## SYNOPSIS OF THE FAMILIES AND GENERA OF THE HYDROMEDUSAE OF THE WORLD, WITH A LIST OF THE WORLDWIDE SPECIES.

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Abstract: This report provides a systematic review of the pelagic Hydrozoa, Siphonophores excluded; diagnoses and keys are given for the different families and genera with a short description of their hydroid stage where known; a list of the world-wide hydromedusae species is established.

Key words: Hydrozoa, Automedusae, Hydroidomedusae, systematics, diagnosis

## A: INTRODUCTION:

The hydromedusae are on the whole one of the best known groups of all the Hydrozoa, three great monographs covering the world-wide described species having been dedicated to them, the first by Haeckel (1879-1880), the second by Mayer (1910) and the last by Kramp (1961). A generic revision has been done by Bouillon, 1985, 1995 and several large surveys covering various

geographical regions have been published in recent times, more particularly, those by Kramp, 1959 the "Atlantic and adjacent waters", 1968 "Pacific and Indian Ocean", Arai and Brinckmann-Voss, 1980 "British Columbia and Puget Sound"; Bouillon, 1999 "South Atlantic"; Bouillon and Barnett, 1999 "New-Zealand"; Boero and Bouillon, 1993 and Bouillon et al, (in preparation) " Mediterranean"; they all largely improved our knowledge about systematics and hydromedusan biodiversity.

The present work is a compilation of all the genera and species of hydromedusae known, built up from literature since Kramp's 1961 synopsis to a few months before publication. Keys and diagnoses are given for the families and genera; where known a brief description is given of the hydroid stage. Such work, although as extensive as possible, can never been considered complete, presenting both errors and omissions and of is course essentially not definitive needing continuous updates. It may nevertheless be a useful tool and assist students of the group.

In all, 1086 hydromedusae species have been recorded from modern literature; 244 of them are however considered either as doubtful species, or as conspecific, or as being insufficiently or improperly described or known only as medusa buds, in consequence 842 hydromedusae species may been estimated as valid. Two hundred sixty two genera of Hydrozoan medusae have been recorded, 41 belong to the Automedusae, 222 to the Hydroidomedusae. Less than half of the 222 Hydroidomedusae genera have one or some species with their cycle known. A great effort has thus to be done by Hydrozoan specialist to study Hydroidomedusae life cycles, the knowledge of which is an essential condition for establishing valid species definition and a sound phylogenetic classification of those animals.

The exclusion of species with no medusa stage is due to an even more complex taxonomic situation than that of the hydromedusae. A host of thecate species, for instance, has been described on the basis of tiny skeletal details that might be simply due to environment-induced variations. Careful revisions are badly needed to "clean" a possible list of all Hydroidomedusae from synonymies.

### **B: OUTLINE CLASSIFICATION:**

Subclass Actinulidae Swedmark and Teissier, 1959 Family Halammohydridae Remane 1927 Family Otohydridae Swedmark and Teissier, 1958 Subclass Anthomedusae Haeckel, 1879 Order Filifera Kühn, 1913 Suborder Margelina Haeckel, 1879 Family Australomedusidae Russell, 1971 Family Bougainvillidae Lütken, 1850 Family Clavidae McCrady, 1859 Family Cytaeididae L. Agassiz, 1862 Family Eucodoniidae Schuchert, 1996 Family Hydractiniidae L. Agassiz, 1862 Family Ptilocodiidae Coward, 1909 Family Rathkeidae Russell, 1953 Family Trichydridae Hincks, 1868 Suborder Pandeida Haeckel, 1879 Family **Bythotiaridae** Maas, 1905. (= Calycopsidae;) Family Niobiidae Petersen, 1979 Family Pandeidae Haeckel, 1879 Family Proboscidactylidae Hand and Hendrickson, 1950 Family Protiaridae, Haeckel 1879 Family Russelliidae Kramp, 1957 Order Capitata Khün, 1913 Suborder Moerisiida Poche, 1914 Family Moerisiidae Poche, 1914 Family Halimedusidae Arai and Brinckmann-Voss, 1980 Family Polyorchidae Agassiz, 1862 Family Urashimeidae Mills 2000 (in press) Suborder Sphaerocorynida Petersen, 1990

Family Hydrocorynidae Rees, 1957 Family Sphaerocorynidae Prévot, 1959 Family Zancleopsidae Bouillon, 1978 Suborder Tubulariida, Fleming, 1828 Family Boeromedusidae Bouillon, 1985 Family Cladonematidae Gegenbaur, 1857 Family Corynidae Johnston, 1836 Family Corymorphidae Allman, 1872 Family Dicyclocorynidae Petersen, 1979 Family Eleutheriidae Russell, 1953 Family Euphysidae Haeckel, 1879 Family Margelopsidae Uchida, 1927 Family Pennariidae McCrady, 1859 Family Tubulariidae Fleming, 1828 Suborder Zancleida Russell, 1953 Family Asyncorynidae Kramp, 1949 Family Cladocorynidae Allman, 1872 Family Porpitidae Goldfuss, 1818 Family Rosalindidae Bouillon, 1985 Family Teissieridae Bouillon, 1974 Family Zancleidae Russell, 1953 Subclass Laingiomedusae Bouillon, 1978 Family Laingiidae Bouillon, 1978 Subclass Leptomedusae Haeckel, 1866 (1879) Order Conica Broch, 1910 Family Aequoreidae Eschscholtz, 1829 Family Aglaopheniidae Marktanner-Turneretscher, 1890 Family Barcinidae Gili, Bouillon, Pagès, Palanques and Puig, 1999 Family Blackfordiidae Bouillon, 1984 Family Cirrholoveniidae Bouillon, 1984 Family Clathrozoidae Hirohito, 1967 Family Dipleurosomatidae Russell, 1953

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Family Eirenidae Haeckel, 1879 Family Haleciidae Hincks, 1868 Family Lafoeidae Hincks, 1868 Family Laodiceidae Agassiz, 1862 Family Lovenellidae Russell, 1953 Family Malagazziidae Bouillon, 1984 Family Melicertidae Agassiz, 1862 Family Mitrocomidae Haeckel, 1879 (part); Torrey, 1909 Family Octocannoidae Bouillon, Seghers and Boero, 1991 Family Orchistomatidae Bouillon, 1984 Family Parateclaiidae Bouillon, Pages and Gili, 2000 Family Phialellidae Russell, 1953 Family Plumulariidae Agassiz, 1862 (Hincks, 1868) Family Sertulariidae Lamouroux, 1812 Family Sugiuridae Bouillon, 1984 Family Teclaiidae Bouillon, Pagès, Gili, Palanques, Puig and Heusner, 1999 Family Tiarannidae Russell, 1940 Family Tiaropsidae Boero, Bouillon and Danovaro, 1987 Order Proboscoida Broch, 1910 Family Campanulariidae Jonhston, 1836 Family Phialucidae Bouillon, 1984 Subclass Limnomedusae Kramp, 1938 Family Armorhydridae Swedmark and Teissier, 1958 Family Olindiidae Haeckel, 1879 Subclass Narcomedusae Haeckel, 1879 Family Aeginidae Gegenbaur, 1857, emend. Maas, 1904 Family Cuninidae Bigelow, 1913 Family Solmarisidae Haeckel, 1879 Subclass Polypodiozoae Raikova, 1988 Family Polypodiidae Poche, 1914 Subclass Siphonophorae Eschscholtz, 1829 not treated here Subclass Trachymedusae Haeckel, 1866 (1879)

Family **Geryoniidae** Eschscholtz, 1829 Family **Halicreatidae** Fewkes, 1886 Family **Petasidae** Haeckel, 1879 Family **Ptychogastriidae** Mayer, 1910 Family **Rhopalonematidae** Russell, 1953

## **C: SIMPLIFIED KEY FOR SUB-CLASSES IDENTIFICATION:**

A- without statocysts:

A1-gonads on manubrium occasionally on manubrium and extending for a short distance along most basal region of radial canals; marginal tentacles solid or hollow, peripheral on exumbrellar rim; exumbrella entire, not divided into lobes; usually with marginal tentacular bulbs; with radial canals and circular canal; sense organs, where present, ocelli; medusa typically bell-shaped; life cycle with hydroid stage: **Anthomedusae**.

A2-gonads exclusively on manubrium; marginal tentacles solid, leaving umbrella some distance above exumbrella margin; with or without marginal tentacular bulbs; with umbrella divided by peronial grooves or similar structures so that umbrellar margin is more or less lobed; with radial canals, but without typical circular canal but a solid core of endodermal cells around umbrellar margin; anatomically visible sense organs apparently missing; umbrella roughly hemispherical; hydroid stage unknown: **Laingiidae**.

B-statocysts, where present, formed exclusively by the velar ectoderm, open or enclosed;

gonads on radial canals, exceptionally contiguous with base of manubrium; marginal tentacles usually hollow, peripheral on exumbrellar rim; with marginal tentacular bulbs; exumbrella entire, not divided into lobes; with radial and

circular canal; sometimes cordyli, rarely ocelli; umbrella usually flattened; life cycle with hydroid stage: **Leptomedusae**.

C-statocysts, where present, as ecto-endodermal statocysts with endodermal axis issued from ring canal:

C1- pelagic hydromedusae:

C1a- gonads only on radial canals; marginal tentacles solid (rarely, Geronyidae, with a mixture of solid and hollow tentacles), tentacles peripheral on exumbrella margin; exumbrella entire, not divided into lobes; with an exumbrellar marginal cnidocyst ring; without marginal tentacular bulbs; with radial canals and circular canal; umbrella tall to hemispherical; usually with free, more rarely enclosed, statocysts usually growing out of umbrella margin; without ocelli; without hydroid stage: **Trachymedusae**.

C1b- gonads only on manubrium or on manubrial pouches; tentacles solid, living exumbrella at some distance above exumbrellar margin; without marginal tentacular bulbs; with scalloped exumbrella margin, divided by peronial grooves; usually without radial canals; circular canal absent or present in form of peripheral system; typically with umbrella flatter than an hemisphere, with a central lens-shaped mass of mesoglea; usually with free statocysts growing out of umbrella margin; without ocelli; without true hydroid stage: **Narcomedusae**.

C1c- gonads either on manubrium or on radial canals; tentacles hollow, peripheral on exumbrellar margin; without marginal tentacular bulbs; exumbrella entire, not divided into lobes; with radial canals and circular canal; with statocysts enclosed, embedded into the mesoglea near ring canal or in the velum; without ocelli; life cycle with hydroid stage: **Limnomedusae**.

C2-present as free living, solitary, minute hydrozoa members of the interstitial fauna of marine sand, recalling more or less the structure of actinula larvae;

without or with reduced umbrella; with elongated manubrium terminating in a simple mouth-opening, without gastrovascular system: **Actinulidae**.

## **D: SYSTEMATIC ACCOUNT:**

Remarks: the sign? before a genus name means doubtful generic position and affinities; the same sign ? after a species name means doubtful species; the numbers following the classes, subclasses and families names represent the number of valid species in each of them, the term gonads is in brackets because there are no real organs in Hydrozoa.

1) CLASS AUTOMEDUSAE Lameere, 1920 sens.emend. (see Bouillon and Boero 2000):

(Actinulidae, Narcomedusae, Trachymedusae) (101 valid species).

Hydrozoa with direct development and entirely pelagic life cycle, the planula never settles and each planula transforms usually directly into a single young medusa, except in a few parasitic forms; no modular colonial hydroid phase; medusa formation without medusary nodule, the subumbrellar cavity and velum are formed by folds and deepening of the oral embryonic ectoderm and are analogous but not homologous to the subumbrellar cavity and velum of the Hydroidomedusa; during embryonic development and medusa budding the primary marginal tentacles are always formed before the subumbrellar cavity and the gastrovascular system; the marginal tentacles do not have tentacular bulbs (see peronia); the sensory organs are ecto-endodermal statocysts, with an endodermal axis, growing out from the circular canal, their sensory cells are innervated by the upper nerve ring, their lythocytes and statoliths are of endodermal origin, their sensory cells are characterised by numerous kinocilium-lacking rootlets and are surrounded by stereocilia; asexual reproduction is absent in Actinulidae and Trachymedusae but present in larvae and adults of Narcomedusae, no frustules or cysts known; sexes are separated;

sex cells generally mature in the ectoderm and each fertilised egg will give a single medusae, except in some Narcomedusae where the larval or polypoid structures issued from the egg may by asexual budding give rise to several medusae.

The fertilised oocytes give rise by gastrulation to short-lived planulae (= stereogatrulae) which develop into young medusae either directly or through intermediate tentaculated post-embryonic stages inappropriately called «Actinulae». Automedusa «actinulae» have been considered identical with the Anthomedusae actinula, but the two are not homologous having a different type of development, those of Automedusa immediately possessing structural characters of medusae and not of polyps. The Automedusa planulae have a very simple didermic cellular organisation lacking the specialised neural and glandular cells characterising the Hydroidomedusa planulae. With the exception of the Actinulidae living in marine sand, the Automedusa are all oceanic, mainly represented by deep sea or open sea species, their typically diploblastic "bauplan" limited their evolution and the Automedusa, although having a very wide geographical distribution, show a very limited generic and specific diversity. They may be considered as the most primitive of the recent Hydrozoa and as similar to hypothetical ancestral Hydrozoa.

## Subclass Actinulidae Swedmark and Teissier, 1959 (12 valid species).

Diagnosis: Free living, solitary, minute (up to 1,5-2 mm) hydrozoa, members of the interstitial fauna of marine sand, recalling more or less the structure of an «actinuloid» larvae (e. g. *Solmundella* larvae); with or without reduced umbrella; with an elongated manubrium or gastric tube terminating into a simple mouth-opening, without gastrovascular system; with or without a cone-shaped aboral adhesive organ formed by incurved ectoderm; with one or two amphicoronate rings of solid tentacles; with or without brood chamber (= remains of subumbrellar cavity); with sexual cells in the endoderm of the manubrium wall; with free ecto-endodermal statocysts similar to those of the Trachy- and Narcomedusae, inserted between and alterning with the tentacles; with body covered by flagella; with direct development and no classical

planula-like stage, embryonic development giving rise immediately to a transitory larval phase or halhydrula; no asexual reproduction; with cnidome containing either stenoteles or microbasic mastigophores and, among others, atrichous anisorhizas and two very particular cnidocysts: spirotele and aspirotele spironemes. The Actinulidae appears by their statocysts and embryonic development close to the Automedusa; the existence of a nerve ring as well as the formation of the brood chamber (subumbrellar cavity) by means of a circular invagination around the manubrium as in the Automedusa show that they are reduced representatives of this class.

1.- with a cone-shaped aboral adhesive organ; with a nerve ring; with two aboral amphicoronate rings of tentacles; gonochoristic; without brood pouch (= subumbrellar cavity) = Halammohydridae

2.- without aboral adhesive organ; without nerve ring; with one oral ring of tentacles of two kinds, adhesive and armed ones; with or without a brood pouch (= subumbrellar cavity); hermaphrodite, viviparous = Otohydridae

#### Family Halammohydridae Remane 1927 (10):

Actinulidae consiting in a long gastric tube and a small aboral cone joined by a neck-like part; aboral cone with an adhesive organ; the manubrium ends blindly close behind the neck and opens orally through the mouth; with an aboral nerve ring; with two aboral whorls of amphicoronate solid tentacles and an altenating ring of ecto-endodermic statocysts; gonochoristic; without brood pouch (= subumbrellar cavity).

Genus Halammohydra Remane, 1927: With the characters of the family. Halammohydra andamanensis Rao, 1978 Halammohydra adherens Swedmark and Teissier, 1958 Halammohydra chauhani Rao, 1975 Halammohydra coronata Clausen, 1967

Halammohydra intermedia Clausen, 1967? Halammohydra intermedius Rao, 1993 = has to be renamed see *H. intermedia* Causen, 1967? Halammohydra octopodides Remane, 1927 Halammohydra sagarensis Rao and Misra, 1980 Halammohydra schulzei Remane, 1927 Halammohydra vermiformis Swedmark and Teissier, 1957

## Family **Otohydridae** Swedmark and Teissier, 1958 (2): Actinulidae with an ovoid body containing the gastric cavity; without aboral adhesive organ; no nerve ring observed; with one ring of oral tentacles of two kinds: adhesive and armed ones, surrounding mouth; with or without a brood pouch (= subumbrellar cavity); hermaphrodite, viviparous.

**Genus** *Otohydra* Swedmark and Teissier, 1958: With the characters of the family. *Otohydra tremulans* Lacassagne, 1973? = description? *Otohydra vagans* Swedmark and Teissier, 1958

#### Subclass Narcomedusae Haeckel, 1879 (38 valid species).

Diagnosis: Medusae usually flattened, with a central lens-shaped mass of mesoglea and much thinner rim. Umbrellar margin lobed, i. e. divided by peronial grooves. Tentacles solid, inserted on exumbrella at some distance from margin, just above peronial grooves, without tentacular bulbs, their endodermal core in contact with the manubrial endoderm and continuing in the mesoglea of the umbrella as a "root"; sometimes small secondary tentacles on margin itself. Manubrium very broad and short with entire circular periphery or with perradial or interradial peripheral pouches. Generally without radial canals; circular canal absent or looped into the marginal flaps to form a "peripheral canal system". «Gonads» on manubrium walls and/or on manubrial pouches. Development with planula or with tentacled larval stages, the longitudinal axis of the larval and adult Narcomedusae correspond to the transversal axis of the planula, in the

other medusae those axes coincide. Marginal sense organs in form of free ectoendodermal statocysts (only one species with closed ecto-endodermal statocysts known). With or without otoporpae. Cnidome: atrichous isorhizae and apotrichous isorhizae. Medusae with direct development or presenting larvae which parasitize other medusae, polychaetes, or fishes; those larvae may originate polypoid structures (polypoid stages, stolo-prolifers) which by successive budding will give rise to numerous juvenile medusae or to secondary larvae which will transform later on into juvenile medusae, both types of asexual reproduction give rise to rapid generation successions and represent perhaps the first step to colony formation and modular life.

1.- without manubrium pouches = Solmarisidae
 1.a. with manubrium pouches = 2
 2.- pouches perradial = Cuninidae
 2.a.- pouches interradial = Aeginidae

Family **Aeginidae** Gegenbaur, 1857, emend. Maas, 1904 (6): Narcomedusae with interradial divided manubrial pouches containing the «gonads»; with or without peripheral canal system. With perradial primary tentacles leaving umbrella between marginal pouches, in number at least half than manubrial pouches; with or without secondary tentacles on umbrellar margin. Pouches extending beyond the point of origin of primary tentacles. With or without otoporpae.

