

Cladistic analysis of Medusozoa and cnidarian evolution

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Abstract. A cladistic analysis of 87 morphological and life history characters of medusozoan cnidarians, rooted with Anthozoa, results in the phylogenetic hypothesis (Anthozoa (Hydrozoa (Scyphozoa (Staurozoa, Cubozoa))). Staurozoa is a new class of Cnidaria consisting of Stauromedusae and the fossil group Conulatae. Scyphozoa is redefined as including those medusozoans characterized by strobilation and ephyrae (Coronatae, Semaestomeae, and Rhizostomeae). Within Hydrozoa, Limnomedusae is identified as either the earliest diverging hydrozoan lineage or as the basal group of either Trachylina (Actinulida (Trachymedusae (Narcomedusae, Laingiomedusae))) or Hydroidolina (Leptothecata (Siphonophorae, Anthoathecata)). Cladistic results are highly congruent with recently published phylogenetic analyses based on 18S molecular characters. We propose a phylogenetic classification of Medusozoa that is consistent with phylogenetic hypotheses based on our cladistic results, as well as those derived from 18S analyses. Optimization of the characters presented in this analysis are used to discuss evolutionary scenarios. The ancestral cnidarian probably had a sessile biradial polyp as an adult form. The medusa is inferred to be a synapomorphy of Medusozoa. However, the ancestral process (metamorphosis of the apical region of the polyp or lateral budding involving an entocodon) could not be inferred unequivocally. Similarly, character states for sense organs and nervous systems could not be inferred for the ancestral medusoid of Medusozoa.

Additional key words: Staurozoa, Scyphozoa, Hydrozoa, Cubozoa

Cnidarian species are often used as model organisms in evolutionary studies (of development, cell biology, gene families, etc.) because Cnidaria diverged relatively early in the history of Metazoa. The presumption in these studies is that cnidarian species may exhibit relatively underderived character states that can be compared with those of other animals, particularly bilaterians. As an example, a recent study made inferences about the ancestral paired domain (a conserved DNA-binding domain present in developmental control genes) in animals based on the condition of *Pax* genes in a hydrozoan cnidarian (Sun et al. 2001). Though character states in cnidarians are possibly ancient, features under study in a given cnidarian species may certainly be derived at some level within Cnidaria and to assume the opposite could be misleading. Thus, the utility of comparative studies is enhanced as more taxa are investigated (Lowe et al. 2002) and as knowledge of phylogeny increases. In the case of Cnidaria, neither its position within Metazoa nor the relation-

ships among its component groups are known with precision (Marques 1996; Nielsen et al. 1996; Jenner & Schram 1999; Nielsen 2001; Collins 2002).

Prior studies focusing on relationships among cnidarian classes contain many contradictions (Salvini-Plawen 1978, 1987; Petersen 1990; Bridge et al. 1992; Bridge et al. 1995; Schuchert 1993; Odorico & Miller 1997; Marques 2001; Nielsen 2001; Collins 2002). However, in the last decade Anthozoa has emerged as the most likely sister group of the remaining cnidarians, first dubbed Tesserazoa (Salvini-Plawen 1978), but more commonly known as Medusozoa (Petersen 1979). Monophyly of the medusozoans is particularly well supported by their shared possession of linear mtDNA, in contrast to anthozoans and other metazoans (Bridge et al. 1992). To move toward a consensus view of cnidarian phylogeny that will enlighten further comparative studies using cnidarians, we present a cladistic analysis of 87 morphological and life history characters to generate a hypothesis of relationships among medusozoan cnidarians. We compare the cladistic results with those of recent phylogenetic analyses of Medusozoa using molecular characters (Collins

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2002), and present a classification that is consistent with phylogenetic hypotheses derived from both analyses. Finally, we make inferences about the evolution of morphological and life history traits within Cnidaria based on our cladistic analysis.

Methods

In our cladistic analysis, we used the class Anthozoa as an outgroup, a position supported by previous morphological and molecular studies. As terminal taxa, we adopted the class Cubozoa (Werner 1975; Franc 1994b), the fossil group Conulatae (Wade 1994), the 4 orders of Scyphozoa (after Franc 1994a), and the 8 subclasses of Hydrozoa (following Bouillon 1994a,b with 2 exceptions). Higher-level hydrozoan taxonomy has suffered from the legacy of early specialists of hydroids and hydromedusae, who developed independent naming schemes. To be inclusive, we use the names Anthoathecata and Leptothecata (Cornelius 1992) rather than relicts of older classifications, such as Anthomedusae, Athecata, Leptomedusae, and Thecata. As in any parsimony analysis, all terminals are considered to be monophyletic. Although hydrocorals and velellids are sometimes classified as higher taxonomic groups of Hydrozoa (e.g., Milleporina, Stylasterina, Chondrophora, etc.), these groups are well established as part of Anthoathecata, based on their morphology (e.g., Bouillon 1985; Schuchert 1996) and on molecular evidence (Collins 2002). Hydridae and *Otohydra* are difficult hydrozoan groups and were considered here to be part of Anthoathecata and Actinulida respectively. Neither of these inclusions impact our scoring of Anthoathecata and Actinulida. That said, if future work indicates that any of our terminal taxa are not monophyletic, our analyses should be emended accordingly.

For each taxon, we scored 87 characters, of which 48 were informative (Appendices 1 and 2). Non-informative characters either have incomplete documentation or were judged to be shared by all terminals. We hope that including these characters here will inspire further studies. Scoring characters for supraspecific taxa requires some generalizations unless one includes only characters that are constant for all species in higher taxa or relies on a phylogenetic hypothesis of the group that permits optimization of all ancestral states (Whiting et al. 1997). In general, the character states scored were represented uniformly in each of the terminals (see Appendix 1 for exceptions and discussion). Because of the taxonomic breadth of this study, characters and their states were taken mostly from the literature. Characters were coded as binary or multi-state and considered unordered. Information that was

not available was coded as a question mark (?) and non-comparable structures were coded in the matrix as N. Polymorphic characters were treated as uncertainties.

Cladistic analyses were carried out using the branch and bound algorithm of the software PAUP* 4.0 (Swofford 2001). First, we searched for most parsimonious trees without weighting any of the characters. Strict and semi-strict consensus trees were calculated from the trees obtained in these primary analyses. Then, a complementary analysis was performed using successive approximation weighting (Farris 1969, see also Carpenter 1988, 1994) by maximum values of re-scaled consistency indices (RC). Bootstrap indices were calculated for 500 replicate searches using both weighted and unweighted characters, and Bremer support indices were calculated using unweighted characters.

Results

The unweighted analysis of the data matrix (Appendix 2) yielded 48 trees (14 trees using “amb-” option of PAUP; L=126; CI=0.730; RI=0.728), for which the strict and semistrict consensus trees have the same highly polytomic topology, including only 3 monophyletic groups: (1) (Coronatae (Semaestomeae, Rhizostomeae)); (2) (Siphonophorae, Anthoathecata); and (3) (Actinulida, Trachymedusae (Narcomedusae, Laingiomedusae)). The successive weighting analysis resulted in 3 fully resolved trees (3 using “amb-”; L=76.65; CI=0.928; RI=0.925), in which Limnomedusae appears in 3 different positions: (1) sister-group of all other hydrozoans; (2) sister-group of (Actinulida (Trachymedusae (Narcomedusae, Laingiomedusae))); and (3) sister group of (Leptothecata (Siphonophorae, Anthoathecata)). The phylogenetic hypothesis (strict consensus) generated by this cladistic analysis (Fig. 1) suggests that Hydrozoa is the monophyletic sister group of all other medusozoans. Within Hydrozoa, Limnomedusae has an unstable position, whereas the other hydrozoan groups form 2 clades (Actinulida (Trachymedusae (Narcomedusae, Laingiomedusae))) and (Leptothecata (Siphonophorae, Anthoathecata)). Non-hydrozoan medusozoans are also monophyletic, but Scyphozoa, as traditionally circumscribed is not. Instead, 3 scyphozoan groups form a clade (Coronatae (Rhizostomeae, Semaestomeae)) that is the sister group to the clade ((Stauromedusae, Conulatae) Cubozoa).

This cladogram (Fig. 1) represents hypotheses that are both consistent with and contradictory to various views of cnidarian relationships that have been proposed in the past. Conulatae, which is comprised of

