

Staurozoans Taxonomy and Relationships to Other “Scyphozoans”

Staurozoans are sessile, stalked jellyfish. In other words, they look like a cross between an anemone and a medusa. This has led to confusion about their position within the phylum Cnidaria and as to whom they are most closely related. Descriptions and placement of this group have changed several times since it was first recognized.

The group of stauromedusae was first designated by Ernst Haeckel (1881) in the Challenger Reports. It was one of four orders in the class that Haeckel referred to as Acraspedae. The other orders were Peromedusae, Cubomedusae, and Discomedusae. Acraspedae were defined as possessing no velum, lobes on the umbrella, gastric filaments, and often had life histories that involved an alternation of generations between benthic polyps and pelagic medusae. Order Stauromedusae was defined as an acraspedid medusa with eight principle tentacles, possibly with secondary tentacle bunches on the ends of the primary tentacles and possessing a stomach and genitalia divided into four segments. Haeckel did not include the stalked adults as part of the order description. Two families were identified, Tesseridae and Lucernaridae. The Tesseridae were first described by Haeckel. They were said to be free swimming medusae with an apical elongation. The family Lucernaridae had first been described in 1847 by Johnston but had not been part of a separate order. In Haeckel's redescription of the family, he does not mention that they are benthic. The only mention of the benthic lifestyle is one phrase when describing the peduncle (what was referred to as an apical elongation in Tesseridae) of the newly described species *Lucernaria bathyphila*.

In 1910, Mayer summarized what was known about the world's medusae. He discussed the class Scyphozoa, the class that Haeckel referred to as the Acraspedae. The term Scyphozoa was first used by Lankester in 1881. The description of the scyphozoans was very similar to the description given by Haeckel for the acraspedans. According to Mayer, the class Scyphozoa contained five classes: Stauromedusae, Carybdeidae (referred to as Cubomedusae by Haeckel), Cornatae (referred to as Peromedusae by Haeckel), Semaestomeae and Rhizostomae (together comprised the Haeckel's Discomedusae). Mayer described the Stauromedusae as primarily sessile, possessing eight tentacles with clusters at the ends, and having non-ciliated planula larvae. Mayer said that stauromedusae were the “most degenerate of all scyphomedusae.” He described the same two families that were mentioned by Haeckel but said that Tesseridae were known only from Haeckel.

The first volume of Libbie Hyman's treatise of the invertebrates was published in 1940. Hyman listed class Scyphozoa as containing five orders similar to those described by Mayer (Cubomedusae, Stauromedusae, Cornatae, Semaestomeae, and Rhizostomae). She describes all staurozoans as being sessile and attached by a stalk. She does not discuss Tesseridae or any exception to the sessile lifestyle.

In 1961, Kramp reviewed the medusae of the world. He described the same five families of Scyphozoa as Hyman. His description of order

Stauromedusae was similar to that of Hyman. He discussed two families of staurozoans: Eleutherocarpidae and Cleistocarpidae. Lucernariinae (=Lucernariidae) is listed as a subfamily of Eleutherocarpidae.

A few years later, Thiel (1966) reviewed the evolution of scyphozoans. He listed the same five orders as Hyman and Kramp. However, he grouped the Cubomedusae and the Stauromedusae into subclass Scyphostomidae, saying that they comprised the base of the Scyphozoa.

In 1973, a jellyfish symposium was held in Japan. During this conference, results were presented suggesting that cubomedusae were significantly different from other scyphozoans and should therefore be placed in their own group: class Cubozoa (Werner, 1973). The cubozoans were placed at the base of the medusa-like organisms. Uchida (1973) examined the systematic position of the stauromedusae. He disagreed with Thiel and other authors who believed that staurozoans were near the base of the scyphozoans, and were most closely related to cubomedusae. Uchida argued that based on their distribution and morphology, Stauromedusae was a more advanced order than Cornatae, and were most closely related to Semaestomeae. He also discussed several versions of the families of stauromedusae, and determined that there were four valid families: Lipkeidae, Kishinouyeidae, Haliclystidae (=Lucernariidae from Haeckel), and Cleisocarpidae.

