

Recent Insights into Cnidarian Phylogeny

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ABSTRACT. With representatives of more than 10,000 species from diverse clades scattered throughout the world's oceans, Cnidaria is a moderately diverse phylum of Metazoa. As such, various taxa within Cnidaria have been the subjects of recent phylogenetic analyses. Because of its diversity, it has not yet been possible to conduct any extensive phylum-level phylogenetic analyses. In addition, new information suggests that the large group of parasites known as Myxozoa is part of Cnidaria. The present contribution summarizes recent findings to create a picture of a current working hypothesis of cnidarian phylogeny. This summary, which treats the relationships among taxa down to the approximate level of order, likely provides a suboptimal estimation of cnidarian phylogeny as compared to a detailed phylogenetic analysis of data sampled densely from all the Cnidaria component clades. Nevertheless, it should provide points of comparison for upcoming efforts to more comprehensively assess cnidarian phylogeny. Even at the basic level of order, many taxa are thought to be polyphyletic. Understandably, current classifications are not fully reflective of recent phylogenetic advances.

INTRODUCTION

Early in the history of Metazoa, the nematocyst evolved. This capsular organelle encloses venom and a tightly coiled, hollow, dart-like thread that is discharged at incredibly rapid accelerations of up to 5 million g (Nüchter et al., 2006). This explosive discharge can be achieved because of extreme osmotic pressures (Holstein and Tardent, 1984; Weber, 1989) within the highly stable nematocyst wall, the molecular structure and function of which are becoming ever clearer (e.g., Meier et al., 2007). Cnida is the more general term for this organelle, the nematocyst being just one type. However, it is reasonably clear, based on the distribution across cnidarian taxa, that the ancestral form of the cnida was as a nematocyst (Marques and Collins, 2004). The lineage in which the nematocyst originated gave rise to the moderately diverse phylum Cnidaria, most likely during the Ediacaran period (Peterson and Butterfield, 2005; Cartwright and Collins, 2007). Since this time, cnidarians have evolved an enormous variety of forms and a great diversity of life history strategies. Representative cnidarians build reefs, fish the depths, and parasitize other species. Extant valid species number a bit more than 11,000 (Daly et al., 2007),

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or more than 13,000 when roughly 2,200 myxozoan species (Lom and Dyková, 2006) are included (see following), and can be found living in all marine environments. Many myxozoans infect freshwater taxa, but just a small number of other cnidarian species live in freshwater (Jankowski et al., 2008).

Daly et al. (2007), in honor of the 300th anniversary of the birth of Linnaeus, recently provided a summary of phylogenetic knowledge about currently recognized cnidarian taxa (exclusive of Myxozoa) typically ranked at ordinal and family levels in current classifications. I aim to provide a summary of recent insights into cnidarian phylogeny focusing on relationships among the different cnidarian orders. No phylum-level analyses of the evolutionary relationships among these taxa have been carried out, although attempts have been made to assess phylogenetic hypotheses for large subclades of Cnidaria; i.e., Anthozoa (Berntson et al., 1999; Won et al., 2001), Hexacorallia (Daly et al., 2003; Brugler and France, 2007), Octocorallia (Berntson et al., 2001; McFadden et al., 2006); Medusozoa (Collins, 2002; Marques and Collins, 2004; Collins et al., 2006a; Van Iten et al., 2006), and Myxozoa (Kent et al., 2001; Fiala, 2006). In addition, several recent studies have assessed the phylogenetic affinities of taxa that have been problematic (Collins et al., 2006b; Van Iten et al., 2006; Dyková et al., 2007; Jiménez-Guri et al., 2007). The approach taken here is to cobble together results from these various analyses to provide a reasonable picture of our present understanding of cnidarian relationships (Figure 1). Representative cnidarians are illustrated in Figures 2 and 3.

As it concentrates on recent insights, the present paper does not provide a thorough review of the history of ideas about relationships among cnidarian orders, nor does it attempt to summarize what recent phylogenetic results tell us about cnidarian character evolution. For that type of information, one should consult the studies referenced herein. The working hypothesis of cnidarian relationships (see Figure 1), as well as the summary provided by Daly et al. (2007), should provide points of comparison for phylum-wide analyses of cnidarian phylogeny, which will soon be attempted by researchers engaged in the cnidarian tree of life project (<http://CnidToL.com>). Because it is a representation of a hypothetical history of Cnidaria, every node in Figure 1 is uncertain and is subject to change in light of new information. In a couple of instances, question marks are inserted on the working hypothesis to indicate relationships that are particularly tentative at present.

