

Phylogeny and Classification of Hydroidomedusae

THE HYDROZOA: A NEW CLASSIFICATION IN THE LIGHT OF OLD KNOWLEDGE.

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ABSTRACT

The Hydrozoa, on the basis of embryological, developmental and morphological features, are considered as a superclass of the phylum Cnidaria comprising three classes: the Automedusa (with the subclasses: Actinulidae, Narcomedusae and Trachymedusae), characterised by direct development of the planula into a medusa; the Hydroidomedusa (with the subclasses: Anthomedusae, Laingiomedusae, Leptomedusae, Limnomedusae, and Siphonophorae), characterised by a polyp stage budding medusae through a medusary nodule; and the Polypodiozoa, with complex endocellular parasitic life cycles.

KEY WORDS: Cnidaria, Hydrozoa, Automedusa, Hydroidomedusa, Polypodiozoa, life cycles, development, classification, phylogeny

"If you look for new ideas, read old literature!!" Pierre Tardent, 1993.

INTRODUCTION

The high-rank systematics of the Hydrozoa is complicated and confused, being a mosaic of different approaches reflecting the specialisation of taxonomists on single hydrozoan groups and/or morphs. The Actinulidae, Anthomedusae, Laingiomedusae, Leptomedusae, Limnomedusae, Narcomedusae, Siphonophorae, and Trachymedusae are generally recognised as the higher taxa comprised in the Hydrozoa, but specialists often disagree about ranking them as either orders or subclasses (see Cornelius, 1990, 1992, 1995, and Bouillon *et al.*, 1992, for reviews).

The definition of the phylogenetic affinities of these eight taxa, here considered as subclasses, is the main problem in Hydrozoan systematics. Cornelius (1995, p. 67), with the statement "(the) subclasses currently recognised cannot at present be grouped other than an all", considered the Hydrozoa as monophyletic (see Bouillon, 1995; Carré & Carré, 1995, for detailed treatment of the group). Other authors considered them as polyphyletic, but most simply avoided tackling the problem of their affinities.

Haeckel (1879), mainly on the basis of the embryological origin and structure of the statocysts, grouped the Anthomedusae and Leptomedusae in the Leptolinae, and the Trachymedusae and Narcomedusae in the Trachylinae; he did not consider the Siphonophorae. No other general system has been proposed until recent years, when two attempts were made. Cornelius (1990, 1992, 1995) reintroduced the term Leptolida widening its scope "to include all hydroids and hydromedusae regardless of group and or life cycle pattern", and dividing the Hydrozoa into Leptolida and Siphonophora; whereas Bouillon *et al.*, (1992) divided the Hydrozoa into two subclasses, the Hydroidomedusae and the Siphonophora. Leptolida and Hydroidomedusae have identical systematic meaning and comprise the same sub-groups, namely Actinulidae,

Anthomedusae, Laingiomedusae, Leptomedusae, Limnomedusae, Narcomedusae, and Trachymedusae.

Both proposals were made mainly to give a single name to animals that are usually referred to in different ways (i. e., Athecata or Anthomedusae, and Thecata or Leptomedusae) by specialists of either polyps or medusae. Both the Leptolida and the Hydroidomedusae, thus, were not proposed as the result of phylogenetic analyses, and the Siphonophorae were kept separate from the other taxa mostly for convenience (Schuchert, 1996).

We will examine the embryological, developmental and morphological features of each Hydrozoan sub-group to identify key characters allowing the formulation of a phylogenetic hypothesis that will be testable with other tools, such as molecular ones. As stressed in the title, most of the information dealt with is scattered in old literature, and the results are nothing else than the review and re-assembly of often neglected old knowledge.

RESULTS

The medusa-producing Cnidaria (i. e., the subphylum Medusozoa) comprise three universally recognised classes, mainly distinguished by how medusae are formed from polyps. The Scyphozoa produce medusae by strobilation, the Cubozoa by polyp metamorphosis and the Hydrozoa by budding. In the Hydrozoa, however, the Actinulidae, Trachymedusae and Narcomedusae do not include a polyp stage in their life cycles and their planulae transform either directly into medusae or into larval stages that transform into medusae. Medusa production and life cycle patterns in general, thus, occur by different processes in the groups making up the Hydrozoa, allowing to assemble the hydrozoan subclasses into three classes, the Hydrozoa being considered as a superclass.

The Superclass Hydrozoa

Definition: symmetry either tetramerous, polymerous or, exceptionally, biradial; gastrovascular system simple, deprived of stomodeum (pharynx,

actynopharynx), septa, and gastric tentacles; mesoglea acellular; sexes generally separated; gametes, with a few exceptions, ectodermal in origin (endodermal in the Polypodiozoa, Actinulidae, *Boreohydra simplex*, *Pegantha clara*, *Protohydra leuckarti* and *Solmaris flavescens*), ripening usually in the ectoderm and shed directly to the outside, never into the gastrovascular cavity (except *Polypodium?*); medusae with velum (except *Obelia*), a muscular membrane projecting inwards from the umbrellar margin and partially occluding the umbrellar opening; polyps, when present, solitary or, most often, colonial, modular, with interconnected coelenterons, often polymorphic, with chitinous exoskeleton (perisarc), some secreting extensive calcium carbonate exoskeletons (coenosteum); cnidocysts of about 24 types (see Werner 1984, Bouillon, 1985, Bouillon et al, 1988 for a review) generally restricted to the ectoderm, the atrichous isorhiza is the only type of cnidocysts found in all the classes of Hydrozoa; these nematocysts are never very common, but all the classes have some species with them (this type of cnidocyst occurs also in Anthozoa, Cubozoa and Scyphozoa); life cycles involving: 1) direct development of planulae into medusae; 2) indirect development of planulae into either solitary or modular, asexual polyps, generally benthic, generating planktonic, individual, sexual medusae by budding via a medusary nodule; many paedomorphic species exhibiting various degrees of medusa reduction, reduced medusoids generally producing gametes without breaking away from polyp colony; 3) planulae developing into pelagic, swimming or floating, highly polymorphic, integrated colonies composed of several modified types of polyps and reduced medusae (formed via a medusary nodule) attached to a stem; 4) endocellular parasitic (polypoid?) stages producing free-living (medusoid?) tentacled stages.

Remarks:

The Hydrozoa are a wide and heterogeneous group, comprising taxa that share few derived features, namely the velum, absent only in *Obelia* (see Boero *et al.*, 1996 for a detailed treatment of the peculiarities of this medusa and on its possible origin), and the ectodermal gonads. On the basis of the present

revision, the Hydrozoa are a superclass comprising three classes: the Automedusa, the Hydroidomedusa and the Polypodiozoa (Fig. 1).

The Class Automedusa Lameere, 1920 emended

Definition: development direct, either entirely pelagic or meiobenthic, planulae simple, never attaching to the bottom and usually transforming directly into a single young medusa, except in some parasitic forms where the embryonic stages may undergo asexual reproduction; no colonial hydroid stage; subumbrellar cavity and velum formed by an annular fold and by deepening of the oral embryonic ectoderm (Fig. 2, 3, 4); primary marginal tentacles always formed before subumbrellar cavity (Fig. 2, 3, 4) and before gastrovascular system, except in parasitic forms; marginal tentacles without tentacular bulbs; statocysts (= tentaculocysts = lithostyles = sensory clubs) ecto-endodermal, growing out from the circular canal, generally in form of "free sensory clubs", sometimes enclosed in the mesoglea (Geryonidae) or located in the mesoglea and secondarily incompletely or completely enclosed by an ectodermal fold or vesicle (*Rhopalonema*, *Sminthea*), the solid inner endodermal axis of the sensory club forms the lithocytes containing the statolith; the outer ectodermal layer is composed by sensory cells innervated by the upper nerve ring (= exumbrellar nerve ring) and characterised by numerous kinocilia lacking rootlets and surrounded by stereocilia (Fig. 5); asexual reproduction only in "actinuloid" larvae and some adults of Narcomedusae; sexes separated; sex cells generally ripening in ectoderm, each zygote developing into a single medusa, except in some Narcomedusae where the "actinuloid" larvae or polypoid structures issued from the egg may give rise to several medusae by asexual budding.