During the late 1990's, the staurozoans were back to being considered the most basal scyphozoans. Bridges et al (1995) discussed four orders of scyphozoans (Stauromedusae, Cornatae, Semaestomeae, and Rhizostomae), and placed the staurozoans at the base of the scyphozoans. In 1997, Arai also placed the stauromedusae at the base of the scyphozoans. She mentioned two families, Cleistocarpidae and Eleutherocarpidae (the same families described by Kramp in 1961). In 1998, Lutz et al. discussed stauromedusae in the deep sea. They found *Lucernaria* (a genus discussed by Haeckel) at hydrothermal vents. This study was a return to some of the work done by Haeckel, which had been largely ignored for over 100 years. In 1999, Claudia Mills started a website with a list of all of the currently recognized species of staurozoans. This list was compiled because there were no reliable references containing this information. Mills listed 50 species in five families (Depastridae, Kyopodiidae, Lipkeidae, Kishinouyeidae, and Lucernariidae). She considered the two families listed by Arai (Cleistocarpidae and Eleutherocarpidae) to be suborders. This was the classification system that she used in her gelatinous zooplankton guide, published in 2003 (Wrobel and Mills).

In 2004, Marques and Collins took the first serious look at scyphozoan phylogenetics. They determined that the stauromedusae (along with the extinct Conulatae) were molecularly and morphologically distinct enough to warrant their own class, Staurozoa. They argued that the medusa-like organisms were more similar to one another than any of them were to the Anthozoa (corals and anemones). Based on this, they created the subphylum Medusozoa containing the classes Staurozoa, Cubozoa, Scyphozoa (with three orders), and Hydrozoa. The staurozoa were the base of the medusozoan lineages.

Collins and Daly described a new species of *Lucernaria* from the deep sea in 2005. Molecular studies were done to determine where the new stauromedusae should be placed within class Staurozoa. These studies provided further evidence that Staurozoa should be its own class. They also questioned the validity of the usage of the suborders Cleistocarpidae and Eleutherocarpidae.

In 2006, Collins et al. clarified some lingering questions about medusozoan phylogenetics and proposed a working hypothesis for the relationships among cnidarian groups, which is the current standard (Figure 1). This paper provided further evidence that Staurozoa is the basal group of Medusozoa. This paper also reintroduced the term Acraspeda (used by Haeckel) to describe the clade containing classes Cubozoa and Scyphozoa.