1.- with only 2 tentacles = *Solmundella*1.a.- with 4 or more tentacles = 2
2.- with 8 (or more) primary tentacles; with or without secondary tentacles = 3
2.a.- with 4-6 primary tentacles, without secondary tentacles = 4
3.- without secondary tentacles; with 8 manubrial pouches (7-9), with peripheral canal; with otoporpae = *Otoporpa*3.a- with secondary tentacles; with 16 manubrial pouches; peripheral canal absent or degenerated; without otopotpae = *Aeginura*



4.- with 4 tentacles, 8 peronia and 16 manubrial pouches = *Aeginopsis* 4a.-with 4 to 6 tentacles, 4-6 peronia and 8-12 manubrial pouches = *Aegina* 

### Genus Aegina Eschscholtz, 1829:

Aeginidae typically with 8 (but occasionally 10 to 12) primary manubrial pouches; with peripheral canal system; usually with 4 (sometimes 5 or 6) marginal primary tentacles; without secondary tentacles; without otoporpae. One species.

Aegina citrea Eschscholtz, 1829

## Genus Aeginopsis Brandt, 1838:

Aeginidae with 16 manubrial pouches; peripheral canal system absent; four primary tentacles and twice as many peronia; without secondary tentacles; without otoporpae.

Aeginopsis laurentii Brandt, 1838

## Genus Aeginura Haeckel, 1879:

Aeginidae with 16 manubrial pouches; peripheral canal system absent or degenerated; 8 primary tentacles and peronia; with secondary tentacles on umbrella margin; without otoporpae.

Aeginura beebei Bigelow, 1940 Aeginura grimaldii Maas, 1904

#### Genus Otoporpae Xu and Zhang, 1978:

Aeginidae with 8 manubrial pouches; peripheral canal present; with eight primary tentacles and same number of peronia; without secondary tentacles; with otoporpae.

Otoporpa polystriata Xu and Zhang, 1978

Genus Solmundella Haeckel, 1879:

Aeginidae with 8 manubrial pouches; without peripheral canal system; 4 peronia but only 2 long tentacles; without secondary tentacles; without otoporpae. One species. *Solmundella bitentaculata* (Quoy and Gaimard, 1833)

#### Aeginidae incertae sedis:

**Genus** *Aeginodiscus* Haeckel, 1879: Aeginidae with 16 peronial strands, 8 tentacles and 32 (16 clefts) peripheral stomach pouches. *Aeginodiscus actinodiscus* Haeckel, 1879 = insufficient description?

**?Genus** *Teraotoporpae* Zamponi and Suarez Morales, 1991: ?Aeginnidae with 4 tentacles, 4 manubrial pouches; 4 peronia and 4 otoporpae. *Tetraotoporpae siankaanensis*, Zamponi and Suarez Morales, 1991 = inconsistent and insufficient description (presence of 2-6 cirri per tentacle?; marginal bulbs?; microbasic semiophore euryteles? gastric peduncle?).

#### Family Cuninidae Bigelow, 1913 (19):

Narcomedusae with perradial and undivided manubrial pouches; with or without secondary tentacles on umbrellar margin; with or without peripheral canal system; with tentacles leaving umbrella opposite to the centre of each manubrial pouch and thus equal in number to that of the pouches; pouches not extending beyond point of origin of tentacles; with or without otoporpae.

1.- with secondary tentacles = Sigiweddelia
1a.- without secondary tentacles = 2
2.- without otoporpae = Solmissus
2.a.- with otoporpae = Cunina
Uncertain genus: Cunissa

Genus Cunina Eschscholtz, 1829:

Cuninidae with otoporpae, with or without peripheral canal system. Cunina becki Bouillon, 1985 Cunina duplicata Maas, 1893 Cunina fowleri (Browne, 1906) Cunina frugifera Kramp, 1948 Cunina globosa Eschscholtz, 1829 *Cunina lativentris* Gegenbaur, 1857 = *C. globosa*? *Cunina mucilaginosa* (Chamisso and Eysenhardt, 1821) = unrecognisable species Cunina octonaria McCrady, 1859 *Cunina oligotis* Haeckel, 1879 = doubtful species Cunina peregrina Bigelow, 1909 *Cunina polygonia* (Haeckel, 1879) = doubtful species Cunina proboscidea E. and L. Metschnikoff, 1871 Cunina sp. Uchida, 1928 Cunina sp. Vanhöffen, 1912 Cunina simplex Gili, Bouillon, Pagès, Palanques, Puig and Heussner, 1998 Cunina tenella (Bigelow, 1909) *Cunina vitrea* Gegenbaur, 1857 = *C. proboscidea*?

#### Genus Cunissa (Haeckel, 1879):

Cuninidae with nine ore more tentacles and peronial strands; manubrial pouches equal in number to tentacles, but with cleft by the insertion of the tentacles so as to appear twice as numerous as tentacles; peripheral canal?; otoporpae? *Cunissa polyphera* Haeckel, 1879 = not found since Haeckel, uncertain species? *Cunissa polypora* Haeckel, 1879 = not found since Haeckel, uncertain species?

**Genus** *Sigiweddelia* Bouillon, Pagès and Gili, 2000: Cuninidae without otoporpae; with secondary tentacles on umbrella margin; with enclosed sensory clubs, with peripheral canal. *Sigiweddelia bathypelagica* Bouillon, Pagès and Gili, 2000

Genus Solmissus Haeckel, 1879: Cuninidae without otoporpae, without peripheral canal system. Solmissus albescens (Gegenbaur, 1857) Solmissus atlantica Zamponi, 1983= doubtful affinity, poorly preserved material, probably an Aeginidae Solmissus bleekii Haeckel, 1879 = doubtful species Solmissus faberi Haeckel, 1879 Solmissus incisa (Fewkes, 1886) Solmissus marshalli Agassiz and Mayer, 1902 Solmissus sp. Ganapati and Nagabhushanan, 1958

#### Family Solmarisidae Haeckel, 1879 (13):

Narcomedusae without manubrial pouches, manubrium periphery circular and unbroken; with or without peripheral canal system; «gonads» on manubrial wall or on manubrial wall diverticula; with numerous tentacles leaving umbrella at manubrium periphery. With or without otoporpae.

1.- with peripheral canal system; with otoporpae = *Pegantha*1.a.-. without peripheral canal system; without otoporpae = *Solmaris* 

## Genus Pegantha Haeckel, 1879:

Solmarisidae with «gonads» forming diverticula of margin of oral manubrium wall; with peripheral canal system; with otoporpae. *Pegantha aureola* (Haeckel, 1879) = unrecognisable species *Pegantha biloba* Haeckel, 1879 = *P. triloba*? *Pegantha clara* R.P.Bigelow, 1909 *Pegantha cyanostilys* (Eschscholtz, 1829)= unrecognisable species *Pegantha dactyletra* Maas, 1893 = *P. triloba*? *Pegantha dodecagona* (Péron and Lesueur, 1810) = unrecognisable species *Pegantha forskäli* (Haeckel, 1879) = doubtful, not found since original description? *Pegantha godeffroyi* (Haeckel, 1879) = unrecognisable species

Pegantha laevis H.B. Bigelow, 1909
Pegantha lunulata (Haeckel, 1879) = P. clara?
Pegantha magnifica Haeckel, 1879
Pegantha martagon Haeckel, 1879
Pegantha mollicina (Forskål, 1775) = doubtful species
Pegantha pantheaon (Haeckel, 1879) = P. triloba?
Pegantha quadriloba Haeckel, 1879 = probably P. triloba?
Pegantha rubiginosa (Kölliker, 1853)
Pegantha sieboldi (Haeckel, 1879) = P. triloba?
Pegantha triloba Haeckel, 1879
Pegantha weberi (Haeckel, 1879) = unrecognisable species
Pegantha zonaria (Haeckel, 1879) = doubtful species
Pegantha zonorchis (Haeckel, 1879) = unrecognisable species

## Genus Solmaris Haeckel, 1879:

Solmarisidae without peripheral canal system; without otoporpae, with simple annular «gonads». Solmaris corona (Keferstein and Ehlers, 1861) Solmaris flavescens (Kölliker, 1853) Somaris lenticula Haeckel, 1879 Solmaris leucostyla (Will, 1844) Solmaris quadrata Bouillon, Boero and Seghers, 1991 Solmaris multilobata Maas, 1893 = S. corona? Solmaris rhodoloma (Brandt, 1838) Solmaris solmaris (Gegenbaur, 1857) Solmaris vanhoeffeni Neppi and Stiasny, 1911= perhaps the juvenile of some other species

Subclass Trachymedusae Haeckel, 1866 (1879) (51 valid species).

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. With solid marginal tentacles or with a mixture of solid and hollow ones, without true tentacular bulbs, with endodermal cores continuing in the mesoglea of the umbrella as short "roots". With or without centripetal canals. Manubrium with or without gastric peduncle. «Gonads» usually on radial canals. Without polyp stage; a differentiated planula stage is lacking in a number of Trachymedusae, the gastrula developing immediately into young medusae, in others, the planula stage is retained and gives rise to a post embryonic tentaculated larval stage before transforming into medusae. No medusa or asexual budding observed. Marginal sense organs as free sensory clubs exceptionally enclosed in the mesoglea or in the velum. Cnidome: generally stenoteles associated with microbasic euryteles or/and atrichous isorhizae.

1.- with numerous tentacles arranged in groups, most of them with a terminal adhesive disk; manubrium broad with eight radial lobes = Ptychogastridae
 1a- tentacles without adhesive disk = 2
 2.-with centripetal canals = Geryoniidae
 2.a- without centripetal canals = 3
 3.- with 4 radial canals = Petasidae
 3a.-with 8, rarely more radial canals = 4
 4.- with broad, circular manubrium and broad radial canals = Halicreatidae
 4.a.- manubrium and radial canals narrow = Rhopalonematidae

Family Geryoniidae Eschscholtz, 1829 (2):

Trachymedusae with gastric peduncle; 4 - 6 radial canals (sometimes more); with centripetal canals; «gonads» on radial canals, flattened and leaf-shaped; 2 kinds of marginal tentacles, solid and hollow; ecto-endodermal statocysts enclosed in mesoglea.

1.- with 6 radial canals, six «gonads», mouth with six lips = *Geryonia* 1.a.- usually with 4 radial canals and «gonads» (sometimes more), mouth with four lips = *Liriope* 

**Genus** Geryonia Péron and Lesueur, 1810: Geryoniidae with six lips; six radial canals and six «gonads». *Geryonia proboscidalis* (Forskål, 1775)

Genus Liriope Lesson, 1843: Geryoniidae with four lips; usually four radial canals and four «gonads», sometimes more. Heptarradiata rioplatensis Zamponi and Genzano, 1988 = Liriope tetraphylla with surnumeral R.C. but mouth with only 4 lips? Liriope tetraphylla (Chamisso and Eysenhardt, 1821) Octorradiata bonaerensis Zamponi and Genzano, 1988 = L. tetraphylla with surnumeral R.C., but mouth with only 4 lips? Pentarradiata estuariensis Zamponi and Genzano, 1988 = L. tetraphylla with surnumeral R.C., but mouth with only 4 lips?

## Family Halicreatidae Fewkes, 1886 (9):

Trachymedusae with wide, circular manubrium; mouth circular, without distinct lips; without peduncle; without centripetal canals; with exceptionally 4 (*Varitentaculata*) usually 8 or more broad radial canals; with numerous marginal tentacles of different size, but all structurally alike and arranged in single series; each marginal tentacle with flexible proximal portion and stiff spine-like distal portion; with free ecto-endodermal statocysts.

1.-with about 16 or more radial canals = *Halitrephes* 1.a-with 4 or 8 radial canals = 2
 2.-with 4 radial canals = *Varitentaculata* 2a.- with 8 radial canals = 3

3.-with tentacles arranged in 16 groups = *Botrynema*3a.-with tentacles in a continuous row = 4
4.-with perradial gelatinous papillae on exumbrella = *Halicreas*4.a- without exumbrellar papillae = *Haliscera*

#### Genus Botrynema Browne, 1908:

With 8 radial canals; with 16 groups of 11-12 tentacles (2 groups with many tentacles in a single row in each octant) and 8 solitary perradial tentacles. *Botrynema brucei* Browne, 1908 *Botrynema ellinorae* (Hartlaub, 1909)

**Genus** *Halicreas* Fewkes, 1882: With 8 radial canals; with continuous row of tentacles; perradial gelatinous papillae on exumbrella. *Halicreas minimum* Fewkes, 1882

**Genus** *Haliscera* Vanhöffen, 1902: Halicreatidae with 8 radial canals; with a continuous row of marginal tentacles; without exumbrellar papillae. *Haliscera alba* Vanhöffen, 1902 *Haliscera bigelowi* Kramp, 1947 *Haliscera conica* Vanhöffen, 1902 *Haliscera racovitzae* (Maas, 1906)

**Genus** *Halitrephes* Bigelow, 1909: Halicreatidae with 16 or more radial canals; with a continuous row of tentacles; without papillae on exumbrella. *Halitrephes maasi* Bigelow, 1909

**Genus** *Varitentaculata* He, 1980: Halicreatidae with only four radial canals. *Varitentacula yantaiensis* He, 1980

### Family Petasidae Haeckel, 1879 (2):

Trachymedusae with four radial canals; without peduncle and centripetal canals; with well developed manubrium; with 4 sac-like «gonads» on radial canals; with marginal tentacles not in clusters, solid, with a terminal club-shaped knob of cnidocysts; with free statocysts.

1.- tentacles asymmetrically arranged = *Petasiella*1a.- tentacles regularly arranged = *Petasus* 

Genus Petasiella Uchida, 1947:

Petasidae with marginal tentacles arising asymmetrically, at unequal intervals. *Petasiella assymetrica* Uchida, 1947

**Genus** *Petasus* Haeckel, 1879: Petasidae with regularly arranged marginal tentacles. *Petasus atavus* Haeckel, 1879 *Petasus digonimus* (Haeckel, 1879) = doubtfuf species *Petasus eucope* (Haeckel, 1879) = doubtful species *Petasus tiaropsis* (Haeckel, 1879) = doubtful species

#### Family Ptychogastriidae Mayer, 1910 (3):

Trachymedusae with either simple manubrium without mesenteries, or with eight-lobed manubrium, with eight mesenterial partitions; with either marginal tentacles grouped into more or less well defined clusters, some with adhesive disks or with very numerous tentacles, not in clusters but inserted at various levels of exumbrella; no centripetal canals or peduncle; with 8 radial canals; «gonads» either attached onto manubrium, on sides of the 8 manubrial lobes, or on radial canals adjacent to manubrial lobe; free ecto-endodermal statocysts.

1.- tentacles into more or less defined clusters, some with adhesive organs = *Ptychogastria* 

1a.- tentacles not in clusters, none with adhesive organs = Tesserogastria

#### Genus Ptychogastria Allman, 1878:

Ptychogastriidae with marginal tentacles in clusters, some with adhesive disks; manubrium with lateral lobes; with eight mesenterial partitions; «gonads» on the sides of the manubrial lobes or on radial canals adjacent to manubrial lobes. *Ptychogastria antarctica* (Haeckel, 1879) = doubtful species *Ptychogastria asteroides* (Haeckel, 1879) *Ptychogastria polaris* Allman, 1878

## Genus Tesserogastria Beyer, 1959:

Ptychogastriidae with a great number of solid tentacle inserted at varying distances from the velum, not in clusters, without adhesive pads; manubrium simple, without peduncle, mesenteries, or pouches; with eight «gonads» attached along manubrium.

Tesserogastria musculosa Beyer, 1959

## Family Rhopalonematidae Russell, 1953 (35):

Trachymedusae with a narrow manubrium; with or without peduncle; without centripetal canals; usually 8, rarely more, narrow radial canals; mouth with distinct lips; with marginal tentacles evenly distributed, sometimes of two kinds, each marginal tentacle of uniform structure throughout or with proximal portion differing from distal one; with «gonads» either on radial canals globular, linear, or hanging in pouches into subumbrellar cavity, or forming a continuous ring around base of manubrium and extending outwards along radial canals; with free, rarely enclosed ecto-endodermal statocysts.

1.- «gonads» in a continuous band around manubrium extending outwards on radial canals = *Homoeonema* 

1a.- «gonads» isolated, on radial canal, sometimes adjacent to manubrium = 2
«gonads» attached to subumbrellar portion of radial canals: *Aglantha*2.- without gastric peduncle = 3



2.a.- with gastric peduncle = 10

3 - with 4 «gonads» only, pendulous; 4 large and 24 small marginal tentacles = *Tetrorchis* 

3a.- with 8 (rarely more)  $\ll$  gonads $\gg$  = 4

4.- with two kinds of marginal tentacles; with enclosed statocysts =

Rhopalonema

4.a.- with all tentacles of one kind; with free club-shaped statocysts = 5

5.- «gonads» adjacent to manubrium (sometimes also 8 «gonads» free from

manubrium); very numerous tentacles = Arctapodema

5a.- «gonads» separated from manubrium = 6

6.- exumbrella with numerous meridional furrows =7

6a.-exumbrella smooth = 8

7.- «gonads» sausage-shaped, pendulous= Crossota

7a.- «gonads» not pendulous, tubular, attached longitudinally to radial canals = *Vampyrocrossota* 

8.- «gonads» globular, distal, contiguous to circular canal; with 8 tentacles = *Sminthea* 

8a.- «gonads» linear, with 32 or more marginal tentacles = 9

9. with 32 tentacles all of one kind developed in succession = Colobonema

9a.- with 48 or more tentacles of equal size = Pantachogon

10.- umbrella with centripetal canals = Voragonema

10a.- without centripetal canals = 11

11.- gastric peduncle short conical (in young specimens almost invisible);

«gonads» attached on subumbrellar portions of radial canals = 12

11a.- gastric peduncle long, slender = 13

12.- with only two pendulous «gonads» = Persa

12.a.- with 8 «gonads» = Amphogona

13- «gonads» linear, wavy, along the radial canals for most of their lenght =14

13a.- «gonads» sausage shaped, definitively pendulous = 15

14.- along peduncle part of radial canals only = Ransonia

14a.- along most of the length of the radial canals = *Benthocodon* 

15.- «gonads» attached to peduncle = Aglaura

15a.- «gonads» attached to subumbrellar portions of radial canals = Aglantha

#### Genus Aglantha Haeckel, 1879:

Rhopalonematidae with a long and slender gastric peduncle; with eight pendulous sausage-shaped «gonads» on subumbrellar portions of the eight radial canals; with numerous tentacles all alike; with free club-shaped marginal statocysts.