A WORKING HYPOTHESIS OF CNIDARIAN PHYLOGENY

Cnidaria is one of the earliest diverging clades within Metazoa, and surprisingly its precise position within the early diverging animal lineages—Porifera, Placozoa, Bilateria, Ctenophora, and Cnidaria—has remained elusive (Collins et al., 2005b; Dunn et al., 2008). That said, it has become ever clearer that Cnidaria is more closely related to Bilateria than is Ctenophora, a finding based on a synthetic consideration of morphology (Salvini-Plawen, 1978), later supported by 18S rDNA data (Wainright et al., 1993; Collins, 1998), and most recently confirmed by a large analysis of many sequences of data from expressed gene transcripts (derived from large-scale sequencing of messenger RNA; known as expressed sequence tags, or ESTs) (Dunn et al., 2008; although note that the analyses published therein suggest that Ctenophora is the earliest diverging extant metazoan lineage, which is either a radical new finding or an indication of bias in the results). Ribosomal data, both 18S (e.g., Collins, 1998) and combined 18S and 28S (Medina et al., 2001; Cartwright and Collins, 2007), strongly suggest that Cnidaria forms a clade with Bilateria and the little-known phylum Placozoa, and that Cnidaria may be the sister group of either taxon or both together. More recently, phylogenetic analyses using entire genomes (unfortunately without any representatives of Ctenophora) found Placozoa to be the sister group of a clade composed of Cnidaria plus Bilateria (Srivastava et al., 2008).

Myxozoa is an interesting group of parasites that very well may be part of Cnidaria. Although some early workers suggested that they are cnidarians, based on the similarity between nematocysts and myxozoan polar capsules (Weill, 1938), they were mainly considered as protists throughout the twentieth century. In 1995, an analysis of 18S and morphological data suggesting that myxozoans were derived from within Cnidaria was published (Siddall et al., 1995). However, this conclusion was doubted by many because the 18S gene of myxozoans appears to have evolved very quickly relative to that of most other metazoans, and different analyses involving different sets of taxa came to conflicting conclusions about the precise position of Myxozoa within Metazoa (Smathers et al., 1994; Siddall et al., 1995; Hanelt et al., 1996; Siddall and Whiting, 1999; Kim et al., 1999; Zrzavý and Hypša, 2003). This uncertainty was claimed to have been resolved when it was discovered that an unusual worm-shaped animal known as *Buddenbrockia* was a myxozoan (Okamura