Remarks:

In spite of the similarity, the subumbrellar cavity and velum of the Automedusa are only analogous to those of the Hydroidomedusa (see below for definition of the class), being formed by a different developmental pattern, not involving the

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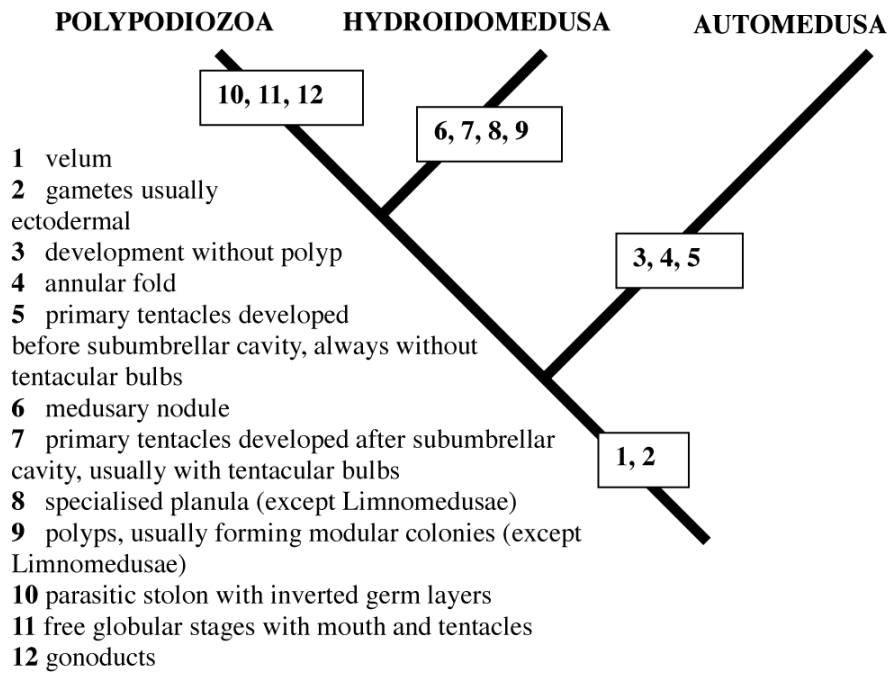


Fig. 1. Phylogeny of the three classes of the superclass Hydrozoa.

formation of a medusary nodule. Asexual reproduction is unknown in both the Actinulidae and the Trachymedusae; it is present only in the Narcomedusae, but without leading to colony formation. Frustules and cysts have never been found in the life cycles of the Automedusae, also chitinous structures of any kind are absent. The fertilised oocytes of the Automedusa give rise by gastrulation to short-lived planulae (= free living gastrulae) which develop into young medusae either directly or through intermediate tentaculated post-embryonic stages inappropriately called "actinulae", as the actinulae of some Anthomedusae. These structures, however, are not homologous since they have different developments: the automedusan actinula has primary medusan features and transforms directly into a medusa, whereas the hydroidomedusan actinula has primary polyp features and transforms into a polyp. The Automedusa planulae have a very simple embryonic didermic cellular organisation lacking the specialised neural and glandular cells characterising most Hydroidomedusa planulae (Figs. 1, 2, 8). The Automedusae have only 9 types of cnidocysts, four of which are not found elsewhere (spiroteles, aspiroteles, atrichous anisorhizae and apotrichous isorhizae) but none is present in the whole class. The number of cnidocysts of the Automedusae (9) is much lower than that of the Hydroidomedusae (21 see below). This might reflect a primitive position of the Automedusa within the Hydrozoa, or might simply be due to the absence of a hydroid stage in their life cycles.

The Automedusa comprise three subclasses: Actinulidae, Narcomedusae and Trachymedusae (Fig. 6 cladogram).

Subclass Actinulidae Swedmark & Teissier, 1959.

Diagnosis: free-living medusae, members of the interstitial fauna of marine sand, solitary, minute (up to 1,5-2 mm); umbrella reduced; manubrium elongated, terminating in a simple mouth; gastrovascular system absent; aboral adhesive ectodermal organ present or not; brood chamber (= subumbrellar cavity, see Salvini-Plawen, 1987; Boero *et al.*, 1998) present or not; sexual cells

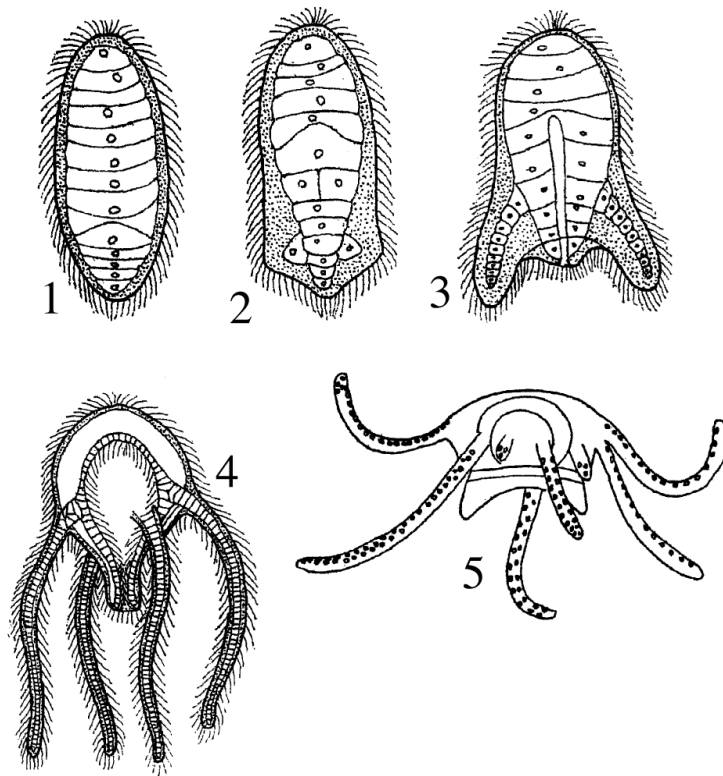


Fig. 2. Early development of *Aglaura hemistoma*, Trachymedusae (after Metschnikoff, 1886).

in the endoderm of the manubrium wall (Ehlers, 1993); tentacles solid, in one or two amphicoronate rings; statocysts open, ecto-endodermal, similar to those of the Limno- Trachy- and Narcomedusae, inserted between adjacent tentacles; there is only one nerve ring, development direct, no classical planula-embryonic stage, the gastrula giving rise immediately to an halhydrula larva; no asexual reproduction. The Actinulidae have a global cnidome of 8 cnidocyst types. Five of them are found also in the other Hydrozoan classes: stenoteles, microbasic mastigophores, atrichous isorhizae, heterotrichous microbasic euryteles, desmonemes. Three are exclusive to the Actinulidae: atrichous anisorhizae, spirotele and aspirotele spironemes, but none of them is common to all species.

Remarks:

The Actinulidae, in spite of their much modified anatomy due to a specialised meiobenthic habit, are close to both Narco- and Trachymedusae, with which they share the structure of statocysts, embryonic development, and the formation of the brood chamber = subumbrellar cavity (see also Salvini-Plawen, 1987) by means of a circular invagination around the manubrium. The Actinulidae are probably the results of paedomorphic processes, recalling the structure of "actinuloid" larvae of other Automedusae (e. g., *Solmundella* larvae).

Subclass Narcomedusae Haeckel, 1879.

Diagnosis: medusae usually flattened, with a central lens-shaped mass of mesoglea and much thinner sides; umbrellar margin lobed, divided by peronial grooves; tentacles solid, inserted on exumbrella at some distance from margin, just above peronial grooves, without tentacular bulbs, with endodermal core in contact with the manubrial endoderm and continuing in the mesoglea of the umbrella as a "root"; sometimes small secondary tentacles on umbrellar margin; manubrium very broad and short, either with even circular periphery or with perradial or interradial peripheral pouches; radial canals generally absent; circular canal absent or looped into the marginal flaps to form a "peripheral canal system"; marginal sense organs in form of free ecto-endodermal statocysts

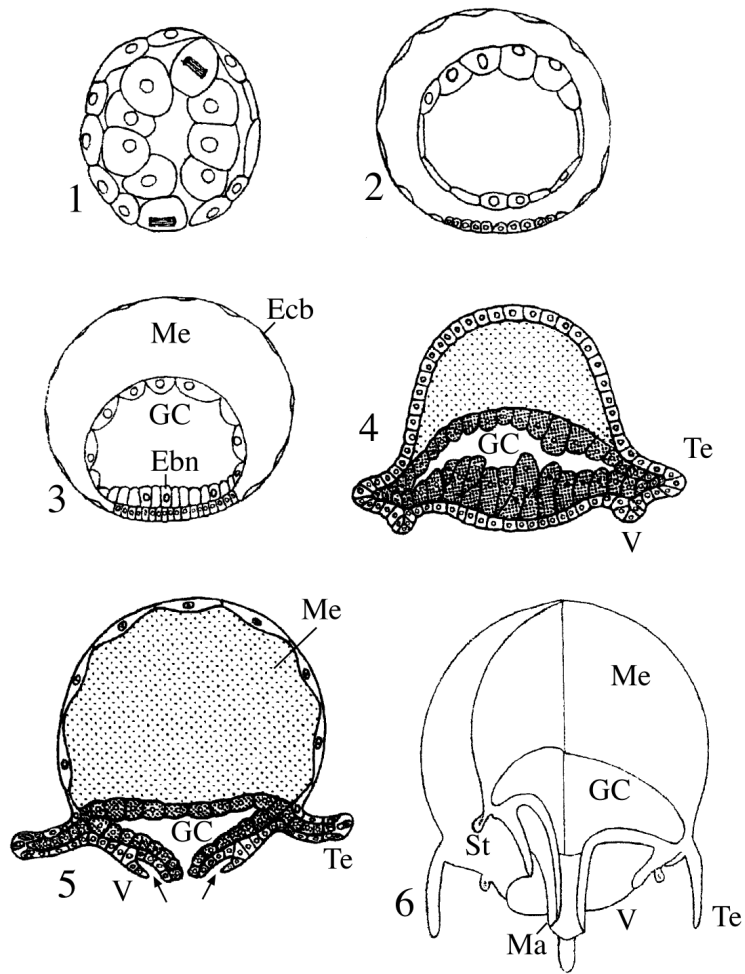


Fig. 3. Early development of *Liriope tetraphylla*, Trachymedusae (1-3, 5 after Metschnikoff, 1886; 4 after Maas, 1905; 6 after Delage & Herouard, 1901). Arrows and asterisk = subumbrellar cavity; Ecb = ectoblast; Ebn = endoblast; GC = gastric cavity; Ma = manubrium; Me = mesoglea; St = statocyst; Te = marginal tentacle; V = velum.

