Contributions to Zoology, 70 (3) 175-179 (2001)
SPB Academic Publishing bv, The Hague

Short notes and reviews

Simplifying hydrozoan classification: inappropriateness of the group Hydroidomedusae in a phylogenetic context

Antonio C. Marques
Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes, 3900, 14040-901, Ribeirão Preto, SP, Brazil. e-mail: marques@ffclrp.usp.br

Keywords: Hydrozoa, Hydroidomedusae, classification, nomenclature, taxonomy

Abstract

The systematics of Hydrozoa is considered from the viewpoint of logical consistency between phylogeny and classification. The validity of the nominal taxon Hydroidomedusae (including all groups of Hydrozoa except the Siphonophorae) is discussed with regard to its distinctness and inclusive relationships. In general, phylogenetic systematic evidence suggest that the use of the term Hydroidomedusae is inappropriate given our current level of understanding. It is concluded that no new, or resurrected, names are necessary before or until a broader phylogenetic revision of the Hydrozoa is accomplished.

Introduction

Classification of organisms is a way to "systematize" biological information within some kind of logical framework. Therefore systematics could be viewed as the science of classifying or organizing organisms into a hierarchical perspective. By the term biological information we mean any property intrinsic to the organism, such as ecology, morphology, molecular constituents, behavior, etc. Hence, taxa formed only by convenience (e.g., assuming economical importance or by the personal preference of its proponent) ought to be discouraged.

Darwin (1859) effectively focused the attention of biologists to reflect on issues of descent and divergence from common ancestors. Subsequently, workers like Julian Huxley, Ernst Mayr, and George G. Simpson, in what came to be called the "Modern Synthesis", accommodated both grades and clades (cf. Mayr & Ashlock, 1991). Cladistics (Hennig, 1950, 1966) excluded grades and generated classifications and models of phylogeny simultaneously. In phenetics, classifications reflect overall similarity, not necessarily phylogeny (Hull, 1988: 122; Mayr and Ashlock, 1991: 128). With regard to the higher levels of hydrozoan classification, no cladistic or phenetic classifications have been proposed. All hydrozoan classifications seem to be based on *gradistic* or essentialistic principles, although the majority of their proponents would not characterize them as such.

In my view, a classification should represent one of the *possible* hypotheses of phylogeny (cf. the principle of logical consistency by Hull, 1964). In other words, "if the cladogram that follows the true phylogeny (assuming that the true phylogeny could be known) is the same as the cladogram expressed by a classification, *then the classification is clearly consistent with phylogeny*" (Platnick, 1979: 542; my italics). For Hydrozoa, Bouillon (1981, 1985) provides examples of a classification logically consistent with proposed hypotheses of phylogeny, although these phylogenies were constructed without the use of rigorous phylogenetic or cladistic methods. Petersen (1990), Marques (1996), Peña Cantero & Marques (1999), and Marques & Migotto (2001) provide examples of phylogenetic and cladistic approaches as a basis for the classification of hydrozoans. The aim of this note is to discuss in light of known aspects of the phylogeny of the Hydrozoa the justification for a taxon "Hydroidomedusae" by Bouillon et al. (1992).

Hydrozoan classification

A historical review of hydrozoan classifications was compiled and discussed by Bouillon et al. (1992). From a methodological perspective, all proposed classifications for the Hydrozoa have been essentialistic, i.e., focused on grades of evolution. Bouillon et al. (1992) also observed that most previous classifications have not been adequate. Although these classifications based their arguments on the assembling of taxa within historical concepts of some proposed names; the idea that a classification should represent some actual phylogenetic knowledge has not been considered. As a substitution for those former inadequate classifications, Bouillon et al. (1992) resurrected the name Hydroidomedusae (originally proposed by Claus, 1877a, 1877b) stating, "Our proposal is to divide the class Hydrozoa into two subclasses, the Hydroidomedusae and the Siphonophorae" (Bouillon et al., 1992: 282). Thus, within the Class Hydrozoa, the siphonophores would be juxtaposed against all other hydrozoans. Although Bouillon et al. (1992) did not justify the existence of such a subclass Hydroidomedusae with any clearly defined features, several authors have followed them, e.g., Pagès et al. (1992), Pagès & Gili (1992), and Boero et al. (1996). Others prefer to use the term Leptolida for this same grouping, e.g., Cornelius (1995), Vervoort (1995), and Brinckmann-Voss & Arai (1998), a name whose use was already denied by Bouillon et al. (1992). Still others simply still consider Hydrozoa to simply include several unnested groups, e.g., Schuchert (1998) and Collins (2000).