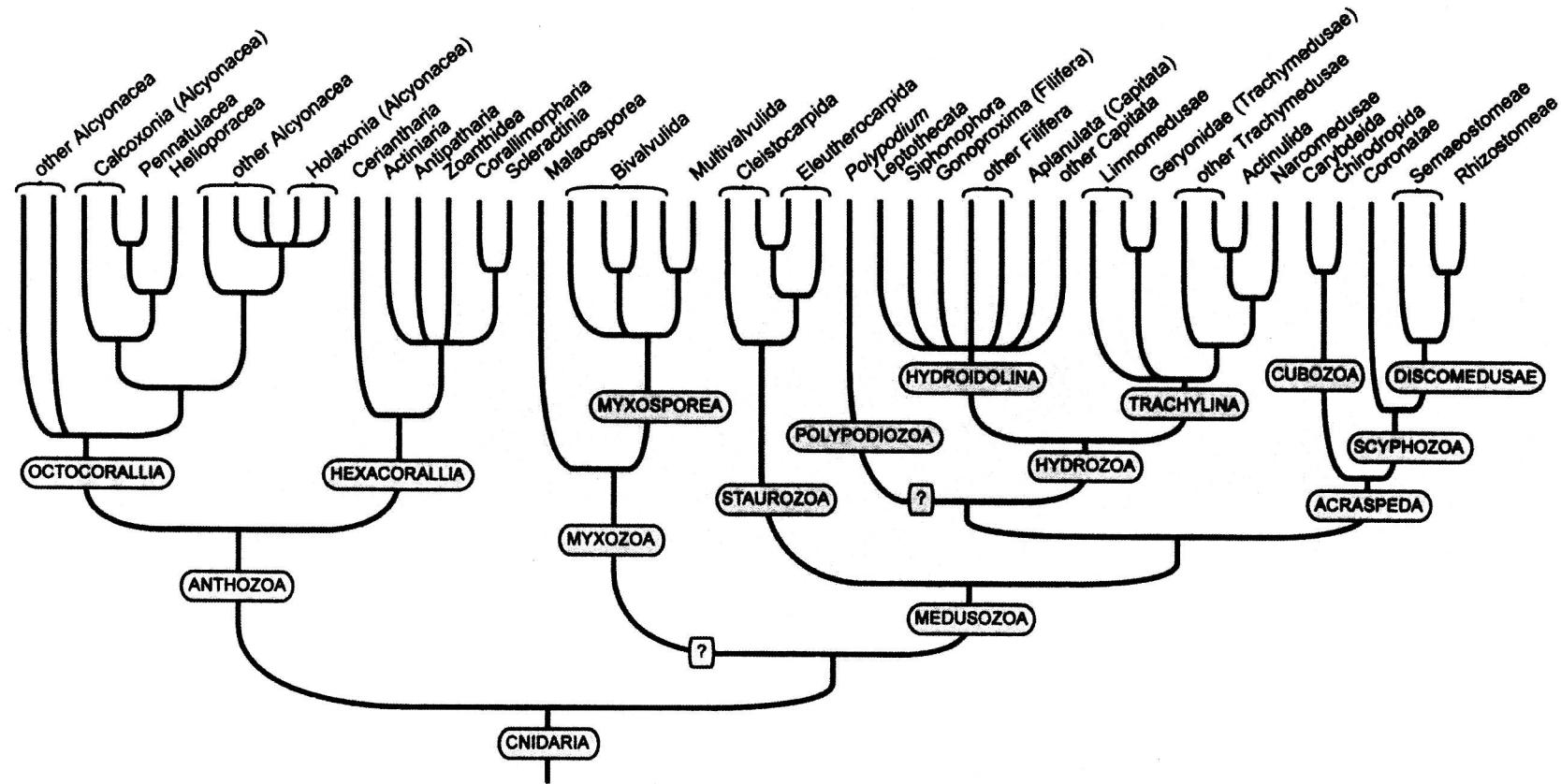


FIGURE 1. Working hypothesis of evolutionary relationships among extant cnidarian taxa usually classified at or near the rank of order.

