

Non-Siphonophoran Hydrozoa: what are we talking about?*

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SUMMARY: The history of nomenclature of non-siphonophoran Hydrozoa is reviewed, showing the existence of many available names. The name Hydroidomedusae CLAUS 1877 is here chosen as appropriate for non-siphonophoran hydrozoans. Different names for the orders are also available, according to the considered stage (hydroid or medusae). To avoid compound names, the medusa-based names are chosen as valid because the medusa is considered to represent the adult stage. The orders of Hydroidomedusae, thus are: Actinulidae, Anthomedusae, Laingiomedusae, Leptomedusae, Limnomedusae, Narcomedusae, Trachymedusae.

Key words: Non-siphonophoran Hydrozoa, nomenclature, historical review.

INTRODUCTION

The systematics and nomenclature of non-siphonophoran hydrozoans is complicated and confused, reflecting the specialization of most researchers on only one of the two different morphological entities, polyps or medusae. Hydroids and medusae of the same species have been given different generic and specific names, but the International Code of Zoological Nomenclature Law of Priority can, in each case, be used to resolve this confusion. Sometimes the hydroid name has priority, and sometimes the medusa. However, the Law of Priority does not extend to taxa above family level and there is no agreed term for the non-siphonophoran Hydrozoa, nor any formal way of agreeing a term. Similarly at the level of the order there is unresolved confusion concerning

organisms of the same species which might be classified as either order Athecata (Gymnoblastera), if a hydroid, or order Anthomedusae, if a medusa. The same applies to the hydroids of the Thecata (Calypthoblastea) and their medusae which are Leptomedusae. (Since medusae are produced asexually the same genotype can be classified differently by the use of two different schemes). In spite of the efforts of some authors (NAUMOV, 1969; BRINCKMANN-VOSS, 1970; BOUILLON, 1985; PETERSEN, 1990) many researchers still restricted their attention to either polyps or medusae and the differences in terminology continue. The aims of this contribution are to present reasoned recommendations to attempt to resolve these terminological confusions.

There are two opposing views on the evolution of the Hydrozoa, the medusan theory derived from the work of BOHM (1878) and BROOKS (1886) (see BOUILLON, 1981 for a review), and the polypoid theo-

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ry (see REES, 1966). Under the medusan theory the polyps represent a prolonged and budding larval stage between the planula and the medusa. This concept was suggested by CLAUS (1881) and has been expressed by many authors subsequently. The alternative view is that the polyp stage is ancestral and the medusae evolved as short lived carriers of the gonads (HUXLEY, 1856). The majority of authors reject expressions such as "alternation of generations" and "metagenic cycles" because the development of hydro-polyps-hydromedusae is regarded as a continuous ontogenetic process from the egg to the adult medusa stage. BOERO and BOUILLON (1987) suggest that hydroids with fixed gonophores, in which medusan development is arrested by precocious sexual differentiation, represent a more highly organized larval stage. The planula¹ larva is a stage derived from the formation of the germ layer (that is by the first arrangement of the primary layers forming the organism), thus corresponding embryologically to a gastrula.

What to call non-siponophoran hydrozoans

At present no common name is **universally** accepted to define the group of hydro-polyps and hydromedusae. The terminology used to define the group is rich and confused.

The following is an *incomplete* list of names² which can be found in the literature:

Cryptocarpae: ESCHSCHOLTZ, 1829.

Gymnophthalmata: FORBES, 1848 (MCCRADY, 1858, in much a wider sense).

Hydromedusida KÖLLIKER, 1833.

Craspedotae³: GEGENBAUR, 1856 (HAECKEL, 1877, 1879; VANHÖFFEN, 1912, 1913; HARTLAUB, 1907-1917; KRAMP, 1933; BRIEN, 1963).

Hydrophorae: HUXLEY, 1856 (DELAGE and HEROUARD, 1901).