Since Darwin hierarchical classifications indicate relationships of subordination within nested sets. Since Hennig, we focus on trying to identify monophyly, natural groups that reflect common ancestry. If we presume that the label "Hydrozoa" (here considered a monophyletic group) is hypothesized to be derived from a single ancestral lineage, then all descendants could be grouped in subordinate patterns. If any of these subgroups are joined together under a taxon name, e.g., the Hydroidomedusae of Bouillon et al. (1992) and posed against another, i.e., the Siphonophorae, this would then necessarily imply that members of these subgroups are related and share a common lineage. The uniqueness of such groups implies that they represent monophyletic lineages that are distinct delineated by a set of autapomorphies.

Are the Siphonophorae monophyletic vis-à-vis the other hydrozoans? This is not clear in Bouillon et al. (1992), and I can see no justification other than that of historical convenience. Students of the Hydrozoa do not deal generally with siphonophores, possibly because of their very derived morphology, ecology, and life history. Obviously, historical convenience is not enough of a reason to separate a group. Perhaps the most striking difference in the siphonophore lineage is its "high degree of determinancy of form" (Mackie et al., 1987: 110-113). The modular construction of siphonophores is based on definite growth zones along an anterior-posterior axis. Derivatives of both polypoid and medusoid stages are found attached to the axial free-floating animal (Kirkpatrick & Pugh, 1984). Observing the singular morphology of the Siphonophorae, one might conclude that this group is highly modified and so, phenetically distant from all other Hydrozoa. Indeed, such phenetic classification reflects similarity relationships, which are not necessarily congruent with, or the result of, rigorous phylogenetic relationships.

However, could siphonophores have a common putative ancestor with some other hydrozoan subgroup(s)? Under such a hypothesis, following an event of cladogenesis, the siphonophore lineage underwent an accelerated process of anagenesis and/or specialization of form, resulting in a long and highly differentiated lineage. In this regard, Petersen (1979: 109 more explicitly; 1990: 105) suggested a possible relationship between Siphonophorae and the Anthomedusae, Leptomedusae, and Limnomedusae. Schuchert (1996: 13) was even more explicit in his statements, considering that "affinities [of Anthomedusae] with the Siphonophora and Laingiomedusae are not established. All three taxa have gonads on the manubrium as a possible synapomorphy. Desmonemes occur only in the Siphonophora and Anthoathecata [= Anthomedusae] and may indicate a closer relationships. *A taxon Hydroidomedusae* (Bouillon et al., 1992) *which includes all Hydrozoa except the Siphonophora is therefore most probably not a natural taxon*" (my italics).