Aglantha digitale (O.F. Müller, 1766) Aglantha elata (Haeckel, 1879) Aglantha ignea Vanhöffen, 1902 = doubtful systematic position Aglantha intermedia Bigelow, 1909

## Genus Aglaura Péron and Lesueur, 1810:

Rhopalonematidae with slender gastric peduncle; with 8 sausage-shaped «gonads» attached on peduncle, not on subumbrella; with numerous tentacles all alike, with free club-shaped statocysts. *Aglaura hemistoma* Péron and Lesueur, 1810

#### Genus Amphogona Browne, 1905:

Rhopalonematidae with short, conical gastric peduncle, exumbrella smooth; with ellipsoidal or sac-shaped, pendulous «gonads» on the 8 radial canals, «gonads» usually of unequal size; with tentacles all alike, not densely crowded; with free club-shaped statocysts. *Amphogona apicata* Kramp, 1957 *Amphogona apsteini* (Vanhöffen, 1902) *Amphogona pusilla* Hartlaub, 1909

## Genus Arctapodema Dall, 1907:

Rhopalonematidae without gastric peduncle; with «gonads» on radial canals adjacent to manubrium; with 8 narrow radial canals; numerous tentacles, all alike, in a single row; free statocysts.

Arctapodema ampla (Vanhöffen, 1902) Arctapodema antarctica (Vanhöffen, 1912) Arctapodema australis (Vanhöffen 1902) Arctapodema macrogaster (Vanhöffen, 1902) Arctapodema sp. Mills, Pugh, Harbison and Haddock, 1996

**Genus** *Benthocodon* Larson and Harbison, 1990: Rhopalonematidae without exumbrellar furrows; without centripetal canals; with eight radial canals; «gonads» linear to wavy, pendulous only distally; with a well developed gastric peduncle; with numerous tentacles superimposed in several rows; marginal sense organs not observed. *Benthocodon pedunculata* Bigelow, 1913 = *Voroganema pedunculata Benthocodon hyalinus* Larson and Harbison, 1990

#### Genus Colobonema Vanhöffen, 1902:

Rhopalonematidae without gastric peduncle; with apical outlines of subumbrellar muscular fields forming a star-shaped figure; elongate «gonads» along 8 radial canals; tentacles all of one kind, developing in succession; free club-shaped statocysts.

Colobonema apicatum Russell, 1961 Colobonema igneum (Vanhöffen, 1902) Colobonema sericeum Vanhöffen, 1902 Colobonema typicum (Maas, 1897)

#### Genus Crossota Vanhöffen, 1902:

Rhopalonematidae without peduncle; numerous meridional exumbrellar furrows; 8 or more radial canals; pendulous sausage-shaped «gonads» on radial canals; numerous densely crowded tentacles, all alike; free club-shaped statocysts.

Crossota alba Bigelow, 1913 Crossota brunnea Vanhöffen, 1902 Crossota norvegica Vanhöffen, 1902

Crossota pedunculata Bigelow, 1913 = Benthocodon pedunculata = Voroganema pedunculata Crossota rufobrunnea (Kramp, 1913)

#### Genus Homoeonema Browne, 1903:

Rhopalonematidae without gastric peduncle; «gonads» forming a continuous band around base of manubrium and extending outwards along proximal half of 8 radial canals; numerous tentacles, all alike; vesicular statocysts. *Homoeonema platygonon* Browne, 1903

## Genus Pantachogon Maas, 1893:

Rhopalonematidae without gastric peduncle; with the apical outlines of the subumbrellar muscular fields forming an entire circle; with «gonads» on the 8 radial canals separated from manubrium; with 48 or more tentacles all alike; free club-shaped statocysts.

Pantachogon haeckeli Maas, 1893 Pantachogon militare (Maas, 1893) Pantachogon scotti Browne, 1910

## Genus Persa McCrady, 1859:

Rhopalonematidae with a short gastric peduncle; with only two oval or sausageshaped «gonads», pendulous, near middle point of the subumbrellar portions of two opposite radial canals; 8 radial canals; with numerous long tentacles, all alike, each with a terminal knob; with free club-shaped statocysts. *Persa incolorata* McCrady, 1859

#### Genus Ransonia Kramp, 1947:

Rhopalonematidae with high conical umbrella (similar to *Aglantha*); with long and narrow gastric peduncle; 8 radial canals; linear, discontinuous «gonads» along peduncular portions of radial canals, not on subumbrella; numerous tentacles, all alike; statocysts unknown. *Ransonia krampi* (Ranson, 1932)

Genus Rhopalonema Gegenbaur, 1857:

Rhopalonematidae without gastric peduncle; with «gonads» along the radial canals separated from manubrium; with solid marginal tentacles of two kinds: large, club-shaped, perradial tentacles with swollen ends and inter-and adradial short, stiff, cirri-like tentacles also with swollen ends; with enclosed statocysts. *Rhopalonema funerarium* Vanhoffen, 1902 *Rhopalonema velatum* Gegenbaur, 1857

#### Genus Sminthea Gegenbaur, 1857:

Rhopalonematidae without gastric peduncle; with globular «gonads» on very distal parts of the 8 radial canals; with only 8 perradial tentacles; with enclosed statocysts.

*Sminthea* (?) *arctica* Hartlaub, 1909 = doubtful species *Sminthea eurygaster* Gegenbaur, 1857

## Genus Tetrorchis Bigelow, 1909:

Rhopalonematidae without gastric peduncle; with only 4 sausage-shaped, pendulous, «gonads» attached to 4 of the 8 radial canals near the middle points; with 4 large perradial and several small marginal tentacles; statocysts unknown. *Tetrorchis erythrogaster* Bigelow, 1909

#### Genus Vampyrocrossota Thuensen, 1993:

Rhopalonematidae without gastric peduncle; with exumbrella furrows; with eight radial canals; with «gonads» attached longitudinally to the radial canal, with tentacles of one kind; statocysts unknown. *Vampyrocrossota childressi* Thuesen, 1993

#### Genus Voragonema Naumov, 1971:

Rhopalonematidae with gastric peduncle; with eight radial canals, with numerous centripetal canals and with up to 500-2000 marginal tentacles superimposed in several rows; with free club-shaped statocysts.

Voragonema laciniata Bouillon, Pagès and Gili, 2000 Voragonema pendunculata (Bigelow, 1913) Vorogonema profundicula Naumov, 1971

### Rhopalonematida incertae sedis:

Genus Stauraglaura Haeckel, 1879:

Rhopalonematidae with a well developed manubrial peduncle; with only four gonads, situated on peduncle on every other of the 8 radial canals, 4 radial canals being without gonads.

Stauraglaura tetragonima Haeckel, 1879 = probably Aglaura hemistoma?

# **2) CLASS HYDROIDOMEDUSA**: Claus, 1877 emend. (Bouillon and Boero, 2000).

(Anthomedusae; Laingiomedusae; Leptomedusae; Limnomedusae; Siphonophorae not included). (740 valid species with medusae). The Hydroidomedusa typically undergo a polymorphic succession of developmental stages during their life cycle. The starting point is a ciliated motile gastrula, the "planula", developing normally into a benthic modular larval stage the polyp (except in the Porpitidae, Margelopsis and Pelagohydra where the hydroid is floating). Polyps will later on, by asexual budding, give rise to planktonic, free-swimming and solitary stages, the hydromedusae, representing the sexual adult state. In many forms the medusae are reduced to sporosacs (fixed gonophores), which no longer leave the hydroids which, by paedomorphosis, secondarily become the sexual stages. The Hydroidomedusa may also form pelagic swimming or floating highly polymorphic modular colonies composed of several modified types of polyps and reduced medusae attached to a stolon supported by floating structures (pneumatophores and nectophores) the all integrated into a single animal (Siphonophores). In the Hydroidomedusae the asexual budding of a medusa or of gonophores involves always the formation of a medusary nodule or entocodon, forming a

coelom like cavity, the subumbrellar cavity, lined by striated muscle cells; during medusa development the primary marginal tentacles always develop after the subumbrellar cavity and the gastro-vascular system has been formed. Both embryonic and larval stages, the planula and the polyp, have a typical diploblastic structure, the adult sexual stage or hydromedusae appear to have acquired during embryonic development (medusary nodule formation) a "triploblastic" kind of organisation (Boero et al., 1998). Hydroids can be solitary but generally form modular colonies by budding. The colonies often produce individual polyps specialised for different functions, all having an interconnected coelenteron (defensive: dactylozooids, reproductive: gonozooids, nutritive: gatrozooids, etc.). The sense organs of the pelagic hydroidomedusa, when present, are ocelli (Anthomedusae, some Leptomedusae), or statocysts (Leptomedusae, Limnomedusae); sometimes cordyli of unknown function are also present (Leptomedusae). The statocysts are closed or open velar ectodermal statocysts formed by the subumbrellar epithelium or velum epithelium (all Leptomedusae) or ecto-endodermal closed statocyst located in the mesoglea near ring canal or in the velum (Limnomedusae).

Velar ectodermal statocysts have their sensory cells innervated by the lower nerve ring (= inner or subumbrellar), their lithocytes and statoliths are ectodermal derivatives and their sensory cells are morphologically distinct from those of the sensory clubs of the Automedusa, lacking stereocilia. Ectoendodermal statocysts exist in the Hydroidomedusa only in the Limnomedusae, they appear close to the Automedusa statocyst being like them innervated by the upper nerve ring and having also their lithocytes and statoliths of endodermal origin, but their development is different, not directly assimilated to a transformed tentacle; their sensory cells are also devoid of stereocilia. They present in fact intermediate characters between Leptomedusan statocysts and Automedusa ones. The presence of a medusary nodule in asexual medusary budding processes and of colonial modular hydroids suggest incluion of the Limnomedusae with the Antho-Leptomedusae.

The Hydroidomedusa have, with a few exceptions, separated sexes; the sex cells generally mature in the ectoderm. The fertilised oocytes give rise by gastrulation to typical planulae which, contrary to Automedusa ones, are very specialised, containing cnidoblasts, different neural and glandular cell types and often-interstitial cells. During the development of the planulae into the polyp stage the embryonic neural and cementing glandular cells are destroyed. Hydroidomedusa are mostly marine but some live in brackish or in freshwater, they are present at all latitudes and at all depths. Hydroidomedusae have frequently only a seasonal existence, their hydroid stage presents several types of resting or dormancy stages (frustules, propagules, cysts, stolon system) allowing them to overcome unfavourable ecological conditions.

## Subclass Anthomedusae Haeckel, 1879 (404 valid species).

Diagnosis: Medusae typically bell-shaped. «Gonads» confined on manubrium, sometimes extending on the most proximal parts of the radial canals. Marginal sense organs, if present, ocelli, never statocysts or cordyli. Marginal tentacles peripheral, hollow or solid, with tentacular bulbs (except, most of the Bythotiaridae, *Eugotoea petalina*, and *Rhabdoon singulare*). Sexual reproduction through a complex planula stage with interstitial cells, neural cells, cnidoblasts and one or two types of glandular cells.

Hydroid: "Athecata hydroids" having the body of their hydranths not covered by rigid perisarcal thecae. Cnidome normally including desmonemes.

#### Order Filifera Kühn, 1913 (226):

Diagnosis: Medusae with «gonads» forming separated interradial, adradial or perradial longitudinal masses on the walls of the manubrium (exceptionally encircling entire manubrium). Mouth either with four simple or complex lips, or with a circular mouth surmounted by oral manubrial tentacles. Marginal tentacles solid or hollow. Cnidome including usually desmonemes and microbasic euryteles, never stenoteles. Planulae having only one type of ectodermal glandular cells: spumous cells. Hydranths with filiform tentacles (except in the dactylozooids of the Ptilocodiidae).

Suborder Margelina Haeckel, 1879 (111):

Diagnosis: Filifera medusae with solid tentacles; ocelli, when present, adaxial; mouth either with simple lips, or with oral solid tentacles armed with cnidocyst clusters or presenting oral arms armed with cnidocyst clusters. Hydroids: Varied in expression.

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1.- with oral tentacles = 2
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1.a.- without oral tentacles = 3

2.- with oral tentacles simple, situated on/or very near mouth rim = Cytaeididae 2.a.- with oral tentacles simple or branched, distinctly inserted above mouth rim

= Bougainvilliidae

3.- mouth with 4 distinct lips = 4

3a.- mouth with 4 inconspicuous lips, each containing a group of about 100 cnidocysts = Eucodoniidae

4.- lips simple, without cnidocyst clusters = 5

4.a- mouth armed with cnidocyst clusters = 6

5.- tentacles in groups, 4-8 simple radial canals = Australomedusidae

5a- tentacles solitary; 4 radial canals with usually fine, branched, anastomosing centripetal canals = Trichydridae

6.- mouth rim and lips covered with a continuous row of cnidocyst clusters along their margin = Clavidae

6a.- mouth lips elongated to form perradial mouth arms with one or many distinct cnidocyst clusters = 7

7.- with exumbrellar didermic centripetal canals or rows of refringent spots issuing from a marginal cnidocyst ring = Ptilocodiidae

7a.- without didermic exumbrellar centripetal canals or refringents spot rows, without marginal cnidocyst ring = 8

8.- marginal tentacles solitary = Hydractiniidae

8.a.- marginal tentacles in 8 groups = Rathkeidae

Family Australomedusidae Russell, 1971 (5):

Anthomedusae with simple mouth lips; with 4 or exceptionally 8 simple radial canals; with 4 groups of perradial tentacles and with or without 4 groups of interradial tentacles or 4 interradial rudimentary bulbs; «gonads» on manubrium or on manubrium and partially on proximal part of radial canals; with or without ocelli.

Hydroid: See Australomedusa.

1.- with 8 radial canals = Octorathkea
1a.- with four radial canals = 2
2.- with only 4 groups of perradial tentacles = Platystoma
2a.- with more than 4 groups of marginal tentacles = 3
3.- with 4 groups of perradial tentacles and 4 interradial rudimentary bulbs = Australomedusa
3a.- with 4 groups of perradial tentacles, 4 groups of interradial tentacles both issued from marginal bulbs and 8 adradial tentacles without marginal bulbs =

Octobulbacea

#### Genus Australomedusa Russell, 1971:

Australomedusidae with cylindrical manubrium, with 4 simple lips; with 4 radial canals, with 4 groups of perradial tentacles and 4 rudimentary bulbs; «gonads» on manubrium and on proximal part of radial canals according sex; with ocelli.

Hydroid: Small stolonal colonies bearing sessile polyps each with a single ring of filiform tentacles located near the middle of their body; medusa buds just below tentacles.

Australomedusa bayili Russell, 1970

#### Genus Octorathkea Uchida, 1927:

Australomedusidae with cruciform manubrium, with 4 simple lips; with 8 radial canals; with 8 groups of marginal tentacles; «gonads» immmature; ocelli? Hydroid: Unknown.

## Octorathkea onoi Uchida, 1927.

Genus Platystoma Zhang Jinbiao, 1982:

Australomedusidae with cruciform manubrium, with 4 simple lips; with 4 radial canals; with 4 groups of marginal tentacles; with «gonads» only on manubrium; with ocelli.

Hydroid: Unknown.

*Platystomma bitentaculata* Xu, Huang and Chen Xu, 1991 = juvenile medusae *Platystoma dongshanensis* Xu and Huang, 1994 *Platystoma nanhaiensis* Zhang Jinbiao, 1982

#### Australomedusidae incertae sedis:

#### Genus Octobulbacea Zamponi, 1983

Medusae with 8 marginal bulbs; 24 molinifom tentacles, 2 per each marginal bulb and 8 adradial without marginal bulbs; gonads interradial. *Octobulbacea montchermosensis* Zamponi, 1983 = not a Margelopsidae as supposed by Zamponi but an Australomedusidae? (see Petersen, 1990)

#### Family Bougainvillidae Lütken, 1850 (51):

Anthomedusae usually bell-shaped; with short manubrium; with simple circular mouth; with oral tentacles simple or dichotomously branched, inserted distinctly above mouth rim and armed with cnidocyst clusters; with 4 radial canals and circular canal; with solid marginal tentacles either solitary or in clusters, borne on 4, 8, or 16 tentacular bulbs; with «gonads» on manubrium either forming a continuous ring or on adradial, interradial or perradial axes; adaxial ocelli absent or present.

Hydroid: Colonies stolonal or erect, branching; perisarc terminating either at base of hydranths or forming a pseudohydrotheca; hydranths with one or more distal whorls of filiform tentacles; free medusae or sporosacs developing mostly on hydrocauli, hydroclades, occasionally on hydrorhiza and rarely from modified hydranths.

1.- oral tentacles simple unbranched = 2
1a.- oral tentacles dichotomously branched = 4
2.- with 4 radial canals = *Nubiella*2a.- with 8 radial canals = 3
3.- eigth equal groups of marginal tentacles = *Lizzella*3a.- marginal tentacles solitary or in eight unequal groups = *Lizzia*4.- with solitary marginal tentacles = *Thamnostoma*4a.- with marginal tentacles in 4 or 8 groups = 5
5.- with marginal tentacles in 4 perradial groups = 7
5.a.- with marginal tentacles in 8 groups, 4 perradial, 4 interradial = 6
6.- marginal groups of tentacles cleft = *Chiarella*6a.- marginal groups of tentacles uncleft = *Koellikerina*7.- in each group a median pair of club-shaped tentacles = *Nemopsis*7a.- marginal tentacles all alike = *Bougainvillia*

## Genus Bougainvillia Lesson, 1830.

Bougainvilliidae with 4 radially placed clusters of solid marginal tentacles; the tentacles of each cluster all alike; with 4 perradial oral tentacles dichotomously branching in normally developed medusae; «gonads» on manubrium in adradial, interradial or perradial position; with or without ocelli. Hydroid: Colonies usually erect, branching or not, more rarely stolonal;

hydranth may be covered by a pseudohydrotheca, with one whorl of tentacles

which are never enveloped by the perisarc of the pseudohydrotheca.

Bougainvillia aberrans Calder, 1993

Bougainvillea alderi (Hodge, 1863) = B. muscus?