(only one species with enclosed ecto-endodermal statocysts); with or without otoporpa; gonads on manubrium walls and/or on manubrial pouches; development with planula or "pseudo-actinuloid" stages, with longitudinal axis perpendicular to the oral-aboral axis of juvenile and adult stages (Fig. 4); primary tentacles of "pseudo-actinula" always aboral; medusae either with direct development or presenting larvae which parasitise other medusae; larvae giving birth to polypoid structures producing, by successive budding, either juvenile medusae or secondary larvae metamorphosing into juvenile medusae. The Narcomedusae have 2 types of cnidocysts, one (apotranchous isorhizae) not found elsewhere but not present in all the species, and atrichous isorhizae.

Remarks:

During the development of planula or of "pseudo-actinuloid" stages, the mouth is formed in a "lateral" position in respect to the planular longitudinal axis; this axis, thus, is perpendicular to the juvenile and adult oral-aboral axis. In the other subclasses the mouth is formed at one end of the planular longitudinal axis, so that this coincides with the oro-aboral axis (Fig. 4); moreover, the primary tentacles of the "pseudo-actinula" of the Narcomedusae are in one aboral circle, whereas in the actinulae of Anthomedusae they are in two or more circles. Like all other Automedusa, the Narcomedusae have no polyp stage, but some parasitic species have polypoid structures (polypoid stages, stolo-prolifera, see Bouillon, 1987) giving rise to a rapid succession of medusae generations and so representing perhaps the first step to colony formation and modular life. These "polypoid" structures, however, are not homologous to the polyps of the Hydroidomedusa since they metamorphose into medusae and do not produce medusary nodules.

Subclass Trachymedusae Haeckel, 1879

Diagnosis: medusae with hemispherical or deep bell-shaped umbrella; margin entire with a thickened peripheral cnidocyst ring; radial canals and circular

canal present; velum often with heavy musculature; marginal tentacles solid, or both solid and hollow, often with endodermal cores continuing in the mesoglea of the umbrella as short "roots", without true tentacular bulbs; centripetal canals present or not; manubrium with or without peduncle; gonads usually on radial canals; with more than 4 radial canals(except the genus *Liriope* where they are usually only four); true planula stage lacking in some species, the gastrula developing immediately into young medusae (Fig. 2); planula stage retained in other species, giving rise to tentacled stages (actinuloid larvae) before transforming into medusae (Fig. 3); marginal sense organs as free sensory clubs exceptionally enclosed in the mesoglea or in the velum. The Trachymedusae have three type of cnidocysts, none being exclusive to the group, generally stenoteles associated with microbasic euryteles or/and atrichous isorhizae.

Remarks:

No kind of asexual reproduction has ever been observed in the Trachymedusae. Both Trachy- and Narcomedusae are oceanic, mainly represented by deep sea or open sea water species. In spite of their very wide geographical distribution, the Automedusa in general show a very limited generic and specific diversity. They may be considered as the most primitive of the recent Hydrozoa, being the nearest living forms to the hypothetical Hydrozoa ancestors.

The Class Hydroidomedusa Claus, 1877 emended

Definition: fertilised oocytes giving rise by gastrulation to a ciliated, polarised motile gastrula, generally called "planula", usually containing cnidoblasts, different neural and glandular cell types and often-interstitial cells (Fig. 11). Specialised planula developing into a solitary or, more often, modular secondary colonial larval stage either benthic, as the hydroids of most Anthomedusae (except in the Porpitidae, *Pelagohydra* and *Margelopsis* where the polypoid phase is floating) Lepto- and Limnomedusae, or planktonic, as the colonies of the Siphonophorae. Sexual adult stage in form of hydromedusa (Fig.

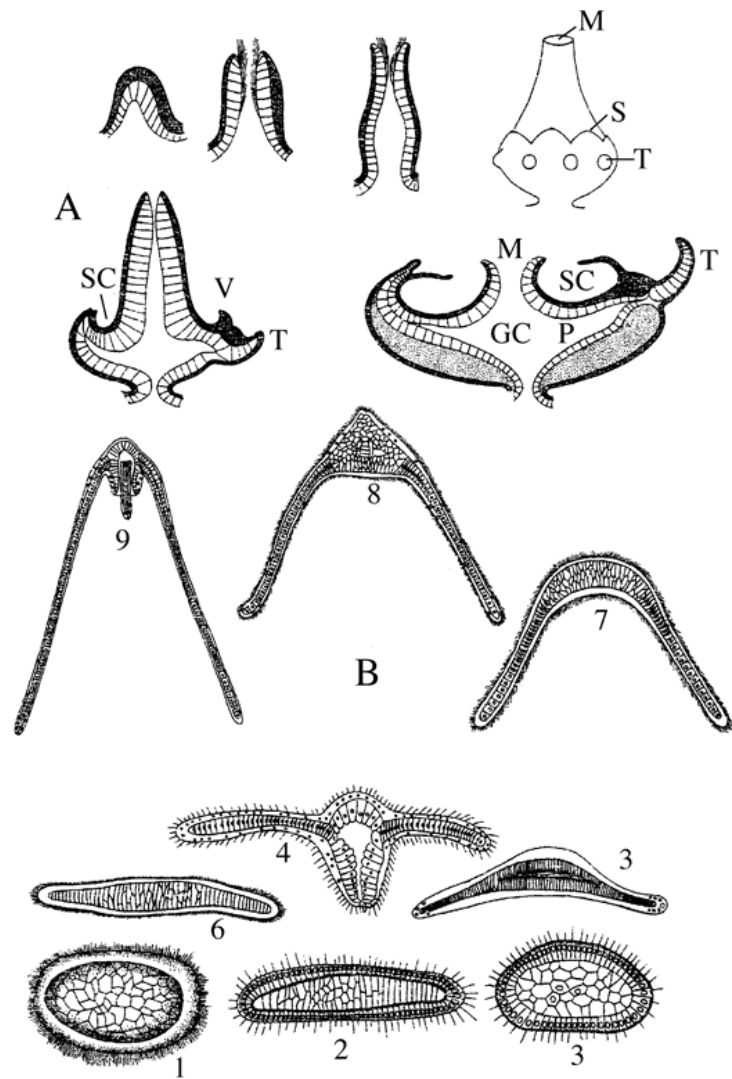


Fig. 4. A. Successive developmental stages of the medusary budding of a stolon prolifer of *Cunina octonaria*, Narcomedusae, parasite of *Liriope tetraphylla*, Trachymedusae (after Chun, 1895 redrawn from Delage & Herouard, 1901). B. 1-4 = early stages of development of *Solmundella bitentaculata*, Narcomedusae , showing the reversal of polarity axes and the

formation of the primary tentacles (after Metschnikoff, 1882, redrawn from Delage & Herouard, 1901); 6-9 = early stages of development of *Solmaris leucostyla*, Narcomedusae, showing the formation of the four primary tentacles and of the manubrium (after Metschnikoff, 1874 redrawn from Bouillon, 1987). GC = gastric cavity; M = mouth; P = manubrial pouch; S = statocyst; SC = subumbrellar cavity; T = tentacle; V = velum.

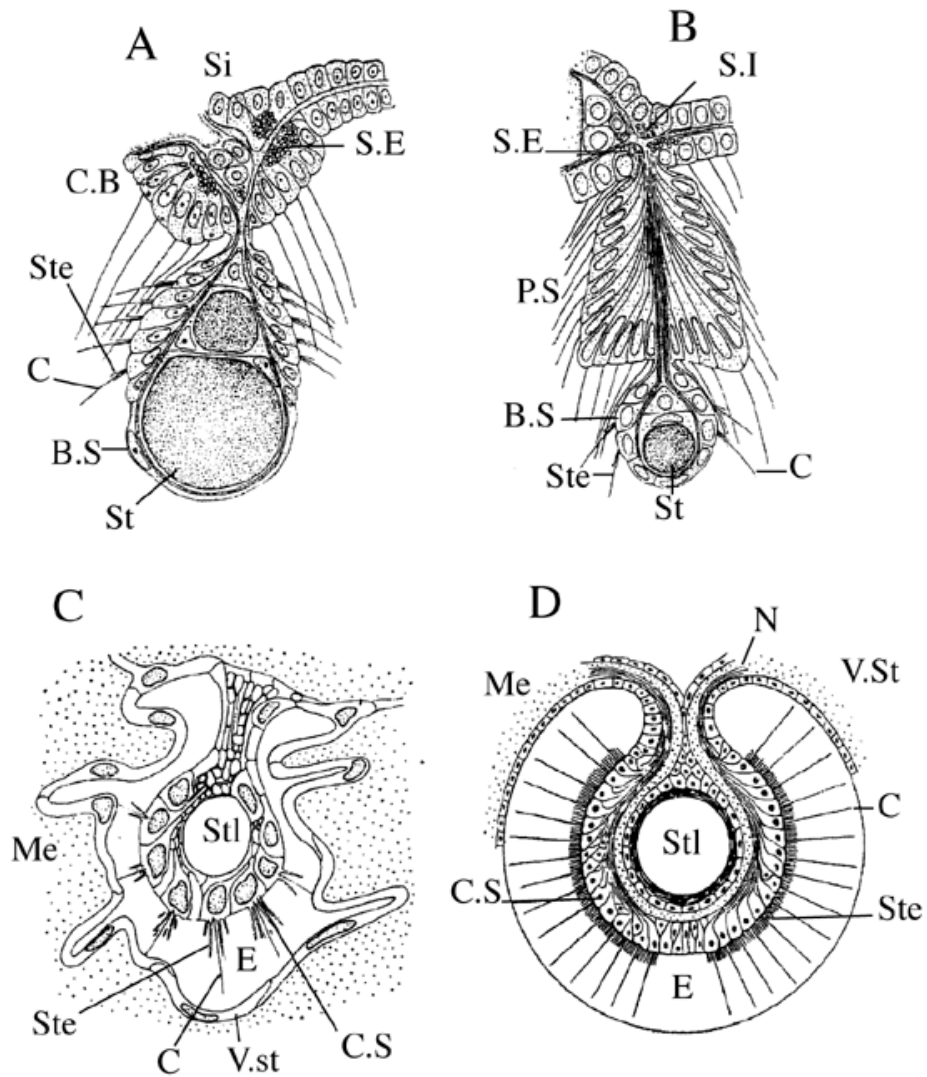


Figure 5. A. Diagram of a radial section of a free ecto-endodermal statocyst of *Aegina citrea*, Narcomedusae. B. Diagram of a radial section of a free ecto-endodermal statocyst of *Solmissus marshalli*, Narcomedusae (A & B after Singla, 1975). C. Diagram of a radial section of an enclosed ecto-endodermal statocysts of *Rhopalonema velatum*, Trachymedusae. D. Diagram of a