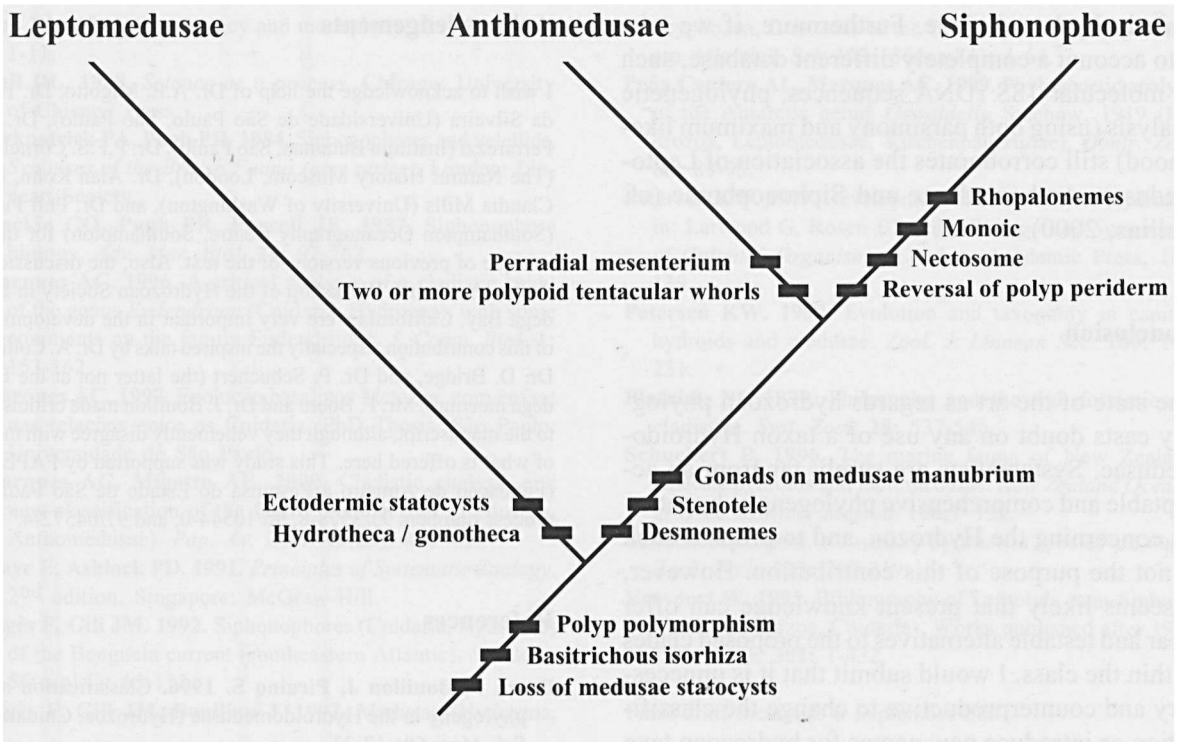

Fig. 1. Relationship among the Leptomedusae, Anthomedusae and Siphonophorae, after Marques (1997).

Indeed, Marques (1997), in a phylogenetic study of the Cnidaria (Fig. 1), concluded there is a relationship among Leptomedusae, Anthomedusae, and Siphonophorae. The Limnomedusae, with no autapomorphy, are a group of uncertain monophyly. They might possibly form a clade with the other hydrozoan subgroups (Trachymedusae, Laingiomedusae, Actinulidae and Narcomedusae). However, that issue is not relevant here. A single group composed of the Leptomedusae, Anthomedusae, and Siphonophorae is supported by the following synapomorphies: 1) polypoid polymorphism; 2) presence of basitrichous isorhizas (homoplastic with Anthozoa, considered by him equivalent to atrichous isorhiza), and 3) loss of the endodermal statocyts on medusae (a reversal, homoplastic with Laingiomedusae, a group that would be eventually included in the Anthomedusae see Schuchert, 1996). The sister-group relationship of the Siphonophorae and Anthomedusae would be supported by the presence of desmonemes, stenoteles (a doubtful character since the nematocyst is lacking in filiferan Anthomedusae; also homoplastic with Cubozoa, Actinulidae, and Trachymedusae), and gonads on the manubrium (a reversal from gonads on the radial canals in the more inclusive subgroups, and another homoplasy with Laingiomedusae). Fig.1 also shows the autapomorphies of Leptomedusae, Anthomedusae and Siphonophorae. It is interesting to note that the Anthomedusae are weakly supported as a subgroup, since one of the putative autapomorphies (perradial mesenteries in the medusa [Petersen, 1990]) is not accepted by some authors (e.g., it is not cited in Schuchert, 1996), and the other (arrangement of the polypoid tentacles in more than one whorl) is reversed in several groups of Anthomedusae. The uncertainty associated with these two characters leaves open the question whether or not the siphonophores are a group belonging within the Anthomedusae (raised by Schuchert, 1996 and also P. Schuchert, pers. comm.). This possibility could be verified in a more detailed analysis in which the subgroups of Anthomedusae would be included, thus probing for anthomedusan paraphyly. Nevertheless, all of the above hypotheses (Petersen, 1979, 1990; Schuchert, 1996; Marques, 1997) cast serious doubt on the validity of the taxon Hydroidomedusae as a phylo-