Bougainvillia aurantiaca Bouillon, 1980

Bougainvillia bitentaculata Uchida, 1925

Bougainvillia bougainvillei (Brandt, 1835)

Bougainvillia britannica (Forbes, 1841)

Bougainvillia carolinensis (McCrady, 1859)

Bougainvillia charcoti Le Danois, 1913 = Nemopsis crucifera and Nemopsis bachei Bougainvillia dimorpha Schuchert, 1996 *Bougainvillia flavida* Hartlaub, 1897 = *B. britannica* Bougainvillia frondosa Mayer, 1900 Bougainvillia fulva Agassiz and Mayer, 1899 Bougainvillia involuta Uchida, 1947 Bougainvillia macloviana (Lesson, 1830) Bougainvillia maniculata Haeckel, 1864 *Bougainvillia meinertiae* Jäderholm, 1923 = colonies living on the parasitic isopod Codonophilus imbricata which live in the buccal cavity of a fish; only medusa buds known; perhaps B. muscus? Bougainvillia multitentaculata Foerster, 1923 *Bougainvillia multicilia* (Haeckel, 1879) = doubtful species Bougainvillia muscoides (M. Sars, 1846) = B. nordgaardi Bougainvillia muscus Allman, 1863 *Bougainvillia nigritella* Forbes, 1834 = *B. muscoides* Bougainvillia niobe Mayer, 1894 Bougainvillia paraplatygaster Xu, Huang and Chen Xu, 1991 Bougainvillia platygaster (Haeckel, 1879) Bougainvillia principis (Steenstrup, 1850) Bougainvillia prolifera (von Ledenfeld, 1884) = doubtful species, juvenile Bougainvillia pyramidata (Forbes and Goodsir, 1853) Bougainvillia ramosa (van Beneden, 1844) = B. muscus Bougainvillia rugosa Clarke, 1882 *Bougainvillia simplex* (Forbes and Goodsir, 1853) = unrecognisable species Bougainvillia superciliaris (L. Agassiz, 1849) Bougainvillia trinema (von Ledenfeld, 1884) = insufficiently described species Bougainvillia vervoorti Bouillon, 1995

Genus Chiarella Maas, 1897:

Bougainvilliidae with eight cleft tentacle-clusters, so that tentacles arise from 16 epaulette-shaped, marginal swellings; oral tentacles dichotomously branched; with adaxial ocelli.

Hydroid: Unknown.

Chiarella centripetalis Maas, 1897

#### Genus Koellikerina Kramp, 1939:

Bougainvilliidae with 8 groups of marginal tentacles, 4 perradial and 4 interradial, all alike in structure; with 4 oral perradial dichotomously branched tentacles; «gonads» on manubrium, adradial, interradial or perradial; with or without ocelli. Endoderm of gastric cavity with numerous conspicuous endodermal expansions sustained by a mesoglean axis and containing excretory vacuoles (see Bouillon, 1988).

Hydroid: Only known for *K. fasciculata*: Colonies arising from a creeping hydrorhiza formed by tubular stolons; hydrocauli and hydroclades erect, branched and recovered by perisarc, encrusted with mud and various detritus; perisarc forming wrinkled pseudohydrothecae covering hydranth and base of tentacles, leaving only hypostome free; hydranth fusiform to pear-shaped, with conical hypostome, with an irregular whorl of up to 14 filiform tentacles, slightly knobbed at end; medusa bud stalked, borne singly on hydrocauli and hydroclades.

Koellikerina constricta (Menon, 1932)

Koellikerina diforficulata Xu and Zhang, 1978

Koellikerina elegans (Mayer, 1900)

Koellikerina fasciculata (Péron and Lesueur, 1810)

Koelikerina heteronemalis Xu, Huang and Chen Xu, 1991 = insufficient

description? perhaps one of the known species of Koellikerina

Koellikerina maasi (Browne, 1910)

Koellikerina multicirrata (Kramp, 1928)

Koellikerina octonemalis (Maas, 1905)

Koellikerina ornata Kramp, 1959
*Koellikerina taiwanensis* Xu, Huang and Chen Xu, 1991 = insufficient description ? perhaps one of the known species of *Koellikerina* 

### Genus Lizzella Haeckel, 1879:

Bougainvilliidae with simple unbranched oral tentacles; with gastric peduncle; with eight marginal bulbs, all alike, the perradial and interradial bulbs having the same number of tentacles. Hydroid: Unknown. ?*Lizzella hyalina* (van Beneden, 1866) = doubtful species and genus

*Lizzella octella* Haeckel, 1879 = doubtful species and genus, probably a juvenile of *Spirocodon saltatrix?* 

## Genus Lizzia Forbes, 1846:

Bougainvilliidae with simple, unbranched oral tentacles; with gastric peduncle; with usually 8 marginal bulbs (exceptionally 16, *Lizzia fulgurans*) each with one solitary marginal tentacle or with unequal groups of marginal tentacles; «gonads» surrounding manubrium; no ocelli.

Hydroid: Unknown

Lizzia alvarinoae Segura, 1980

Lizzia blondina Forbes, 1848

Lizzia ferrarii Segura, 1980

*Lizzia elisabethae* Haeckel, 1879 = doubtful species, probably a juvenile

Bougainvillia (see Schuchert, in preparation).

Lizzia fulgurans (A. Agassiz, 1865)

Lizzia gracilis (Mayer, 1900)

Lizzia octostyla (Haeckel, 1879)

#### Genus Nemopsis L. Agassiz, 1849:

Bougainvilliidae with four clusters of marginal tentacles, each with a median pair of club-shaped tentacles and on both sides a number of simple filiform tentacles; with adaxial ocelli; with four perradial dichotomously branched oral

tentacles; manubrium with four radial lobes extending towards radial canals; «gonads» on manubrial lobes. Hydroid: Colonial or solitary bougainvilliids. *Nemopsis bachei* L. Agassiz, 1849 *Nemopsis crucifera* (Forbes and Goodsir, 1853) *Nemopsis dofleini* Maas, 1909 *Nemopsis heteronema* Haeckel, 1879 *Nemopsis hexacanalis* Huang and Xu, 1994 *Nemopsis* sp. Ganapati and Nagabhushanam, 1958

# Genus Nubiella Bouillon, 1980:

Bougainvillidae with simple unbranched oral tentacles; with 4 solitary marginal tentacles. Hydroid: Unknown. *Nubiella mitra* Bouillon, 1980

Genus Thamnostoma Haeckel, 1879:

Bougainvilliidae with 4 dichotomously branched oral tentacles, with 4, 8 or more solitary marginal tentacles; with interradial «gonads»; with or without ocelli.

Hydroid: Unknown. *Thamnostoma alexandri* (Mayer, 1904) = possibly a *Hydractinia*? *Thamnostoma dibalia* (Busch, 1851) *Thamnostoma eilatensis*, Schmidt, 1972 *Thamnostoma macrostomum* Haeckel, 1879 *Thamnostoma russelli*, Rees, 1938 ?*Thamnostoma* sp. (Neppi and Stiasny, 1911, 1913; Russell, 1953; Hirohito, 1988) *Thamnostoma tetrellum* (Haeckel, 1879)

## Bougainviliidae either incertae sedis or conspecific:

Genus Pachycordyle Weismann, 1883:
Medusa without tentacles, radial canals or circular canal; manubrium simple surrounded by gonads; no sense organs.
Hydroid: Bougainvilliid, only known in the type species Pachycordyle napolitana Weismann, 1883.
The specimens of Pachycordyle listed below correspond to highly reduced medusa stages possibly of different origin.
Pachycordyle conica Kramp, 1959 = gonophores of siphonophores?
Pachycordyle degenerata (Mayer, 1904) = gonophores of siphonophores?
Pachycordyle lineata Kramp, 1959 = gonophores of siphonophores?
Pachycordyle lineata Kramp, 1959 = gonophores of siphonophores?

Genus Silhouetta Millard and Bouillon, 1973:

Only juvenile medusae known, with 4 marginal bulbs, each with one tentacle and an ocellus; manubrium with 4 oral tentacles. Hydroid: Hydranths with 2-4 tentacular rings, without pseudohydrothecae. *Silhouetta puertoricensis* Wedler and Larson, 1986 = *S. uvacarpa* 

Silhouetta uvacarpa Millard and Bouillon, 1973

## Family Clavidae McCrady, 1859 (4):

Anthomedusae with a bell-shaped umbrella; with short manubrium; with a gastric gelatinous peduncle or with vacuolated endodermal cells forming a pseudo-peduncle; mouth armed with a continuous row of sessile cnidocyst clusters along whole margin; with 4 radial canals and circular canal; with solitary solid tentacles, numerous in adults; «gonads» on interradial walls of manubrium; with adaxial ocelli.

Hydroid: Colonies stolonal or branched; hydranths sessile or pedicellated, naked, occasionally retractable into a thin perisarc cone or tube (*Merona, Rhizogeton, Tubiclava*); with filiform tentacles scattered over hydranth body; nematophores present or absent; free medusae or sporosacs developing from hydrorhiza, hydrocaulus, or from reduced hydrants (blastotyles).

1.- with manubrium mounted upon a short, solid, pyramidal, gelatinous, peduncle without endodermal vacuolated cells = *Oceania*1.a.- with manubrium mounted upon a pseudo-peduncle formed by highly vacuolated endodermal cells = *Turritopsis*

## Genus Oceania Kölliker, 1853:

Clavidae with a short, solid, pyramidal, gelatinous, peduncle without endodermal vacuolated cells. Hydroid: Not known from field, Metschnikoff (1886) obtained ramified colonies with claviform hydranths having up to 13 filiform tentacles alternating in three whorls; gonophores not known.

Oceania armata Kölliker, 1853 Oceania tydemani Bleeker and van der Spoel, 1988

## Genus Turritopsis McCrady, 1859:

Clavidae with a pseudo-peduncle formed by highly vacuolated endodermal cells Hydroid: see family characters, known only in *Turritopsis nutricula*. *Turritopsis lata* Ledenfeld, 1884 *Turritopsis nutricula* McCrady, 1859

### Family Cytaeididae L. Agassiz, 1862 (10):

Anthomedusae with a bell-shaped umbrella; manubrium bulbous, with simple, circular mouth; with 4 or more unbranched oral arms, either on or very near mouth rim; with 4 radial canals and circular canal; 4 or 8 marginal solid tentacles; «gonads» in interradial position or encircling manubrium; without ocelli.

Hydroid: Non-polymorphic colonies arising from reticulate stolons covered by perisarc; hydranths sessile, with one whorl of filiform tentacles below conical hypostome, naked, base of hydranths often with a perisarc collar; spines absent; free medusae and sporosacs on hydrorhiza.



1.- with 4 marginal tentacles = *Cytaeis*1a.- with 8 marginal tentacles = *Paracytaeis* 

Genus Cytaeis Eschscholtz, 1829: Medusa with the characters of the family, with only 4 marginal tentacles. Hydroid: See family characters. Cytaeis adherens Bouillon, Boero and Seghers, 1991 Cytaeis nassa Millard, 1959 = medusae unrecognisable from other Cytaeis medusae Cytaeis nuda Rees, 1962 = medusae unrecognisable from other Cytaeis medusae Cytaeis pusilla Gegenbaur, 1857 = medusae unrecognisable from other Cytaeis medusae Cytaes imperialis Uchida, 1964 = medusae unrecognisable from other Cytaeis

medusae

Cytaeis spp.

*Cytaeis tetrastyla* Eschscholtz, 1829 = medusae unrecognisable from other *Cytaeis* medusae

*Cytaeis uchidae* Rees, 1962 = medusae unrecognisable from other *Cytaeis* medusae

*Cytaeis vulgaris* Agassiz and Mayer, 1899 = medusae unrecognisable from other *Cytaeis* medusae

## Genus Paracytaeis Bouillon, 1978:

With general characters of the family, with eight marginal tentacles; with 4 interradial exumbrellar opaque oval spots of special vacuolated cells located midway of umbrella.

Hydroid: Unknown.

Paracytaeis octona Bouillon, 1978

Family Eucodoniidae Schuchert, 1996 (1):

Anthomedusae with a bell-shaped umbrella, without pointed apical projection; exumbrella without cnidocyst tracks; manubrium quadrangular; with a developed, conical, gastric peduncle; mouth quadrangular; with 4 inconspicuous lips armed with cnidocysts; with 4 radial canals and circular canal; «gonads» encircling manubrium; with 4 solid marginal tentacles with a terminal swelling; marginal bulbs small; without ocelli. Hydroid: Unknown.

**Genus** *Eucodonium* Hartlaub, 1907: With the characteristics of the family. *Eucodonium arctica* Hand and Kan, 1961 = *Plotocnide boreale Eucodonium brownei* Hartlaub, 1907

# Family Hydractiniidae L. Agassiz, 1862 (25):

Anthomedusae more or less bell-shaped; with or without slight apical process; manubrium tubular to sac-shaped not extending beyond umbrella margin; with or without gastric peduncle; mouth with 4 simple or branched oral lips elongated to form arms armed with terminal clusters of cnidocysts (exceptionally mouth rim simple and armed with a cnidocysts ring: Kinetocodium); 4, 8 or more solitary, solid, marginal tentacles; with 4 radial canals and circular canal: «gonads» on manubrium, interradial, sometimes extending along the proximal portions of radial canals; with or without ocelli. Hydroid: Where known, colonies with hydrorhiza either stolonal or reticular, formed by stolonal tubes covered with perisarc, sometimes forming protective tubes (Clavactinia protecta), or encrusting, covered with naked coenosarc, or forming a calcareous hydrorhizal skeleton, frequently with chitinous or calcarous spines, sometimes forming branches; hydranths sessile, naked, polymorphic; gastrozooids with one or more whorls of oral filiform tentacles, or with scattered tentacles on the distal half of the body; gonozooids with one or more whorls of oral tentacles or without tentacles and mouth, giving rise to free medusae or sporosacs; dactylozooids, when present, with no tentacles; ectodemal vesicles of unknown function present or not; reproduction by fixed

sporosarcs, eumedusoids, or free medusae generally borne on gonozooids, exceptionally on hydrorhiza.

Genus Hydractinia van Beneden, 1841: See characters of the family for medusae and hydroids. Hydractinia americana Mayer, 1910 Hydractinia apicata Kramp, 1959 Hydractinia areolata (Alder, 1862) Hydractinia arge (Clarke, 1882) = eumedusoid. Hydractinia australis (Schuchert, 1996) *Hydractinia bella* Hand, 1961 = adult medusa unknown Hydractinia borealis (Mayer, 1900) Hydractinia carcinicola (Hiro, 1939) = eumedusoid. Hydractinia carnea M. Sars, 1846 *Hydractinia claviformis* (Bouillon, 1965) = eumedusoid. Hydractinia dubia (Mayer, 1900) Mayer, 1910 *Hydractinia epiconcha* Stechow, 1907 = eumedusoid. Hydractinia exigua (Haeckel, 1880) *Hydractynia hartlaubi* Neppi and Stiasny, 1911 = *H. areolata* Hydractynia hayamaensis Hirohito, 1988 = only juvenile medusae known, similar to those of H. carnea and H. selena Hydractinia hooperii (Sigerfoos, 1899) = eumedusoid. Hydractinia inabai (Hirohito, 1988) = eumedusoid. Hydractinia meteoris Thiel, 1938 Hydractinia minima (Trinci, 1903) Hydractinia minuta (Mayer, 1900) Hydractinia misakiensis (Iwasa, 1934) = eumedusoid. Hydractinia ocellata (A. Agassiz and Mayer, 1902) Hydractinia polystyla (Haeckel, 1879) Mayer, 1910 = doubtful species *Hydractinia pruvoti* Motz-Kossowska, 1905 = eumedusoid. ?Hydractinia sagamiensis (Hirohito, 1988) = juvenile medusa, generic position not known

Hydractinia selena (Mills, 1976) Hydractinia simplex Kramp, 1928 = P. minima? Hydractinia spinipalpillaris (Hirohito, 1988) = eumedusoid. Hydractinia tenuis (Browne, 1902) Hydractinia tournieri (Picard and Rahm, 1954)

## Hydractiniidae incertae sedis:

#### Genus Kinetocodon Kramp, 1921:

Only juvenile medusae known; manubrium flask-shaped; mouth quadrate with an oral ring of cnidocysts; 4 radial canals; 3 marginal tentacles and a rudimentary marginal bulb.

Hydroid: Stolonal colonies living on Pteropods; with gastrozooids having 0-6 short, oval oral tentacles; with filiform dactylozooids entirely covered by cnidocysts; with pedunculate gonophores issued from stolon, each with one medusa.

Kinetocodon danae Kramp, 1921

### Family Ptilocodiidae Coward, 1909 (6):

Anthomedusae more or less bell-shaped; with or without radial exumbrellar furrows; with didermic centripetal tracks or exumbrellar rows of refringent spots; with a marginal cnidocyst ring; when present, marginal tentacles solid, with tips armed with cnidocysts; four radial canals and circular canal; manubrium tubular or bottle-shaped, with mouth arms with terminal cnidocyst clusters, with adradial or interradial «gonads».

Hydroid: Hydractinoidea with stolonal reticular hydrorhiza or with encrusting hydrorhiza covered by naked coenosarc; hydranths sessile, naked and polymorphic; gastrozooids without tentacles; dactylozooids with 4 or more capitate tentacles, sometimes filiform; gonophores or gonozooids or gastrogonozooids; reproduction by fixed sporosacs, eumedusoids or free medusae.

1.- medusae without marginal tentacles = *Tregoubovia* 

1a.- medusae with marginal tentacles = 2
2.- «gonads» adradial = *Hansiella*2a.- «gonads» interradial = *Thecocodium*

## Genus Hansiella Bouillon, 1980:

Ptilocodiidae with conspicuous marginal cnidocyst ring from which several centripetal didermic processes arise; with 4 stiff marginal tentacles from which only tips are armed with cnidocysts; with short mesenteries; manubrium with mouth arms with terminal clusters of cnidocysts; «gonads» adradial; without ocelli.

Hydroid: Unknown. Hansiella fragilis Bouillon, 1980

### Genus Thecocodium Bouillon, 1967:

Ptilocodiidae with marginal cnidocyst ring from which either several centripetal endodermic processes or exumbrellar rows of refringent spots arise; with 4 stiff marginal tentacles located in exumbrellar furrows; with short mesenteries; manubrium with mouth arms with terminal clusters of cnidocysts; «gonads» interradial; without ocelli.

Hydroid: See family characters. *Thecocodium quadratum* (Werner, 1965) *Thecocodium penicillatum* Jarms, 1987

### Genus Tregoubovia Picard, 1958:

Ptilocodiidae without exumbrellar furrows; with didermic centripetal tracks; without marginal tentacles or marginal tentacular bulbs; with interradial «gonads».