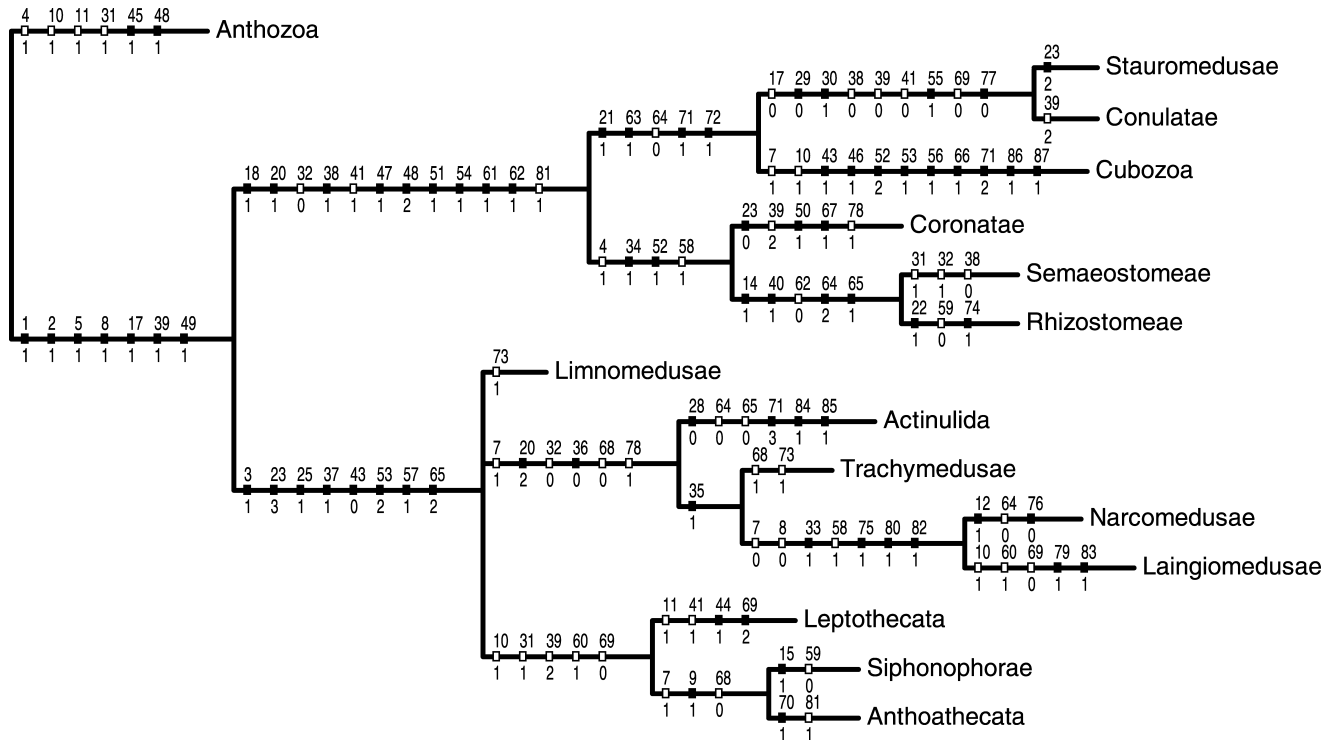


Fig. 1. Strict consensus of 3 most parsimonious trees (L=76.65; CI=.928; RI=.925) resulting from a successive weighting analysis. Apomorphic character states (character number and state above and below nodes respectively) are mapped onto the tree at appropriate nodes, characters optimized using Accelerated Transformation. Homoplastic characters are indicated with open squares.

the fossil genus *Conchopeltis* and the better known conulariids, is an extinct group of animals with conical exoskeletons that are square in cross section. They have often been thought of as early diverging members of Cnidaria (cf. Werner 1973a; Salvini-Plawen 1978; Bouillon 1981; Nielsen 2001). Specifically, Conulatae has been compared to Coronatae because the apatitic tests of conulates and the chitinous thecae of coronate scyphozoan polyps are similarly composed of 2 layers, a thin outer layer and a relatively thicker inner layer (Werner 1966). Moreover, structures on the midlines and corners of conulates are reminiscent of thorn-like projections at the interradial and periradial of coronate polyps (Werner 1966; Van Iten et al. 1996). On the other hand, the mineralized septa of the conulate *Eoconularia loculata* exhibit an ontogeny inferred to be nearly identical to that observed in developing stauromedusans (Kiderlen 1937; Jerre 1994; Wade 1994). The only cladistic analysis addressing the question of conulate affinities treated Scyphozoa as a single evolutionary entity and concluded that Conulatae was the sister group to Scyphozoa (Van Iten et al. 1996). Our analysis supports the hypothesis that Conulatae and Stauromedusae are more closely related to each other

than either is to Coronatae and that Scyphozoa as traditionally circumscribed is not monophyletic (Fig. 1).

Since the elevation of Cubozoa to class status, cubozoans have often been envisioned as the sister group of either Hydrozoa (Werner 1973b; Bouillon 1981; Cornelius 1991; Nielsen 2001) or Scyphozoa (Salvini-Plawen 1978, 1987; Schuchert 1993). However, the authors of some earlier analyses concluded, as have we, that stauromedusans and cubozoans share a relatively close relationship (Haeckel 1879; Uchida 1929; Thiel 1966). Our morphological results are very consistent with those based on molecular data, which likewise suggest that scyphozoans may not be monophyletic, as stauromedusans branch closer to other medusozoans (Collins 2002). As for the other scyphozoan groups (Coronatae, Semaestomeae, and Rhizostomeae), all published hypotheses (to our knowledge) suggest that the latter 2 groups are more closely related to each other than either is to Coronatae, as derived here. Indeed, both molecular data (Collins 2002) and morphology (Mayer 1910; Uchida 1926; Thiel 1966) have suggested that rhizostomes are derived from within semaestomes, a hypothesis that is not tested by our cladistic analysis because we treat Semaestomeae as a terminal taxon.

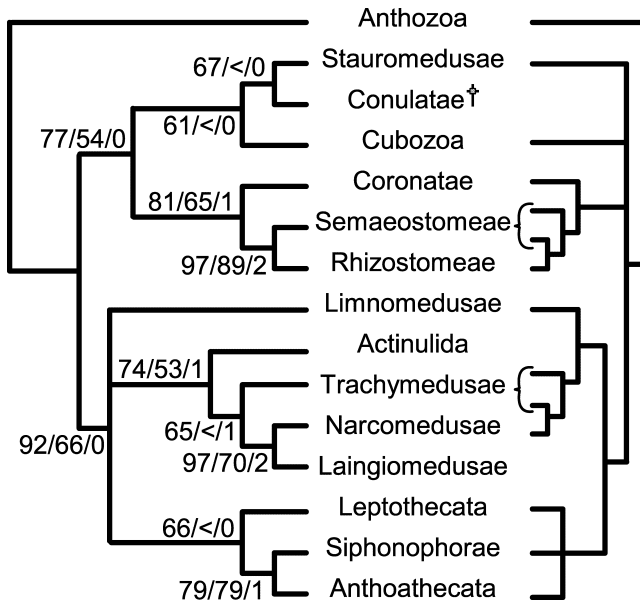


Fig. 2. Congruence of our cladistic-based hypotheses (left) and hypotheses based on 18S sequence data (right, strict consensus of most parsimonious and maximum likelihood trees from Collins (2002)). The marker on Conulatae denotes that the group is extinct. The 3 support indices shown at the nodes in our hypothesis are: bootstrap indices using weighted and unweighted characters, and Bremer support indices using unweighted characters. < indicates a bootstrap index that is less than 50.

Within Hydrozoa, our analysis suggests that Hydroidolina (Leptothecata, Siphonophorae, and Anthoathecata) is a clade, a result corroborated by 18S data (Collins 2000, 2002) and by another hypothesis based on morphological characters (Bouillon & Boero 2000). However, we did not find the clade Hydroidomedusae in its original sense as comprising all non-siphonophore hydrozoans (Bouillon et al. 1992; and see Marques 2001) or in its emended form as a clade containing Limnomedusae, Laingiomedusae, Leptothecata, Siphonophorae, and Anthoathecata (Bouillon & Boero 2000). Because Anthoathecata is a terminal taxon, the present analysis does not test the hypothesis that Siphonophorae is a subgroup of Anthoathecata (Schuchert 1996; Marques 2001).

This analysis identifies Limnomedusae as the most basal group of Hydrozoa, Trachylina, or Hydroidolina. 18S data provided relatively strong support for 1 of these hypotheses, namely that Limnomedusae (though only 2 species were sampled) is the basal group of a clade also containing Trachymedusae and Narcomedusae (Collins 2000, 2002). Our analysis identifies just a single synapomorphy of Limnomedusae, the presence of an urticant ring, a continuous ring of cnidae on the umbrellar margin of the medusae, and this fea-

ture is revealed as homoplastic in Trachymedusae. The lack of identified autapomorphies for Limnomedusae may indicate that the group is polyphyletic, and in fact, there has been a history of various limnomedusan groups being taxonomically linked to either Trachymedusae or Anthoathecata. Future analysis, with the subgroups of Limnomedusae treated as terminals, may result in splitting of the group.

The remaining hydrozoan groups (Actinulida, Trachymedusae, Narcomedusae, and Laingiomedusae) form a clade. Molecular data have not been sampled for Actinulida and Laingiomedusae, but 18S data strongly support the hypothesis that Trachymedusae and Narcomedusae are closely allied (Collins 2002). Thus, our cladistic analysis and molecular data are consistent with Bouillon & Boero (2000), who concluded that Actinulida, Trachymedusae, and Narcomedusae are relatively closely related. However, our cladistic analysis and molecular data contradict the placement of Limnomedusae and Laingiomedusae in a clade with Leptothecata, Siphonophorae, and Anthoathecata (Bouillon & Boero 2000). Laingiomedusae is a particularly problematic group because information is lacking on the polyp stage, reproduction, and 18S rDNA. As these data become available, they may clarify the phylogenetic position of Laingiomedusae within Hydrozoa.

Discussion

Phylogenetic classification

Ranks may convey important information in the context of a classification based on phylogenetic hypotheses. Designating a new class within a phylum is a statement that the phylum is more diverse at a fundamental level than previously appreciated because it contains an additional group that is historically discrete, and correspondingly distinct in its biology, from the other classes that comprise the phylum. It goes without saying that the arbitrary and subjective nature of ranks must also be appreciated. The phylum Cnidaria is generally considered to comprise 4 classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa.

Despite the fact that many cnidarian morphological characters are quite simple (see Appendix 2) and potentially prone to homoplasy, our cladistic analysis has yielded phylogenetic hypotheses for Medusozoa that are quite similar to those based on 18S data (Fig. 2). Both data sets support the monophyly of Hydrozoa and agree in suggesting that Scyphozoa (when defined as including Stauromedusae, Coronatae, Semaestomeae, and Rhizostomeae, but not Cubozoa) may not be monophyletic. In particular Stauromedusae may be more closely related to other medusozoans than to Co-

Table 1. Classification of Cnidaria that is consistent with phylogenetic hypotheses based on the cladistic analysis presented here and analyses of 18S sequence data (Fig. 2.). As noted in the text, Limnomedusae may be polyphyletic and it is possible (and perhaps likely) that some limnomedusans belong in Trachylina (as indicated by 18S data) whereas others belong in Hydroidolina.