radial section of an enclosed ecto-endodermal statocyst of *Geryonia proboscidalis*, Trachymedusae. (C & D after Horridge, 1969). B.S = sensory club; C = kinocilium; C.B = basal cushion; C.S = sensory epithelium; E = seawater; Me = mesoglea; N = nerves; P.S = sensorial papilla; S.E = exumbrellar or external nerve ring; S.I = subumbrellar or internal nerve ring; St = concretion of the statolith; Ste = stereocilia; Stl = statolith; V.St = enclosing vesicle of the statocyst.

7), free swimming, planktonic and solitary, produced by the secondary larvae by asexual budding always involving the formation of a medusary nodule, or entocodon, with a coelom-like cavity, the subumbrellar cavity, lined by striated muscle cells; subumbrellar cavity and gastro-vascular system always developing before primary marginal tentacles (Fig. 8). Both embryonic and larval stages (i. e., planula and polyp) diploblastic; sexual, adult medusa stages acquiring a kind of "triploblastic" organisation during embryonic development. In the Siphonophorae, and in many representatives of the other subclasses (besides poorly known Laingiomedusae), medusae reduced to fixed gonophores no longer leaving the colonies which, thus, become the adult sexual stages by paedomorphosis; hydroids sometimes solitary, but generally forming modular colonies by budding, usually covered by a chitinous exoskeleton; colonies often made up by individual polyps specialised for different functions, all having an interconnected coelenteron (defensive: dactylozooids, reproductive: gonozooids, nutritive: gastrozooids, etc.); siphonophores forming highly polymorphic pelagic colonies composed of several types of polyps and reduced medusae attached to a stolon supported by floating structures (pneumatophores and nectophores); sexes, with few exceptions, separated; gametes generally ripening in the ectoderm; during the development of the planula into the polyp stage the embryonic neural and cementing glandular cells are destroyed; polyp with reversed polarity axis in respect to planula, the anterior or animal pole of the planula becoming the posterior (aboral) pole of the hydroid stage; medusae with a second inversion of polarity, the upper part of the umbrella (apex) being again the anterior pole of the body and the original polarity of the egg being restored (Werner, 1980). Cnidocysts represented by 21 types (the most diversified cnidome of the Hydrozoa), with 12 types exclusive to the group: merotrichous isorhizae, holotrichous isorhizae, atrichous anisorhizae, homotrichous anisorhizae, heterotrichous anisorhizae, macrobasic mesoteles, macrobasic mastigophores, homotrichous microbasic euryteles, telotrichous, merotrichous and holotrichous macrobasic euryteles, anacrophores; acrophores and birhopaloids found elsewhere in the Hydrozoa.

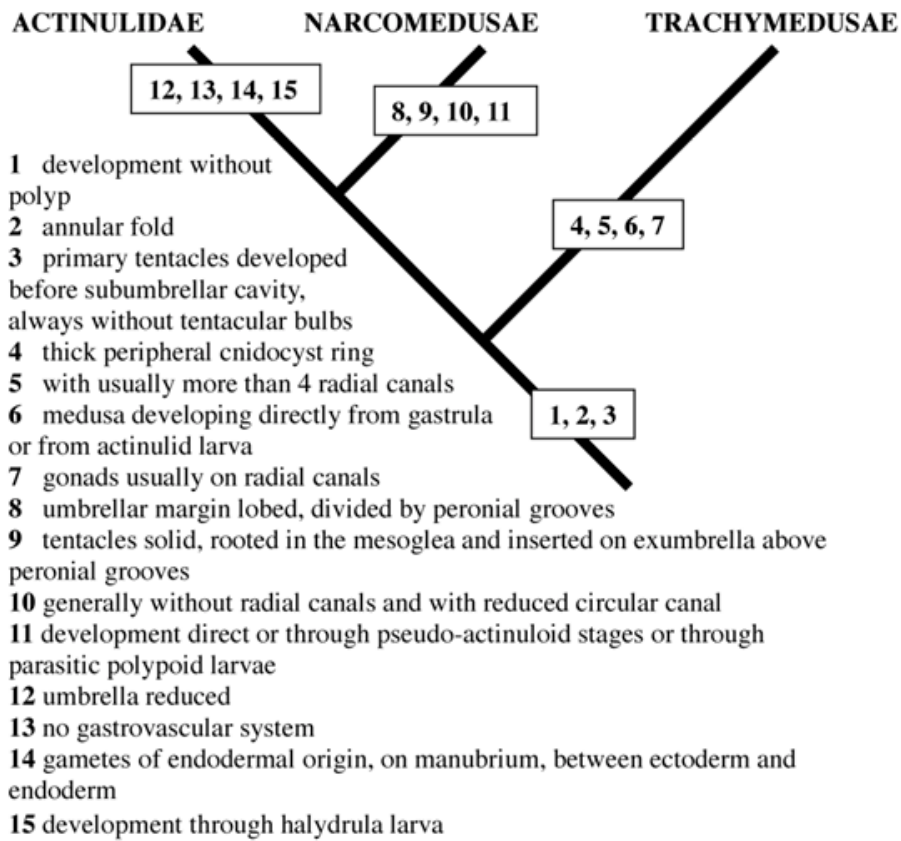


Fig. 6. Phylogeny of the Automedusa.

Remarks:

The sense organs of the medusae, when present, have much different features in the various subclasses. Many Anthomedusae and some Leptomedusae have ocelli; some Leptomedusae have cordyli of unknown function; some Leptomedusae and Limnomedusae have statocysts of two main types: a) closed or open velar ectodermal statocysts formed by either the subumbrellar epithelium or the velar epithelium (Fig. 9) (all Leptomedusae); b) ecto-endodermal closed statocyst located in the mesoglea near the ring canal or in the velum (Limnomedusae). The sensory cells of the velar ectodermal statocysts are innervated by the lower nerve ring (= inner or subumbrellar), the lithocytes and statoliths are ectodermal derivatives and their sensory cells are morphologically distinct from those of the sensory clubs of the Automedusa, lacking stereocilia (Fig. 9).

The ecto-endodermal statocysts of Limnomedusae appear close to the Automedusae statocysts, both being innervated by the upper nerve ring and having their inner axis, lithocytes and statoliths of endodermal origin, but their development is different and their ectodermal sensory cells are devoid of stereocilia, like those of the other Hydroidomedusae. They present in fact intermediate characters between the statocysts of the Leptomedusae and those of the Automedusae. The subclasses comprise mostly marine forms, but some live in brackish- or in fresh-waters, they are present at all latitudes and at all depths. Their occurrence is often seasonal, and they spend the adverse season, or unfavourable ecological conditions in general, with several types of resting or dormancy stages often protected by a chitinous thecae (frustules, propagules, cysts, stolonial system). Such structures are unknown in the Siphonophorae, which, however, are sharply seasonal and should thus possess resting stages to spend unfavourable periods. When known, the number of singlet microtubules of the cnidocil cilium is variable, usually between 6 -10 in Anthomedusae and Limnomedusae except in *Hydra*, with 100 singlet microtubules, and in the Siphonophorae with up to 400-500 singlets.

The Hydroidomedusa comprises five subclasses: Anthomedusae, Laingiomedusae, Leptomedusae, Limnomedusae and Siphonophorae (Fig. 10).

Subclass Anthomedusae Haeckel, 1879.

Diagnosis: medusae typically bell-shaped, with gonads confined on manubrium, sometimes extending on proximal parts of radial canals; marginal sense organs, when present, in form of ocelli; marginal tentacles peripheral, hollow or solid, with tentacular bulbs (except most Bythotiaridae, *Eugotoea petalina* and *Rhabdoon singulare*); sexual reproduction usually leading to planulae or, in some Tubulariidae, actinulae, both stages with several specialised cell types: interstitial cells, cnidoblasts, nerve cells and one or two types of ectodermal glandular cells. In species with encysted planulae (like *Hydra*) generally only interstitial cells and cnidoblast are present, the planulae fixing themselves to the support by their chitinous sheet. Hydroid larval stage athecate and gymnoblastic, i. e. with polyps and gonophores not covered by rigid perisarc; hydroids colonial or solitary; hydranth with one or more whorls of tentacles. Cnidome normally including desmonemes, often stenoteles and microbasic euryteles; the Anthomedusae have 14 types of cnidocysts, 3 of which are exclusive to the group: heterotrichous anisorhizae, homotrichous microbasic euryteles, and macrobasic mesoteles, but none of them is characteristic of all the species.