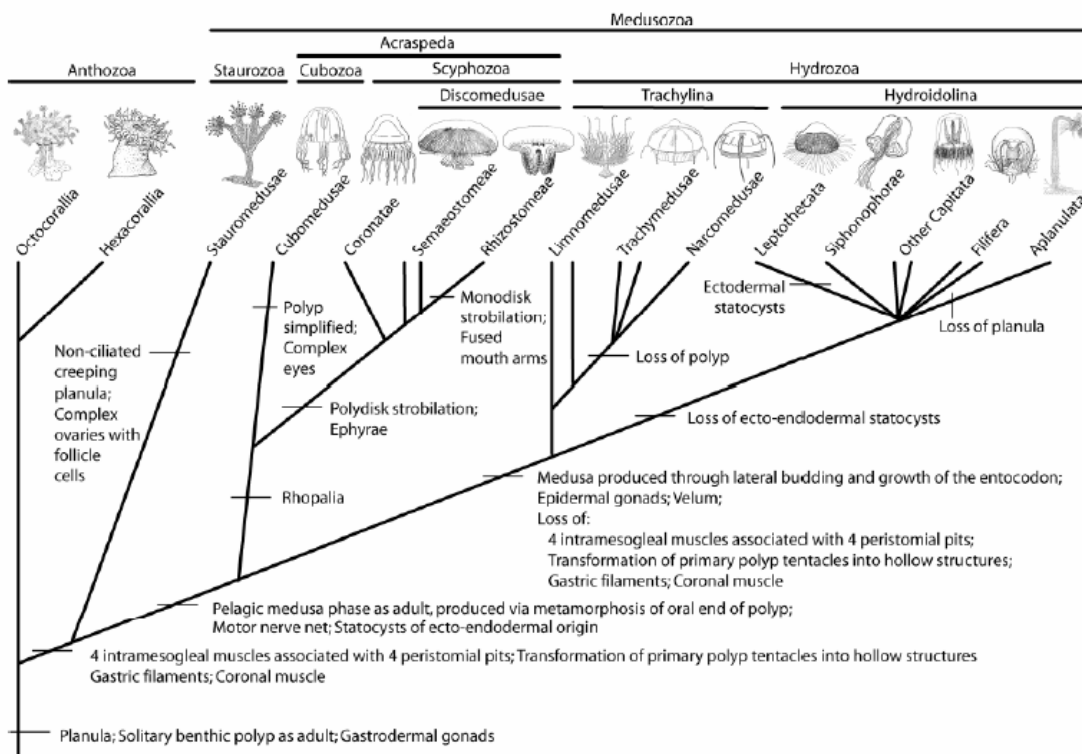


Figure 1. Current View of Cnidarian Relationships, From Collins et al, 2006.

Staurozoans have gone from being a somewhat vaguely described order to being an important evolutionary link within the Cnidaria. A story that began with Haeckel in the 1870's, has taken new directions based on the use of new technology. One hundred years from now when scientists look at the taxonomic position of staurozoans, opinions will have changed, technology will have improved, and the position of the staurozoans may have changed again (perhaps many times over).

Literature Cited:

Arai, M.N., 1997. *A Functional Biology of Scyphozoa*. Chapman Hall, London.

- Bridge, D., C.W. Cunningham, R. DeSalle, L.W. Buss, 1995. Class-level relationships in the phylum Cnidaria: molecular and morphological evidence. *Molecular Biology and Evolution* 12(4): 679-689.
- Collins, A.G. and M. Daly, 2005. A new deepwater species of stauromedusae, *Lucernaria janetae* (Cnidaria, Staurozoa, Lucernariidae), and a preliminary investigation of stauromedusan phylogeny based on the nuclear and mitochondrial rDNA data. *Biological Bulletin* 208: 221-230.
- Collins, A.G., P. Schuchert, A.C. Marques, T. Jankowski, M. Medina, and B. Schierwater, 2006. Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Systematic Biology* 55(1): 97-115.
- Haeckel, E.H. 1881. Report on the deep sea medusae dredged by the H.M.S. Challenger during the years 1873-1876. *Reports from the Challenger Expedition (Zoology)* 4:1-154.
- Hyman, L.H., 1940. *The Invertebrates*. Vol 1 Protozoa through Ctenophora. McGraw-Hill, New York.
- Kramp, P.L., 1961. Synopsis of the Medusae of the World. *J Mar Biol Asso of the United Kingdom* 40: 292: 303.
- Lankester, 1881. *Encyclopedia Britannica*, Ed. 9. Hydrozoa.
- Lutz, R.A., D. Desbruyeres, T.M. Shank, R.C. Vrijenhoek, 1998. A deep-sea hydrothermal vent community dominated by stauromedusae. *Deep-Sea Research II* 45: 329-334.
- Marques, A.C. and A.G. Collins, 2004. Cladistic analysis of Medusozoa and cnidarian evolution. *Invertebrate Biology* 123 (1): 23-42.
- Mayer, A.G., 1910. *Medusae of the World*. Vol. 3 the Scyphozoa. Carnegie Institute of Washington, Washington, D.C.
- Mills, C.E., 1999. Internet 1999-Present. Stauromedusae: list of all valid species names. <http://faulty.washington.edu/cemills/Staurolist.html>.
- Thiel, H., 1966. The evolution of the Scyphozoa: A Review p 77-118 in *The Cnidaria and Their Evolution*, W.J. Röss ed. Academic Press, London.
- Uchida, T., 1973. The systematic position of the stauromedusae. *Publ. Seto Mar. Biol. Lab.* 20: 133-139.
- Werner, B., 1973. New investigation on the systematics and evolution of the class Scyphozoa and the phylum Cnidaria. *Publ. Seto Mar. Biol. Lab.* 20: 35-61.
- Wrobel, D. and C.E. Mills, 2003. *Pacific Coast Pelagic Invertebrates: A Guide to the Common Gelatinous Animals*. 2nd Edition. Monterey Bay Aquarium, Monterey, CA.