Hydroid: Unknown. *Tregoubovia atentaculata* Picard, 1958

## Ptilocodiidae with eumedusoids:

**Genus** *Hydrichtella* Stechow, 1909: Eumedusoid. Hydroid: See family characters. *Hydrichtella epigorgia* Stechow, 1909

**Genus** *Ptilocodium* Coward, 1909: Eumedusoid. Hydroid: See family characters. *Ptilocodium repens* Coward, 1909

### Family Rathkeidae Russell, 1953 (8):

Anthomedusae with somewhat globular umbrella, with slight apical process; manubrium short, cylindrical, not extending beyond umbrellar margin; with gastric peduncle; mouth with 4 lips elongated to form either simple or branched oral arms armed with terminal and usually also lateral cnidocyst clusters; with 4 to 8 radial canals and circular canal; with «gonads» generally completely surrounding manubrium; with 8 groups of solid marginal tentacles; without ocelli.

Hydroid: Hydranths arising from ramified, creeping stolons; hydranths monomorphic, sessile, with one whorl of filiform tentacles surrounding a rounded hypostome; free medusa developing on hydrorhiza or more rarely at the base of hydranths.

1.- with 4 radial canals = *Rathkea*1a.- with 8 radial canal = *Allorathkea* 

### Genus Allorathkea Schmidt, 1972:

Rathkeidae with 8 radial canals; mouth arms divided once or dichotomously several times and ending in cnidocyst clusters. Hydroid: Unknown. *Allorathkea ankeli* Schmidt, 1972

## Allorathkea macrogastrica Xu and Huang, 1990

### Genus Rathkea Brandt, 1838:

Rathkeidae with 4 radial canals and with 4 elongated oral arms, simple or divided and armed with a various number of cnidocyst clusters pending the species. Hydroid: With the characters of the family. *Rathkea africana* Kramp, 1957 *Rathkea antarctica* Uchida, 1971 *Rathkea formosissima* (Browne, 1902) *Rathkea formosissima* (Browne, 1902) *Rathkea jaschnowi* Naumov, 1956 = *Chiarella centripetalis Rathkea lizzoides* O'Sullivan, 1984 *Rathkea octopunctata* (M. Sars, 1835) *Rathkea rubence* Nair, 1951

## **Rathkeidae conspecific:**

*Pseudorathkea macrogastrica* Xu and Huang, 1990 = *Allorathkea macrogastrica* 

# Family Trichydridae Hincks, 1868 (1):

Anthomedusae without gastric peduncle; mesoglea especially thick in upper part of umbrella; with four large, simple, pleated lips; with 4 radial canals; with numerous fine, lateral branched, anastomosing centripetal canals connecting non perradial marginal bulbs to the radial canals; «gonads» interradial; marginal tentacles solid, with triangular marginal bulbs; without ocelli or any other apparent sense organ.

Hydroid: Colonies stolonal, with creeping stolon covered by thin perisarc; hydranths sessile, with base surrounded by a collar-like tube of perisarc, with one amphicoronate whorl of filiform tentacles; gonophores unknown.

The systematic position of this family remains uncertain, they are here tentatively included in the Margelina because of their solid tentacles. The

medusae of *Trichydra* were previously included in the Proboscydactilidae (as *Pochella*) but the «gonads» are not radial outgrowths of the stomach and there are no exumbrellar cnidocyst chambers characteristic of this latter family. The discovery of their alleged cycle does not resolve the problem of their taxonomical position; *Trichydra* polyps have been considered as Corynidae, as Campanulariidae, or to being next to the Lafoeidae and also tentatively as being the hydroid of *Lizzia blondina* (See Edwards, 1973 for a review). They present great morphological affinities with the polyps of *Halitiara inflexa* Bouillon, 1980 (see Bouillon, 1985a). The medusae have typical Anthomedusae characters in the structure and the form of the manubrium and of the «gonads» and in the structure of the tentacles but they differ from *Halitiara* medusae by several important characters.

Perhaps the study of the cnidome will give enough information to solve this systematic puzzle; *Halitiara* has very particular cnidocysts for Anthomedusae: merotrichous isorhizae.

Genus Trichydra Wright, 1858:

Medusae and hydroids with the characters of the family. *Trichydra pudica* Wright, 1858

### Suborder Pandeida Haeckel, 1879 (116):

The name Tiarida Haeckel, 1879 is invalid, *Tiara* Lesson, 1843 being a junior homonym of *Tiara* Swainson, 1832, a mollusc (see Calder, 1988). The name Pandeida has therefore been proposed for the suborder (Bouillon, 1999; Bouillon and Barnett, 1999).

**Diagnosis:** 

Filifera medusae with hollow tentacles; ocelli, when present, abaxial; mouth simple, lips usually without specialised cnidocyst armed structures, without oral tentacles (except Russsellidae).

Hydroid: Colonies generally stolonal, not branching, monomorphic; hydranths when known with conical hypostome; usually with one whorl of filiform tentacle exceptionally with two or three or scattered (*Stomotoca atra*).



1.- marginal tentacles without basal bulbs or swellings, terminated in a terminal cnidocyst cluster = Bythotiaridae

1.a.- marginal tentacles usually with basal bulbs, without terminal cnidocyst clusters or capitations = 2

2.- with branched or divided radial canals = 3

2a.- with undivided radial canals = 4

3.- with two simple and two bifurcated radial canals; tentacular bulbs develop into medusae = Niobiidae

3a.- with 4-6 branched radial canals, exumbrella with exumbrellar cnidocyst tracts; manubrium with radial gastric pouches; with usually no circular canal; without rudimentary bulbs = Proboscidactylidae

4.- with 4 unbranched oral tentacles, without terminal cluters of cnidocyst,

situated above mouth opening = Russellidae

4a.- without oral tentacles = 5

5.- with 4 radial canals; with only 4 marginal tentacles in adults and without rudimentary bulbs; cnidome with merotrichous isorhizas = Protiaridae 5.a- with two or more tentacles in adults; with 4 unbranched radial canals (rarely 8, *Octotiara*); manubrium usually without radial gastric pouches (except *Annatiara*) with or without rudimentary bulbs; cnidome without merotrichous isorhizas = Pandeidae

Family Bythotiaridae Maas, 1905 (= Calycopsidae) (28):

Pandeoidea without apical projection and gastric peduncle; mouth with 4 simple or crenulated lips; with or without centripetal canals; with simple or folded, adradial or interradial «gonads» on manubrial wall; with 4 or 8 simple or branching radial canals and circular canal; with 4 or 8 or more hollow marginal tentacles\* either with highly reduced or without basal marginal bulbs, each terminating in a large cnidocyst cluster, their basal portion often adnate to exumbrella; with or without rudimentary or dwarf solid tentacles (*Eumedusa*); rarely with abaxial ocelli.

\*The mesoglea of the distal part of the tentacles is often enlarged and reduces strongly the endodermal axis (see Bouillon, 1988, Arai and Brinckmann-Voss, 1998).

Hydroid: Hydroids, when known, living in the prebranchial cavity of ascidians; hydrorhiza formed as a plate giving rise to unbranched colonies; hydranths sessile with up to five irregular whorls of filiform tentacles; medusae arise from polyps.

1.- with centripetal canals, blind or joining base of manubrium = 2

1.a.- without centripetal canals = 4

2.- all tentacles hollow, cnidocysts only in the terminal knob = Calycopsis 2a.- two kind of tentacles = 3

3.- with 8-16 large, hollow tentacles, with rings of cnidocysts and terminal knob; with numerous small solid dwarf tentacles without terminal knob = *Eumedusa* 

3.a- with four perradial and numerous small tentacles without terminal knob = *Meator* 

4.- radial canals simple, unbranched = 5

4a.- radial canals branched, «gonads» folded = 7

5.- «gonads» smooth interradial = 6

5a.- «gonads» smooth adradial = *Pseudotiara* 

6.- with eight radial canals, marginal tentacles with abaxial basal ocelli = *Bhytocellata* 

6a.- with four radial canals; no ocelli = Heterotiara

7.- radial canals bifurcated (some few additional branches may occur as abnormalities) = *Bythotiara* 

7a.- radial canals branching repeatedly at various levels = Sibogita

# Genus Bythocellata Nair, 1951:

Bythotiaridae with cnidocyst rows on exumbrella; with eight separated unbranched radial canals; without centripetal canal; with eight marginal tentacles; tentacle bases with abaxial ocelli; without secondary tentacles.

Hydroid: Unknown. Bythocellata cruciformis Nair, 1951

# Genus Bythotiara Günther, 1903:

Bythotiaridae with 4 simple or branching radial canals; without centripetal canals; «gonads» interradial with transverse furrows; with or without rudimentary or dwarf tentacles entirely covered with cnidocysts; without ocelli. Hydroid: Where known see family diagnosis. Bythotiara capensis Pagès, Bouillon and Gili, 1991 Bythotiara depressa Naumov, 1960 Bythotiara drygalskii Vanhöffen, 1912 Bythotiara drygalskii Vanhöffen, 1912 Bythotiara hunstmani (Fraser, 1911) Bythotiara metschnikovii Bouillon, Seghers and Boero, 1988 Bythotiara murrayi Günther, 1903 Bythotiara parasitica (Kirk, 1915) Bythotiara sp. Schuchert, 1996 Bythotiara sp. Raskoff, 2000 Bythotiara stilbosa Mills and Rees, 1979

# Genus Calycopsis Fewkes, 1882:

Bythotiaridae with unbranched radial canals; with centripetal canals; «gonads» transversely folded, often forming 8 adradial rows; marginal tentacles of similar structure with cnidocysts only on the terminal knob and with adnate base; without ocelli.

Hydroid: Unknown. Calycopsis bigelowi Vanhöffen, 1911 Calycopsis borchgrevinki (Browne, 1910) Calycopsis borealis (Linko,1913) = Calycopsis birulai = Eumedusa birulai Calycopsis chuni Vanhöffen, 1911 Calycopsis gara Petersen, 1957 Calycopsis krampi Petersen, 1957 Calycopsis lipi van der Spoel and Bleeker, 1988

Calycopsis nematophora H.B. Bigelow, 1913 Calycopsis papillata Bigelow, 1818 Calycopsis simplex Kramp and Damas, 1925 Calycopsis simulans (Bigelow, 1909) Calycopsis typa Fewkes, 1882

## Genus Eumedusa Bigelow, 1920:

Bythotiaridae with primarily four unbranched radial canals and with 4 or more? centripetal canals arising from ring canal; «gonads» folded; with two kinds of tentacles, large hollow tentacles with rings of cnidocysts and terminal knob, and small solid tentacles without terminal knob; without ocelli. Hydroid: Unknown. *Eumedusa birulai* (Linko, 1913)

## Genus Heterotiara Maas, 1905:

Bythotiaridae with thick walls; with 4 simple radial canals; without centripetal canals; «gonads» interradial, without transverse folds; without secondary tentacles; without ocelli. Hydroid: Unknown. *Heterotiara anonyma* Maas, 1905 *Heterotiara minor* Vanhöffen, 1911

### Genus Meator Bigelow, 1913:

Bythotiaridae? with four simple radial canals; without centripetal canals; with eight smooth adradial «gonads», tentacles without terminal knob of cnidocysts and of different size; without ocelli.

Hydroid: Unknown.

Meator rubatra H.B. Bigelow, 1913 species with uncertain affinities.

## Genus Pseudotiara Bouillon, 1980:

Bythotiaridae with 4 marginal tentacles, with very reduced basal swellings; with 4 small, simple lips; usually without centripetal canals; with 4 radial canals,

usually simple; with 8 longitudinal «gonads» on perradial ridges of manubrium; without ocelli.

Hydroid: Unknown.

Pseudotiara tropica (Bigelow, 1912)

## Genus Sibogita Maas, 1905:

Bythotiaridae primarily with 4 radial canals that branch repeatedly at various levels; without centripetal canals; with transversely folded «gonads»; without ocelli. Hydroid: Unknown.

Sibogita geometrica Maas, 1905 Sibogita geometrica occidentalis Kramp, 1959 = S. geometrica

# Bythotiaridae incertae sedis:

## Genus Gymnogonium Xu and Huang, 1994:

Bythotiaridae with 2 simple and 2 bifurcated radial canals; without centripetal canals; with perradial gonads; with 6 hollow tentacles tipped by a spherical knob of cnidocysts; marginal tentacles linving umbrella at some distance from margin, with basal swellings embedded in mesoglea; without ocelli. Hydroid: Unknown.

*?Gymnogonium zhengzhongii* Xu and Huang, 1994 = perhaps a juvenile medusae *Heterotiara anonyma ?* 

### Genus Kanaka Uchida 1947:

Bythotiaridae with 4 radial canals with differentiated upper and lower halves; without centripetal canals; 8 long hollow tentacles with terminal cnidocysts knob; without secondary tentacles; manubrium short; mouth with 4 well developed lips; gonads seem to develop on the lower part of radial canals?; without ocelli.

Hydroid: Unknown.

Kanaka pelagica Uchida 1947= Heterotiara minor?

## Family Niobiidae Petersen, 1979 (1):

Anthomedusae without gastric peduncle; with 2 simple and 2 bifurcating radial canals, so that six canals reach the circular canal; without mesenteries; with interradial «gonads»; with marginal tentacular bulbs developing into medusa buds; without ocelli.

Hydroid: Unknown.

**Genus** *Niobia* Mayer, 1900: Medusae and hydroids with characters of family. *Niobia dendrotentaculata* Mayer, 1900

# Family Pandeidae Haeckel, 1879 (69):

Anthomedusae with or without an apical projection; manubrium quadrate, usually large; with or without gastric peduncle; mouth with either 4 simple, or crenulated, or complexly folded lips; with 4 radial canals (exceptionally 8 as in *Octotiara*) often broadened or ribbon-like or with jagged margin; rarely centripetal canals; with or without mesenteries; «gonads», either with smooth surface or complexly folded, on manubrium walls in adradial or interradial positions, sometimes extending along radial canals or completely perradial; with 2 or more hollow marginal tentacles; mostly with tapering, elongated, conical (almost carrot-shaped) and often laterally compressed bulbs; with or without rudimentary tentacles, tentaculae or marginal warts; with or without abaxial ocelli; cnidome usually containing microbasic euryteles.

Hydroid: Where konwn, colonies usually stolonal, not branching; hydranths bearing normally one whorl of filiform tentacles, exceptionally two or more whorls, or scattered tentacles, or no tentacles; perisarc developed to a variable degree, occasionally forming a pseudohydrotheca or missing completely; reproduction mainly by free medusae except in some genera of questionable affinity like *Nudiclava*.

1.- radial canals with long lateral diverticula; marginal tentacles numerous with

stalked cnidocyst knobs along most of their length = Zanclonia

1a.- radial canals without long lateral diverticula; marginal tentacles without stalked cnidocyst knobs = 2

2.- with centripetal canals = 3

2a.- without centripetal canals = 4

3.- with 4 interradial centripetal canals; without gatric peduncle = *Eutiara* 

3a.- with up to 12 centripetal canals; with a very large peduncle = *Timoides* 

4.- with only two well developed marginal tentacles in adults = 5

4.a.- with more than two well developed tentacles in adults = 8

5.- without gastric peduncle = 6

5a.- with a gastric peduncle = 7

6.- «gonads» horseshoe-shaped = *Codonorchis* 

6a.- «gonads» not horseshoe-shaped = Amphinema

7.- with simple mouth rim, with simple «gonads»; with rudimentary tentacles = *Stomotoca* 

7a.- with complexly crenulated lips; with complexly transversally folded

«gonads»; with rudimentary marginal warts = Larsonia

8.- with more than two marginal tentacles and with marginal cirri = Cirrhitiara

8a.- with more than two marginal tentacles and without marginal cirri = 9

9.- with 4 perradial marginal bulbs with hollow tentacles and 4 broad interradial bulbs rimmed by a cluster of short solid tentaculae = *Geomackiea* 

9a.- with perradial and internadial bulbs identical, all marginal tentacles hollow = 10

10.- without mesenteries = 11

10.a.- with mesenteries = 13

11.- with 4 perradial manubrial lobes = Annatiara

11.a.- without perradial manubrial lobes =12

12.- «gonads» oval smooth = Barnettia

12.a.- «gonads» horseshoe-shaped, folded = Halitholus

13.- «gonads» not reticulated or folded, smooth, sometimes corrugated; 4 fairly simple lips = 14

13.a.- «gonads» reticulate or folded, or both; oral lips more or less folded or crenulated = 16

14.- with exumbrellar intertentacular longitudinal ridges = Janiopsis 14a.- without exumbrellar intertentacular longitudinal ridges =15 15.- manubrium quadrangular, very short and broad, with large base, its entire upper surface attached to the subumbrella; «gonads», large, sheet-like, smooth, completely covering all interradial surface and with 3-4 dark red spots in living specimens = *Pandeopsis* 15a.- manubrium cruciform, fairly long, flask-shaped; «gonads», usually adradial, smooth or exceptionally weakly corrugated = Merga 16.- «gonads» folded, mainly in four adradial masses; lips slightly folded = **Hvdrichthvs** 16a.- «gonads» reticulate = 17 17.- «gonads» reticulate, without isolated interradial pits, horseshoe-shaped, with diverging horizontal folds, connected by interradial transverse bridge = Leuckartiara 17.- «gonads» reticulate, with isolated interradial pits, with or without additional folds, not horseshoe-shaped = 1818.- «gonads» altogether reticulate without surrounding folds = Pandea 18a.- «gonads» with combined folds and pits = 1919.- «gonads» in eight vertical, adradial series of transverse folds, interradial portion of manubrium walls with isolated pits; no ocelli = *Neoturris* 19a.- «gonads» mainly in irregular, more or less vertical folds surrounding a

reticulate area, with ocelli = Catablema

## Genus Amphinema Haeckel, 1879:

Pandeidae generally with a considerable apical projection; sometimes with an apical chamber; typically with never more than 2 opposite hollow marginal tentacles; with marginal warts or tentaculae; without gastric peduncle; manubrium with broad base; with or without mesenteries; mouth with 4 simple

lips; «gonads» either adradial, interradial or perradial, occasionally extending along radial canals; with or without ocelli.

Hydroid: Hydroids, when known, forming stolonal colonies, with creeping hydrorhiza, giving rise to well developed unbranched hydrocauli with a terminal hydranth, hydrocaulus perisarc often infested by detritus and extending to the base or the middle of the hydranth body but not developing in a real pseudohydrotheca, hydranths with one whorl of amphicoronate filiform oral tentacles; polyps bending back with mouth facing towards substratum when stressed; medusa buds borne on short peduncles arising from hydrorhiza, from hrydrocauli or from both.