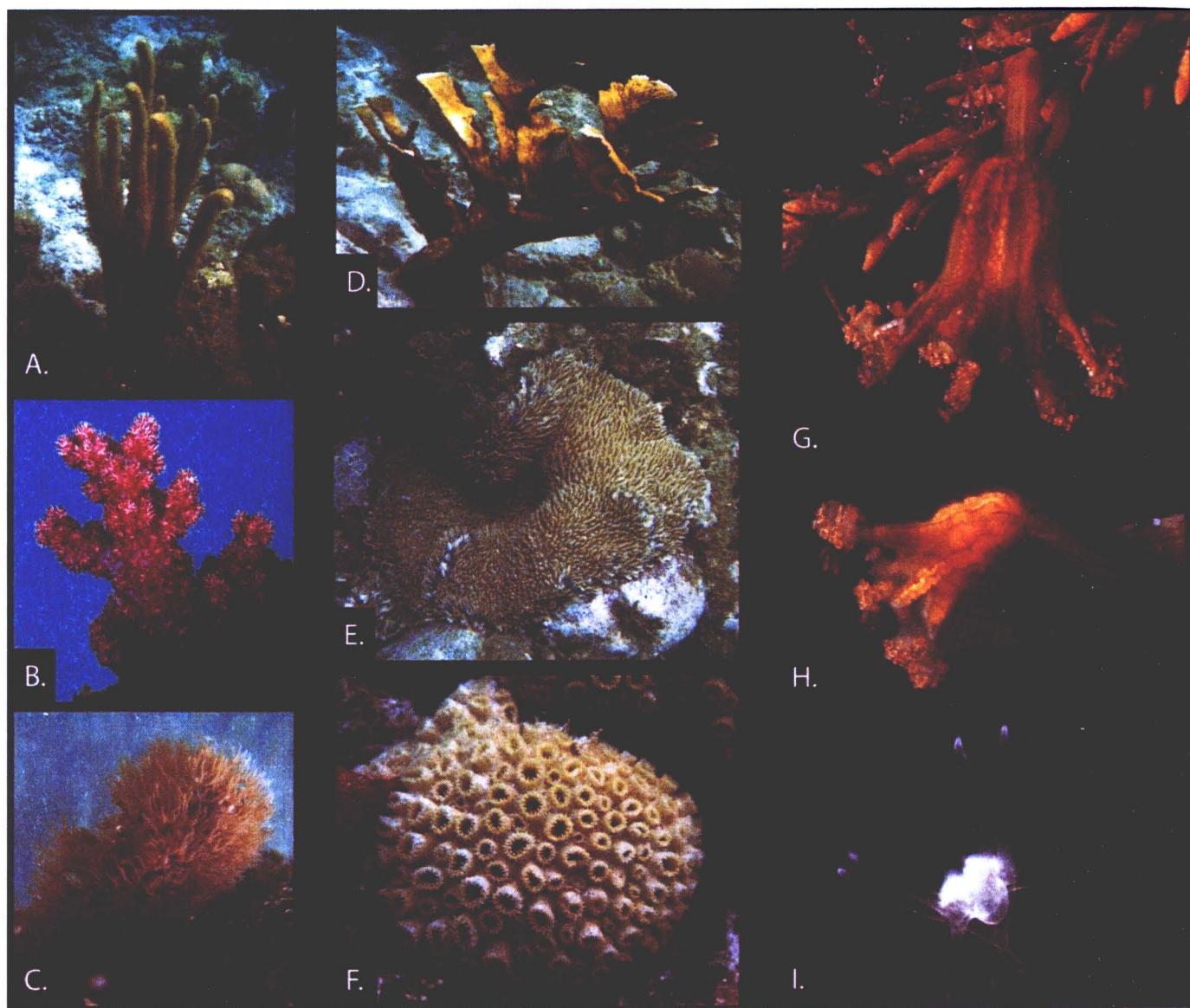


FIGURE 2. Representative cnidarians: Anthozoa, Staurozoa, and Polypodiozoa. A, Octocorallia, Holaxonida, *Plaxaura* from St. John, U.S. Virgin Islands; B, Octocorallia, Alcyonacea (part of the unnamed clade including Holaxonida), *Dendronephthya* from Shirahama, Japan; C, Octocorallia, Alcyonacea, *Briareum* from St. John, U.S. Virgin Islands; D, Hexacorallia, Scleractinia, *Acropora* from St. John, U.S. Virgin Islands; E, Hexacorallia, Actiniaria, *Thalassianthus* from Shirahama, Japan; F, Hexacorallia, Zoanthidea, *Palythoa* from St. John, U.S. Virgin Islands; G, Staurozoa, Eleutherocarpida, *Haliclystus* from Hokkaido, Japan; H, Staurozoa, Cleistocarpida, *Manania* from Hokkaido, Japan. I, Polypodiozoa, *Polypodium* (photographed by N. Evans).

et al., 2002; Okamura and Canning, 2003). Okamura and colleagues showed that the morphology and DNA of *Buddenbrockia* firmly placed it within Myxozoa. However, they also argued that the presence of four muscles located between the endoderm and ectoderm of *Buddenbrockia* indicated that it, and by extension Myxozoa as a whole,

was a close relative of nematodes and firmly derived from within Bilateria. Most recently, this hypothesis was falsified by analyses of EST data taken from *Buddenbrockia* and other metazoans indicating that Myxozoa is part of Cnidaria (Jiménez-Guri et al., 2007), as suggested by earlier workers (Weill, 1938; Siddall et al., 1995).

