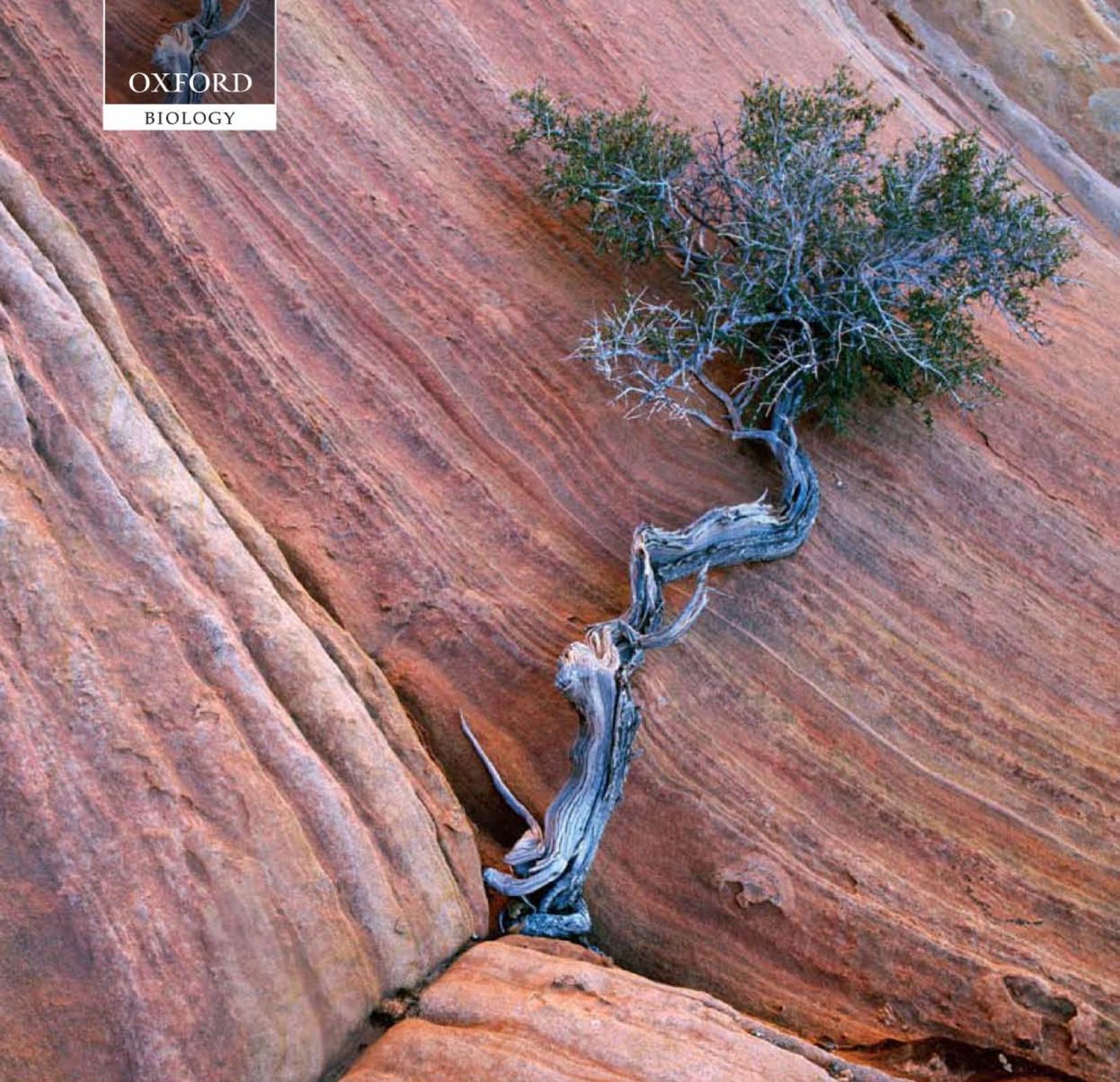


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the **TIMETREE** *of* **LIFE**

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Cnidarians (Cnidaria)

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Abstract

Cnidarians, which show a remarkable diversity of morphology and lifestyles, are important as reef-constructors, predators, and parasites in marine ecosystems. Few data currently exist on the timing of the evolutionary events among major groups of cnidarians (~7 classes and ~25 orders) and some of these are associated with high levels of uncertainty. However, fossil evidence, and molecular estimates of divergence times among members of the subclass Hexacorallia (Class Anthozoa), indicate that past climate-change events have had a significant impact on the evolution of reef-building corals and related groups.

