## AFFINITIES AND CLASS-LEVEL SYSTEMATICS OF THE PHYLUM CNIDARIA

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Phylogenetic relationships among the cnidarian classes Anthozoa, Hydrozoa and Scyphozoa, and between Cnidaria and other metazoan phyla, continue to be subject to widely divergent interpretations. Also controversial are the affinities of numerous fossil groups, including Byronia Bischoff, Sphenothallus Hall and conulariids, that have been interpreted as extinct cnidarians. Currently favored interpretations of evolution within Cnidaria are generally consistent with one of two alternative hypotheses of phylogenetic relationships: scyphozoans and anthozoans are members of a monophyletic group that excludes hydrozoans; or scyphozoans and hydrozoans are members of a monophyletic group that excludes anthozoans. Putative anthozoan-scyphozoan synapomorphies include (1) gastric septa present; (2) cnidae present in both ectoderm and gastroderm; (3) sex cells gastrodermal; and (4) mesoglea contains amoeboid cells. Putative hydrozoan-scyphozoan synapomorphies include (1) medusa present; (2) tetraradial symmetry; (3) rhopaloid nematocysts; and (4) similarities in sperm structure.

Evaluation of alternative hypotheses of relationships within Cnidaria is complicated by uncertainty surrounding relationships between this and other metazoan phyla. While some investigators have interpreted Cnidaria and Ctenophora as members of a monophyletic group that excludes other phyla, others have argued that ctenophorans are more closely related to platyhelminths than they are to cnidarians. Putative cnidarian-ctenophoran synapomorphies include (1) production of cells modified for prey capture; and (2) presence of a medusa. Putative ctenophoran-platyhelminth synapomorphies include (1) presence of gonoducts; (2) ciliated cells with several to many cilia; (3) determinate cleavage; and (4) muscle cells developed from mesoderm. Comparisons of these and other phyla indicate that the strongest hypotheses of synapomorphy are those between cnidarians and ctenophorans. Ctenophorans do not have a mesoderm, and they lack complex reproductive structures that can be homologized with platyhelminth gonoducts. Similarities between ctenophorans and platyhelminths in ciliation and cleavage type are either non-homologous or shared primitive. The most recent common ancestor of ctenophorans and cnidarians was probably a medusa-like animal with circular and meridional muscle fibers and a non-septate digestive cavity having four radial canals. This cavity probably lacked cells specialized for prey capture, but glutinant prey-capture structures may have been present on tentacles. Sperm produced by this common ancestor were most similar to sperm of extant ctenophorans, hydrozoans and scyphozoans. Anatomical features unique to ctenophorans or cnidarians, regarded by some investigators as evidence against a close relationship between these two groups, are autapomorphies. These interpretations imply that putative hydrozoan-scyphozoan synapomorphies are actually shared primitive, and that the presence of gastric septa and cnidae-bearing gastric filaments in scyphozoans and anthozoans is shared derived. This would mean that the most parsimonious hypothesis of phylogenetic relationships within Cnidaria is that anthozoans and scyphozoans are members of a monophyletic group that excludes hydrozoans.

Debate over relationships among these extant taxa has heightened interest in the affinities of prominent groups of problematic fossil cnidarians. Byronia Bischoff, Sphenothallus Hall and conulariids, all characterized by an apatitic, multilamellar theca, show detailed anatomical similarities to hydrozoans and/or scyphozoans. Putative synapomorphies linking Byronia and coronatid scyphozoans include the presence of multiple whorls of thorn-like nodes projecting into the thecal cavity, with each whorl consisting of eight nodes arranged in two sets of four nodes each. Sphenothallus, characterized by a pair of tentacles and, in some species, multiple branching, is most similar to hydrozoan and scyphozoan polyps, many of which are colonial or exhibit a single pair of tentacles early in their development. Similarities in hard- and soft-part anatomy between scyphozoans and conulariids suggest that conulariids, like scyphozoans, possessed four gastric septa and produced medusae through polydisc strobilation. Although conulariids have been interpreted as ancestral to extant cnidarians, they are more likely either a sister group to Scyphozoa or members of this class.