Phylum Cnidaria
Class Anthozoa
Subphylum Medusozoa
Class Staurozoa nov.
Order Stauromedusae
Order Conulatae (extinct)
Class Cubozoa
Class Scyphozoa
Order Coronatae
Subclass Discomedusae
Order Semaestomeae
Order Rhizostomeae
Class Hydrozoa
Order Limnomedusae
Subclass Trachylina
Order Actinulida
Order Trachymedusae
Order Narcomedusae
Order Laingiomedusae
Subclass Hydroidolina
Order Leptothecata
Order Siphonophorae
Order Anthoathecata

ronatae, Semaestomeae, and Rhizostomeae. In the present analysis, monophyly of Cubozoa and Anthozoa is assumed, hypotheses that are supported by molecular studies (Kim et al. 1999; Collins 2002). An advantage of morphological analyses over molecular studies is that fossil groups can be sampled as well. Here, for instance, we find that the fossil conulates are probably more closely related to the benthic stauromedusans than they are to other cnidarian groups (cf. also Wade 1994). In light of the congruence of 18S- and morphology-based hypotheses, we present a classification for Cnidaria that includes the recognition of a new class, Staurozoa (represented by the sessile stauromedusans and fossil conulates) and re-circumscribe Scyphozoa as those groups that are characterized by strobilation and distinctive juvenile medusae known asephyrae (Table 1).

Character evolution in Cnidaria

Whether the ancestor of cnidarians was a polyp or a medusa (or even an actinula or a planula) has been debated for over a century (Brooks 1886) and is still under dispute. A medusoid ancestor of Cnidaria was

envisioned by Hyman (1940) and Hand (1959). Schuchert (1993) also assumed that the ancestral cnidarian possessed a pelagic medusoid stage, arguing that the loss of such a stage in the lineage leading to Anthozoa was a more likely evolutionary event than was the origin of a complex medusa. On the other hand, there has also been a long history of numerous supporters of the alternative, namely that Cnidaria had a polypoid ancestor (Haeckel 1879; Brooks 1886; Hadzi 1953; Werner 1973a, 1975; Salvini-Plawen 1978, 1987), though details of this hypothetical ancestor are at odds. In particular, a biradial sexual polyp without periderm was considered ancestral by Salvini-Plawen (1978, 1987), whereas others (Werner 1973a; Bouillon 1981) viewed the ancestral polyp as tetrameros and surrounded by a peridermal tube.

In our analysis, we adopted Anthozoa as an outgroup in order to root the tree and to produce a working hypothesis for Medusozoa. Simply choosing an outgroup for rooting purposes would not normally allow for a formal optimization of characters in a cladistic analysis. However, a clear consensus view has emerged that Anthozoa is the sister group of Medusozoa (Werner 1973a; Salvini-Plawen 1978, 1987; Bridge et al. 1992; Bridge et al. 1995; Schuchert 1993; Kim et al. 1999; Medina et al. 2001; Collins 2002). Therefore, character optimization is appropriate. Throughout the remaining discussion when referring to characters and states listed in Appendices 1 and 2, we use the following abbreviations: (ch#, st#).

We conclude that our cladistic hypothesis is most consistent with the inference that the adult cnidarian ancestor was a sessile animal (ch17, st0) with a polyp form (ch36, st1). Further, if the hypothesis generated by our analysis is correct, then the ancestral polyp probably possessed complete septa (ch43, st1or2). Whether or not this polyp possessed periderm (ch39) or gastrodermal musculature (ch48) is equivocal. The probable symmetry of the ancestral cnidarian is biradial (ch18, st2), as previously concluded by Salvini-Plawen (1978, 1987). This result reinforces the conclusion drawn from a recent study demonstrating that anthozoan cnidarians and bilaterians share molecular mechanisms responsible for body axis formation and that these were most likely inherited from a common biradial ancestor (Hayward et al. 2002).

If the ancestral cnidarian was polypoid as an adult, then the addition of a medusa stage (ch49, st1) to the life cycle very likely happened in the lineage leading to Medusozoa. This suggests that a medusa is a synapomorphy of Medusozoa. However, distinct variations in how medusae develop in the various medusozoan subgroups raise the possibility that not all medusozoan groups share their respective medusae

due to common descent from a medusa-bearing ancestor (Salvini-Plawen 1987). Given our cladistic hypothesis, the ancestral process of medusa development (ch20) in Medusozoa is unclear. In one clade, ((Staurozoa, Cubozoa) Scyphozoa), the ancestor appears to have formed medusae by metamorphosis of the apical (= oral) portion of the sessile polyp (ch20, st1). In contrast, the ancestral hydrozoan probably produced medusae through development of lateral buds originating from groups of undifferentiated cells (entocodons) located between ectoderm and endoderm (ch20, st0). Although these 2 types of medusa production could have evolved independently, the overall similarity in medusa morphology suggests that it is more likely that one process evolved from the other. At the same time, the 2 processes are rather different, and it is difficult to imagine how one might have evolved from the other.

That said, hydrozoan medusa production seems to be somewhat more complicated and we offer a speculative scenario describing how hydrozoan-type medusa production may have been derived from apical metamorphosis. One can imagine an early medusozoan lineage with a colonial polyp stage, in which new polyps are laterally budded from existing polyps. If apical production of medusae subsequently became limited to polyps specialized for this process, still later evolution could have resulted in the complete reduction of these specialized polyps. The resulting medusa development would be localized to the lateral portions of polyps, as seen in many hydrozoans. It remains to be seen if future studies of the molecular basis of medusa development can determine whether medusae and the processes that produce them are homologous in diverse medusozoan groups.

Even within the 2 primary medusozoan clades, life cycles are dramatically variable. Within Hydrozoa, the polyp stage has apparently been lost in Trachylina (ch20, st2), whereas in Hydroidolina, complex colonies with polymorphism have arisen (ch37, st1) and many hydroidolins exhibit strong reduction of the medusa, including its complete disappearance in Hydridae. In Scyphozoa, medusae are produced by strobilation (ch21, st0), when the apical part of the polyp transforms (e.g., tentacles are resorbed) concomitant with constriction, ultimately resulting in the liberation of ephyrae by transverse fission. Evidently, polydisk strobilation (ch22, st0) preceded monodisk strobilation (ch22, st1), which is known only in rhizostomes. In Stauromedusae, the apical transformation takes place without transverse fission (ch21, st1), resulting in a sessile polyp-like adult (Kikinger & Salvini-Plawen 1995). We infer a similar process for Conulatae. In cubozoans, metamorphosis of the polyp has typically

been thought of as complete, resulting in a single planktonic medusoid adult, though in *Tripedalia cystophora* the basal portion of the polyp is sometimes (only 2%) retained and capable of re-growth and the production of a subsequent medusa (Werner 1973a). In a recent study of the cubozoan *Carybdea marsupialis*, Stangl et al. (2002) reported striking similarity between this cubozoan's metamorphosis and what is observed in Stauromedusae. In both cases, metamorphosis and the development of adult characteristics are largely restricted to the oral end of the polyp (Stangl et al. 2002). A primary difference is that stauromedusans remain sessile and retain the aboral portion of the polyp, whereas these cubomedusans liberate themselves from the substrate, often with the aboral portion of the polyp still attached to the apex of the medusa before it is fully resorbed (Stangl et al. 2002).

Our cladistic hypothesis also yields equivocal inferences about the ancestral sense organs (ch51, ch69) of medusae. The medusoid phase of the ancestor of Staurozoa, Cubozoa, and Scyphozoa probably possessed structures (rhopalioids) that were ontogenetically transformed into sense organs when tentacles of the polyp were resorbed (ch51, st1). These structures apparently are secondarily simplified (ch52, st0) in staurozoans, perhaps because of their sessile habit. In the lineage leading to cubozoans, sense organs have instead become more complex, involving eyes with compound lenses (ch52, st2), possibly associated with the evolution of intricate behaviors for which some of these species are known. Hydrozoans possess ontogenetically very different organs that sense equilibrium and/or light (ch69), suggesting that these organs evolved independently of those in staurozoans, cubozoans, and scyphozoans. Differences in the nerve ring (ch53) between hydrozoans and other medusozoans may be tied to differences in sensory structures. In many hydrozoans, the nerve ring is most closely associated with structures involved in swimming (e.g., the velum), whereas in other medusozoans the nervous system is most intimately connected to the sense organs (rhopalia).

Our cladistic hypothesis suggests that the primitive cnidae for cnidarians were probably isorhizas (ch13, st1), the most morphologically simple nematocysts, which are distributed throughout the cnidarian classes. This stands in accordance with the conclusion of Bozhenova et al. (1988), but in contrast to the view that haploneme nematocysts are ancestral for Cnidaria (Salvini-Plawen 1978, 1987). Other nematocyst types, such as microbasic euryteles (ch8) and mastigophores (ch9; probably the most primitive nematocyst type with a shaft in medusozoans) and heterotrichous anisorhizas (ch14; displaying slight differentiation of the

tubule), are probably derived from that primitive cnidome. Nevertheless, nematocyst types may have undergone some parallel evolution, which might explain why nematocyst types correlate well with diet among pelagic hydrozoans (Purcell & Mills 1988). That said, it is reasonable to suspect that the distribution of cnidomes across Cnidaria has been strongly influenced by phylogenetic history (Bozhenova et al. 1988). Detailed investigation of medusozoan nematocysts, focusing on those groups which exhibit polymorphism, will help in illuminating the extent of convergent evolution of nematocyst types in Medusozoa.