The Phylum Cnidaria is ancient and diverse in terms of size and body shape, and includes the sea fans, sea pens, sea anemones, corals, hydroids, and jellyfish (Fig. 1). Cnidarians possess two cell layers (diploblastic), the outer ectoderm and the inner endoderm, separated by an acellular mesoglea, or partially cellular mesenchyme (1). The animals are radially symmetrical, although this may be modified, and have two basic forms, the polyp and the medusa. The sessile polyp is sac like, with a single body cavity (coelenteron) opening through the mouth which is surrounded by one or more rows of tentacles. The pelagic medusa is umbrella- or bell-shaped with a mouth located in the center of the concave underside surrounded by tentacles positioned around the margins of the animal. In polyps and medusae, the tentacles are armed with stinging or adhesive structures called cnidae, each produced by a stinging cell, the cnidocyte (1, 2).

In cnidarians, the alternation of an asexual benthic polypoid form, with the sexually reproducing medusoid phase, is the primitive life-history state in extant taxa (e.g., many hydroids). Depending on the taxon, the polypoid or medusoid phase may be reduced or completely absent. In anemones and corals, for example, the medusoid phase is eliminated with the gonads developing within the polyps. Colonies of many species of benthic cnidarians can grow or reproduce through asexual

production of new polyps or colonies (e.g., corals), the overall size of which can be large. Cnidarians are carnivores, suspension feeders, or parasites, and many species within the phylum have symbiotic intracellular algae in their tissues. They are ecologically important animals in marine environments, although some are also found in freshwater. Corals have been important framework-building species in reefs from the Paleozoic (359 million years ago, Ma) to the present day in both shallow and deep waters, although the main hermatypic groups have changed over time with a dramatic turnover from rugose and tabulate corals before the great Permian extinction (251 Ma) to the scleractinian corals from the mid-Triassic (245–228 Ma) (3). Jellyfish and siphonophores are also ancient and are important in coastal and oceanic marine ecosystems as pelagic predators.

Today the phylum has a high species diversity, with the Class Anthozoa containing more than 6100 species: >3000 in Subclass Octocorallia (4); >1113 in Subclass



Fig. 1 A scyphozoan from the Irish Sea (*Aurelia aurita*; upper left), an actiniarian from southwest Britain (*Metridium senile*; upper right), and a scleractinian from Maldives (*Acropora* sp., lower). Credit: A. Rogers.

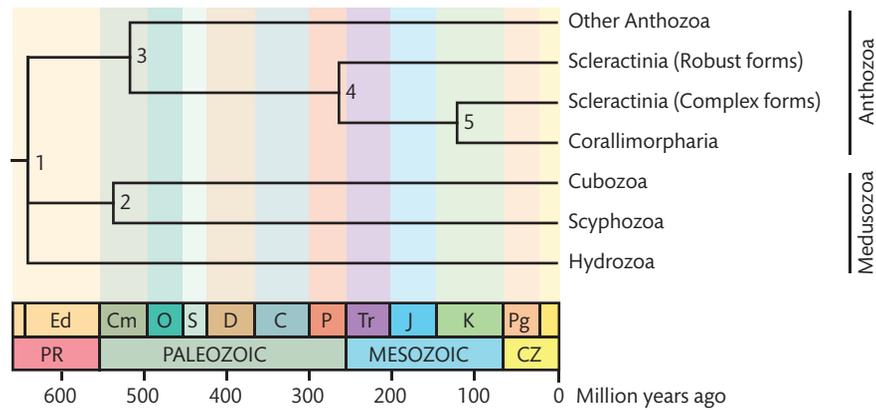


Fig. 2 A timetree of cnidarians. Divergence times are shown in Table 1. *Abbreviations:* C (Carboniferous), Cm (Cambrian), CZ (Cenozoic), D (Devonian), Ed (Eidacaran), J (Jurassic), K (Cretaceous), O (Ordovician), P (Permian), Pg (Paleogene), PR (Proterozoic), S (Silurian), and Tr (Triassic).

Hexacorallia Order Actiniaria (5); >1600 in Order Scleractinia (5); >461 in Subclass Ceriantharia, and hexacoral Orders Zoanthidea, Corallimorpharia, and Antipatharia combined (5). The remaining cnidarians of the Medusozoa comprise more than 5954 species: 2184 in Class Myxozoa (6); 1 in the Class Polydipodiozoa; 51 in Class Stauromedusae (7); 32 in Class Cubozoa (8); 212 in Class Scyphozoa (9); >166 in Class Hydrozoa, Subclass Trachylinae (10); >1900 in Subclass Hydroidolina, Order Leptomedusae (10); >1200 in Order Anthomedusae (10); and 199 in Order Siphonophora (10). The groups that are holopelagic or which have a mainly pelagic life history generally are less species-rich than the groups with a benthic or parasitic lifestyle. This is probably a result of the homogeneity and open nature of the pelagic environment, offering less opportunity for niche specialization and allopatric speciation than in groups where the dominant life-history phase is parasitic or benthic.