Amphinema australis (Mayer, 1900)

Amphinema dinema (Péron and Lesueur, 1810)

Amphinema krampi Russell, 1956

Amphinema modernisme Bouillon, Pagès and Gili, 2000

Amphinema physophorum (Uchida, 1927)

Amphinema platyhedos Arai and Brinckmann-Voss, 1985

Amphinema rubrum (Kramp, 1957)

Amphinema rugosum (Mayer, 1900)

Amphinema shantungensis Chow and Huang, 1958 = A. rugosum

*Amphinema tsingtauensis* Kao, Li Fung-Lu, Chang and Li Hien-Lun, 1958 = *A.rugosum* 

Amphinema turrida (Mayer, 1900)

# Genus Annatiara Russell, 1940:

Pandeidae without apical projection; exumbrella with meridional cnidocyst tracks; manubrium short, very broad, cruciform, with 4 large perradial lobes closely connected with proximal half or more of 4 radial canals; mouth very broad, cruciform, with folded margin; several hollow marginal tentacles of 2 sizes, regularly alternating; with ocelli.

Hydroid: Unknown.

Annatiara affinis (Hartlaub, 1913)

Annatiara lempersi Bleeker and van der Spoel, 1988

## Genus Barnettia Schuchert, 1996:

Pandeidae with eight hollow, long tentacles between each pair of which are cirri-like small tentacles without bulbs, with chordal endoderm; the cirri-like tentacles are evenly spaced and not associated with the larger tentacles; manubrium small, with four simple perradial lips; «gonads» interradial, smooth; four radial canals present, without mesenteries; apical projection may be present; no ocelli.

Hydroid: Unknown. Barnettia caprai Schuchert, 1996

### Genus Catalbema Haeckel, 1879:

Pandeidae with large dome-shaped apical projection; with numerous tentacles, with or without marginal bulbs between adjoining tentacles; no gastric peduncle; manubrium large with broad base, with 4 short mesenteries; mouth rim with 4 large, crenulated lips; radial canals broad, denticulate; «gonads» adradial, reticular with interradial connection, with irregular or parallel folds running either in vertical or perpendicular direction; with ocelli. Hydroid: Unknown.

Catablema multicirratum Kishinouye,1910 Catablema nodulosum H.B. Bigelow, 1913 Catablema vesicarium (A. Agassiz, 1862)

## Genus Cirrhitiara Hartlaub, 1913:

Pandeidae with large, solid apical projection; with 4 or 8 large hollow marginal tentacles and a number of rudimentary marginal bulbs, each carrying a lateral cirrus on one side; all marginal bulbs with ocelli; «gonads» interradial, horseshoe-shaped, with diverging folds directed perradially; with long mesenteries.

Hydroid: Unknown.

*Cirrhitiara simplex* Xu, Huang and Chen Xu, 1991 *Cirrhitiara superba* (Mayer, 1900)

## Genus Codonorchis Haeckel, 1879:

Pandeidae with an apical projection; with only 2 opposite hollow marginal tentacles; with marginal tentaculae; without gastric peduncle; manubrium with broad base; with mesenteries; mouth cruciform with 4 simple lips; «gonads» horseshoe-shaped; with ocelli.

Hydroid: Colonies stolonal with simple creeping hydrorhiza; hydranths small (0,25 mm), sessile, naked, fusiform; hypostome short, conical; with a single whorl of 4-6 filiform tentacles; medusa buds on hydrorhiza with a pedicel of variable length, generally longer than hydranth. *Codonorchis octaedrus* Haeckel. 1879

# Genus Eutiara Bigelow, 1918:

Pandeidae with exumbrellar longitudinal ribs; with blind centripetal canals alternating with radial canals; radial canals large, with lateral diverticulae, with well developed mesenteries; complex «gonads» forming eight series of adradial folds.

Hydroid: Unknown. Eutiara mayeri H.B. Bigelow, 1918 Eutiara russeli Bouillon, 1981

## Genus Geomackiea Mills, 1985:

Pandeidae without apical projection; with four hollow perradial tentacles and 4 broad, flat, interradial bulbs each rimmed by 5-8 closely packed solid short tentaculae, the longest occupying the central position; without peduncle; with simple unarmed mouth; with smooth interradial «gonads» extending along radial canal to nearly half of the distance to bell margin; no ocelli. Hydroid: Unknown.

Geomackiea zephyrolata Mills, 1985

Genus Halitholus Hartlaub, 1913:

Pandeidae with large dome-like apical projection; manubrium cubic, rather square in cross-section; «gonads» adradial, more or less horseshoe-shaped, folded; mouth rim faintly crenulated; radial canals comparatively narrow, not or very faintly jagged; no mesenteries; 4 or more hollow marginal tentacles; with or without ocelli.

Hydroid: When known, forming "*Perigonimus* type" reptant colonies, hydranths with 6-10 tentacles. *Halitholus cirratus* Hartlaub, 1913

Halitholus intermedius (Browne, 1902)

Halitholus pauper Hartlaub, 1913

Halitholus sp. Arai and Brinckmann-Voss, 1980

## Genus Hydrichthys Fewkes, 1887:

Umbrella dome-shaped; with a large apical projection; manubrium cruciform; mouth with 4 well developed sligtly folded lips; with 4 or more radial canals, jagged, some with lateral crest; with conspicuous mesenteries; with up to 6 marginal tentacles with conical bulbs; «gonads» covering interradial surface of manubrium but developed in 8 adradially folded masses; without ocelli. Hydroid: Parasite of fishes, hydrorhiza forming a naked encrusting plate; with tubular gastrozooids without tentacles; gonozooids branched or unbranched with clusters of medusa buds.

Hydrichthys boycei Warren, 1916 = complete cycle unknown?
Hydrichthys cyclothona Damas, 1934 = complete cycle unknown?
Hydrichthys mirus Fewkes, 1887
Hydrichthys pacifica Miyashita, 1941 = complete cycle unknown?
Hydrichthys pietschi Martin, 1975 = Stomotoca pietschi
Hydrichthys sarcotretis (Jungersen, 1911) = complete cycle unknown?

## Genus Janiopsis Bouillon, 1980:

Pandeidae with a conspicuous apical projection; with numerous (up to 48) exumbrellar intertentacular ridges and ribs ending to the origin of the apical projection; manubrium with long mesenteries; «gonads» smooth covering

interradial apical part of manubrium, at maturity extending adradially along the mesenteries and along radial canals; proximal part of manubrium elongated, prominent with 4 crenalated lips; with up to sixteen marginal tentacles with laterally compressed bulbs; with ocelli.

Hydroid: Unknown.

Janiopsis costata Bouillon, 1980

Genus Larsonia Boero, Bouillon and Gravili, 1991:

Pandeidae with thick apical mesoglea and usually with sharply pointed apex, manubrium swollen on a broad gastric peduncle extending beyond umbrella margin, mouth with prominent complexly crenualted lips; «gonads» in eight adradial rows, complexly transversely folded, with two opposite perradial tentacles, with numerous rudimentary warts; without ocelli.

Hydroid: Parasite of fishes, naked with plate like hydrorhiza, hydranth with no tentacles; gonozooids branched.

Larsonia pterophylla (Haeckel, 1879)

## Genus Leuckartiara Hartlaub, 1914:

Pandeidae usually with an apical projection of varying shape; with large manubrium connected to radial canals by mesenteries; mouth with extensively folded or crenulated margin; «gonads» interradial, bipartite but connected interradially, typically horseshoe-shaped, with horizontal folds directed perradially; radial canals broad and ribbon-like, often with jagged edges; with numerous hollow tentacles with elongated, laterally compressed basal bulbs; often with rudimentary tentacles; usually with ocelli.

Hydroid: Hydroids, when known, forming stolonal colonies; hydrocauli not or sparingly branched, covered by perisarc extending on hydranth body forming more or less gelatinous pseudohydrothecae that do not envelop the tentacles; hydranths with one whorl of oral filiform tentacles; medusa buds develop on hydrocauli or hydrorhiza and are covered by a thin perisarc.

Leuckartiara abyssi (G.O. Sars, 1874)

Leuckariara adnata Pagès, Bouillon and Gili, 1991

Leuckartiara annexa Kramp, 1957 Leuckartiara brownei Larson and Harbison, 1990 Leuckartiara eckerti Bouillon, 1985 Leuckartiara foersteri Arai and Brinckmann-Voss, 1980 Leuckartiara gardineri Browne, 1916 Leuckartiara grimaldii Ranson, 1936 Leuckartiara hoepplii Hsu, 1928 Leuckartiara nobilis Hartlaub, 1913 Leuckartiara octona (Fleming, 1823) Leuckartiara orientalis Xu, Huang and Chen Xu, 1991 Leuckartiara simplex Bouillon, 1980 Leuckartiara sp. Arai and Brinckmann-Voss, 1980 Leuckartiara zacae Bigelow, 1940

## Genus Merga Hartlaub, 1914:

Pandeidae with cruciform manubrium, with perradial edges of manubrium connected with radial canals by long mesenteries; manubrium never twisted; with smooth or exceptionally slightly folded or weakly corrugated «gonads», generally adradial; with simple or faintly crenulated oral lips; with 4-8 or more marginal tentacles; with or without rudimentary bulbs or tentaculae; with or without ocelli.

Hydroid: Hydroids, when known, colonial, stolonal, arising from a ramified hydrorhiza; hydrocauli slightly branched or not; hydranths on hydrocauli or almost sessile; with or without pseudohydrothecae which, when present, do not envelop the tentacles; hydranths with one whorl of filiform tentacles; medusa buds arising from hydrocauli and hydrorhiza.

Merga bulbosa Bouillon, 1980

Merga galleri Brinckmann, 1962 Merga macrobulbosa Xu, Huang and Chen Xu, 1991 Merga reesi Russell, 1956 Merga tergestina (Neppi and Stiasny, 1912) Merga tregoubovii Picard, 1960

*Merga treubeli* Schuchert, 1996 = perhaps a Bythotiaridae *Merga violacea* (Agassiz and Mayer, 1899)

## Genus Neoturris Hartlaub, 1914:

Pandeidae with apical projection varying much in shape and size, often reduced; manubrium very large and broad, with well developed mesenteries; «gonads» in 8 adradial series with transverse folds directed towards interradii; depressed interradial parts of manubrium with isolated pits of «gonads»; with 8 or more hollow marginal tentacles with laterally compressed basal bulbs; without rudimentary tentacles or marginal warts; mostly without ocelli. Hydroid: Hydroids, where known, arising from stolonal hydrorhiza; hydrocauli unbranched, with terminal hydranth; perisarc of hydrocauli continuing up to the hydranth body but not surrounding tentacles; hydranths with one whorl of filiform oral tentacles; free medusae developing from hydrocauli sometimes from hydrorhiza, gonophores completely covered with perisarc. Neoturris bigelowi Kramp, 1959 Neoturris brevicornis (Murbach and Shearer, 1902) Neoturris crockeri Bigelow, 1940 Neoturris fontata (H.B. Bigelow, 1913) Neoturris papua (Lesson, 1843) Neoturris pelagica (Agassiz and Mayer, 1902) Neoturris pileata (Forskål, 1775)

### Genus Octotiara Kramp, 1953:

Pandeidae with eight simple radial canals, with or without gastric peduncle; with transversely folded «gonads»; without mesenteries. Hydroid: Colonies symbiotic with bryozoans; with stolonal hydrorhiza; hydrocaulus short, covered by thin perisarc; hydranth with a single row of 3-4 filiform tentacles; medusa buds borne isolated on hydrorhiza. *Octotiara russelli* Kramp, 1953

Genus Pandea Lesson, 1843:

Pandeidae with or without apical projection; with or without longitudinal exumbrellar cnidocyst ribs; «gonads» at first in the adradii and eventually encircling manubrium, forming a complex irregular network of ridges with pits in between; lips wide and folded; radial canals ribbon-like; with long mesenteries; with more than 8 hollow marginal tentacles; without rudimentary marginal tentacles or marginal warts; with or without ocelli. Hydroid: Hydroids, where known, forming stolonal colonies arising from a creeping, ramified hydrorhiza fixed on the planktonic gastropod *Clio cuspidata*; hydranths naked, almost sessile; hydranths with filiform oral tentacles in 2 closely set whorls; free medusae borne on short pedicels covered by perisarc and arising directly from hydrorhiza. *Pandea conica* (Quoy and Gaimard, 1827) *Pandea cybeles* Alvarino, 1988

*Pandea minima* von Ledenfeld, 1884 = indeterminable doubtful species *Pandea rubra* Bigelow, 1913

## Genus Pandeopsis Kramp, 1959:

Pandeidae with voluminous, quadrangular manubrium with large base attached to subumbrella; with long mesenteries; «gonads» sheet-like, smooth, covering all interradial surface of manubrium and with 3-4 dark red spots in living or recently fixed specimens; mouth with four simple lips; up to 16 marginal tentacles and up to 24 rudimentary bulbs; tentacular cirri or reduced tentacles absent; tentacle bulbs without spur, with abaxial ocelli.

Hydroid: Not known from nature, only from rearing; planulae aggregating and attaching to substrate forming a common hydrorhiza giving numerous hydranths with one whorl of three filiform tentacles; medusa buds unknown; hydrorhiza forming long stolons giving rise to dispersal buds *Pandeopsis ikarii* Kramp, 1959

### Genus Stomotoca L. Agassiz, 1862:

Pandeidae with bell-shaped umbrella; with two marginal perradial tentacles and numerous marginal rudimentary tentacles; manubrium on broad peduncle

extending beyond bell margin, mouth rim smooth; «gonads» in eight well separated adradial rows, with simple transverse folds.

Hydroid: Where known, stolonal colonies growing on algae, bryozoans and sponges; with unbranched stems; hydranth with three rows of filiform tentacles, oral whorl held upwards, aboral rows perpendicular to column; gonophores on hydrorhiza.

Stomotoca atra L. Agassiz, 1862 Stomotoca mira M. Sars, 1874 Stomotoca pietschi Martin, 1975 Stomotoca pterophylla Haeckel, 1879 = Larsonia pterophylla

#### Genus Timoides Bigelow, 1924:

Pandeidae with blindly ending centipetal canal, with large gastric peduncle twice as long as subumbrellar cavity; manubrium very long with four long lancet-shaped lips; «gonads» on lower part of peduncle, just above manubrium; with numerous tentacles and marginal cirri. No sense organs. Hydroid: Unknown. *Timoides agassizi* Bigelow, 1904

## Genus Zanclonia Hartlaub, 1913:

Pandeidae with 20 long, transverse diverticula at right angles on both sides of four radial canals; with 24-32 marginal tentacles, each with adaxial series of stalked cnidocyst knobs.

Hydroid: Unknown. Zanclonia weldoni (Browne, 1910).

## Pandeidae incertae sedis or juveniles or conspecific:

## Genus Campaniclava Allman, 1864:

Only juvenile medusae known with 4 tentacles issued from conspicuous marginal bulbs; manubrium quadratic; mouth simple.

Hydroid: Stolonal colonies living on Pteropods; hydranths on a short pedicel, with 9-10 distally scattered filiform tentacles and one larger below them; with pedunculated gonophores issued from hydrorhiza. *Campaniclava clionis* Vanhöffen, 1910 = perhaps *Pandea rubra*?

**Genus** *Cnidotiara* Uchida, 1927: *Cnidotiara gotoi* Uchida, 1927 = *Zancleopsis gotoi* 

Genus Dissonema Haeckel, 1879:

Anthomedusae with two or four perradial tentacles, without marginal clubs; tentaculae sometimes present; with abaxial ocelli; gonads extend from manubrium outwards along the radial canals *Dissonema gaussi* Vanhöffen, 1912 = doubtful species of doubtful affinity?

Dissonema saphenella Haeckel, 1879 = doubtful species of doubtful affinity?

**Genus** *Pelagiana* Borstad and Brinckman-Voss, 1979: Only juvenile medusae known with 4 marginal bulbs and two perradial tentacular bulbs. Hydroid: Colonies living in the blue-green algae *Trichodesmia Pelagiana trichodesmiae* Borstad and Brinckman-Voss, 1979

Genus Perigonella Stechow, 1921:

Only newly released medusae known, with 4 marginal tentacles; manubrium simple without oral differentiation. Hydroid: Stolonal colonies living on the Pteropod *Hyalacea tridentata*; hydranths solitary, almost sessile, with one ring of filiform tentacles; gonophores pedunculate, borne on hydrorhiza. *Perigonella sulfura* (Chun, 1889)

Family **Proboscidactylidae** Hand and Hendrickson, 1950 (8): Anthomedusae without statocysts and ocelli; without centripetal canals; manubrium with 4-6 or more radial gastric lobes extending along proximal

portions of radial canals; with «gonads» surrounding manubrium and extending on gastric lobes; radial canals branched, obliterated canals may be present; usually without circular canal but with a solid endodermal marginal core; with numerous exumbrellar cnidocyst clusters or bands alternating with tentacles; marginal tentacles hollow, with swollen hollow base connected to the lumen of the radial canals.

Hydroid: Colonies of single hydroids arising from creeping naked stolons located around the lips of sabellid polychaete tubes; hydranths almost sessile, polymorphic with gastrozooids and gonozooids, sometimes dactylozooids, gastrozooids with rounded hypostome, separated from the body by a constriction, with a large cluster of cnidocysts or "cap" somewhat displaced onto one side of the hypostome, with 2 filiform tentacles arising close together, under the hypostomial constriction, opposite to the cnidocyst cluster; gonozooids and dactylozooids without tentacles, mouthless and smaller than gastrozooids; medusa buds very close to gonozooid tip.

The systematic position of the Proboscidactylidae is not clear; they have traditionally been included in the Limnomedusae, mostly by convenience and ignorance of their real affinities. Several authors consider that by some characters, mainly the structure of their tentacular base and the presence of desmonemes, they should be referred to the Anthomedusae Filifera (see Werner, 1984; Petersen, 1990; Schuchert, 1996). We tentatively follow here this suggestion and include them in the Pandeida because of their hollow tentacles, but even in this suborder their relationships with the other families are not obvious.

**Genus** *Proboscidactyla* Brandt, 1834: Medusa and hydroid with the characters of the family. *Proboscidactyla abyssicola* Uchida, 1947 *Proboscidactyla brooksi* (Mayer, 1910) = *P. stellata*? *Proboscidactyla circumsabella* Hand, 1954

Proboscidactyla flavicirrata Brandt, 1835 Proboscidactyla furcata (Haeckel, 1879) = P. stellata Proboscidactyla menoni Pagés, Bouillon and Gili, 1991 Proboscidactyla mutabilis (Browne, 1902) Proboscidactyla occidentalis (Fewkes, 1889) = P. flavicirrata? Proboscidactyla ornata (McCrady, 1859) Proboscidactyla pacifica (Maas, 1909) = P. flavicirrata? Proboscidactyla sp. Schuchert, 1996 Proboscidactyla stellata (Forbes, 1846)

# Family Protiaridae, Haeckel 1879 (8):

Anthomedusae with only four fully developed marginal tentacles arising from conspicuous hollow tentacular bulbs, four simple radial canals and a circular canal, mouth with four simple lips; «gonads» interradial, with smooth surface; with or without mesenteries; without rudimentary bulbs; margin with or without cirri-like tentacles; exceptionally with ocelli.