When interpreting the results of evolutionary studies that use cnidarians as model organisms, the various medusozoan groups should be appreciated as being derived in many respects (Fig. 1). For instance, it was recently proposed that hydrozoans possess a third tissue layer that is homologous with the mesoderm of bilaterians (Boero et al. 1998). In hydrozoans producing a medusa via lateral budding, this third tissue layer—the entocodon—is ephemerally located between ectoderm and endoderm and becomes the striated muscle layer lining the subumbrella when the medusa is liberated. Based on the relative phylogenetic positions of Hydrozoa within Cnidaria and Cnidaria within Metazoa, the hypothesis that this hydrozoan layer is homologous to the mesoderm of Bilateria would imply independent losses of mesoderm in numerous lineages, which seems unlikely (Collins 2002). On the other hand, recent studies have shown strong similarities between expression patterns of genes involved with the development of mesoderm and muscles in bilaterians and expression patterns of similar genes in a hydrozoan medusa (Spring et al. 2000, 2002). That similar genes would be involved in the specification of muscle systems in both cnidarians and bilaterians is of great interest, but not all that surprising because muscles were presumably present in the common ancestor of cnidarians and bilaterians. In the absence of evidence for an entocodon in other cnidarians, this structure probably does not play a central role in understanding the origin of bilaterian mesoderm. Nevertheless, future studies aimed at understanding the molecular mechanisms underlying muscle differentiation in other cnidarians are certainly warranted.

Many comparative studies aimed at understanding the evolution of features in more complex animals have relied upon cnidarians (e.g., *Hydra*, *Nematostella*, *Podocoryne*, *Aurelia*, *Acropora*, etc.) to represent early diverging animals. For each such species, one might ask if its phylogenetic position within Cnidaria makes it a particularly good or poor representative for comparative purposes. However, this question is too simple. Choosing an anthozoan representative rather

than a hydrozoan species because Anthozoa is basal is nonsensical. After all, hydrozoan species are part of Medusozoa, which is just as basal within Cnidaria as is Anthozoa. In our view, any cnidarian species is appropriate for these types of studies so long as both a hypothesized position for the species within Cnidaria and the relevant character states of other cnidarians are considered. As additional data for diverse cnidarians are accumulated, a more complete understanding of the evolution of features of interest will be achieved.

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Appendix 1

Characters used in this study. It is our hope that this list of characters, many of which have not been investigated for various taxa (see Appendix 2), will inspire further studies. Accordingly, our list includes several characters that are non-informative in the present parsimony analysis because information is incomplete or we judge them to be shared by all terminals.

Cell and microstructure

1. Cnidocil (0—mobile; 1—immobile). For medusozoan species investigated, the basal rootlet of the cnidocil is absent, rendering it immobile (Holstein & Hausmann 1988; Schuchert 1993). For anthozoans, the structure is more typical (see Schuchert 1993 and references therein). Information appears to be lacking for many groups.
2. Mitochondrial DNA (0—circular; 1—linear). Diverse medusozoans have a linear mitochondrial genome, whereas that of anthozoans is circular (Bridge et al. 1992), like that of other metazoans.
3. Gap junction plaques (0—absent; 1—present). Gap junctions resembling those seen in other animal groups have been documented for a number of hydrozoan groups (Mackie et al. 1984; Lesh-Laurie & Suchy 1991; Scemes & McNamara 1991; Thomas & Edwards 1991; Carré & Carré 1994), whereas investigations of several other cnidarian groups have revealed none (Mackie et al. 1984; Lesh-Laurie & Suchy 1991) and still other groups have apparently not been investigated. We coded gap junction plaques as absent in Cubozoa because their electrophysiological responses are inconsistent with the presence of these junctions (Mackie et al. 1984). Germain & Anctil (1996) documented intercellular coupling involving connexin-like proteins at very tiny zones in an anthozoan, hinting that gap junctions may be very small in cnidarians other than hydrozoans. Similar studies of other cnidarians could be most fruitful.
4. Mesoglea (0—non-cellular; 1—cellular). Cells are found in the mesoglea of anthozoans (Fautin & Mariscal 1991), as well as in many coronates, semeanostomes, and rhizostomes (Hyman 1940; D. Chapman 1966; G. Chapman 1966). Although the

character appears to be somewhat variable, e.g., the semaestome genus *Cyanea* contains species either with or without cellular mesoglea, we have scored cellular mesoglea as present in Semaestomeae and Rhizostomeae. In stauromedusans, cubozoans, and hydrozoans, mesoglea is non-cellular (Clark 1878; Conant 1898; D. Chapman 1966; G. Chapman 1966; Werner 1973a, 1979; Thomas & Edwards 1991).

5. Collagen structure (0—homotrimerous; 1—heterotrimerous). Collagen of *Stomolophus* (Rhizostomeae) is heterotrimerous, resembling that of vertebrates, and is the only report of this type of collagen for invertebrates (Miura & Kimura 1985; Lesh-Laurie & Suchy 1991). Collagen of Anthozoa is homotrimerous (Lesh-Laurie & Suchy 1991); we found no information on collagen structure for other cnidarians.

Cnidome

6. Cnidae (0—absent; 1—present).
7. Stenoteles (0—absent; 1—present). Present in Cubozoa (Werner 1984; Hartwick 1991) and hydrozoans generally (Schuchert 1993). Rare in Filifera (Anthoathecata), but present in capitate anthoathecans, Siphonophorae (Carré & Carré 1994), Actinulida, and Trachymedusae (Bouillon 1985). Absent from Anthozoa.
8. Euryteles (0—absent; 1—present). Documented in Stauromedusae, Coronatae, Semaestomeae, Rhizostomeae (Calder 1983; Lesh-Laurie & Suchy 1991), and Cubozoa (Schuchert 1993; Franc 1994b). Absent in Anthozoa (Schuchert 1993). Among hydrozoans, euryteles are present in Trachymedusae (except in the family Petasiidae), Limnomedusae, Anthoathecata (Bouillon 1985), and Siphonophorae (Clausen 1967: 368). In Leptothecata, euryteles are present in a few species (Weill 1934; Russel 1940; Bouillon 1985) and although these occurrences may be homoplastic, they are scored as polymorphic here. Euryteles scored as polymorphic for Actinulida; have been described in some species of Actinulida (Swedmark & Teissier 1967; Clausen 1967), but published figures are difficult to distinguish from stenoteles.
9. Desmonemes (0—absent; 1—present). Appear to be absent from non-hydrozoan cnidarians. Among hydrozoans, they are present in Anthoathecata (both Filifera and Capitata), Siphonophorae (Carré & Carré 1994), and possibly in a species of Actinulida (Clausen 1967). The record for Actinulida is doubtful because only aspiroteles (Lacassagne 1968), which are very similar to desmonemes, were reported in a subsequent investigation of the same species, and the majority of actinulid species investigated do not possess desmonemes (Bouillon 1985).
10. Mastigophores (0—absent; 1—present). Absent in Stauromedusae, Coronatae, Rhizostomeae, and Semaestomeae (Lesh-Laurie & Suchy 1991; Schuchert 1993), but present in Cubozoa (Lesh-Laurie & Suchy 1991; Franc 1994b), Anthozoa (Fautin & Mariscal 1991), Laingiomedusae (Bouillon 1985), Leptothecata, Siphonophorae, and Anthoathecata. In Actinulida, Bouillon (1985) reported microbasic mastigophores in 2 species, quoting Clausen (1967) and Swedmark & Teissier (1967), but the original records of those authors appear to us to be euryteles, not mastigophores. Rare in Limnomedusae (Bouillon 1985), and scored as polymorphic.
11. Basitrichous isorhizas (0—absent; 1—present). Present in Anthozoa (Picken & Skaer 1966; Fautin & Mariscal 1991), but absent from Cubozoa, Coronatae, Semaestomeae, and Rhizostomeae (Lesh-Laurie & Suchy 1991; Schuchert 1993). Also scored as absent from Stauromedusae, though 1 species is an exception (Hirano 1986). Among hydrozoans, several groups do not possess basitrichous isorhizas (Actinulida, Trachymedusae, Narcomedusae, Laingiomedusae, and Siphonophorae) whereas others do (Leptothecata). Anthoathecata scored as polymorphic because basitrichous isorhizas are widely distributed in Capitata, but rare to absent in Filifera. Scored as absent in Limnomedusae even though basitrichous isorhizas were recorded for 1 species (Nagao 1969; Kubota 1976). In Kubota (1976), identification of the nematocyst is inconsistent with the illustrations.
12. Apotrichous isorhizas (0—absent; 1—present). Reported for the narcomedusan families Aeginidae and Cuninidae (Bouillon 1985).
13. Holotrichous or atrichous isorhizas (0—absent; 1—present). Two distinct nematocyst types, holotrichous and atrichous isorhizas, are combined here because when studied by optical microscopy, their differences may not be perceptible. Present for Anthozoa, Stauromedusae, Cubozoa, Coronatae, Semaestomeae, Rhizostomeae (Calder & Peters 1975; Calder 1983; Rifkin & Edean 1983, 1988; Fautin & Mariscal 1991; Lesh-Laurie & Suchy 1991; Franc 1994b), and widely distributed among hydrozoan groups (Bouillon 1985; Carré & Carré 1994).
14. Heterotrichous anisorhizas (0—absent; 1—pre-

sent). Common in Semaestomeae and less so in Rhizostomeae (Calder 1983). Absent from Coronatae and Stauromedusae (Calder 1977, 1983; Lesh-Laurie & Suchy 1991), unreported for Anthozoa, and absent in Cubozoa, with 1 known exception (Franc 1994b). For hydrozoans, absent in Actinulida, Trachymedusae, Narcomedusae, and Laingiomedusae (Bouillon 1985). For Limnomedusae and Leptothecata, present in only 1 species of each (Bouillon 1985), and we considered them absent for these taxa. The character was scored as polymorphic for Siphonophorae and Anthoathecata because the nematocyst is present only in some subgroups of these taxa (Bouillon 1985; Carré & Carré 1994).