The cnidarians originated in the early stages of metazoan evolution, in the Precambrian (>542 Ma) (11, 14). Some of the oldest metazoan fossils, part of the Ediacaran biota, have been attributed to three extant cnidarian groups, including the Chondrophorina (sailors by the wind), the Pennatulacea (sea pens), and the Scyphozoa (jellyfish). Modern chondrophorinans are assigned to the Family Porpitidae, within the Anthomedusae, on the basis of morphology. However, molecular phylogenetic analyses, based on nuclear small subunit (SSU) ribosomal DNA (rDNA) sequences, have suggested that the Ediacaran fossils attributed to the Chondrophorina are from another unrelated taxon (11). This study is, however, consistent with the existence of pennatulids in

the Ediacaran, 565 Ma, and the scyphozoans in the late Ediacaran 545 Ma (12, 13). Using calibration from the fossil record, and a Quartet-based method for estimating the divergence dates between cnidarian taxa from a phylogeny based on nuclear SSU rDNA, the root of the Cnidaria has been placed in the Proterozoic, 800–1000 Ma (11). Phylogenetic analysis of all available protein sequence data and the use of well-constrained calibration points from the fossil record, to estimate secondary calibration points in the Precambrian (>542Ma), similarly estimate the divergence of the Cnidaria and Bilateria at 1298 ± 74 Ma (14). These dates confirm the origin of cnidarians at the base of the metazoan radiation and show that they have a substantial hidden Precambrian history (11).

Cnidarians have been an integral part of theories relating to the origin of metazoans for more than 100 years, because they have been regarded as primitive animals (15). Whether the ancestral cnidarian was polypoid or medusoid, the nature of the relationships between the classes of the phylum has been important to resolving how the diversity of metazoan life arose. The discovery that the Cubozoa, Scyphozoa, and Hydrozoa, including the Siphonophora, possess a unique derived structural alteration in their mitochondrial DNA (linear mitochondrial DNA, mtDNA) (16) was strong evidence that the medusoid groups are monophyletic, forming the clade Medusozoa. Support for the close association of Medusozoa and Anthozoa (circular mtDNA as for all other metazoans) has been provided by nuclear SSU rRNA-based phylogenies (17). The derivation of the Medusozoa from the ancestral anthozoans is the likely

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among cnidarians.

Timetree		Estimates									
Node	Time	Ref. (17)		Ref. (18)		Ref. (19)(a)		Ref. (19)(b)		Ref. (26)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	640.9	709	777–641	711.7	1035–389	548	519–579	595	561–626	-	-
2	537.5	-	-	537.5	943–191	-	-	-	-	-	-
3	517.5	-	-	517.5	2308–0	-	-	-	-	-	-
4	264.0	-	-	-	-	-	-	-	-	264	240–288
5	121.0	-	-	-	-	-	-	-	-	121	110–132

Note: Node times in the timetree represent the mean of time estimates from different studies. Estimates from ref. (19) are from two different nodes.

path of evolution for these taxa, because it would require a single origin of the medusa as opposed to an origin and subsequent loss in the Anthozoa if they were the derived group (17).

The origin of the Medusozoa has been estimated from nuclear SSU and large subunit (LSU) rRNA as probably during the Cryogenian (850–630 Ma; Table 1, Fig. 2) in the Neoproterozoic. These dates range from the early Neoproterozoic to early Cambrian (11, 18, 19), and the dates for the origins of the Medusozoa, the Scyphozoa, and the Hydrozoa are inconsistent, so the relationships between these taxa are shown as a polytomy (Table 1, Fig. 2). The Cryogenian was a period of severe global glaciations including the so-called “Snowball Earth” events (20). Recent work has suggested that despite the extreme conditions during parts of this period it is likely that areas of the oceans remained open even during glaciations (21).