The differences between the diagnoses of the Protiaridae and Pandeidae appear at first sight rather small, but the cnidome of the Protiaridae is very particular, containing, among others, merotrichous isorhizas a type of cnidocysts which characterises normally only Leptomedusae families (Eirenidae, Eucheilotidae, Haleciidae, Lovenellidae and Tiaropsidae).

Hydroid: The hydroids are known only in *Halitiara inflexa* (Bouillon, 1985a, b; Bouillon *et al.*, 1988b) and *Halitiara formosa* (Brinckmann-Voss, pers. comm.) and are also very different from Pandeidae polyps, showing some resemblance to certain Campanulinidae hydroids and mainly with *Trichydra* polyps (Bouillon *et al.*, 1988b). Colonies arising from creeping stolons, hydranths issued from very short hydrocauli; hydrorhiza and hydrocauli covered by perisarc, which forms a cup at hydranths' base; hydranths with one whorl of filiform tentacles, large cnidocysts alternating with the tentacles; gonophores unkown.

1.- with marginal cirri = 2

1a- without marginal cirri = 3
2.- with adaxial ocelli = *Halitiarella*2a.- without ocelli =*Halitiara*3.-without mesenteries; «gonads» 4 or 8 on interradial walls of manubrium = *Protiara*3a.- with mesenteries = 5
4.- «gonads» interradial; marginal tentacles with abaxial spurs = *Paratiara*4a.- «gonads» entirely surrounding manubrium; marginal tentacles without abaxial spurs = *Latitiara*

# Genus Halitiara Fewkes, 1882:

Pandeidae with 4 straight radial canals; with 4 perradial marginal tentacles and several intermediate, solid cirrus-like marginal tentacles; without rudimentary marginal bulbs; mouth a simple cruciform opening; with or without mesenteries; interradial «gonads»; without ocelli, cnidome with merotrichous isorhizae.

Hydroid: See family characters. Halitiara formosa Fewkes, 1882 Halitiara inflexa Bouillon, 1980 Halitiara rigida Bouillon, 1980

Genus Halitiarella Bouillon, 1980:

Protiaridae with 4 radial canals; with 4 marginal tentacles; mouth with 4 simple lips; with marginal cirri; with smooth interradial «gonads»; with no mesenteries; with adaxial ocelli on marginal tentacular bulbs. Hydroid: Unkown.

*?Halitiarella minuta* Xu, Huang and Chen Xu, 1991= does not belong to the genus *Halitiarella*, doubtful systematic position *Halitiarella ocellata* Bouillon, 1980

Genus Latitiara Xu and Huang, 1990:

Protiaridae with «gonads» entirely surrounding manubrium; with gastric mesenteries; with 4 radial canals; with 4 marginal tentacles without abaxial spurs; with no marginal cirri; with no ocelli. Hydroid: Unknown. *Latitiara orientalis* Xu and Huang, 1990

## Genus Paratiara Kramp and Damas, 1925:

Protiaridae with smooth interradial «gonads»; manubrium more or less twisted, with well developed mesenteries; mouth with 4 simple lips; marginal tentacles with abaxial spurs; without ocelli; without marginal cirri. Hydroid: Unknown. *Paratiara digitalis* Kramp and Damas, 1925

### Genus Protiara Haeckel, 1879:

Protiaridae with 4 or 8 longitudinal «gonads», interradial or perradial?; 4 marginal tentacles, without marginal cirri or tentaculae; without mesenteries; mouth with 4 simple lips; with or without ocelli. Hydroid: Unknown. *Protiara haeckeli* Hargitt, 1902 ?*Protiara* sp. Bouillon and Barnett, 1999 = doubtful position, insufficient description *Protiara tetranema* (Péron and Lesueur, 1810)

### Family Russellidae Kramp, 1957 (1):

Anthomedusae with apical projection; manubrium mounted upon a gastric peduncle, with four small perradial manubrial pouches along the proximal part of the 4 radial canals; with four unbranched oral tentacles attached above mouth margin, without terminal cnidocyst clusters; mouth with four perradial lips; marginal tentacles hollow, without basal swellings, in 8 groups, 4 perradial and 4 adradial, each group with one large and two small tentacles; basal part of large tentacles sunken into deep furrows of umbrella margin; with 8 adradial «gonads»; with adaxial red ocellus at base of free portion of each tentacle.

Hydroid: Unknown.

**Genus** *Russellia* Kramp, 1957a. With the characters of family. *Russellia mirabilis* Kramp, 1957

## Order Capitata Khün, 1913 (176):

Diagnosis: Medusae with «gonads» typically completely surrounding the manubrium. Mouth simple and circular. Marginal tentacles usually hollow (except in Margelopsidae and Porpitidae, where they are solid). Cnidome of the medusae characterised by the presence of stenoteles. Sexual reproduction through planulae or actinulae. Planulae with usually two types of ectodermal embryonic glandular cells: spumous and spheroulous ones. Hydranths usually with capitate tentacles either in the adult polyps or during their larval life; gonophores generally borne on hydranth body.

1.- marginal tentacles developed only at junction between radial canals and circular canal = 2

1a.- marginal tentacles developed at junctions between radial canals and circular canal and along entire circular canal (except *Tiaricodon*); manubium quadrate; mouth cruciform; interradial «gonads» on manubrium and radial lobes or on radial lobes only = Moerisiida

2.- manubrium with quadrate or octogonal base and cylindrical mouth tube; interradial «gonads»; usually with exumbrellar cnidocyst pouches or tracks; tentacles with cnidophores (except the Porpitidae) = Zancleida 2a.- generally with cylindrical manubrium with circular base; mouth usually simple and circular; «gonads» normally completely surrounding manubrium =

Tubulariida

Suborder Moerisiida Poche, 1914 (27):

Capitata with quadrate manubrium forming radial lobes; mouth cruciform; interradial «gonads» on manubrium and radial lobes or on radial lobes only;

marginal tentacles developed at junctions between radial canals and circular canal and along entire circular canal (except *Tiaricodon*); tentacular bulbs usually with abaxial ocelli. Planulae with usually two types of ectodermal embryonic glandular cells: spumous and spheroulous ones.

Hydroid: Hydroids claviform; with long hypostome; tentacles scattered or in one or more whorls under hypostome; free medusae or reduced gonophores.

## 1.- without gastric peduncle = 2

1a.- with gastric peduncle = 3

2.- with perradial manubrial lobes along proximal parts of radial canals;

"gonads" on manubrium and perradial lobes = Moerisiidae

2a.- without perradial manubrial lobes; gonads on manubrium, in 8 -16 adradial pouches = Urashimeidae

3.- gastric peduncle conspicuous; "gonads" on perradial manubrial pouches on gastric peduncle = Polyorchidae

3a.- gastric peduncle short; "gonads" either on manubrium or on manubrium and perradial manubrium lobes = Halimedusidae

### Family Moerisiidae Poche, 1914 (7):

Anthomedusae with prismatic manubrium presenting radial lobes on proximal parts of the 4 radial canals; without gastric peduncle; with or without centripetal canals; with simple cruciform mouth; usually without lips except in oldest specimens; «gonads» on manubrium and surrounding manubrial lobes or only on manubrial lobes overlying the radial canals; with 4, 16-32 or several hundreds moniliform or modified moniliform hollow marginal tentacles with adnate bulbs; with abaxial ocelli; without statocysts.

Hydroids with moniliform or modified moniliform tentacles scattered or in one whorl around middle part of the hydranth body; medusa buds borne on short pedicels between or just under the tentacles; polyp buds produced from lower part of the hydranth, short hydrocaulus ending in pedal disc forming podocysts, or with short stolon-like tubes ending in podocysts or hydranths.
1.- radial lobes of manubrium twisted; «gonads» lobed = *Halmomises*1a - radial lobes of manubrium not twisted; «gonads» smooth = 2
2.- marginal tentacles moniliform; «gonads» on manubrium continuous with those on manubrium lobes = *Moerisia*

2a.- marginal tentacles with irregularly transverse cnidocysts claps or bands; «gonads» on manubrium usually separated from those on manubrial lobes in adults = *Odessia* 

### Genus Halmomises von Kennel, 1891:

Moerisiidae with radial lobes of manubrium with twisted and folded «gonads» extending along proximal portion of radial canals; marginal tentacles with rings of cnidocysts throughout their lenght.

Hydroid: Unknown.

Halmomises lacustris Von Kennel, 1891 = unrecognisable

# Genus Moerisia Boulenger, 1908:

Moerisiidae with 4, 16-32 moniliform marginal tentacles; without centripetal canals; with «gonads» on interradial walls of manubrium, continuous with those on manubrial lobes.

Hydroid: With the general characters of the family, tentacles moniliform.

Moerisia carine Bouillon, 1978

Moerisia gangetica Kramp, 1958

Moerisia gemmata (Ritchie 1915)

Moerisia horii (Uchida and Uchida, 1929)

Moerisia inkermanica (Paltschikowa-Ostroumova, 1925)

Moerisia lyonsi Boulenger, 1908

Moerisia pallasi (Derzhavin, 1912)

## Genus Odessia Paspaleff, 1937:

Moerisiidae with «gonads» on perradial manubrial lobes usually separated from those on manubrium walls in adults; without centripetal canals; 16-32 marginal tentacles with cnidocysts in irregular transverse claps or bands.

Hydroid: With the general characters of the family but tentacles scattered under hypostome, each with one large terminal knob of cnidocysts and several adaxial knobs.

Odessia maeotica (Ostroumoff, 1896)

*?Odessia multitentaculata* Xu, Huang and Chen Xu, 1991= does not belong to the genus *Odessia*, doubtful systematic position

# Family Polyorchidae Agassiz, 1862 (5):

Medusae usually with a well pronounced gastric peduncle; with prismatic manubrium, with perradial manubrial pouches, with four oral lips crowded with cnidocysts; with four radial canals with or without blind side branches; «gonads» either spiral or sausage-shaped on perradial manubrial pouches only; with numerous tentacles (24-260) with stout elongate bulbs; with abaxial ocelli. Hydroids unknown.

Remarks: Where known, the young medusae of Polyorchidae have 4 tentacles, no gastric peduncle, a simple cruciform mouth and short perradial manubrial pouches along proximal parts of the 4 radial canals. During further development of the species with conspicuous gastric peduncle, the manubrium is gradually pushed downwards by the growth of the peduncular mesoglea and the perradial manubrial pouches become so attached along the gastric peduncle between manubrium and the proximal parts of the radial canals. In the majority of Polyorchidae the «gonads» differentiate only on the manubrial pouches and they appear so wrongly issued from the proximal or peduncular part of the radial canals.

1.- marginal tentacles in eigth marginal clusters; «gonads» on peduncular manubrium pouches spirally twisted = *Spirocodon*1 a.- marginal tentacles not in clusters; «gonads» on peduncular manubrium pouches sausage-shaped, pendent = 4
2.- radial canals with lateral branches = *Polyorchis*2a.- radial canals without lateral branches = *Scrippsia*

## Genus Polyorchis A. Agassiz, 1862:

Medusa with numerous marginal hollow tentacles in simple row along exumbrella margin; tentacular bulbs tubular, adnate, with ocellus on short spur; with 4 radial canals with numerous, short, blind lateral diverticula; ring canal with or without branched diverticula; with well pronounced gastric peduncle; manubrium prismatic with pendent sausage-shaped peduncular manubrium pouches; mouth with four crenulated lips with distinct row of cnidocyst; with «gonads» along peduncular manubrium pouches.

Hydroid: Unknown.

Polyorchis haplus Skogsberg, 1948

Polyorchis karafutoensis Kishinouye, 1910 Polyorchis montereyensis Skogsberg, 1948 = P. penicillatus Polyorchis penicillatus (Eschscholtz, 1829)

## Genus Scrippsia Torrey, 1909:

Medusa with numerous marginal tentacles with clasping, adnate marginal bulbs which continue to grow up over exumbrella, making tentacles appear in cycles on exumbrella according to age; tentacles of youngest cycle with abaxial ocelli; with a large gastric peduncle; manubriulm short, with sausage-shaped peduncular manubrium pouches; mouth with crenulated lips with distinct row of cnidocyst; radial canals without diverticula; with «gonads» along peduncular manubrial pouches.

Hydroid: Unknown. Scrippsia pacifica Torrey, 1909

#### Genus Spirocodon Haeckel, 1880:

Medusa with umbrella margin drawn up in eight broad lobes making tentacles appear to be arranged in eight clusters, tentacles hollow, marginal tentacular bulbs adnate, with abaxial ocelli; 4 radial canals with dendritic side branches; 4 interradial arborescent centripetal canals in each interradius; gastric peduncle broad, manubrium prismatic, with elongated, spirally twisted perradial

peduncular manubrial pouches, with long frilled lips with a row of cnidocysts; with «gonads» along peduncular manubrial pouches. Hydroid: Unknown. *Spirocodon saltator* (Tiselius, 1818)

# Family Halimedusidae Arai and Brinckmann - Voss, 1980 (2).

Medusae with 4 radial canals; usually with a low gastric peduncle; manubrium cruciform, with perradial manubrial lobes; mouth quadratic, with lips lined by cnidocysts; either with 4 perradial marginal tentacles or with 4 perradial marginal tentacles and 4 interradial groups of tentacles, all hollow; "gonads" either on manubrium or on manubrium and perradial lobes; marginal bulbs with abaxial ocelli.

Hydroid: Where known, small, solitary with perisarcal base and protective perisarcal spine above hydranth; with 3 - 8, generally 4 oral capitate tentacles with a few scattered cnidocysts along their lenght; medusa buds single, just below tentacles.

1.- with only four perradial marginal tentacles = *Tiaricodon*1a.- with four perradial marginal tentacles and 4 interradial groups of marginal tentacles = *Halimedusa*

### Genus Halimedusa Bigelow, 1916:

With mouth studded with a row of tightly packed round cnidocyst knobs; manubrium cruciform, with perradial manubrial lobes; with 4 peradial marginal tentacles and with 4 interradial groups of 10-11 tentacles, all covered with scattered spherical cnidocyst batteries and with a small round terminal cluster; "gonads" smooth on entire interradial surface of manubrium, unpouched, not extending on perradial manubrial lobes.

Hydroid: With the characters of the family.

Halimedusa typus Bigelow, 1916

Genus Tiaricodon Browne 1902:

Medusae with four imperfectly moniliform marginal tentacles; with stout, elongated marginal bulb surrounded by thickened, cnidocyst-studded epidermis; manubrium prismatic with quadrate base, with short sac-like perradial pouches; with a small or without gastric peduncle; mouth with 4 distinct frilled lips, mouth margin thickened with cnidocyst; with «gonads» on manubrium surface and on manubrial pouches; with 4 radial canals without diverticulae; with abaxial ocelli.

Hydroid: Unknown *Tiaricodon coeruleus* Browne, 1902 *Tiaricodon* sp. Schuchert, 1996

#### Family Urashimeidae Mills, 2000 (1)

Medusae with four jagged radial canals; with 4 hollow marginal tentacles with numerous stalked cnidocyst knobs over all surface; exumbrella with several (about 20) meridional cnidocyst tracks more or less definitively in 4 groups; manubrium square, short; mouth cruciform, lips prominent, frilled, covered by cnidocysts; with «gonads» as 8-16 sac-like pouches in adradii of upper part of manubrium; with abaxial ocelli.

Hydroid: Only young hydranths known, small, solitary; with 4-5 capitate oral tentacles.

**Genus** *Urashimea* Kishinouye, 1910: With the characters of the family. *Urashimea globosa* Kishinouye, 1910

# Suborder Sphaerocorynida Petersen, 1990 (11):

Capitata medusae with flask-shaped, quadrate or cruciform manubrium in crosssection; with interrardial, adradial or circular «gonads»; with 2-4 perradial marginal capitate tentacles.

Hydroid: Where known, with numerous long capitate tentacles arranged in 3-6 irregular aboral whorls around middle part of the hydranth body or in 5-6 close alternate oral whorls surrounding hypostome; with stolonal hydrorhiza, creeping

or mat-like, forming a basal plate; free medusae or sporosacs borne on middle part of the body or on basal part of hydrocaulus or on hydrorhiza.

1.- with evenly rounded umbrella = Hydrocorynidae
1a.- umbrella conical or dome-shaped = 2
2.- with marginal tentacles terminating in a hollow ellipsoid cnidocyst knob; with apical chamber = Sphaerocorynidae
2a.- with normal capitate marginal tentacles with or without abaxial side branches; without apical chamber = Zancleopsidae

# Family Hydrocorynidae Rees, 1957 (2):

Medusae with evenly rounded umbrella; with or without gastric peduncle; with four marginal tentacles with scattered, round cnidocyst knobs and with a small terminal knob; with clasping tentacular bulbs with ocelli; manubrium broadly flask-shaped or tubular, quadrate or cruciform in cross section; mouth tube prismatic, ending in a cruciform mouth with or without cnidocyst clusters; «gonads» interradial without longitudinal groove, surrounding nearly the whole manubrium.

Hydroid: Colonies with spindle-shaped hydranth not well demarcated from hydrocaulus, carrying numerous long oral hollow capitate tentacles in 5-6 closeset whorls around a conical hypostome, hydrocaulus long, naked with thickened mesolamella issuing from a chitinised hydrorhizal stolonal plate; medusa buds in clusters on basal part of hydrocaulus.

**Genus** *Hydrocoryne* Stechow, 1907: With the characters of the family *Hydrocoryne bodegensis* Rees, Hand and Mills, 1976 *Hydrocoryne miurensis* Stechow, 1907

# Family Sphaerocorynidae Prévot, 1959 (3):

Anthomedusae bell-shaped, ovoid; apical mesoglea very thick with a conical or dome-shaped apical projection and a broad apical chamber; manubrium flask-

shaped with quadrate base, or cruciform in cross section; mouth simple, round or cruciform; in non mature specimens «gonads» interradial with a longitudinal median groove which apparently divide them in adradial masses, adult medusae with «gonads» confluent in perradii; with four hollow, marginal tentacles with adaxial or spirally arranged cnidocysts clusters and terminating in a ellipsoid cnidocyst knob; marginal bulbs large, clasping exumbrella, with an adaxial expansion; with abaxial ocelli.