15. Birhopaloids (0—absent; 1—present). Most likely an autapomorphy of Siphonophorae (Carré & Carré 1994).
16. Rhopalonemes (0—absent; 1—present). May be an autapomorphy of Siphonophorae (Carré & Carré 1994).

Life habit and symmetry

17. Life habit (0—benthic adults; 1—planktonic adults). Despite considerable variation within some groups, all taxa were scored as planktonic as adults except for Anthozoa, Stauromedusae, and Conulatae, which is considered benthic in light of taphonomic data (Simões et al. 2000)
18. Symmetry (0—radial; 1—radial tetramerous; 2—biradial). Scoring this character is difficult because of considerable variation within our terminal taxa, often within the same individual depending on the body parts or life-cycle stages being considered (e.g., radial canals and gonads or polyp and medusa). For the medusoid phases, all our terminal taxa are radially tetramerous or probably derived from such a state, as indicated by the number and disposition of radial canals, and/or oral arms, and/or gonad location, with a few exceptions (e.g., Salvini-Plawen 1987). Similarly, cnidarian planulae are typically bilateral. Therefore, scoring of this character across our terminal taxa applies to the respective polypoid stages. Stauromedusans, cubozoans, coronates, semaestomes, and rhizostomes are all radial-tetramerous (D. Chapman 1966; Lesh-Laurie & Suchy 1991), whereas hydrozoan polyps, in the groups that have them, are basically radial. However, 2 primary tentacles develop early in the ontogeny of polyps in many medusozoan groups (Salvini-Plawen 1978). Therefore, these groups are also biradial, and we score them as polymorphic (0/2 or 1/2). In Anthozoa, symmetry is variable (reviewed by Salvini-Plawen 1978), but a bilateral planula symmetry that persists in the polyp or transforms to biradial is common. We score this character as biradial for Anthozoa and await further resolution of anthozoan phylogeny, which should clarify the plesiomorphic condition of this character for Anthozoa and Cnidaria as a whole.

Reproduction and development

19. Sexual condition (0—hermaphroditic; 1—gonochoric). This variable character requires generalizations for the terminals. We considered a taxon to be gonochoric when this condition is present in more than just a few isolated species. Within Cnidaria, Siphonophorae is among the rare hermaphroditic groups, though hermaphroditism is not necessarily simultaneous in the majority of species (Kirkpatrick & Pugh 1984). In other hydrozoans, the predominant condition is gonochorism (see exceptions in Bouillon 1994b).
20. Location of medusa formation (0—lateral, budding from an entocodon; 1—apical/oral; 2—direct development without polyp stage). Strobilation in Coronatae, Semaestomeae, and Rhizostomeae produces medusae at the apical ends of polyps, with very few exceptions (e.g., *Pelagia*). Transformation of the stauromedusan polyp to the adult form involves a transformation of the oral end of the polyp (Kikinger & Salvini-Plawen 1995). A similar process of metamorphosis and development of adult characteristics largely toward the oral end of the polyp is observed in cubozoans (Stangl et al. 2002). In many hydrozoan groups, medusae form on the lateral portions of polyps and involve the entocodon, whereas in others the medusa is produced by direct development without any polyp stage. Information is missing for Laingiomedusae because the polyp stage, if it exists, is unknown (Bouillon & Boero 2000).
21. Type of apical medusa formation (0—strobilation; 1—metamorphosis without transverse fission). Strobilation involves transverse fission and is typical only of Coronatae, Semaestomeae, and Rhizostomeae. In both Stauromedusae and Cubozoa, adult medusae are produced by a metamorphosis which involves the resorption of polyp tentacles and the development of new tentacles and which is not accompanied by transverse fission (Werner et al. 1971; Kikinger & Salvini-Plawen 1995; Stangl et al. 2002).
22. Strobilation type (0—polydisk; 1—monodisk).
23. Oocyte development (0—oocytes develop without

accessory cells; 1—oocytes develop with accessory cells; 2—oocytes develop within follicles; 3—oocytes develop with uptake of somatic or other germ line cells). Oocytes develop with accessory cells in anthozoans, semaeostomes, and rhizostomes (Eckelbarger & Larson 1993; Eckelbarger 1994). Ovaries of Stauromedusae, in which oocytes develop within follicles, appear to be uniquely complex among cnidarians, though only 1 species has so far been investigated (Eckelbarger & Larson 1993). Hydrozoans differ in the development of their oocytes, which take up nutrients from other cells, including degenerating oocytes (Campbell 1974; Tardent 1985; Eckelbarger 1994).

24. Spermatophores (0—absent; 1—present). Known only for some cubozoans (Werner 1973b; Bouillon 1994a; Franc 1994b).
25. Location of gonads (0—gastrodermis; 1—epidermis). In non-hydrozoans, the gonads are of gastrodermal origin and location (Fautin & Mariscal 1991; Bouillon 1994a). In hydrozoans, the gonads are located in the epidermis (Bouillon 1994a; Nielsen 2001), although for many species the gonads originate in the gastrodermis (Tardent 1985). In most species of Narcomedusae, the gonads seem to originate in the epidermis, although in some species (*Pegantha clara* and *Solmaris flavescens*) the gonads are of gastrodermal origin (Bigelow 1909; Bouillon 1987).

Siphonophore features

26. Nectosome (0—absent; 1—present). Present in siphonophores other than those in Cystonectae.
27. Pneumatophore (0—absent; 1—present). Present in siphonophores other than those in Physonectae.

Planula

28. Planula in the life cycle (0—absent; 1—present). Absent only from actinulids, which have direct development (Swedmark & Teissier 1966; Bouillon 1985; Clausen & Salvini-Plawen 1986).
29. Planula ciliation (0—absent; 1—present). Typically ciliated. In Stauromedusae, the planula of only 1 species has been investigated and was found not to be ciliated (Otto 1976, 1978). Although Thiel (1966) and Franc (1994a) considered the character generalized for Stauromedusae, the universality of this and other planula characters in the group is currently unknown.
30. Number of endodermal cells of the planula (0—variable; 1—constant, n=16). The endodermis of the stauromedusan planula possesses 16 supporting cells arranged linearly (Otto 1976, 1978), a

condition that appears to be unique in Cnidaria (Lesh-Laurie & Suchy 1991).

31. Glandular cells in the planula (0—absent; 1—present). Histological studies of cnidarian planulae are not common and much remains to be learned from future studies. Glandular and nerve cells are lacking in the planulae of *Halicylistus* (Otto 1976, 1978) and *Cassiopeia* (Martin & Chia 1982), in Stauromedusae and Rhizostomeae, respectively, but they are present in semaeostomes (Widersten 1968). Within Hydrozoa, anthoathecatan planulae appear to be best studied and reveal glandular and nerve cells (Martin & Chia 1982; van de Vyver 1994; Bouillon & Boero 2000). For Anthozoa, Fautin & Mariscal (1991) report that all cell types present in the adult were already in the planula (nematocysts, sometimes spirocysts, supporting cells, secretory, nervous, and sensory).
32. Nerve cells in the planula (0—absent; 1—present). See comments for ch31. Nerve cells have been observed in the planulae of limnomedusan species (Bouillon & Boero 2000).
33. Relationship between axes of planula and adult (0—oral-aboral axis in the adult derived from the longitudinal axis of the planula; 1—oral-aboral axis in the adult derived from the transverse axis of the planula). The oral-aboral axis found in adult narcomedusans develops from the transverse axis of the planula, presumably a unique characteristic of this group (Bouillon 1987). This character is probably not known for most taxa.

Post-planula

34. Ephyrae (0—absent; 1—present). Information is scarce for Coronatae (Lesh-Laurie & Suchy 1991), but it appears that only coronates, semaeostomes, and rhizostomes have ephyrae in their life cycles (Thiel 1966).
35. Actinula (0—absent; 1—present). Stages described as actinulae occur sparsely among hydrozoan groups, in the superfamily Tubularioidea (Petersen 1990), in Trachymedusae (Thomas & Edwards 1991), and in Narcomedusae. Although they are morphologically similar, the anthoathecatan actinula (present in Tubularioidea) is not considered homologous to those of Trachymedusae and Narcomedusae, because in anthoathecata the actinula precedes the polyp whereas in Trachymedusae and Narcomedusae it precedes the medusa (Petersen 1990; Bouillon 1994b). Here we refer to the actinula that precedes the medusa. The name Actinulida also refers to the similarity between representatives of this group and the actin-