Phylogenetic analyses based on partial sequences of the mitochondrial SSU rRNA (22), partial and complete sequences of the nuclear SSU rRNA (23, 24), a combination of those data (25), or the entire mitochondrial genome (26, 27), have suggested that the Subclass Octocorallia is the closest relative of the group containing all other anthozoan orders. Some studies have placed the Ceriantharia (tube-dwelling anemones) basal to all other Anthozoa (28, 23), although the majority favor this group to be the closest relative of the Hexacorallia (22, 24, 25, 27, 29). The relationships between the orders of the Hexacorallia remain unresolved. In particular, the relationships between the Zoanthidea (zoanthids—colonial anemones), Actiniaria (sea anemones), and Antipatharia (black corals) are unclear and studies based on different genes have estimated different relationships between these taxa (24, 27). Estimates from nuclear SSU and LSU

data place the origin of the hexacorallians in the Lower Cambrian (542–513 Ma) (18), a date consistent with the earliest well-preserved fossil anemones. This period was a time when early reefs, comprising archaeocyath sponges and tabulate corals developed, although these collapsed at the end of the Lower Cambrian (30).

Of all the hexacorals, the scleractinians are unusual in their sudden and late appearance in the fossil record in the Middle Triassic (Anisian stage, 237 Ma, 3). This followed the great Permian extinction which destroyed 96% of all marine species (31) and wiped out the Orders Rugosa and Tabulata, the main reef-building corals of the Paleozoic (542–251 Ma) (3). The cause of the Permian extinction is still a subject of significant debate. Large-scale volcanism probably led to global warming, resulting from increased atmospheric CO₂ and subsequent methane hydrate release. Oceanic anoxia, together with release of toxic hydrogen sulfide from the deep ocean and decreased marine productivity, are thought to have also occurred (31). The changes in ocean biochemistry and in other environmental parameters at the end of Permian (251 Ma) led to a prolonged recovery well into the Triassic (251–200 Ma) (3, 31).

The appearance of numerous higher taxa of the Scleractinia on the margins of the Tethys Sea is abrupt in the fossil record and the origination of stony corals has been a topic of much debate to which molecular studies have made a significant contribution. Several potential ancestors to scleractinians have been postulated (3), including rugosan corals, the Scleractiniomorpha, and soft-bodied Hexacorallia from the Orders Actiniaria, Corallimorpharia, or Zoanthidea (the “naked coral” hypothesis, 32).

Phylogenetic analyses of the Scleractinia, based on SSU rRNA, have identified two distinct clades, the “robust”

and the “complex” stony corals (33–36). Sequence divergence between these clades suggested that they originated about 300 Ma (34), a date that is older than the fossil appearance of the scleractinians in the Anisian stage of the Middle Triassic (245–237 Ma). However, subsequent analyses of the mitochondrial genome sequences of Anthozoa have refined the estimate for the origination of the Scleractinia at 288–240 Ma (26). This also supports the theory that the stony corals arose from naked hexacorallian ancestors in the Permian/Triassic and expressed the ability to secrete aragonite skeletons when ocean chemistry became conducive to the accretion of aragonite from seawater (3, 32). Experiments on growing scleractinian corals in seawater with a lowered pH may support this hypothesis. These show that at least some species can respond to the absence of conditions for the accretion of a skeleton by dissociation of the colonial form and complete skeletal dissolution (37). This may provide an explanation as to how corals might have survived large-scale environmental changes in the Permian and thus appeared abruptly within the fossil record at a later date. However, more than 40% of extant Scleractinia live in deep waters where preservation potential is reduced compared to shallow environments. Thus, the early history of skeletonized corals may have been obscured in the fossil record (26).

At least one hexacorallian group has been eliminated as ancestors of the scleractinians. The corallimorpharians were found to have been derived from the “complex” clade of the Scleractinia through the analyses of mitochondrial genome sequence (26) (but see 27). This was dated as to have occurred in the mid- to late-Lower Cretaceous, 132–110 Ma. This was a time when changing seawater chemistry increasingly favored the secretion of calcitic skeletons over aragonitic skeletons in marine organisms (38) and reefs became dominated by rudist bivalves (3). The corallimorpharians lost the coral skeleton presumably as an adaptation to increasingly unfavorable conditions for the uptake of calcium carbonate and secretion of aragonite.

The rise and fall of reef-building cnidarians through geological time is intimately connected with changes in marine chemistry which have been driven by climate change (3, 38). Present-day climate change has impacted scleractinians through global temperature increases, causing coral bleaching. Increasing levels of ocean acidification have the potential to reduce calcification rates and increase dissolution rates of coral skeletons that form reefs (39, 40). Geological history tells us that if current trends in environmental change continue, even if corals

survive through physiological refugia as “naked” polyps, there will be profound changes in the distribution, diversity, and structure of coral reef communities.