genetically-based clade. Furthermore, if we take into account a completely different database, such as molecular 18S rDNA sequences, phylogenetic analysis (using both parsimony and maximum likelihood) still corroborates the association of Leptomedusae, Anthomedusae and Siphonophorae (cf. Collins, 2000).

Conclusion

The state of the art as regards hydrozoan phylogeny casts doubt on any use of a taxon Hydroidomedusae. Systematists are surely far from an acceptable and comprehensive phylogenetic hypothesis concerning the Hydrozoa, and to propose such is not the purpose of this contribution. However, it seems likely that present knowledge can offer clear and testable alternatives to the proposed clades within the class. I would submit that it is unnecessary and counterproductive to change the classification or introduce new names for hydrozoan taxa before any broader phylogenetic analysis is accomplished. All current classifications are very subjective.

In order to respect the traditional or historical groups, as well as retain the principle of monophyly of each group, a more rational classification for the Hydrozoa would be the simple acceptance of all known subgroups. This would require that we restrain ourselves from proposing nested, inclusive hierarchies within the class – effectively maintaining a polytomy for subgroups with Hydrozoa. This polytomy can then be resolved when researchers start to discover and/or choose other characters within the frame of comprehensive analyses and thus produce consistent hypotheses rather than of a miscellany of names. Thus, the class Hydrozoa would include eight subclasses, keeping the names proposed by Bouillon et al. (1992), simplifying the use of some of them and avoiding other cumbersome combinations (Cornelius, 1990). These eight subclasses are: Actinulidae, Anthomedusae (orders Capitata & Filifera), Laingiomedusae, Leptomedusae (orders Conica and Proboscoida), Limnomedusae, Narcomedusae, Siphonophorae (orders Calycophorae, Cystonectae, Physonectae), and Trachymedusae.

Acknowledgements

I wish to acknowledge the help of Dr. A.E. Migotto, Dr. F.L. da Silveira (Universidade de São Paulo, São Paulo), Dr. H. Ferrarezzi (Instituto Butantan, São Paulo), Dr. P.F.S. Cornelius (The Natural History Museum, London), Dr. Alan Kohn, Dr. Claudia Mills (University of Washington), and Dr. Phil Pugh (Southampton Oceanography Centre, Southampton) for their critique of previous versions of the text. Also, the discussions during the Fourth Workshop of the Hydrozoan Society in Bodega Bay, California were very important in the development of this contribution, especially the inspired talks by Dr. A. Collins, Dr. D. Bridge, and Dr. P. Schuchert (the latter not at the Bodega meeting). Mr. F. Boero and Dr. J. Bouillon made criticisms to the manuscript, although they vehemently disagree with most of what is offered here. This study was supported by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo), process numbers 93/3578-8, 96/10544-0, and 97/04572-4.

References

Boero F, Bouillon J, Piraino S. 1996. Classification and phylogeny in the Hydroidomedusae (Hydrozoa, Cnidaria). *Sci. Mar.* **60:** 17-33.

Bouillon J. 1981. Origine et phylogénèse des cnidaires et des hydropolypes-hydroméduses. *Annls. Soc. R. Zool. Belg.* **111:** 45-56.

Bouillon J. 1985. Essai de classification des hydropolypes-hydroméduses (Hydrozoa- Cnidaria). *Indo-Malayan Zool.* **2:** 29-243.

Bouillon J, Boero F, Cicogna F, Gili JM, Hughes RG. 1992. Non-siphonophoran Hydrozoa: what are we talking about ? *Sci. Mar.* **56:** 279-284.