- ula stage of Trachymedusae and Narcomedusae, but homology in this case is uncertain.
36. Polypoid phase (0—absent; 1—present). A polypoid phase (a body structure consisting of a column and an aperture originating from the blastopore surrounded by tentacles) is present in all major cnidarian groups other than Actinulida and Trachymedusae. A polyp-like form is present in some narcomedusans, but this structure is almost certainly not homologous to the polyps of other cnidarian groups (Bouillon 1987). Information about the life cycle of laingiomedusans is unknown (Bouillon 1978, 1985), though polyp-like forms have been found appearing from medusoid budding (J. Bouillon, pers. comm.)—a possible link between this group and the Narcomedusae. Within Semaestomeae, Leptothecata, and Anthoathecata, some members do not have a polyp phase, but in each of these cases, the lack probably represents a secondary loss. Stauromedusae was scored as possessing a polyp phase because the adult form is separated ontogenetically from the juvenile polyp-like form by a distinct metamorphosis.
 37. Polymorphic polyps (0—absent; 1—present). Common in Leptothecata, Siphonophorae, and Anthoathecata (Bayer & Owre 1968; Kirkpatrick & Pugh 1984), and also present in some members of Limnomedusae (Bouillon 1994b), which was scored as polymorphic. Anthozoa is also scored as polymorphic because octocorals have polymorphic polyps.
 38. Desmocytes (0—absent; 1—present). Desmocytes are hardened dead cells ontogenetically derived from secretory epidermal cells (Marcum & Diehl 1978) linking cuticle to mesoglea. Common in many sessile cnidarians (D. Chapman 1966; Lesh-Laurie & Suchy 1991). Documented in a number of semaestomes (Hérouard 1911; Widersten 1966; Lesh-Laurie & Suchy 1991), but appear to be absent in cubozoans, rhizostomes, and perhaps coronates (Lesh-Laurie & Suchy 1991, and references therein). Stauromedusans have supporting cells resembling desmocytes (Lesh-Laurie & Suchy 1991), but are scored here as absent. Desmocytes are common in anthozoans and hydrozoans (Fautin & Mariscal 1991; Lesh-Laurie & Suchy 1991). Even in a siphonophore, a non-sessile hydrozoan, Mackie (1960) described desmocytes between the stem and the float of *Physalia*. Homology of desmocytes across Cnidaria has been doubted (Tidball 1982; Fautin & Mariscal 1991; Thomas & Edwards 1991).
 39. Periderm (0—absent; 1—present but limited to the basal area of polyp or to podocysts; 2—present and covering most of polyp). According to Salvini-Plawen (1978) and Lesh-Laurie & Suchy (1991), periderm is secreted only by some coronates among the traditional scyphozoans. However, D. Chapman (1966) reported a vestigial cuticle in scyphistomae of *Aurelia* and pointed out that groups with podocysts, such as Semaestomeae and Rhizostomeae, necessarily have periderm involved in forming the resistant structure (D. Chapman 1966). A small basal periderm has been reported for cubopolyps (Werner 1984; Bouillon 1994b). No indication of periderm has been reported for stauromedusans. Among hydrozoans, polyps and colonies of many Limnomedusae, Leptothecata, and Anthoathecata produce perisarc, which is similar to the periderm of scyphozoans (Thomas & Edwards 1991). Some siphonophores also may produce a kind of “perisarc” that extends over most of the organism (cf. Mackie 1960). In the fossil group Conulatae, a periderm was present (Salvini-Plawen 1978). Anthozoans secrete no periderm.
 40. Podocysts (0—absent; 1—present). Resting stages appearing in unfavorable conditions are found in Semaestomeae and Rhizostomeae (Lesh-Laurie & Suchy 1991). Also present in a small number of anthoathecans (D. Chapman 1966; Petersen 1990); we consider them to be secondarily derived. Information concerning cubopolyps is still indefinite (Schuchert 1993).
 41. Structure of polyp tentacles (0—hollow; 1—solid). Hollow in anthozoans, cubozoans, and the traditional scyphozoan groups (Schuchert 1993). In hydropolyps, the character is not uniform: hollow in Limnomedusae, chord-like in Leptothecata (scored as solid), and polymorphic in Anthoathecata (Petersen 1990).
 42. Number of tentacular whorls (0—one; 1—two or more). Polyp tentacles in 2 or more whorls occur broadly only in Anthoathecata (Petersen 1990), which we score as polymorphic. Some groups within Anthozoa (e.g., Ceriantharia) and Stauromedusae (*Stylocoronella variabilis*; see Kikinger & Salvini-Plawen 1995) also have 2 whorls of tentacles, but this condition is not representative.
 43. Septa in polyp (0—absent; 1—gastrodermal folds present; 2—present). Except in polyps of Cubozoa and Hydrozoa, the gastrovascular cavity is divided by septa. Salvini-Plawen (1987) argued that cubopolyps exhibit reduced septa and septal muscles; these septa are gastrodermal folds in which the mesoglea is never present (e.g., in *Tripedalia*, Chapman 1978, also Lesh-Laurie & Suchy 1991).

Except for Cubozoa, we score simply the presence or absence of septa, rather than considering the many characters that could be derived from them (e.g., the arrangement of muscle bundles), because of difficulty in determining character states and judging homology.

44. Hydrotheca/gonotheca (0—absent; 1—present). Unique to Leptothecata. Similar structures occur in other hydrozoans, e.g., families Stylasteridae and Milleporidae, but these are not constituted by perisarc.
45. Stomodeum (0—absent; 1—present). Stomodeum, corresponding to the pharynx, is unique to Anthozoa. The structure called a scyphopharynx in some scyphozoans (discussed in Lesh-Laurie & Suchy 1991) is probably not homologous to the anthozoan pharynx, nor is it widely distributed.
46. Organization of the nervous system (0—in 1 or 2 nets; 1—with nerve rings). Cubopolyps have 2 nerve rings near the oral cone, 1 in the gastrodermis and 1 in the epidermis, a condition unique among cnidarian polyps (Lesh-Laurie & Suchy 1991; Bouillon 1994a). Cf. ch77.
47. Canal system (0—absent; 1—present). Werner (1973a) noted a canal system in the polyp of a coronate and pointed out similar canal systems in scyphopolyps of Semaestomeae and Rhizostomeae. Canals also occur in Stauromedusae and Cubozoa (Thiel 1966). There are no indications of any canal system in the well-known polyps of Hydrozoa and Anthozoa.
48. Gastrodermal musculature (0—not organized in bunches; 1—organized in bunches of gastrodermal origin; 2—organized in bunches of ectodermal origin). The gastrodermal musculature among anthozoans is organized into longitudinal bundles of gastrodermal origin, except for Ceriantharia, in which the musculature is organized in longitudinal layers, with retractor muscles occurring in the mesenteries (Fautin & Mariscal 1991). In hydro-polyps, the musculature consists of a layer of longitudinal epidermal muscular fibers and circular gastrodermal fibers (Werner et al. 1976; Lesh-Laurie & Suchy 1991; Thomas & Edwards 1991). In Stauromedusae, Coronatae, Semaestomeae, and Rhizostomeae, polyps have 4 main muscles of ectodermal origin, in an interradial position, and located in the mesoglea (Thiel 1966). Cubopolyps also possess intramesogleal muscles organized in bunches of ectodermal origin, though the number is not fixed. Fossil conulates with 4 opercular flaps can be inferred to have had 4 muscle bundles with a position topologically equivalent to those of Stauromedusae, Coronatae, Semaestomeae, and Rhizostomeae (Moore & Harrington 1956; D. Chapman 1966).

Medusae

These characters apply to an adult life phase that typically follows an intermediate polyp stage. Although homology between cnidarian medusoid phases has long been debated, the strong morphological similarity of various medusae leads us to score these characters across the medusozoan groups. Anthozoa has no comparable phase and is scored accordingly throughout.

49. Medusoid phase (0—absent; 1—present).
50. Pedalium of coronate type (0—absent; 1—present). This type of pedalium, present only in Coronatae, is part of the umbrella, and should not be confused with the pedalia of Cubozoa, which are the thickened bases of tentacles or tentacle bunches (Thiel 1966). Cf. ch56.
51. Rhopalia/rhopalioids (0—absent; 1—present). Hollow structures ontogenetically derived from tentacles are present in Cubozoa, Coronatae, Semaestomeae, and Rhizostomeae, in which they are associated with statocysts and photoreceptors. Rhopalia of cubozoans contain strikingly complex sensory structures, including ocelli with corneas, vitreous body, lenses, and retinas (Pearse & Pearse 1978). The simpler hollow structures of Stauromedusae are known as rhopalioids or anchors, and have a similar ontogeny involving the reduction of primary tentacles. Statocysts of Trachymedusae and Narcomedusae are also of tentacular origin, but they do not appear to be homologous with rhopalia because they are not associated with photosensitive structures.
52. Complexity of rhopalium/rhopalioid (0—rhopalioids; 1—rhopalia; 2—rhopalia with complex eyes). Cf. ch51.
53. Nerve ring(s) (0—absent; 1—one; 2—two). Scoring of this character follows Schuchert (1993). The medusae of Stauromedusae, Coronatae, Semaestomeae, and Rhizostomeae have 2 epidermal nerve nets connected in marginal centers or ganglia (Lesh-Laurie & Suchy 1991). Hydrozoan medusae have 2 nerve rings, 1 internal and the other external (Thomas & Edwards 1991) in Limnomedusae, Trachymedusae, Leptothecata, Siphonophorae (2 rings in the nectophore, Thomas & Edwards 1991; Carré & Carré 1994), and Anthoathecata. Cf. ch77.
54. Gastric filaments (0—absent; 1—present). Present in the adult stages of Stauromedusae, Cubozoa,