Hydroidea (including Trachymedusae, placing Narcomedusae into the Discophora) AGASSIZ, 1862 (ALLMAN, 1871; PERRIER, 1893; CLAUS and GROBBEN, 1910; NAUMOV, 1969; TARDENT, 1978; WERNER, 1984; etc. This term is used with a variable meaning, often differing from the original meaning given by Agassiz: for instance Actinulidae, Laingiomedusae, Narcomedusae and Trachymedusae are often excluded).

¹ The term "planula" was created by DALYELL (1847-1848) and is the result of the erroneous comparison of this stage of hydrozoan development to a *Planaria* (see ALLMAN 1871, p. 88).

² Some of these expressions sometimes cover larger or, rarely, more restricted groups the Hydro-polyps-Hydromedusae *sensu stricto*.

³ Used in general for medusae only.

Hydromedusae: VOGT, 1851 (CARUS, 1863, 1868-1875; HAECKEL, 1866; GEGENBAUR, 1859, 1878; ZITTEL, 1876, 1910; SICARD, 1883; WEISSMANN, 1883; CLAUS, 1880, 1844, 1891-1892; VOGT and YOUNG, 1888; CHUN, 1889-1902; NEUMAYER, 1889; R. HERTWIG, 1891; LANKESTER, 1891; LANG, 1893; SHIPLEY, 1893; PERRIER, 1894; GIARD, 1895; SEDGWICK, 1898; FOWLER, 1900; KÜHN, 1910; A. HERTWIG, 1919; BOERO and BOUILLON, 1987; etc.).

Hydramedusae-Polypomedusae: CLAUS, 1868.

Hydromedusae-Polypomedusae: CLAUS, 1880-1882.

Hydroidmedusen: CLAUS, 1877a.

Cycloneura: EIMER, 1878.

Aphacellae: HAECKEL, 1879.

Ectocarpus: O. and R. HERWIG, 1879.

Polypomedusae: LENDENFELD, 1884 (SICARD, 1883; CLAUS, 1884, 1892; GIARD, 1895; LAMEERE, 1938).

Hydroidea-Trachylina: BROCH, 1923-1925 (WERNER, 1984).

Hydropolypes-Hydromedusae: (see BOUILLON 1981, 1985, 1992).

Most of the authors of recent general textbooks avoid a general term, dividing the Hydrozoa into different orders or subclasses. HYMAN (1940), for instance, divided the Hydrozoa into five orders, Hydroidea (Gymnoblastera and Calyptoblastera), Milneporina, Stylasterina, Trachylina (Trachymedusae and Narcomedusae), and Siphonophora. Different variations but on the same theme were given by: BORRA-DAILE *et al.* (1959); WERNER (1965); REES (1966); HICKMAN (1967); WILMOTH (1967); BRINCKMANN-VOSS (1970); MILLARD (1975); TARDENT (1978); BARNES (1980); BRUSCA and BRUSCA (1990), etc. This above list illustrates the lack of consistency which highlights the necessity for an adequate name for this group of organisms. The most widely used terms are Craspedota (for medusae only), Hydroidea, and Hydromedusae.

The name "Hydroidea" is not satisfactory since, as originally defined (AGASSIZ, 1862) it excludes the Narcomedusae and for many authors if used in isolation it might be confused with "hydroids" alone (CORNELIUS, 1990). BOERO and BOUILLON (1987) proposed that the term "hydromedusae" was to be used as a general name for this group. This proposal was not new since the term "hydromedusae" has often been used to include hydroid polyps and hydromedusae by many authors. For instance, LANKESTER (1891, 1900) divided the Hydrozoa into two classes: Hydromedusae and Scyphomedusae. At that time the Hydromedusae already included several of the sub-groups accepted at present:

1. Gymnoblaster - Anthomedusae
2. Calyptoblastea - Leptomedusae
3. Trachymedusae
4. Narcomedusae
5. Hydrocorallinae
6. Siphonophorae

HERTWIG (1891) divided the Hydrozoa into two subclasses: Hydromedusen and Scyphomedusen. The "Hydromedusen" included six orders:

1. Hydrarien
2. Hydrocorallinen
3. Tubularien-Anthomedusen
4. Campanularien-Leptomedusen
5. Trachymedusen
6. Siphonophoren

BOERO and BOUILLON (1987) acknowledged that the term "hydromedusae", is not favoured by specialists of hydropolyps and presents some inconsistencies. For example it could lead people to talk about the polyps of hydromedusae or to refer to species with no medusa in the life cycle. In addition "hydromedusa" and "medusa" are often used as synonyms.