Brinckmann-Voss A, Arai MN. 1998. Further notes on Leptolida (Hydrozoa: Cnidaria) from Canadian Pacific waters. *Zool. Verh.* **323:** 37-68.

Claus C. 1877a. *Grundzüge der Zoologie. I.* 53-86 (Hessen, Marburg).

Claus C. 1877b. Studien über Polypen und Quallen der Adria. *Denkschr. Akad. Wiss. Wien.* **38:** 1-64.

Collins, AG. 2000. Towards understanding the phylogenetic history of Hydrozoa: hypothesis testing with 18S gene sequence data. *Sci. Mar.* **64:** 5-22.

Cornelius PFS. 1990. Evolution in leptolid life-cycles (Cnidaria: Hydroida). *J. Nat. Hist.* **24:** 579-594.

Cornelius PFS. 1995. North-west European thecate hydroids and their medusae. *Synopses of the British Fauna (new series),* London: Linnean Society .

Darwin CR. 1859. *On the origin of species.* A facsimile of the first edition (1859) with introduction by Ernst Mayr (1966). Cambridge: Harvard University Press

Hennig W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik.* Berlin: Deutscher Zentralverlag.

Hennig W. 1966. *Phylogenetic systematics.* Urbana: University of Illinois Press.

Hull DL. 1964. Consistency and monophyly. *Syst. Zool.* **13:** 1-11.

Hull DL. 1988. *Science as a process*. Chicago: University of Chicago Press.

Kirkpatrick PA, Pugh PR. 1984. Siphonophores and velellids, *Synopses of the British Fauna (new series)*. London: Linnean Society.

Mackie GO, Pugh PR, Purcell JE. 1987. Siphonophore biology. *Adv. Mar. Biol.* **24:** 97-262.

Marques AC. 1996. A critical analysis of a cladistic study of the genus *Eudendrium* (Cnidaria: Hydrozoa), with some comments on the family Eudendriidae. *J. Comp. Biol.* **1:** 153-162.

Marques AC. 1997. Evolução basal nos Metazoa, com ênfase nas relações entre os Cnidaria. PhD Thesis. São Paulo: Universidade de São Paulo.

Marques AC, Migotto AE. 2000. Cladistic analysis and new classification of the family Tubulariidae (Hydrozoa, Anthomedusae). *Pap. Av. Zool.* **41**(25): 465-488.

Mayr E, Ashlock PD. 1991. *Principles of Systematic Zoology*. 2nd edition. Singapore: McGraw-Hill.

Pagès F, Gili JM. 1992. Siphonophores (Cnidaria, Hydrozoa) of the Benguela current (southeastern Atlantic). *Sci. Mar.* **56**(supl.1): 65-112.

Pagès F, Gili JM, Bouillon J. 1992. Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela current (southeastern Atlantic). *Sci. Mar.* **56**(supl.1): 1-64.

Peña Cantero AL, Marques AC. 1999. Phylogenetic analysis of the Antarctic genus *Oswaldella* Stechow, 1919 (Hydrozoa, Leptomedusae, Kirchenpaueriidae). *Contr. Zool.* **68:** 83-93.

Petersen KW. 1979. Development of coloniality in Hydrozoa, in: Larwood G, Rosen BR. eds. *Biology and Systematics of Colonial Organisms*. London: Academic Press, 105-139.

Petersen KW. 1990. Evolution and taxonomy in capitate hydroids and medusae. *Zool. J. Linnean Soc.* **100:** 101-231.

Platnick NI. 1979. Philosophy and the transformation of cladistics. *Syst. Zool.* **28:** 537-546.

Schuchert P. 1996. The marine fauna of New Zealand: athecate hydroids and their medusae. *New Zealand Oceanographic Institute Memoir* **106:**1–159.

Schuchert P. 1998. How many hydrozoan species are there? *Zool. Verh.* **323:** 209-219.

Vervoort W. 1995. Bibliography of Leptolida (non-Siphonophoran Hydrozoa, Cnidaria). Works published after 1910. *Zool. Verh.* **301:** 1-432.

Final draft received: 6 September 2001