- Coronatae, Semaestomeae, and Rhizostomeae (Thiel 1966; Bouillon 1994a).
55. Coronal muscle (0—well developed; 1—marginal and tiny). The coronal muscle of medusae is responsible for swimming, and according to Lesh-Laurie & Suchy (1991), the muscles of Stauro-medusae, Cubozoa, Coronatae, Semaestomeae, Rhizostomeae, and Hydrozoa have the same location, structure, and arrangement of myofibrils, despite some structural differences, e.g., the presence of a velum in Hydrozoa. A coronal muscle occurs in all hydrozoan groups, including Siphonophorae (Carré & Carré 1994). In Stauromedusae this musculature is present as a tiny subumbrellar marginal strip (Gwilliam 1960; Bayer & Owre 1968), or even absent (as in *Stylocoronella*, Salvini-Plawen, pers. comm.).
 56. Pedalium of the cubozoan type (0—absent; 1—present). As stated above (ch50), the pedalia of Coronatae and Cubozoa are homonyms rather than homologous structures.
 57. Velum (0—absent; 1—present). A circular membrane of tissue projecting toward the center of the bell opening acts in the swimming of some medusae. The velum comprises 2 epidermal epithelia, one subumbrellar and the other exumbrellar, with a mesolamella in between. It is connected to the subumbrella by a non-muscular zone containing the nerve rings. This structure is characteristic of most hydrozoan groups; a few exceptions (e.g., Anthoathecata Milleporidae) appear to be character losses. Actinulida also lacks a velum (Bouillon 1985), but it is scored as non-comparable because of its diminutive umbrella.
 58. Umbrellar margin (0—smooth and continuous; 1—lobed). The umbrellar margin in Coronatae, Semaestomeae and Rhizostomeae is lobed, whereas that in Stauromedusae and Cubozoa is not (Thiel 1966). Among Hydrozoa, medusa margins are lobed in Narcomedusae and Laingiomedusae (*Laingia jaumotti* with 4 lobes and *Kantiella enigmatica* with 8 lobes; Bouillon 1978).
 59. Tentacles (0—absent; 1—present). Present at the umbrella margin in all groups of Medusozoa except Rhizostomeae (Thiel 1966) and Siphonophorae.
 60. Tentacular bulbs (0—absent; 1—present). Scoring of this character is based on data from Bouillon & Boero (2000).
 61. Statolith composition (0— $MgCaPO_4$; 1— $CaSO_4$). Statoliths of hydrozoans (at least in 7 species of Leptothecata and 1 of Trachymedusae) are composed of $MgCaPO_4$, whereas those of Coronatae, Rhizostomeae, Cubozoa (1 species), and Semaestomeae (2 species) are made of $CaSO_4$ (Chapman 1985; Lesh-Laurie & Suchy 1991). Chapman (1985) also noted that the ratio of Mg to Ca differs between Limnomedusae and Leptothecata, possibly indicating independent origins. The character is non-comparable for Stauromedusae, Laingiomedusae, Siphonophorae, and Anthoathecata because members of these groups do not have statocysts, and consequently lack statoliths. Statolith composition can be related to physiological factors, but the character is included to inspire future investigations.
 62. Septa (0—absent; 1—present). Septa in the gastrovascular cavity of the medusa occur in Stauromedusae, Cubozoa, and Coronatae (though diminutive) (Thiel 1966). Comparable septa are absent in Semaestomeae, Rhizostomeae (Thiel 1966), and Hydrozoa. Because the location of gastric filaments should be influenced by the presence or absence of septa (Thiel 1966), we have avoided double weighting of the character by not scoring characters related to its position.
 63. Septal shape (0—straight; 1—y-shaped). The septa of Stauromedusae, Cubozoa, and Conulatae are y-shaped (Kiderlen 1937; Thiel 1966; Jerre 1994). These septa often form a claustrum, a lamella constituted by 2 endodermal layers, located between 2 contiguous septa in medusoids (see Thiel 1966).
 64. Radial canals (0—absent; 1—present; 2—present and complex). Absent in Stauromedusae, but present in Coronatae (in a simple form) and in Semaestomeae and Rhizostomeae (in complex morphological arrangements). In Semaestomeae, the canals ramify, join, and even extend into the marginal lobules, tentacles, and statocysts. In Rhizostomeae, the morphology is still more complicated, as the canals anastomose in a wide zone (see Thiel 1966 and references therein). In Cubozoa, canals are absent. However, cubozoans have gastrovascular spaces that topologically correspond to radial canals. We score the character as polymorphic, states 0 and 1, to reflect our uncertainty about whether these spaces do or do not constitute radial canals. In Hydrozoa, radial canals are absent in Actinulida and Narcomedusae, but present in all other groups (Bouillon 1994a; Carré & Carré 1994).
 65. Circular canal (0—absent; 1—partially present; 2—fully present). Absent in Stauromedusae, Cubozoa (though there is a morpho-physiologically similar structure in the velarium), and Coronatae, but partially present in Semaestomeae and Rhizostomeae (Thiel 1966). In Hydrozoa, a circular canal is absent in Actinulida, but present in other

- groups with some variation. For instance, narcomedusans have a system in which the circular canal is arranged around the peronia and tentacular bases (Bouillon 1985, 1994b), a condition similar to that seen in Laingiomedusae (Bouillon 1978).
66. Velarium (0—absent; 1—present). Occurs only in Cubozoa. It has a gross structure similar to that of the velum, but is entirely of subumbrellar origin (Hyman 1940).
 67. Coronal furrow (0—absent; 1—present). Present only in Coronatae (Mayer 1910).
 68. Gonadal location (0—manubrium; 1—radial canals). In Hydrozoa, members of Narcomedusae (Bouillon 1985), Laingiomedusae (Bouillon 1978, 1985), Siphonophorae (Kirkpatrick & Pugh 1984), and Anthoathecata (Bouillon 1994b) have gonads on the manubrium, though sometimes gonads extend along the radial canals. Following the topological equivalencies of Clausen (1967), the area of the gastric tube of Actinulida, where actinulids bear gonads, corresponds to the manubrium of other medusae (Clausen 1967; Bouillon 1985). In Limnomedusae, gonads are located on radial canals (except in *Limnocrnida*, an African and Indian freshwater group). In most trachymedusans, gonads are also located on the area of the radial canals, but some species have them on the pseudo-manubrium (Bayer & Owre 1968), dubbed pseudo because the radial canals are present. In Leptothecata, gonads are also on the radial canals (Bouillon 1994b), with a few exceptions. In Cubozoa, gonads occur along the interradial septa (Mayer 1910), an area equivalent to where the radial canals are in those medusae that possess them.
 69. Statocysts (0—absent; 1—endodermal; 2—ectodermal). Stauromedusae, Laingiomedusae (Bouillon 1994a), Siphonophorae (Carré & Carré 1994), and Anthoathecata lack statocysts. The statocysts of Coronatae, Semaestomeae, and Rhizostomeae are reported to be of endodermal origin (Mayer 1910). In Hydrozoa, statocysts of endodermal origin are present in Limnomedusae, Actinulida, Trachymedusae, and Narcomedusae, whereas Leptothecata is the only group to have statocysts of exclusively ectodermal origin (Bouillon 1985, 1994b).
 70. Perradial “mesenteries” (0—absent, 1—present). The so-called perradial mesenteries are triangular pouches adjacent to the base of the stomach and located along the radial canals of many species of Anthoathecata (Petersen 1990).
 71. Adult medusoid shape (0—bell; 1—pyramidal; 2—cubic; 3—actinuloid). Adults of medusozoans are medusae in most groups, and are typically bell-shaped, more or less narrowing in the oral-aboral axis. However, the shape in Stauromedusae is pyramidal, in Cubozoa cubic, and in Actinulida actinuloid (Mayer 1910; Thiel 1966).
 72. Shape of horizontal cross-section (0—circular; 1—quadrate, i.e., with 4-parted symmetry). A quadrate horizontal cross-section is seen in Stauromedusae, Cubozoa, and Conulatae.
 73. Urticant rings (0—absent; 1—present). Urticant rings are rings of cnidae in the basal area of the umbrellar margin and are present in some Limnomedusae (P. Shuchert, pers. comm.) and Trachymedusae (Bouillon 1994b).
 74. Oral arms with suctorial mouths (0—absent; 1—present). Present in Rhizostomeae, whose 8 fused oral arms are ontogenetically derived from the 4 oral lobules of the manubrium of the ephyrae (Thiel 1966).
 75. Tentacular insertion (0—umbrellar margin; 1—away from the umbrellar margin). Tentacles most commonly arise at the umbrellar margin, but never in Narcomedusae and Laingiomedusae, in which the tentacular insertion is near the apex of the umbrella (Bayer & Owre 1968; Bouillon 1978, 1985). Rhizostomes and siphonophores were scored non-comparable because their medusoids do not have tentacles.
 76. Manubrium (0—absent; 1—present). Members of Narcomedusae often lack a manubrium (cf. Bayer & Owre 1968). However, at least 1 species has a conspicuous manubrium, which even extends outside the bell (*Cunina proboscidea*, Bouillon 1994b). We score this character absent for Narcomedusae, while anticipating more complete information in the future.
 77. Nervous system organization (0—GFNN absent; 1—GFNN present). Coronates, semaeostomes, and rhizostomes have 3 basic components in the nervous system: a giant fiber nerve net (GFNN), which transmits pulses to the marginal ganglion and to the swimming muscle; a diffuse nerve net (DNN), in which neurons are located in the subumbrellar epidermis, oral arms, and tentacles (if present); and marginal centers, which include the marginal ganglion and the rhopalium (Horridge 1956; Lesh-Laurie & Suchy 1991). No GFNN is present in Stauromedusae (Gwilliam 1960; Passano 1982). In cubozoans, there is evidence of DNN fibers organized in a diffuse system, as well as of a GFNN organized in the subumbrellar epidermis and in the nerve ring (Werner et al. 1976; Chapman 1978; Satterlie 1979; Satterlie & Spencer 1979; Passano 1982; Lesh-Laurie & Suchy 1991). Hydrozoan medusae also have DNN fibers,