Remarks:

The Anthomedusae and the Leptomedusae are the most speciose groups of the Hydrozoa. Many species have reduced medusae, which remain attached to the hydroid colonies as fixed gonophores. The taxonomic value of medusa reduction has been discussed by Boero & Bouillon (1987), Cornelius (1990), Petersen (1990), Boero *et al.* (1996), Boero *et al.* (1997). Petersen (1990) convincingly argued that medusa reduction occurred independently in many capitate-anthomedusan clades, so not having any phylogenetic meaning. This view has been then extended to all Anthomedusae and Leptomedusae, the two

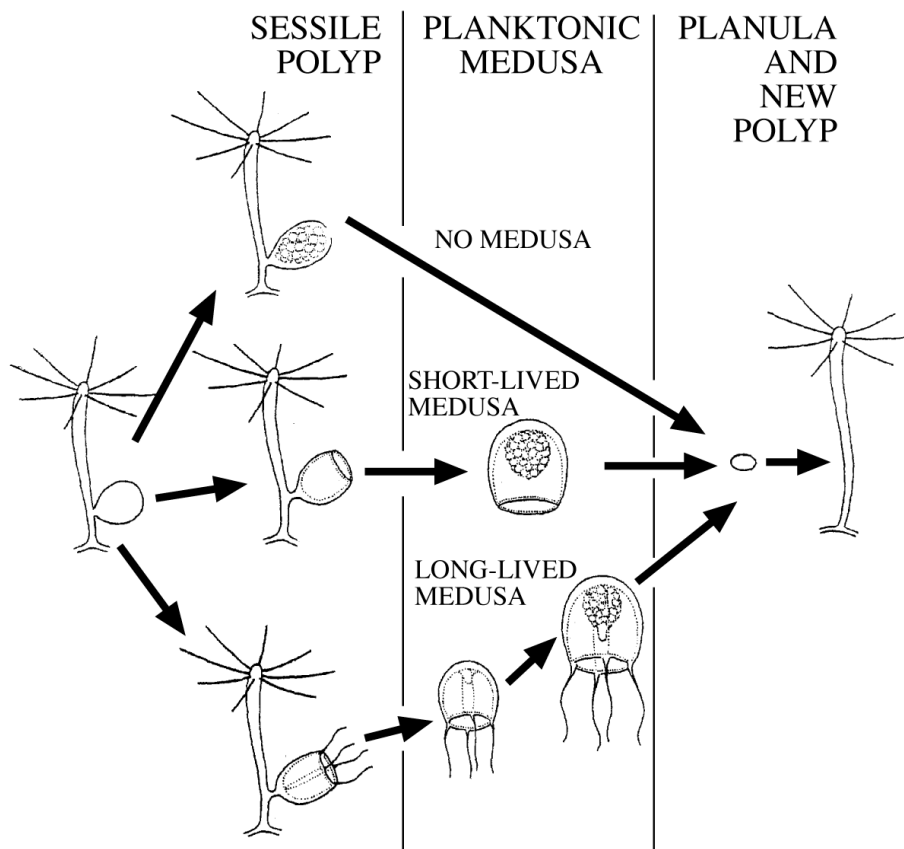


Fig. 7. Simplified diagram of the hydroidomedusan life cycle.

classes with the highest rate of medusa reduction of all Hydrozoa besides Siphonophorae.

Subclass Laingiomedusae Bouillon, 1978

Diagnosis: medusae with almost hemispherical umbrella with lobed margin, i. e. divided by "peronial" grooves or similar structures; four radial canals; no typical circular canal, a solid core of endodermal cells around umbrellar margin; tentacles solid, inserted on the exumbrellar surface above margin; tentacular bulbs sometimes in direct contact with the endodermal circular core; narrow exumbrellar cnidocyst bands or triangular ciliated fields sometimes alternating with tentacles; manubrium simple, either quadrangular, tubular or conical; mouth simple, quadrangular to circular; gonads in four masses on the manubrium or as epidermal lining of interradial pockets of the manubrium; asexual medusa budding, with the formation of a medusary nodule, in two of the four species presently included in the Laingiomedusae, *Kantiella enigmatica* and *Laingia jaumotti*. Cnidome: including macrobasic mastigophores or macrobasic euryteles.

Remarks:

Marginal sense organs apparently absent. Sexual reproduction and life cycle unknown. The presence of a medusary nodule and of marginal tentacular bulbs are characteristic of the Hydroidomedusa, whereas the tentacles inserted on the exumbrella and the absence of a circular canal are typical of the Narcomedusae, so that the Laingiomedusae might be considered as a mosaic of the two groups. The medusary nodule (i. e., the trademark of the Hydroidomedusa) is too a complex and specialised structure to have been originated independently in the Laingiomedusae which, thus, are included in the Hydroidomedusa. However, more information about their life cycle is needed to clarify their phylogenetic affinities. The Laingiomedusae are the smallest group of Hydroidomedusae.

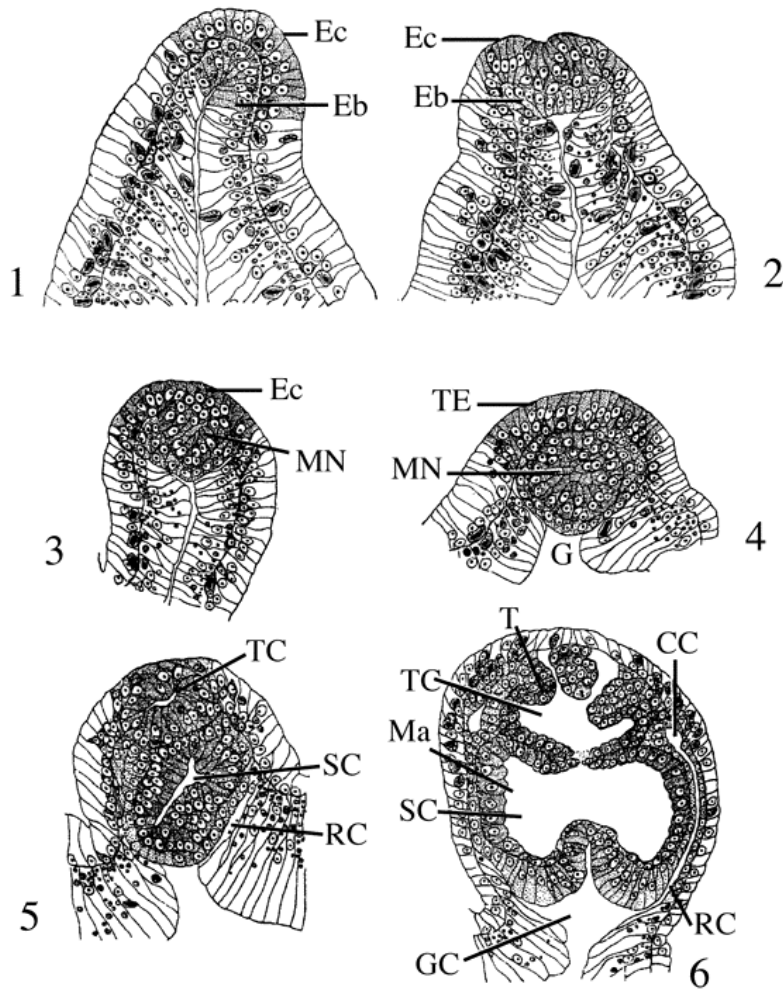


Fig. 8. Organogenesis of the medusa budding in Hydroidomedusae (*Limnocoñida*). 1: Dedifferentiation of the ectoderm and endoderm in ectoblast en endoblast at the beginning the budding processes. 2: ectoblastic proliferation and formation of the endoblastic plate. 3: origin of the medusary nodule and the endodermal cup. 4: growth of the medusary nodule, formation of the ectodermal tentacular plate and origin of the radial canal from the endodermal cup. 5: appearance of the subumbrellar cavity within the medusary nodule, formation of the tentacular cavity within the ectodermal tentacular mass and of the radial canals. 6: almost fully grown medusae, showing

the subumbrellar cavity, the manubrium, the radial canals, the circular canal, the gastric cavity, the velum, and the tentacles. (All after Bouillon, 1957, redrawn from Berrill, 1961). Eb = endoblast; Ec = ectoblast; CC = circular canal; G & GC = gastric cavity of the budding polyp or medusa; Ma = manubrium; MN = medusary nodule; RC = radial canal; SC = subumbrellar cavity; T = tentacular bud; TC = tentacular cavity; TE = tentacular ectodermal plate; V= velum.