Molecular studies of the Medusozoa have led to a much greater understanding of non-anthozoan relationships, but have resulted in few data on the timing of evolutionary events within the group, because of relatively few fossil records for calibration. Phylogenetic analyses of the Class Staurozoa, including a new species from deep-sea hydrothermal vents, using SSU rRNA sequences (7), have supported morphological studies suggesting this group is the closest relative of all other Medusozoa (41). This is consistent with the hypothesis that the medusoid form evolved from benthic ancestors (15). Gene sequences of the SSU and LSU of nuclear rRNA indicate that the group containing Cubozoa and Scyphozoa (named the Acraspeda, 15) is the closest relative of Hydrozoa and that these groups may have evolved in the Cryogenian (Table 1) (18). The mean dates for the node between the Hydrozoa and Scyphozoa/Cubozoa actually predate those for the origin of the medusozoans and so this is shown as a polytomy (Fig. 2). This reflects the high levels of uncertainty in present estimates of the timing of events in the evolution of the medusozoans. The timing of divergence between the hydrozoans and scyphozoans must have come after the evolution of the first medusozoans (15, 41). These dates again point to a substantial evolutionary history of the cnidarians in the Precambrian.

The cubozoans and scyphozoans show marked differences in their life histories, but their relationship is supported by morphological similarities in the medusae of both groups (15). Nuclear SSU and LSU rRNA data place the node between these classes in the Early Cambrian at 538 Ma (18). Within the scyphozoan jellyfish, the Rhizostomeae has previously been considered as derived from the Semaestomeae, because of similarities in the radial canal systems, which has been confirmed by molecular data (15, 17). The Coronatae (crown jellyfish) is a close relative of the Semaestomeae and the Rhizostomeae.

On the basis of mitochondrial SSU rRNA and nuclear SSU and LSU rRNA sequences, the Hydrozoa have been separated into two major clades, the Trachylina (Orders Limnomedusae, Trachymedusae, and Narcomedusae) and the Hydroidolina (Orders Anthoathecata, Lep-tothecata, Siphonophorae) (15, 42). The Trachylina consists mainly of marine medusoid forms (a few are freshwater) with simple, reduced, or even absent polyp stages. The Trachylina generally fall into the previously

recognized orders, although there is evidence of paraphyly in the Limnomedusae and Trachymedusae (15). Although the athecate hydroids, thecate hydroids, and siphonophores form separate clades, the relationships between the orders of the Hydroidolina are largely unresolved. This may be a result of rapid evolution in the early history of this group. In these analyses, the monotypic Subclass Langiomedusae falls within the Athecata, and the classification of athecate hydroids into the suborders Capitata and Filifera is not supported (14). However, a new clade, the Aplanulata, united by a shared-derived character (development from egg to polyp via a nonciliated stereogastrula stage, rather than a ciliated planula stage, 43) is resolved by the molecular analyses (15, 42). This clade comprises the Tubulariidae, Corymorphidae, Candelabridae, and Hydridae. Other anthoathecate hydroid groups that exhibit this type of development may also fall within this group, although they are yet to be sampled for molecular studies (15).

Ultrastructural studies and analyses of the SSU of the nuclear rRNA have suggested that the parasitic myxozoans, previously regarded as protists, are cnidarians (44). Phylogenetic analyses of 129 protein sequences have provided strong support for this hypothesis and furthermore suggest that the myxozoans are highly derived medusozoans (45). At present the relationship of the myxozoans to other medusozoan taxa has not been resolved, but this discovery has changed understanding of the diversity of species and lifestyles adopted by cnidarians. Myxozoans are parasites of a variety of animals including annelids, bryozoans, and fish and can be economically significant, especially in the aquaculture industry.

Molecular phylogenetic approaches are now being employed to examine the evolution and systematics of cnidarians below the level of Order. Within the Anthozoa, poor correspondence between the preexisting morphological taxonomy and molecular phylogenetics trees has been discovered, especially within the Octocorallia (46–48) and Scleractinia (33–36). This suggests that previous interpretation of the homology of the characters of the skeletons of anthozoans, and other aspects of morphology, are unreliable as a result of convergent or parallel evolution (47).

At the subordinal taxonomic levels, biogeographic and historical factors also become an important influence in the evolution and systematics of coral (49) and other cnidarian taxa (e.g., hydroids, 50). DNA sequence analyses are also demonstrating the existence of many cryptic taxa at the lower taxonomic levels such as Scleractinia (51), Octocorallia (48), Scyphozoa (52, 53), and Hydrozoa

(50, 54). Some of these groups have been viewed as having species with cosmopolitan or very wide geographic distributions resulting from pelagic life-history stages or hydrochory of sessile adults and a lack of barriers to dispersal across the oceans. This is leading to a reevaluation of the systematics, distribution, and overall species diversity of cnidarian taxa.

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