CORNELIUS (1990), trying to ease the problem, proposed re-introducing the term "leptolids", but without defining his concept of the term and its limits. This name was introduced by HAECKEL (1877, 1879) and as originally defined included only the Anthomedusae and the Leptomedusae (for definition of these terms see below), Haeckel proposed "Trachylinae" to include Narcomedusae and Trachymedusae. Thus, by definition, the distinction between Leptolinae and Trachylinae is *essentially* based on the embryological origin of the statocysts, these being *exclusively ectodermal* in the Leptolinae (when present), and *ecto-endodermal* in the Trachylinae. In addition, according to HAECKEL (1879) most Leptolinae have an "alternance of generations", a feature not shared by most Trachylinae.

The embryological origin of the statocysts still remains the essential criterion to separate the Leptomedusae from all other hydromedusae with statocysts.

The term "leptolid" has not been widely used. DELAGE and HEROUARD (1901) used it in the sense of HAECKEL, but added the Hydrida (*Hydra*, *Protohydra*, *Microhydra*, etc.). PARKER and HASWELL (1910) mentioned it in their "Textbook of Zoology". KRAMP (1932) cited the Leptolina in the introduction of his revision of the Mitrocomidae, in the conclusions of his paper on the alternance of generations

(KRAMP, 1943) and in the zoogeographical section of his work on the systematics of the medusae of the Atlantic Ocean and adjacent waters (KRAMP, 1959)⁴. Surprisingly, KRAMP (1943, 1959) included the Limnomedusae into the Leptolidae, contrary to the definitions given by Haeckel that Kramp has accepted in a previous paper (KRAMP, 1932). The Limnomedusae have statocysts of ecto-endodermal origin as have the Trachymedusae and the Narcomedusae and should be placed with them into the Trachylinae.

NAUMOV (1969) used HAECKEL's terms Leptolinae and Trachylinae. He defined them and added the Hydrida for the genera *Protohydra* and *Hydra*. He included the Limnomedusae in the Leptolida, a decision that is incompatible with the definition of the group, and also with that proposed by NAUMOV himself (1969, page 194). MILLARD (1975) in her "Monograph of the Hydroids of South Africa" mentioned the term "Leptolina" as a synonym of Hydroida. For her the Hydroida comprise the Athecata (Gymnoblaster-Anthomedusae), the Thecata (Calyptoblastea-Leptomedusae), the Chondrophora, and even the Limnomedusae. Some authors used Leptolida exclusively in the title of their papers (e.g. THIEL, 1938; POLTEVA and KVADE, 1980).

It is evident that the term "Leptolida" is the cause of some confusion, and as originally defined covers just the Athecatae-Anthomedusae and the Thecatae-Leptomedusae, and while these contain the greatest majority of non-siphonophoran hydrozoans it is an inappropriate term for the whole group. Its re-introduction to include all non-siphonophoran hydrozoans could cause more confusion. Besides a small number of specialists, nobody knows this term, whereas hydroid, medusa, and hydromedusa are in current usage.