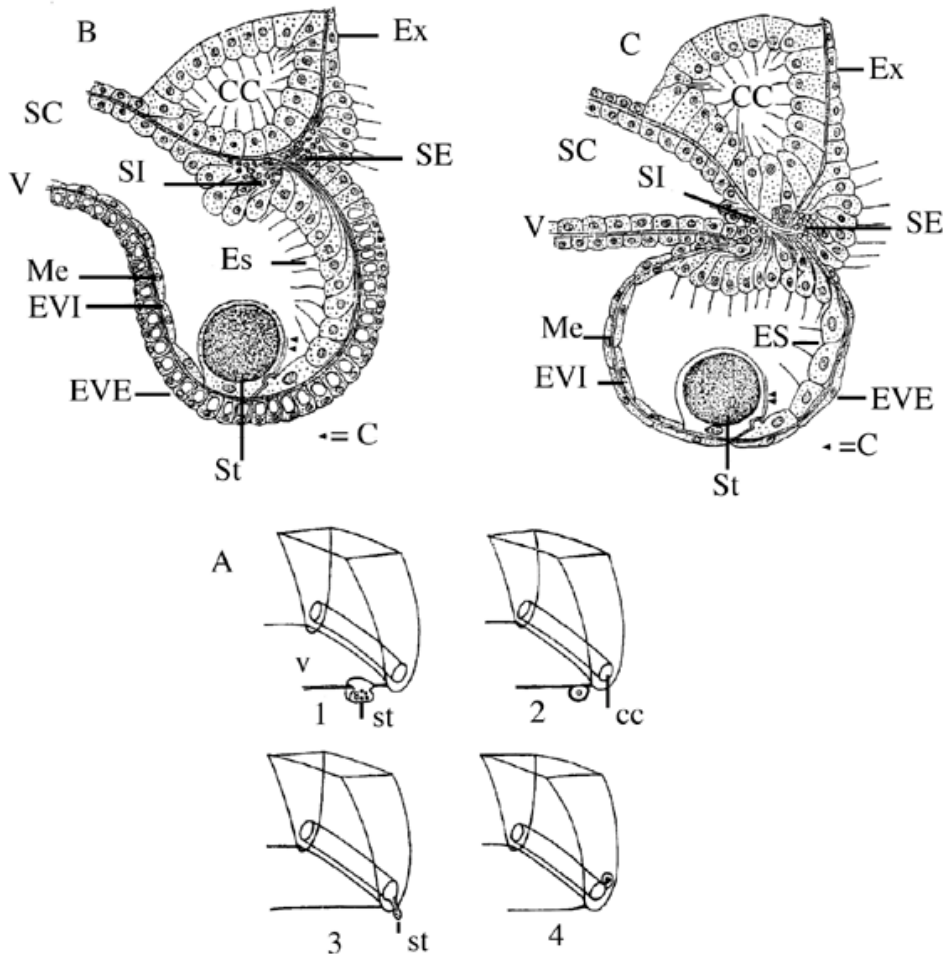


Fig. 9. A. Different types of statocysts. 1- open ectodermal velar statocyst; 2- closed ectodermal velar statocyst; 3- free ecto-endodermal statocyst; 4- enclosed ecto-endodermal statocyst. (c.c = circular canal; st = statocyst; v = velum). B. Diagram of a radial section of an open ectodermal velar statocyst. C. Diagram of a radial section closed ectodermal velar statocyst. C = kinocilium; CC = circular canal; Ex = exumbrella; E.S = sensory epithelium; E.V.E. = external epithelium of the statocyst vesicle; E.V.I. = internal epithelium of the statocyst vesicle; Me = mesoglea; S.C = subumbrellar cavity; S.E = exumbrellar or external nerve ring; S.I = exumbrellar or internal nerve ring; St = concretion of the statolith; V = velum (A. after Russell, 1953; B. and C. after Singla, 1975).

Subclass Leptomedusae Haeckel, 1879

Diagnosis: medusae more flat than bell-shaped, typically with hemispherical or flattened umbrella; gonads confined to radial canals, exceptionally extending on the proximal part of manubrium; marginal sense organs, when present, in form of ectodermal velar statocysts, rarely cordyli, occasionally adaxial ocelli; marginal tentacles peripheral and hollow (except in *Obelia* where they are solid), with tentacular bulbs; sexual reproduction leading to planulae presenting numerous specialised cell types: interstitial cells, cnidoblasts, nerve cells and usually two types of ectodermal glandular cells; hydroid larval stage colonial, thecate and calyptoblastic, i. e. with polyps and gonophores generally protected by rigid perisarc, forming hydrothecae, nematothecae and gonothecae, a few species with naked hydranths and gonophores; tentacles all oral, in one, two or more rows, often amphicoronate. Cnidome: often microbasic mastigophores and merotrichous isorhizae. The Leptomedusae have only a few general types of cnidocysts (5, none being exclusive to the group) in comparison with the Anthomedusae (14) and even with the Actinulidae (8), the Linnomedusae (9) and the Siphonophorae (9).

Remarks:

See the remarks for the Anthomedusae.

Subclass Linnomedusae Kramp, 1938

Diagnosis: medusae with gonads either on manubrium only, or on manubrium and continuing along the radial canals, or on radial canals only; marginal tentacles peripheral, hollow, without true basal bulb, usually with a parenchymatic endodermal core at base, embedded in the umbrellar mesoglea; when present, marginal sense organs internal, in form of enclosed ecto-endodermal statocysts located in the mesoglea, near the ring canal or in the velum; medusae exceptionally reduced to medusoids (*Monobrachium*); planulae

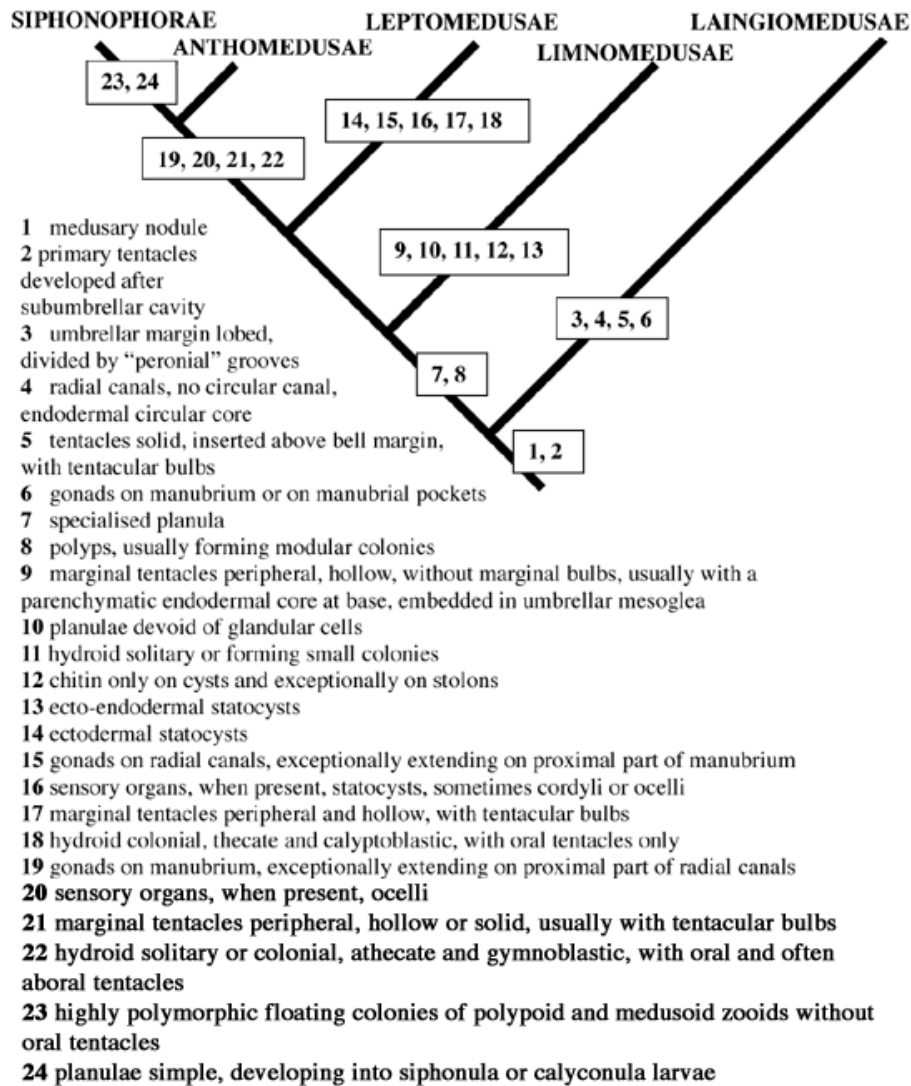


Fig. 10. Phylogeny of the Hydroidomedusa.

with cnidoblasts and interstitial cells but devoid of glandular cells. Hydroid larval stage solitary or colonial, small, sessile, with or without tentacles; often close to planula structure with a clear gradation of forms going from: species without mouth and permanent gastric cavity = feeding planula (Microhydrulidae, *Olindias*), to forms with a hypostome, but without tentacles, forming transitory colonies or definitive colonies with a limited number of individuals (*Craspedacusta*, *Limnocnida*), to solitary or colonial forms with hypostome and with one or more tentacles (*Calpasoma*, *Eperetmus*, *Gonionemus*, *Monobrachium*, *Scolionema*, *Vallentinia*), polyps exceptionally polymorphic (*Monobrachium*). They present usually active asexual reproduction by planula-like structures (frustules) and by chitin covered cysts (except in the stolonial colonies like *Eperetmus* and *Monobrachium*). Some solitary forms (Microhydrulidae, *Olindias*) and the stolonial colonial species are partially protected by a perisarc. The Limnomedusae have 9 types of cnidocysts, only one type is peculiar, the semiophore euryteles existing in one genus of Microhydrulidae: *Rhaptapagis*.