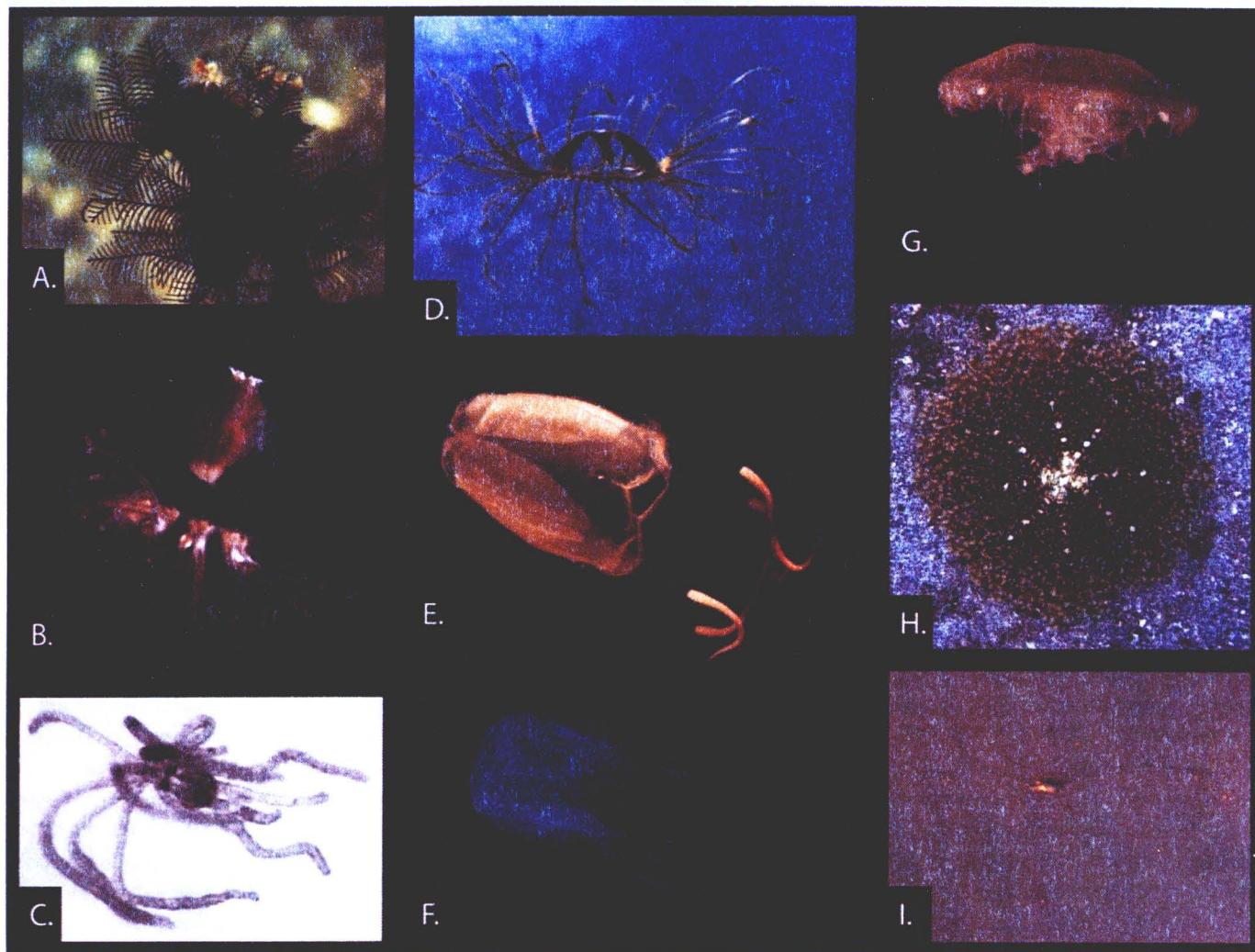


FIGURE 3. Representative cnidarians: Hydrozoa, Cubozoa, Scyphozoa, and Myxozoa. A, Hydrodolina, Leptothecata, *Lytocarpia* from Shirahama, Japan; B, Hydrodolina, other Capitata, *Cladonema* from Hokkaido, Japan; C, Trachylina, Actinulida, *Halammohydra* from Bocas del Toro, Panama (still taken from video by J. Norenburg); D, Trachylina, Limnomedusae, *Gonianemus* from Hokkaido, Japan; E, Cubozoa, Carybdeida, *Carybdea* from Bocas del Toro, Panama; F, Cubozoa, Chirodropida, *Chironex* from Southern Japan (photographed in Enoshima Aquarium); G, Scyphozoa, Semaeostomeae, *Chrysaora* from Bocas del Toro, Panama; H, Scyphozoa, Rhizostomeae, *Cassiopea* from St. John, U.S. Virgin Islands; I, Myxozoa, Myxosporea, Bivalvulida, actinospore stage of *Myxobolus* (photographed by A. Nawrocki and N. Evans).

Not surprisingly, given the type of data analyzed, taxon sampling for the EST analysis was rather limited, with just two anthozoans, two hydrozoans, and one scyphozoan included. The myxozoan was shown to fall as the earliest diverging lineage in a clade including the two hydrozoans and the scyphozoan (Jiménez-Guri et al., 2007). In contrast, even more recent analyses of rDNA data with excellent taxon sampling resulted in best trees in which Myxozoa was the sister group of Bilateria, a result thought to be biased by long-branch attraction (Evans et al., 2008). Figure 1 shows

Myxozoa as the sister lineage of Medusozoa, as indicated by the EST results, but the branch also includes a question mark because of the small number of taxa included in the analysis by Jiménez-Guri et al. (2007). Knowing whether myxozoans possess linear or the typical circular mitochondrial genomes could help place Myxozoa within Cnidaria, as this is a major distinction between Anthozoa and Medusozoa (Bridge et al., 1992, 1995; see following).

The inclusion of Myxozoa's 2,200 species (Lom and Dyková, 2006) within Cnidaria increases the richness of

the phylum significantly. As parasites with complex life cycles involving multiple hosts, the diversity of Cnidaria is substantially enriched as well. In recent years, relationships within Myxozoa have mainly been addressed using 18S rDNA data. These data give a strong signal that species parasitic of freshwater bryozoans in the class Malacosporea (=order Malacovalvulida) form a small clade (just three species are known) that is sister to the remaining myxozoans classified in the class Myxosporea (Canning et al., 2000; Kent et al., 2001). Recent classifications of Myxosporea break the class into two orders, Bivalvulida and Multivalvulida. While neither taxon as traditionally recognized is monophyletic, including one aberrant bivalvulid member in Multivalvulida renders Bivalvulida paraphyletic and Multivalvulida monophyletic (as shown in Figure 1; Kent et al., 2001; Whipples et al., 2004; Fiala, 2006; Lom and Dyková, 2006). The great majority of myxosporeans appear to fall into two large clades, one dominated by species inhabiting freshwater hosts, and the other including Multivalvulida and other species that primarily infect marine hosts (Kent et al., 2001; Holzer et al., 2004). Examples of reversals in freshwater and marine habits continue to accumulate, and a third smaller clade has been identified (Fiala, 2006). Considerable diversity of Myxozoa remains to be sampled, but existing studies indicate that many myxozoan taxa, even genera, are polyphyletic. Continued efforts to identify morphological features reflecting shared ancestry, which could be used to improve the existing classification, are necessary (Fiala, 2006).