The Trachylida, according to HAECKEL's definition, comprise the hydrozoans with statocysts of ecto-endodermal origin, that is the Limnomedusae, the Narcomedusae, the Trachymedusae, and the Actinulidae. In spite of this common feature, the heterogeneity of the members of this group makes the term Trachylida as inadequate as the term Leptolida. The Limnopolypae-Limnomedusae have similar polyp stages and life cycles to those of Athecatae-Anthomedusae and Thecatae-Leptomedusae. The Trachymedusae have direct development which can be condensed (e.g. Geroniidae), or pass through a gastrula (planula) (e.g. Rhopalonematidae). The Actinulidae

⁴ CORNELIUS (1990), discussing the "Leptolids" and citing KRAMP (1943) wrote: "and several earlier authors cited by Kramp, long ago provided a satisfactory term", but we could not trace such literature.

show features, including direct development, associated with specialized characters linked to their interstitial life. Some Narcomedusae have direct development to the medusa, some pass through a polyp stage, in this respect showing a cycle similar to that of Antho-Lepto and Limnomedusae, some have parasitic polypoid larval stages (see BOUILLON, 1987 for a review).

The Narcomedusae are morphologically so different from the other hydromedusae that many authors (e.g. GOETTE, 1907; MAYER, 1910; RUSSELL, 1953) expressed some doubt about their common origin, but the discovery of the Laingiomedusae has resolved this doubt (BOUILLON, 1978, 1985, 1987).

The main difference between the Narcomedusae and all other hydromedusae is inversed polarity of their planulae and their way of budding medusae (see BOUILLON, 1987 for a review). The oral-aboral axis of Narcomedusae is differentiated along the transversal axis of their planulae, rather than along the longitudinal axis, as is the case for the planulae of all other hydropolyps-hydromedusae. The medusae are budded without the formation of an entocodon (or "glockenkern" or "medusary nodule"), a characteristic feature of the budding of all other hydrozoans.

So the two Haeckelian terms "Leptolida" and "Trachylida" are not appropriate and overburden the already complex nomenclature of the hydrozoans. We feel the need to find a single term to group the orders (or sub-classes, according to the authors) at present recognized in non-siphonoporan Hydrozoa, namely:

1. Athecatae-Anthomedusae
2. Thecatae-Leptomedusae
3. Limnopolypae-Limnomedusae
4. Laingipolypae (if a polyp stage exists)-Laingiomedusae
5. Narcopolypae-Narcomedusae
6. Trachymedusae
7. Actinulidae

Compound names such as hydropolyps-hydromedusae, Athecatae-Anthomedusae, etc., have been considered as cumbersome by CORNELIUS (1990); but such expressions have long been used to bridge the "cultural" separation between polyp and medusan specialists.

Our proposal is to divide the class Hydrozoa into two subclasses, the Hydroidomedusae and the Siphonophorae. Hydroidomedusae is the latinized "Hydroidmedusen" of CLAUS (1877b). The names hydro-

polyps (or hydroids) and hydromedusae remain as general terms to refer to the two main stages of Hydroidomedusae, but are here considered as having no formal taxonomic value.

What to call the orders

The use of compound scientific names such as Athecatae-Anthomedusae are not used for any other zoological taxa, and we feel their use is also cumbersome despite the necessity to unify the nomenclature for hydroids and medusae. In this case the use of the name of the adult could be taken as a sound criterion with precedents; thus the name "Trematoda" covers the various larval stages of these parasitic platyhelminths and "Ephemeroptera" refers to the brief adult stage of animals that spend most of their time as larvae. For this reason we propose to divide the subclass Hydroidomedusae into seven orders:

Actinulidae
 Anthomedusae
 Laingiomedusae
 Leptomedusae
 Limnomedusae
 Narcomedusae
 Trachymedusae

The disadvantage of this is that it leads to reference to hydroids with no medusae as, for example, Leptomedusae. But it respects the phylogenetic patterns which lead to species with no medusae via medusa suppression. In recognition of this problem CORNELIUS (1992, page 246 of the present book) proposes new names for Athecatae/Anthomedusae and Thecatae/Leptomedusae (namely Anthoathecatae and Leptothecatae). Many names are already available for these groups and it seems unwise to introduce further names which could further confuse the nomenclature. As a logical consequence of CORNELIUS proposal, furthermore, the other orders of Hydroidomedusae (Laingiomedusae, Limnomedusae and narcomedusae) should bear both hydroid and medusa names, leading to the creation of unnecessary and cumbersome new names again.

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