Remarks:

The Limnomedusae are a small group of hydroidomedusa with a dimorphic benthic-pelagic cycle, but the hydroids are small, poorly developed and never form large modular colonies so that medusa production is lower than in the Antho- and Leptomedusae. Many of the present-day Limnomedusae inhabit either fresh- or brackish-waters, their medusae are often of irregular occurrence, whereas their hydroids, and the resting stages they usually produce, are perennial, resisting to prolonged adverse conditions: the cysts of *Craspedacusta* survived 40 years of complete desiccation.

Subclass Siphonophorae Eschscholtz, 1829

Diagnosis: pelagic, swimming, or floating Hydrozoa (except the deep-water, epibenthic Rhodaliidae), forming highly polymorphic modular colonies of

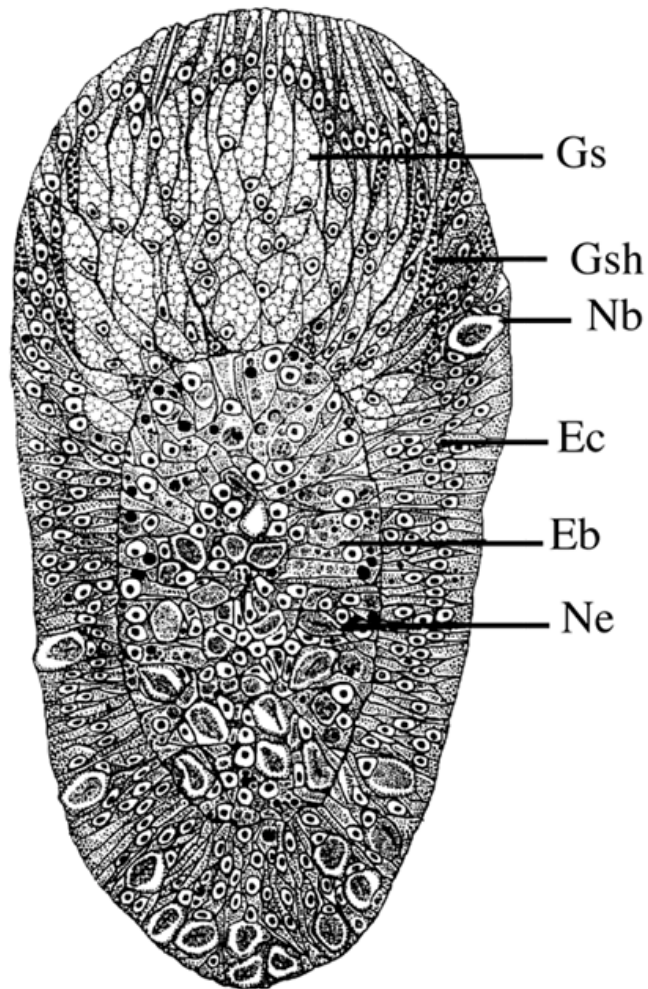


Fig. 11. Histological structure of a hydroidomedusan planula (*Sarsia eximia*) (after Bodo & Bouillon, 1968).Eb = endoblast; Ec = ectoblast ; Gs = spumous glandular cell; Gsh = spherulous glandular cell; Nb = nematoblast; Ne = nematocyst.

polypoid and medusoid zooids attached to a stem or stolon, supported by a floating and swimming system comprising one or several modified medusae; polypoid zooids in form of gastrozooids with a trailing tentacle, dactylozooids, cystozooids (excretion), bracts or aspidozooids and gonophores often associated in repetitive groups or cormidia along the stolon; all without oral tentacles; medusoid zooids of three sorts: pneumatophores, nectophores or swimming bells and sexual medusoids; pneumatophores: inverted and very reduced medusae, without mesoglea, consisting of an exumbrellar wall or pneumatocodon, a subumbrellar wall or air sac and a gas gland; nectophores or swimming bells: less reduced medusae with umbrella, velum, 4 radial canals, a circular canal, 2 nerve rings and striated subumbrellar muscle, without mouth, manubrium, tentacles, and sense organs; cormidia develop successively from the coenosarc of the base of the stolon near the floating system; elaborated visible sense organs like ocelli or statocysts absent; survival of isolated zooids impossible; cormidia of most Calycophora, the real colony units, breaking loose and leading an independent existence, being then termed eudoxia; sexual reproduction by monoecious or dioecious gonophores rarely liberated as eumedusoids; medusa budding with the formation of a medusary nodule; planulae pelagic, without the cellular differentiation typical of the other hydroidomedusa planulae, with a very short lifetime, usually much less than 24 hours, metamorphosing into more specialised pelagic larvae, the siphonula and calyconula, further on developing into the adult sexual form or cormus. The Siphonophorae have a global cnidome of 9 cnidocyst types depending the suborders: acrophores, anacrophores, desmonemes, stenoteles, homotrichous anisorhizae, atrichous isorhizae, microbasic mastigophores and birhopaloids, 4 of them being exclusive to the group: acrophores, anacrophores, homotrichous isorhizae and birhopaloids but non common to all the species. The Cystonectae posses only isorhizae.

Remarks:

The Siphonophorae can be considered as colonies of cormidia, formed by polypoid structures that are so specialised to be assimilated to the organs of an

individual (the colony), they are sometimes considered as nurse carriers, similar to hydroid colonies not coming sexually mature but budding off sexual medusoids which may be released along with other stem constituents (Totton, 1965). The cnidome suggests affinity with the Anthomedusae since desmonemes, typical of this subclass, are present in some groups; also stenoteles are typical of Anthomedusae but are shared also with some Automedusae. The singlet microtubules of the cnidocyst cilium are very high in number, varying from 300 to 400. There is no alternation of benthic and pelagic life, the colonies remaining pelagic and exploiting a single environment all their cycle. Each gonophore has a limited number of eggs (1 in the Physonects, 2 to 20 in the Calycophores), but a cormidium can form successive gonophores increasing so the number of eggs, and the modular colonies, furthermore, are formed by numerous cormidia. Compared to most Antho- and Leptomedusae, whose benthic colonies are long-lived, can undergo a resting phase and produce higher numbers of eggs or medusae, the Siphonophorae have a much lower reproductive rate; this possibly explaining why they are much less successful and have a lower diversity and geographical distribution.

The Class Polypodiozoa Raikova, 1988

Diagnosis: earliest known parasitic stages as binucleate cells occurring in previtellogenetic fish oocytes (Fig. 12); further parasitic development of *Polypodium* in the fish egg may take several years, leading to the formation of a convoluted didermic stolonal structure, with inverted germ layers, growing at the expenses of the fish eggs' yolk and forming numerous inverted buds; germ layers taking their normal position (ectoderm outwards, endoderm inwards) by eversion before liberation, at the spawning of the mature fish; free stolons fragmenting into individual buds giving rise to free creeping globular stages that can multiply by longitudinal fission; globular stages mobile and feeding, with oral mouth-cone and tentacles; specimens usually with 24 tentacles, but in mid summer individuals with 12 tentacles are also common and in late summer specimens with only 6 tentacles may be found; germ cells endodermal, females

with two kinds of "gonads" each with a gonoduct opening in the gastral cavity, males with gonads forming gametophores carrying cnidocysts. The main characteristic features of the Polypodiozoa are: separated epithelial and muscle cells, inversion of germ layers during the period of parasitic life, aberrant meiosis; complex female gonads with gonoducts, position of the cnidocil above the operculum and the adaptation to intracellular parasitism. Cnidome: atrichous isorhiza

Remarks:

This class comprises *Polypodium hydriforme* Ussow, 1885 which, until recently, was the only known metazoan adapted to an intracellular parasitic life, with a cycle involving the succession of a free living stage and of an intracellular parasitic stage of the eggs of some Acipenseridae and Polyodontidae fishes, living in fresh water basins of Russia, Romania, Iran, and North America. It is not known how the parasite gets into the previtellogenic oocytes of young fish. The free-living stage presumably represents the sexual medusae, the parasitic stages being considered as polypoid (Fig. 12).

Siddal *et al.* (1995) provided evidence that the Myxozoa are closely related to *Polypodium*, proposing their demise as a phylum of protists and suggesting their inclusion in the Cnidaria, Hydrozoa. Pending more detailed studies on the life cycles of the ex Myxozoa, we provisionally include them in the Polypodiozoa.

DISCUSSION

The Automedusa appears the most simple and primitive hydrozoan group, with simple holopelagic planulae, transforming directly into young medusae by simple cellular processes.