In analyses of Cnidaria (exclusive of Myxozoa), it has generally become accepted that Anthozoa is the sister clade of Medusozoa, a hypothesis that is buttressed by morphology (Salvini-Plawen, 1978; Bridge et al., 1995), mitochondrial genome structure (Bridge et al., 1992), and rDNA sequences (e.g., Berntson et al., 1999; Kim et al., 1999; Medina et al., 2001; Won et al., 2001; Collins, 2002). One recent exception is a study by Kayal and Lavrov (2008) based on complete mitochondrial genome sequences, which found Medusozoa (just two representatives) derived from within Anthozoa as the sister group of three sampled representatives of Octocorallia. Although certainly worthy of consideration and future testing, limitations in taxon sampling in the Kayal and Lavrov (2008) analysis cast some doubt on the veracity of this finding. Similar arrangements were also presented in early rDNA analyses that similarly suffered from poor taxon sampling, as shown by pioneering work of Bridge et al. (1995). As indicated in Figure 1, Anthozoa is hypothesized to consist of two well-supported sister clades with diverse representatives, Octocorallia and Hexacorallia. Anthozoa is usually considered to be a class

within the phylum (e.g., Daly et al., 2007), but making it a subphylum, with Hexacorallia and Octocorallia as its classes, would go some way toward balancing the classification of Anthozoa with that of Medusozoa.

The phylogeny of Octocorallia has posed some of the most troublesome questions in recent cnidarian systematics because of a relatively dramatic incongruence between traditional taxonomy and molecular-based hypotheses of relationships (Berntson et al., 2001). Nevertheless, consistent progress has been made; many of the alliances first suggested by the rDNA analyses of Berntson et al. (2001) have been confirmed, and some morphological synapomorphies of recently recognized clades have been identified (McFadden et al., 2006). It has been premature, given the great diversity of Octocorallia remaining to be sampled, to erect a new classification for the group, but some patterns are emerging. There appear to be two major clades and a minor clade or grade that branched early in the history of Octocorallia (McFadden et al., 2006). One of the three octocoral orders, Alcyonacea (soft corals and sea fans), which is by far the most diverse and least distinctive, is clearly paraphyletic. The other two orders, Pennatulacea (sea pens) and Helioporacea (blue corals), are monophyletic, and each appears to be independently descended from a paraphyletic Calcoxonaria (one group of sea fans), a suborder of Alcyonacea (McFadden et al., 2006). Another group of sea fans known as Holaxonaria all appear in one of the major clades, along with other alcyonaceans, but there is no strong evidence for holaxonian monophyly.

In contrast to Octocorallia, the overall picture of the phylogeny of Hexacorallia has been relatively clear. Of the six hexacorallian orders, several lines of evidence indicate that Ceriantharia (tube anemones) is the earliest diverging lineage (Berntson et al., 2001; Won et al., 2001; Daly et al., 2002, 2003; Brugler and France, 2007). Similarly, this same set of studies all concur in finding a close relationship between Scleractinia (stony corals) and Corallimorpharia. However, there has been some confusion about whether Corallimorpharia might be derived from within Scleractinia, that is, one version of the “naked coral hypothesis,” which posits that one or more hexacorallian groups without skeletons are derived from stony coral ancestors. Abundant evidence refutes the idea that Actiniaria (true anemones) or Zanthideida are derived from scleractinian ancestors (Berntson et al., 2001; Won et al., 2001; Daly et al., 2002, 2003; Brugler and France, 2007), but several analyses of mitochondrial genes, including whole mitochondrial genomes, have found corallimorpharians to be derived from within Scleractinia (France et al., 1996; Romano and Cairns, 2000; Medina et al., 2006). In contrast,

however, better taxon sampling of mitochondrial genomes (Brugler and France, 2007) and analyses of other genes with better taxon sampling (Fukami et al., 2008) favor the hypothesis that Corallimorpharia and Scleractinia are monophyletic sister groups. No clear picture of the relationships between this clade, Actiniaria, Antipatharia (black corals), and Zoanthidea has emerged from recent work, as different data sets or analytical approaches have yielded conflicting results (Berntson et al., 2001; Won et al., 2001; Daly et al., 2002, 2003; Brugler and France, 2007).

In present classifications, Medusozoa is usually presented as including four classes: Cubozoa, Hydrozoa, Scyphozoa, and Staurozoa. As mentioned earlier, a recent analysis of EST data suggested that Myxozoa is derived from within Cnidaria, as the sister group of the three medusozoans included in the analysis (Jiménez-Guri et al., 2007). Another taxon, Polypodiozoa, which is sometimes considered a class because of the unusual nature of the parasitic species within its single genus, *Polypodium* (Raikova, 1988), has also recently been hypothesized to fall within Medusozoa, most likely as a close relative of Hydrozoa (Evans et al., 2008). Thus, Medusozoa may have as many as six classes representing rather distinct, evolutionarily independent lineages. Evidence for the monophyly of Medusozoa, albeit with the exclusion of Myxozoa and Polypodiozoa, comes from rDNA data (Collins, 1998, 2002; Medina et al., 2001; Collins et al., 2006a) and observations of morphology (Werner, 1973; Salvini-Plawen, 1978; Schuchert, 1993; Bridge et al., 1995).