- as well as ganglia (Thomas & Edwards 1991), and a GFNN also occurs in Anthoathecata (e.g., *Polyorchis*, *Stomotoca*, *Amphinema*: Chapman 1974; Mackie & Singla 1975; Anderson & Mackie 1977; Singla 1978a; Spencer 1979; Thomas & Edwards 1991), Leptothecata (e.g., *Obelia*, Chapman 1968), Limnomedusae (e.g., *Limnocrnida*, Bouillon 1956), Trachymedusae (e.g., *Aglantha*: Singla 1978b), and Siphonophorae (e.g., *Nanomia*, Mackie 1973).
78. Structure of medusa tentacles (0—hollow; 1—solid). Hollow primary or secondary tentacles are present in Cubozoa, Stauromedusae, and Semaestomeae. In Hydrozoa, hollow tentacles occur in Limnomedusae (Bouillon 1994a) and Leptothecata (except for *Obelia* and perhaps *Dipleurosoma pacificum*) (Bouillon 1994b). Tentacles are solid in Coronatae, Actinulida, Laingiomedusae, and Narcomedusae (Thiel 1966; Bouillon 1985). In Trachymedusae, the majority of species have solid tentacles and determine the scoring, despite species with hollow tentacles in Geryonidae (Bouillon 1994a, 1994b). Anthoathecata is polymorphic for this character.
 79. Tentacular morphology (0—straight tentacles; 1—tentacles with an angular inflection). The tentacles of *Laingia jaumotti* and *Kantiella enigmatica* (Laingiomedusae) have a right-angle inflection close to where the tentacles meet the umbrella (Bouillon 1978a).
 80. Peronia (0—absent; 1—present). A peronium, found only in Narcomedusae and Laingiomedusae, is a structure formed when the tentacular ectoderm extends up to the umbrellar margin, and lines the umbrellar furrow with cnidae (Bouillon 1978a).
 81. Ocelli (0—absent; 1—present). Present in the medusae of Cubozoa, Coronatae, Semaestomeae, and Rhizostomeae. Although stauromedusans generally do not have ocelli as adults, some interstitial forms do appear to possess them (Blumer et al. 1995), and we score the character as polymorphic for the group. In Hydrozoa, ocelli are generally not present (Bouillon 1978, 1985, 1994b; Carré & Carré 1994), except in Anthoathecata and rarely in Leptothecata (Bouillon 1994b).
 82. Peripheral canal system (0—absent; 1—present). Present only in Narcomedusae and Laingiomedusae, this is a limited circular canal encircling peronia and tentacular bases (Bouillon 1978).
 83. Umbrellar furrow (0—absent; 1—present). Present only in Laingiomedusae (Bouillon 1978).
 84. Development of the umbrella (0—fully developed; 1—aboral cone). The aboral cone occurs only in Actinulida (Clausen 1967).
 85. Number of tentacular whorls (0—one whorl; 1—two whorls). Actinulids have 2 tentacular whorls as adults, 1 aboral and 1 subaboral (Clausen 1967). Two whorls of tentacles are also present in the interstitial *Armohydra*, an unusual member of Limnomedusae, which we code as polymorphic for this character.
 86. Velar canals (0—absent; 1—present). Present in the velarium of cubozoans, varying in number and morphology (Franc 1994b). No equivalent structures are known in other medusozoans.
 87. Frenulae (0—absent; 1—present). Frenulae are supporting structures of the velarium, perradially located in Cubozoa (Franc 1994b). No equivalent structures are known in other medusozoans.

Appendix 2

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Anthozoa	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	2	1	N	N	N
Stauromedusae	?	1	0	0	?	1	0	1	0	0	0	0	1	0	0	0	0	{12	1	1	1	N
Conulatae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?
Cubozoa	1	1	0	0	?	1	1	1	0	1	0	0	1	0	0	0	1	{12	1	1	1	N
Coronatae	?	?	0	1	?	1	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0	0
Semaeostomea	1	1	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	{12	1	1	1	0
Rhizostomeae	?	1	0	1	?	1	0	1	0	0	0	0	1	1	0	0	1	{12	1	1	0	1
Limnomedusae	1	1	?	0	?	1	0	1	0	{01	0	0	1	0	0	0	1	{02	1	0	N	N
Actinulida	?	?	?	0	?	1	1	{01	?	0	0	0	1	0	0	0	1	N	1	2	N	N
Trachymedusae	?	1	1	0	?	1	1	1	0	0	0	0	1	0	0	0	1	N	1	2	N	N
Narcomedusae	?	?	?	0	?	1	0	0	0	0	0	1	1	0	0	0	1	N	1	2	N	N
Laingiomedusae	?	?	?	0	?	1	0	0	0	1	0	0	1	0	0	0	1	N	?	?	N	N
Leptothecata	1	1	?	0	?	1	0	{01	0	1	1	0	1	0	0	0	1	{02	1	0	N	N
Siphonophorae	1	1	1	0	?	1	1	1	1	1	0	0	1	{01	1	{01	1	{02	{01	0	N	N
Anthoathecata	1	1	1	0	?	1	{01	1	1	1	{01	0	1	{01	0	0	1	{02	1	0	N	N

TAXA	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Anthozoa	1	0	0	0	0	1	1	0	1	1	0	0	0	1	{01	0	0	0	0	0	2	0
Stauromedusae	2	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	2	0
Conulatae	1	?	?	0	0	?	?	?	?	?	?	?	?	1	0	?	2	?	?	?	2	0
Cubozoa	?	{01	0	0	0	1	1	0	?	?	0	0	0	1	0	1	1	?	1	0	1	0
Coronatae	0	0	0	0	1	1	0	?	?	0	1	0	1	0	1	2	0	1	0	2	0	0
Semaeostomea	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	1	1	1	0	2	0
Rhizostomeae	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	1	1	1	0	2	0
Limnomedusae	3	0	1	0	0	1	1	0	0	1	0	0	0	1	{01	0	1	0	0	0	0	0
Actinulida	?	0	1	0	0	0	N	N	N	N	0	0	0	N	N	N	N	N	N	N	N	N
Trachymedusae	3	0	1	0	0	1	1	0	0	0	0	0	1	0	N	N	N	N	N	N	N	N
Narcomedusae	3	0	1	0	0	1	1	0	0	0	1	0	1	0	N	N	N	N	N	N	N	N
Laingiomedusae	?	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Leptothecata	3	0	1	0	0	1	1	0	1	1	0	0	0	1	1	0	2	0	1	0	0	1
Siphonophorae	?	0	1	{01	{01	1	1	0	1	1	0	0	0	1	1	0	{02	0	0	?	0	0
Anthoathecata	3	0	1	0	0	1	1	0	1	1	0	0	0	1	1	0	2	0	{01	{01	0	0

TAXA	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Anthozoa	1	0	0	1	0	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Stauromedusae	0	0	1	2	1	0	1	0	0	1	1	0	0	0	1	?	N	1	1	0	0	0
Conulatae	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?
Cubozoa	0	1	1	2	1	0	1	2	1	1	0	1	0	0	1	0	1	1	1	{01	0	1
Coronatae	0	0	1	2	1	1	1	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0
Semaeostomea	0	0	1	2	1	0	1	1	0	1	0	0	0	1	1	0	1	0	N	2	1	0
Rhizostomeae	0	0	1	2	1	0	1	1	0	1	0	0	0	1	0	N	1	0	N	2	1	0
Limnomedusae	0	0	0	0	1	0	0	N	2	0	0	0	1	0	1	0	?	0	N	1	2	0
Actinulida	N	N	N	N	1	0	0	N	?	0	?	0	N	0	1	0	?	0	N	0	0	0
Trachymedusae	N	N	N	N	1	0	0	N	2	0	0	0	1	0	1	0	0	0	N	1	2	0
Narcomedusae	N	N	N	N	1	0	0	N	?	0	0	0	1	1	1	0	?	0	N	0	2	0
Laingiomedusae	?	?	?	?	1	0	0	N	?	0	?	0	1	1	1	1	N	0	N	1	2	0
Leptothecata	0	0	0	0	1	0	0	N	2	0	0	0	1	0	1	1	0	0	N	1	2	0
Siphonophorae	0	?	0	0	1	0	0	N	2	0	0	0	1	0	0	1	N	0	N	1	2	0
Anthoathecata	0	0	0	0	1	0	0	N	2	0	0	0	1	0	1	1	N	0	N	1	2	0

TAXA	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	
Anthozoa	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	0	0
Stauromedusae	0	1	0	0	1	1	0	0	0	1	0	0	0	0	{01	0	0	0	0	0	0	0
Conulatae	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cubozoa	0	1	1	0	2	1	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1
Coronatae	1	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0
Semaeostomea	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Rhizostomeae	0	1	1	0	0	0	0	1	N	1	1	N	N	0	1	0	0	0	N	0	0	0
Limnomedusae	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	{01	0	0	0
Actinulida	0	0	1	0	3	0	0	0	0	1	?	1	0	0	0	0	0	0	1	1	0	0
Trachymedusae	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Narcomedusae	0	0	1	0	0	0	0	0	1	0	?	1	0	1	0	1	0	0	0	0	0	0
Laingiomedusae	0	0	0	0	0	0	0	0	1	1	?	1	1	1	0	1	1	0	0	0	0	0
Leptothecata	0	1	2	0	0	0	0	0	0	1	1	0	0	0	{01	0	0	0	0	0	0	0
Siphonophorae	0	0	0	0	0	0	0	0	N	1	1	N	N	0	0	0	0	0	N	0	0	0
Anthoathecata	0	0	0	1	0	0	0	0	0	1	1	{01	0	0	1	0	0	0	0	0	0	0