The main "innovations" in Hydroidomedusa, the main group of the Hydrozoa, are:

1 - the evolution of a benthic post-planular larval stage, the hydroid, primitively simple (Limnomedusae) but becoming colonial, modular and usually protected

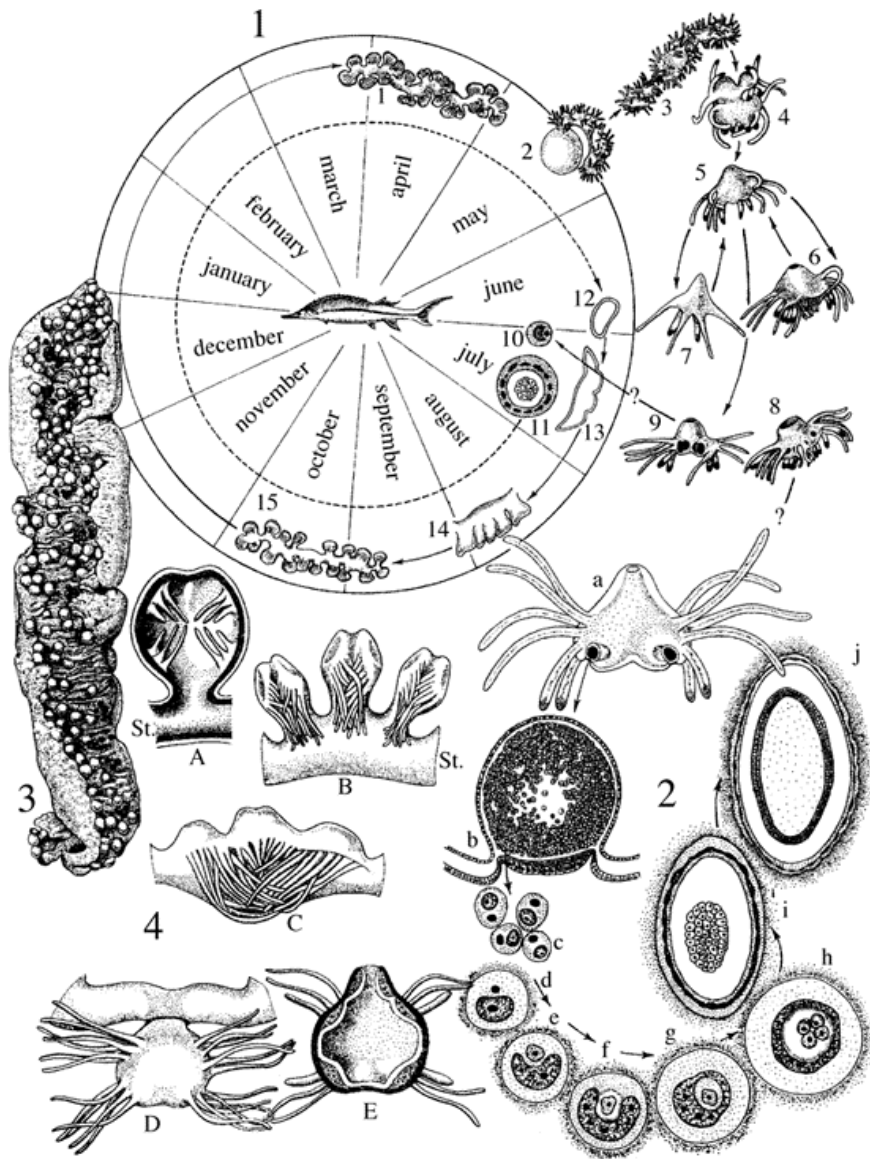


Fig. 12. Life cycle of *Polypodium hydriforme* (Polypodiozoa), internal parasite of Acipenserid fishes (redrawn from Bouillon, 1987). 1. General cycle: 1-reversed stolon prolifer; 2-stolon prolifer living an infected Acipenserid egg; 3- stolon prolifer in the water; 4- fragment of a stolon;

5- polyp with 12 tentacles; 6- polyp with 24 tentacles; 7- polyp with 6 tentacles; 8- female polyp; 9- male polyp; 10-binucleate cell parasite of an Acipenserid oocyte; 11- morula encapsulated in the trophamion 12- planula; 13- budding planula; 14- stolon prolifer without tentacles; 15- stolon prolifer reversed with internal tentacles. 2. Diagram of the formation of the trophamion. a. - sexual medusa; b. - gonad with binucleated cells; c. -binucleated cells; d. to g. - binucleated cells parasite of a fish oocyte; h. - segmentation of the embryo; i. - morula stage inside the trophamion; j. - planula stage inside the trophamion. 3. ovary of an *Acipenser*, the large eggs are parasitised, the small ones are not. 4. A-C reversed buds with internal tentacles on a stolon prolifer (St.); D stolon prolifer with external tentacles; E. medusae liberated from an infected fish egg.

by a chitinous exoskeleton in most species (Antho- Leptomedusae), having as first consequence a structural complication of the planulae; these have only a transitory pelagic life and must develop specialised cells for settlement on the substratum; the Siphonophorae are modular too, but their planulae remain pelagic and so conserve a simple structure, resting at an embryonic cellular level until transformation in post embryonic Calyconula or Siphonula stages;

2 - larval hydroid stages with great possibilities of asexual reproduction, forming buds of different types: polyp budding to increase the size of the colony; medusary or gonophoral budding for sexual reproduction; varied propagules for rapid colonisation of the surrounding environment or of different habitats; resting stages, like cysts, frustules, and stolonial systems allowing not only survival under adverse environmental conditions but also the colonisation of new biota. Asexual reproduction is one of the main features explaining the success of the Hydroidomedusa;

3 - an asexual budding of medusae characterised by a unique formation, the medusary nodule (glockenkern or entocodon), which accelerates and condenses the differentiation of the morphological structures of a medusa; the formation of a medusary nodule is the developmental pattern leading to medusa formation in all the subclasses of Hydroidomedusa: from the budding of medusae from both polyps and medusae (even when the medusary budding is exceptionally only of ectodermal origin), to medusoid formation in the Siphonophorae.

In our opinion, post-planular polypoid larval stages, modularity, apparition of chitin and of medusary nodule are linked and concomitant evolutionary phenomena. They have as main consequences that single zygotes will give rise to modular larvae, forming usually rather large colonies metabolically able to produce a tremendous number of medusae by asexual budding (in some species up to 4.450 in 3 days) each of which will give rise, on its turn, to very large numbers of eggs and, in some species, may even produce new medusae again by budding (see Boero *et al.*, 1992). In paedomorphic groups, furthermore, the hydroid colonies produce a great number of gonophores each emitting a large number of eggs or planulae. The presence of post-planular larvae, the hydroids, with their great possibilities of asexual

budding, leading to a dimorphic life history allowing exploitation of different environments and resources possibly explains why the Hydroidomedusa (and especially Antho- and Leptomedusae) have presently the greatest generic and specific diversity and are the most widespread and successful groups of the Hydrozoa.

The Hydrozoa, like all other Cnidaria, are considered as diploblastic organisms having only a tissue level of organisation, without the true anatomically distinct organs characteristic of the triploblasts. The development of the medusary nodule, however, together with the very elaborated "sense organs", the condensation of the sexual cells, nerve cells and the striated epithelial muscle cells in well defined positions are possibly the premises of a triploblastic organisation. In the many lines of derived paedomorphic Hydroidomedusa, characterised by medusa reduction, in fact, the subumbrellar cavity remains closed, is lined by striated muscle and contains the sexual elements, a condition that much resembles a coelomic cavity. The Hydroidomedusa, thus, could represent a first step, or a first attempt, towards coelomisation. The Cnidaria might so represent a living centre of metazoan radiation, having structures that represent the premises of the main steps of animal evolution (Boero *et al.*, 1998).

The Polypodiozoa are intra-cellular parasites, they are very specialised and modified Hydrozoa having very few characters in common with the members of the other classes. Their stolonial parasitic budding stage and their cnidome might suggest, nevertheless, some affinities with the Narcomedusae to which they were previously associated (Bouillon, 1985).

CONCLUSION

The old debate about "who came first", whether the polyp or the medusa (see Bouillon, 1981), has been possibly resolved by Bridge *et al.* (1992) who provided convincing evidence to identify in the polypoid Anthozoa the most primitive living Cnidaria. The medusa, thus, should be the result of peramorphosis, with further complication of polypoid features. As far as the

Hydrozoa are concerned, however, we are inclined to consider the Automedusa (represented by medusae only) as the nearest group to the ancestral Hydrozoan condition. In the other Medusozoa, namely the Scyphozoa and the Cubozoa, the medusa is the main morph, and the polyp is reduced or even absent, without the sharp tendency towards modularity encountered in many Hydrozoa. In the Cubozoa, in fact, the ratio one polyp-one medusa is the rule, whereas in the Scyphozoa a single polyp can produce many medusae by strobilation, with a stronger tendency towards modularity in the developing medusae (the strobila) than in the polyps (see Werner, 1973, 1980). The radially symmetrical polyp of the Hydroidomedusa is different from the tetramerous polyp of both Scypho- and Cubozoa, and it produces medusae via a medusary nodule, possibly the greatest innovation of the Hydrozoa in respect to the rest of the Medusozoa. As suggested by Boero *et al.* (1992), thus, the ancestral hydrozoan might have been a medusa with direct life cycle (i. e., an Automedusa); the hydropolyp represents a re-introduced polyp stage in a group of Cnidaria in which the polyp had been abolished. The “actinula”, proposed by Rees (1966) as the ancestral cnidarian, is a larval stage of Automedusa and a juvenile polyp of some Hydroidomedusa, the two having nothing in common besides the name and, in the light of the present treatment, representing no ancestral cnidarian state. The ranking of the Hydrozoa as a superclass and the introduction of three classes disrupts traditional treatments of the Cnidaria, although Cornelius (1995) used already the same level of classification. Whatever the formal ranking of the Automedusa, Hydroidomedusa and Polypodiozoa, each has numerous original features and might well represent a phylogenetically sound taxonomic unit. At this level, convenience is often the main reason for taking decisions on how to rank a monophyletic taxon. The Hydrozoa might still be considered as a class, and the Automedusa, Hydroidomedusa and Polypodiozoa as subclasses, but this would require many changes of rank in the elaborate classification set up by Bouillon (1985, 1995). It is more convenient, at this stage, to “push up” the Hydrozoa to the rank of superclass than “push down” a host of lower taxa, from subclasses to superfamilies.

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