfish is either a female or a male, whereas some *Eleutheria* are reported to be hermaphroditic, which means that each jellyfish is both male and female, producing both sperm and eggs, often sequentially. In the case of some *Eleutheria* and some species of *Staurocladia*, the fertilized embryos are protected for a short while within the central disk before they are then released; in other cases the gametes are fertilized externally in the sea without maternal protection, as is typical for most other hydromedusae. The fertilized embryos develop into free-swimming planula larvae and then settle to the bottom where they form tiny, inconspicuous hydroids, which will eventually produce more medusae. The hydroids of these species have only rarely been found in nature, but for a few of these species, are quite easily raised in the laboratory.

It is difficult to estimate age of individuals in populations where asexual reproduction can be so prolific at times and where individuals are so tiny that it is nearly impossible to keep track of them. It is thought that most of these crawling hydromedusae live less than about one month. However, some individual crawling hydromedusae may successfully overwinter in the field and medusae of at least one species of *Staurocladia* are known to persist as long as one year in the laboratory.

There are a few other species of benthic hydromedusae, which live at least partially attached to the bottom in shallow water, including species of *Cladonema* and *Gonionemus*, but these are characteristic of quieter water including bays with abundant sea grass, rather than exposed rocky shorelines.

ECOLOGY

These tiny crawling jellyfish feed primarily on harpacticoid copepods, which also move over the surfaces of seaweed blades and rock. The jellyfish creep slowly along by raising one tentacle off the surface at a time and throwing it forward in the direction of movement. Some species have been observed to release from the surface and swim for brief periods, but most of these crawling species of jellyfish are unable to swim.

Little is known about the predators of these little hydromedusae. At least one species of aeolid nudibranch feeds on a *Staurocladia*, and it is likely that other such predator–prey associations exist between various species of these hydromedusae and other nudibranchs in the field.

Eleutheria dichotoma has recently been found to be well established as an introduced species along approximately 400 km of the New South Wales (Australia) shoreline. Although these medusae, with central disk diameters of less than 0.5 mm, occur in densities up to about 100 individuals per 10 cm^2 of algal surface (especially *Ulva*) in some places along the rocky shore (Fraser *et al.* 2006), we still do not know what impact they might have in the intertidal communities in which they live. *Staurocladia* species in Japan have been shown to have high asexual reproductive rates when conditions are good, allowing rapid increase of the microscopic medusa populations at times; the same is likely true for *Eleutheria*.

TAXONOMY AND PHYLOGENY

Both *Staurocladia* and *Eleutheria* are anthomedusan hydromedusae and produce athecate hydroids. They are usually now placed in the family Cladonematidae, although some authors still recognize the Eleutheriidae as a separate family for these two genera. Recent morphological comparison studies indicate that this is a polyphyletic group (Schuchert 2006); distinction of the two genera is problematic and has varied widely between authors.

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FURTHER READING

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