Attempts to incorporate data from Myxozoa and Polypodiozoa in analyses of cnidarian phylogeny have been complicated by the relatively rapid rate of molecular evolution in these two taxa. In many analyses of rDNA, representatives of these two groups appear to be artificially attracted to bilaterian exemplars and end up forming sister group relationships with Bilateria (Siddall et al., 1995; Kim et al., 1999; Zrzavý and Hypsa, 2003). In a recent study of 18S and 28S data, dense taxon sampling of medusozoans appears to have overcome some of this long-branch attraction problem, at least so far as Polypodiozoa is concerned (Evans et al., 2008). Although the optimal trees of Evans et al. (2008) had Myxozoa branching as the sister group of Bilateria, perhaps because the 28S marker was only partially sampled for the myxozoans, Polypodiozoa consistently fell within Medusozoa, as one would expect based on its morphology (Raikova, 1980, 1994). Unfortunately, however, the exact position of Polypodiozoa within Medusozoa was shown to be dependent upon method of analysis and the inclusion or exclusion of

myxozoan representatives (Evans et al., 2008), prompting the question mark shown in Figure 1.

Among the taxa more traditionally considered as part of Medusozoa, Staurozoa (or Stauromedusae) may possibly be the earliest diverging lineage, a result obtained through the analysis of both molecular and morphological data (Collins, 2002; Dawson, 2004; Collins and Daly, 2005; Collins et al., 2006a; Van Iten et al., 2006). As benthic, so-called stalked medusae, the finding that Staurozoa might branch early in the history of Medusozoa was of some interest because it very clearly implied that the pelagic medusa stage was a feature derived within this clade. However, Collins et al. (2006a) noted that some methodological choices in their phylogenetic analyses impacted the position of Staurozoa. Further, although not specifically addressed, the position of Staurozoa was not stable in the analyses of Evans et al. (2008). Thus far, no strong evidence has been published suggesting that Staurozoa is not an early diverging lineage of Medusozoa. Within Staurozoa, there are two main taxa, Cleistocarpida and Eleutherocarpida, neither of which appears to be monophyletic despite the fact that taxon sampling was relatively limited (Collins and Daly, 2005).

Another small class of Medusozoa is Cubozoa (box jellyfishes). Although 18S data provide no clear signal about the precise position of Cubozoa within Cnidaria (Collins, 2002; Evans et al., 2008), 28S data strongly suggest that Cubozoa is the sister group of Scyphozoa (true jellyfishes), together forming the clade Acraspeda (Collins et al., 2006a; Evans et al., 2008). Both 18S and 28S strongly support cubozoan monophyly, as well as that of its two main subtaxa, Carydeida and Chirodropida (Collins, 2002; Collins et al., 2006a). Similarly, there is relatively strong and stable evidence concerning the evolutionary relationships among the scyphozoan orders Coronatae, Rhizostomeae, and Semaeostomeae, although it should be noted that taxon sampling has been sparse. The earliest diverging lineage is Coronatae, and Rhizostomeae is a well-supported clade that is derived from within Semaeostomeae (Collins, 2002; Collins et al., 2006a).

The largest and most diverse class within Medusozoa is Hydrozoa. As indicated in Figure 1, an ancient divergence within Hydrozoa divides the group into two clades, Trachylina and Hydrodolina (Collins, 2002; Marques and Collins, 2004; Collins et al., 2006a). Each clade has been the subject of recent papers aimed at bringing increased taxon and genetic marker sampling to bear on the evolutionary relationships among their respective component groups (Cartwright et al., 2008; Collins et al., 2008). As Figure 1 shows, relationships among the major lineages of

Hydroidolina are uncertain (Collins et al., 2006a; Cartwright et al., 2008). In terms of taxonomy, the clade includes Leptothecata (thecate hydroids and leptomedusae) and Siphonophora (colonial siphonophores including the Portuguese man o' war), two groups with ample evidence for monophyly (Collins, 2002; Collins et al., 2006a; Cartwright et al., 2008). Hydroidolina also includes the large and diverse taxon Anthoathecata (athecate hydroids and anthomedusae), which is typically subdivided into Capitata and Filifera. There is no evidence supporting the monophyly of Capitata, Filifera, or Anthoathecata (Collins, 2002; Collins et al., 2006a; Cartwright et al., 2008). Despite the difficulty in working out the relationships among hydroidolian clades, some advances have been made in identifying large clades that had not been previously recognized. For instance, Capitata appears to be composed of two well-supported clades, one dubbed Aplanulata (includes the well-known model organisms of *Hydra*) in reference to the group's lack of a ciliated planula stage (Collins et al., 2005a, 2006a) and the other consisting of all the other capitate groups (Cartwright et al., 2008). The name Capitata has recently been applied to this more restrictive clade (Cartwright et al., 2008). Similarly, within Filifera, a previously unrecognized alliance of species that bear gonophores, but not on their hydranth bodies, has been given the name Gonoproxima. There is no support for the monophyly of the remaining filiferans.

Trachylina is composed of four orders: Actinulida, Limnomedusae, Narcomedusae, and Trachymedusae. The monophyly of Narcomedusae seems to be relatively certain (Collins, 2002; Collins et al., 2006a, 2006b, 2008), whereas the monophyly of Actinulida has yet to be tested because just a single representative has been included in any phylogenetic analysis (Collins et al., 2008). Trachymedusae, a group of pelagic species that lack polyp stages, appears to be polyphyletic. One family (Geryoniidae) has a close relationship with a subgroup of Limnomedusae (Collins et al., 2006a, 2008), whereas another (Rhopalonematidae) may have given rise to the interstitial Actinulida (Collins et al., 2008). Limnomedusae appears to represent a grade at the base of Trachylina (Collins, 2002; Collins et al., 2006a, 2006b, 2008). As with many cnidarian groups, the classification of Trachylina requires refinement to better reflect our phylogenetic knowledge.

CONCLUSION AND CLASSIFICATION

The working hypothesis of cnidarian phylogeny presented here (see Figure 1), as do all others, requires continued testing and refinement. Many of the studies

behind it have limitations, especially in taxon sampling, and the original papers should be consulted for more detailed assessments of strengths and weaknesses of the analyses that they report. As the working hypothesis results from no single analysis and was instead put together from numerous sources, some of my biases, in the form of judgments, have had an impact on the final form of the working hypothesis. This effect is certainly a weakness in such an exercise and demonstrates why it is less preferable than an analysis that relies on data sampled from diverse representatives across Cnidaria. When such an analysis is conducted, the working hypothesis presented here may provide a helpful reference point for comparison.

Figure 1 makes it clear that the current classification of Cnidaria, even at the basic level of order, has not kept up with phylogenetic advances. A new classification using taxa hypothesized to be monophyletic is not feasible until more thorough and robust phylogenetic analyses are conducted. Conflicting results from different phylogenetic studies create one hindrance to advances in classification, but this is not really new, as different taxonomists have always offered different classifications to reflect their changing perceptions of taxa. More detrimental to progress in classification is the lack of completeness in existing phylogenetic analyses. With molecular data, individuals are sampled, and assessments of the phyletic status (monophyletic, paraphyletic, or polyphyletic) of larger taxa are not very strong until large numbers of component species are included in an analysis. Moreover, the relevant morphological features that distinguish any particular clade (especially if not corresponding to a traditional taxon) are not easily discerned without thorough sampling and examination of its members.

Nevertheless, classifications are made to enhance communication. Therefore, it may be prudent to attempt classifications that better reflect ongoing advances in phylogenetics. Below I present one such attempt for Cnidaria. It is not meant to be adopted, as this author has little expertise in non-medusozoan cnidarians. Instead, it is presented to illustrate one possible system for classifying traditional taxa in light of ongoing phylogenetic advances. It relies on annotation indicating whether a given taxon is likely to be monophyletic, paraphyletic, or polyphyletic. Taxa for which reasonable evidence suggests monophyly are followed by a superscript M. Taxa thought to be paraphyletic are followed by superscript P and a list of taxa [in brackets] hypothesized to be derived from it. Taxa that are likely polyphyletic are placed in quotation marks. Finally,

taxa whose phyletic status is essentially unknown are left with no annotation.

Phylum Cnidaria^M

Subphylum Anthozoa^M

Class Hexacorallia^M

- Order Actiniaria^M
- Order Antipatharia^M
- Order Ceriantharia^M
- Order Corallimorpharia^M
- Order Scleractinia^M
- Order Zoanthida^M

Class Octocorallia^M

- Order "Alcyonacea"^P [Calcoxonia, Helio-poracea, Holaxonia, Pennatulacea]
- Order Calcoxonia^P [Helioporacea, Pen-tulacea]
- Order Helioporacea^M
- Order Holaxonia
- Order Pennatulacea^M

Subphylum Medusozoa^M

Class Cubozoa^M

- Order Carybdeida^M
- Order Chirodropida^M

Class Hydrozoa^M

Subclass Hydroidolina^M

- Order Aplanulata^M
- Order Capitata^M (excluding Aplanulata)
- Order Filifera (excluding Gonoproxima)
- Order Gonoproxima^M
- Order Leptothecata^M
- Order Siphonophora^M

Subclass Trachylina^M

- Order Actinulida
- Order Limnomedusae (including Ger-yonidae)
- Order Narcomedusae^M
- Order Trachymedusae^P [Actinulida, Nar-comedusae]

Class Polypodiozoa^M

Genus *Polypodium*

Class Scyphozoa^M

Order Coronatae^M

Subclass Discomedusae^M

Order Rhizostomeae^M

Order Semaeostomeae^P [Rhizostomeae]

Class Staurozoa^M

Order "Cleistocarpida"

Order "Eleutherocarpida"

Subphylum Myxozoa^M

Class Malacosporea^M

Order Malacovalvulida^M

Class Myxosporea^M

Order Bivalvulida^P, [Multivalvulida]

Order Multivalvulida^M

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