Hydroids: colonies with creeping stolons; with vasiform hydranth; numerous solid capitate tentacles in 3-5 whorls around broadest part of hydranth; free medusa or eumedusoids.

**Genus** Sphaerocoryne Pictet, 1893: With the characters of the family. Sphaerocoryne agassizii (McCrady, 1859) = insufficiently described species? Sphaerocoryne bedoti Pictet, 1893 Sphaerocoryne cocometra Bigelow, 1909 Sphaerocoryne peterseni Bouillon, 1984

## Sphaerocorynidae incertae sedis:

**Genus** *Linvillea* Mayer, 1910 = conspecific of *Sphaerocoryne Linvillea arcuata* (Haeckel, 1879) = doubtful species

### Family Zancleopsidae Bouillon, 1978 (6):

Anthomedusae with conical or dome-shaped umbrella, without apical chamber; 2-4 capitate marginal tentacles, with or without lateral capitate branches; marginal bulbs clasping umbrella margin, with adaxial hemispherical projection studded with cnidocysts; manubrium broadly flask-shaped, with quadrate or cruciform base; mouth square or circular, with or without faint lips; «gonads» 4, interradial with deep interradial grooves which may divide them into 8 adradial patches or «gonads» surrounding manubrium; with or without ocelli on marginal bulbs or on proximal part of tentacles.

Hydroid: Unknown.

1.- without ocelli; «gonads» circular in adults = *Dicnida* 1a.- with ocelli; «gonads» interradial = *Zancleopsis* 

# ?Genus Dicnida Bouillon, 1978:

Medusa with high apical projection; without apical chamber; with only two opposite tentacles ending in a large subspherical cnidocyst knob, tentacles with or without adaxial ramification armed with a cnidocyst knob; with 4 tentacular bulbs with hemispherical adaxial expansion covered with cnidocysts; manubrium with quadrate base, flask-shaped, with cruciform cross-section, ending in a short cylindical mouth tube with circular mouth; «gonads» interradial in non mature specimens, in adults surrounding manubrium; without ocelli.

Hydroid: Unknown. Dicnida rigida Bouillon, 1978

# Genus Zancleopsis Hartlaub, 1907:

Zancleopsidae with or without apical projection; either with 2 long, opposed, capitate tentacles with capitate side branches and 2 opposed, shorter or longer, simple capitate tentacles, or with four simple capitate tentacles; marginal tentacular bulbs clasping umbrella margin, with large hemispherical adaxial expansion covered with cnidocysts; manubrium flask-shaped; mouth more or less cruciform, with or without simple lips; «gonads» interradial, with deep interradial grooves which may divide them into 8 adradial masses; with ocelli. Hydroid: Unknown.

Zancleopsis dichotoma (Mayer, 1900) Zancleopsis elegans Bouillon, 1978 Zancleopsis gotoi Uchida, 1927 Zancleopsis tentaculata Kramp, 1928 Zancleopsis symmetrica Bouillon, 1985

# Suborder Tubulariida, Fleming, 1828 (117):

Capitata medusae generally with cylindrical manubrium with circular base; mouth usually simple and circular; «gonads» normally completely surrounding manubrium; marginal tentacles developed only at junction between radial canals and circular canal; usually with 1 to 4 marginal tentacles, rarely 8 or more in the Cladonematidae and Eleutheriidae. Cnidome of medusae including desmonemes and stenoteles.

Hydroid: Where known, hydroids with solid or parenchymatical oral tentacles in one whorl around hypostome or spreading down over hydranth body; with solid or parenchymatical aboral tentacles in one or three whorls or absent; free medusae or sporosacs. Cnidome of polyps including stenoteles, with or without desmonemes.

1.- reduced medusae, with four rudimentary bulbs = Pennariidae

1.a.- medusae not reduced, exceptionally without tentacles = 2

2.- marginal tentacles simple; with 1- 4 marginal tentacles = 3

2.a.- marginal tentacles branched; usually with more than 4 radial canals = 8

3.- marginal tentacular bulbs with ocelli = Corynidae

3.a- marginal tentacular bulbs without ocelli = 4

4.- exumbrella without cnidocyst tracks = 5

4.a.- exumbrella with cnidocyst tracks = Tubulariidae

5.- marginal tentacles in four groups = Margelopsidae

5a.- marginal tentacles solitary = 6

6.- with four equal marginal tentacles with «gonads» in four pedunculate pendulous perradial pouches hanging into subumbrellar cavity = Boeromedusidae

6.a.- with 1 - 4 unequal marginal tentacles; «gonads» on manubrium, different from 6 = 7

7.- with 1- 4 marginal tentacles, unequally developed or of the same length but all of same structure; without apical projection = Euphysidae

7.a.- with up to four marginal tentacles of different size and structure; umbrella dome-shaped or with pointed apex = Corymorphidae

8.- marginal tentacles bifurcating = Eleutheriidae8a.- marginal tentacles with several branches = Cladonematidae

The Dicyclocorynidae with only juvenile medusa known are not included in this key

### Family Boeromedusidae Bouillon, 1985 (1):

Medusae with apical projection; with cylindrical manubrium; with simple tubular mouth; with 4 radial canals and circular canal; with 4 conical marginal bulbs; with four simple, hollow tentacles with many cnidocyst clusters including a terminal ovoid cluster; «gonads» on manubrium and as four large perradial pouches hanging freely in subumbrellar cavity; without ocelli. Hydroid: Unknown.

**Genus** *Boeromedusa* Bouillon, 1995 Diagnosis as for the family. *Boeromedusa auricogonia* Bouillon, 1995

# Family Cladonematidae Gegenbaur, 1857 (5):

Creeping and swimming Anthomedusae; mouth with short lips armed with 4 to 6 cnidocyst clusters or with ramified oral tentacles; with or without apical chamber above manubrium; with cylindrical manubrium with perradial pouches; with variable number of radial canals, some branched, some simple, final number of canals entering circular canal usually of same number as marginal tentacles; with «gonads» completely surrounding manubrium; with variable number of hollow branching marginal tentacles, each furnished with 1 to 10 branches ending in an organs of adhesion and 1 to 10 branches with clusters of cnydocysts; with ocelli.

Hydroid: When known, colonial, with creeping stolons; stems sparingly branched or unbranched; hydranth with one whorl of 4-5 oral capitate tentacles, with or without an aboral whorl of filiform tentacles; mouth with oral ectodermal gland cells forming a preoral chamber.

1.- mouth with simple armed lips; without apical chamber = *Cladonema*1a.- mouth with branched oral tentacles; with apical chamber = *Dendronema* 

Genus Cladonema Dujardin, 1843:

Cladonematidae with simple mouth armed with cnidocyst clusters; without apical chamber. Hydroid: With the characters of the family. *Cladonema californicum* Hyman, 1947 *Cladonema myersi* Rees, 1949

Cladonema pacificum Naumov, 1955

Cladonema radiatum Dujardin, 1843

Cladonema uchidai Hirai, 1958

Genus Dendronema Haeckel, 1879:

Cladonematidae with branched oral tentacles; with an apical chamber above manubrium.

Hydroid: Unknown. Dendronema stylodendron Haeckel, 1879 = doubtful species?

Family Corynidae Johnston, 1836 (32):

Anthomedusae with bell-shaped umbrella; without cnidocyst tracks; manubrium tubular; with simple circular mouth; with 4 radial canals and circular canal; 2-4 hollow equally developed marginal tentacles; with «gonads» encircling completely the manubrium in one or more rings; mostly with abaxial ocelli. Hydroid: When known, colonies branched or unbranched rising from a creeping stolon or encrusted base; hydranths with an oral whorl of capitate tentacles and often below them more capitate tentacles in whorls or scattered; there may be filiform tentacles below the capitate ones, gonophores develop usually on polyps either as sessile sporosacs or free medusae.

1.- marginal bulbs with adaxial pads of cnidocysts = 21a.- marginal bulbs without adaxial pads of cnidocysts = 3

2.- with 2 - 4 equal marginal tentacles with abaxial pedunculated cnidocyst knobs and bifurcating distally in two terminal cnidocyst knobs = *Cladosarsia*2a.- with 2 - 4? marginal tentacles with a single cnidocyst knob = *Paulinum*3.- «gonads» divided in two or more rings = *Dipurena*3.a.- «gonads» not interrupted, undivided = *Sarsia*

# Genus Cladosarsia Bouillon, 1978:

Corynidae with marginal bulbs presenting large adaxial pads of cnidocysts; 4 perradial tentacles similar with abaxial pedunculated cnidocyst knobs and bifurcating at their end, each branch provided with a terminal cnidocyst knob; with «gonads» surrounding completely the manubrium or only its oral half; with ocelli.

Hydroid: Unknown Cladosarsia capitata Bouillon, 1978 Cladosarsia minima Bouillon, 1978

Genus Dipurena McCrady, 1859:

Corynidae with 4 similar perradial tentacles; marginal bulbs without adaxial cnidocyst pads; «gonads» divided in two or more rings around manubrium; endoderm of sexual parts digestive, endoderm of non sexual parts chordal; manubrium usually extending well beyond umbrellar margin; with ocelli. Hydroid: Where known, with general characters of the family, with a button of ectodermal gland cells around the mouth; with free medusae. *Dipurena baukalion* Pagès, Gili and Bouillon, 1992 *Dipurena bicircella* Rees, 1977 *Dipurena brownei* (Bigelow, 1909) = *D. ophiogaster*? *Dipurena dolichogaster* (Haeckel, 1864) = doubtful species *Dipurena fertilis* Metschnikoff 1871 = doubtful species *Dipurena halterata* (Forbes, 1846) *Dipurena ophiogaster* Haeckel, 1879 *Dipurena pyramis* (Haeckel, 1879) = systematic position doubtful *Dipurena reesi* Vannucci, 1956

Dipurena simulans Bouillon, 1965 Dipurina spongicola Anger, 1972 Dipurena strangulata McCrady, 1859

# ?Genus Paulinum Brinckmann-Voss and Arai, 1997:

Medusa with cone-shaped exumbrella; with wide manubrium with a conical extension of the base into the mesoglea; manubrium not tubular at mouth end; four thick radial canals and circular canal; 4 marginal bulbs with adaxial thickening, at least two of which bear stiff tentacles terminating in a round cnidocyst knob.

Hydroid: Unknown.

*Paulinum lineatum* Brinckmann-Voss and Arai, 1997 = position of the genus uncertain

*Paulinum punctatum* (Vanhöffen, 1911) = position of the genus uncertain, possibly the medusa stage of *Velella velella* (see Schuchert, in preparation).

# Genus Sarsia Lesson, 1843:

Corynidae medusae with undivided «gonads»; marginal bulbs without adaxial cnidocyst pads.

*Sarsia* medusae present a great range of variability, there is considerable confusion about the different species and it is often difficult to distinguish one species from another, the knowledge of their cycle and cnidocysts being often necessary.

Hydroid: Where known, with general character of the family; without ectodermal oral gland cells; with free medusae. *Sarsia angulata* (Mayer, 1900)

Sarsia apicula (Murbach and Shearer, 1902)

Sarsia barentsi Linko, 1905 = doubtful species

Sarsia brevia Uchida, 1947 = Euphysomma brevia

*Sarsia brachygaster* Grönberg, 1898 = doubtful species

Sarsia clavata Keferstein, 1862 = doubtful species

Sarsia cliffordi Brinckmann-Voss, 1989 Sarsia coccometra Bigelow, 1909 = Sphaerocoryne coccometra (see Petersen 1990) Sarsia codonoforum Haeckel, 1879 = perhaps Sarsia prolifera? Sarsia conica (Haeckel, 1880) Sarsia densa (Hartlaub, 1897) = perhaps S.tubulosa? Sarsia erythrops Romanes, 1876 = doubtful species, not found in Mayer (1910) nor in Kramp (1961) Sarsia eximia (Allman, 1859) Sarsia frutescens Allmann, 1871 = doubtful species Sarsia gemmifera Forbes, 1848 Sarsia gracilis Browne, 1902 Sarsia hargitti Mayer, 1910 Sarsia inabai Uchida 1933 Sarsia japonica (Nagao, 1962) Sarsia minima von Ledenfeld, 1884 = indeterminable species Sarsia nipponica Uchida, 1927 Sarsia occidentalis (Fewkes, 1899) = insufficient description Sarsia occulta Edwards, 1978 Sarsia pattersoni Haddon, 1886 = doubtful species, could be S. tubulosa Sarsia piriforma Edwards, 1983 Sarsia polyocellata Uchida, 1927 Sarsia princeps (Haeckel, 1879) Sarsia producta (Wright, 1858) Sarsia prolifera Forbes, 1848 Sarsia radiata von Ledenfeld, 1884 = indeterminable species *Sarsia resplendens* Bigelow, 1909 = *Hydrocoryne miurensis* Sarsia reticulata (Agassiz, 1862) Sarsia rosaria (Agassiz 1862) = unsufficiently described species Sarsia sarsii Genzano and Zamponi, (1991) 1994 = S. tubulosa? Sarsia sp. Arai and Brinckmann-Voss, 1980 and see Kramp, 1961 p.33 Sarsia siphonophora Haeckel, 1879 = probably S. gemmifera

Sarsia striata Edwards, 1983 Sarsia tubulosa (M. Sars, 1835) Sarsia turricula McCrady, 1859 = doubtful species Sarsia viridis Arai and Brinckmann-Voss, 1980

# Corynidae incertae sedis:

Genus Dicodonium Haeckel, 1879:

Corynidae with two well developed tentacles; with or without perradial rudimentary tentacles; without meridional lines of cnidocysts on exumbrella; with or without ocelli.

Several species of *Dicodonium* have been described in the literature, generally observed only once by their author. Petersen (1990) suggest that they should all be considered as obsolete with the exception of *D. floridana* Mayer, 1910 which is probably valid but does not belong to the Corynidae. The other species should thus be regarded as obsolete except *D. punctatum* (see Brinckmann-Voss and Arai, 1998; Schuchert, in preparation).

#### Hydroid: Unknown.

Dicodonium adriaticum Graeffe, 1884 = young pandeid? Dicodonium cornutum Haeckel, 1879 = unrecognisable Dicodonium dissonema Haeckel, 1879 = unrecognisable Dicodonium floridanium Mayer, 1910 = a corymorphid? Dicodonium ocellatum (Busch, 1851) = Sarsiella ocellata = abnormal Sarsia Dicodonium jeffersoni (Mayer, 1910) = unrecognisable Dicodonium punctatum Vanhöffen, 1911 = Paulinum punctatum (see Brinckmann-Voss and Arai, 1998); but more probably correspond to the medusa stage of Velella velella (see Schuchert, in preparation)

#### Genus Sarsiella Hartlaub, 1907:

Corynidae with only two opposite marginal tentacles; with ocelli Sarsiella dinema Hartlaub, 1907= doubtful species Sarsiella ocellata (Bush, 1851) = Dicodonium ocellatum = abnormal Sarsia? Obsolete species

#### Family Corymorphidae Allman, 1872 (23):

Anthomedusae usually with a dome shaped or a pointed apex; without exumbrellar cnidocyst tracks; with manubrium not extending beyond umbrella margin (except in *Yakovia* but this is presumably an artefact due to fixation), sausage-shaped or exceptionally with sac-like processes; simple mouth, circular; with 1- 4 capitate or moniliform marginal tentacles from different size and structure, exceptionally branched and rudimentary tentacles; «gonads» undivided surrounding all length of manubrium and exceptionally also in sac-like processes of manubrium (*Gotoea*).

This family comprises the following genera: *Branchiocerianthus* Mark, 1898; <u>Corymorpha</u> (=Amalthaea) Sars, 1835; <u>Euphysora</u> Maas, 1905; <u>Eugotoea</u> Margulis, 1989; *Furkaurahydra* Yamada *et al.*, 1977; <u>Gotoea</u> Uchida, 1927; *Gymnogonos* Bonnevie, 1898; <u>Paragotoae</u> Kramp, 1942; <u>Vannuccia</u>, Brinckmann-Voss, 1967; <u>Yakovia</u> Margulis, 1989. The underlined genera have a medusa stage.

Hydroid: Solitary, with one whorl of moniliform or capitate oral tentacles or several whorls of filiform oral tentacles; with one to three whorls of moniliform or filiform aboral tentacles; hydrocaulus long, distally pointed or rounded, hollow or more or less filled by parenchymatic endoderm; lower part with short papillae or/and longer anchoring didermic filaments; free medusae or fixed sporosacs.

1.- with 1 fully developed marginal tentacle = 2 1a.- usually with 3 short or rudimentary marginal tentacles and 1 long fully developed marginal tentacle different in structure = *Euphysora* 2.- exumbrella divided in 4 prominent leaf-shaped facets separated by 4 longitudinal large and deep grooves; umbrella without marginal bulb; marginal tentacle ending in a cnidocyst capitation = *Eugotoea* 2a.- exumbrella with uniform surface = 3 3.- umbrella margin slightly oblique to vertical axis, umbrella with no apical

process; principal marginal tentacle short and thick, ending in long and large,

oval to cylindrical ectodermal swelling containing numerous cnidocysts = *Vannuccia*.

3.a.- umbrella margin at right angles to vertical axis, fully developed marginal tentacles different = 4

4.- «gonads» on manubrium and on 4 sausage-like interradial manubrial pouches = *Gotoea* 

4a.- «gonads» simple; manubrium without interradial pouches = 5

5.- fully developed marginal tentacle slender, long, moniliform; umbrella with pointed apical process = *Corymorpha* 

5a- fully developed marginal tentacle ending or in a single cnidocyst capitation or in clusters of cnidocysts capitation; umbrella without pointed apical process = 6

6.- fully developed marginal tentacle with a terminal cnidocyst knob; with one tentacular and three non tentacular bulbs = Paragotoea

6a.- fully developed marginal tentacle with terminal ramifications ending in numerous cnidocyst clusters; with only one marginal bulb bearing the tentacle = *Yakovia* 

### Genus Corymorpha M. Sars, 1835:

Corymorphidae with a dome-shaped or pointed apical process, usually with an apical canal; one long moniliform tentacle and three non tentacular rudimentary bulbs.

Hydroid: With general characters of the family; hydranth vasiform with one or several closely set whorls of oral filiform tentacles, and one whorl of aboral filiform tentacles; with parenchymatc diaphragm; hydrocaulus with thin perisarc, with parenchymatic endoderm with longitudinal peripheral canals; lower part with short papillae or/and long ancoring didermic filaments; free medusae or fixed gonophores.

Corymorpha carnea (Clark, 1876) = only medusa buds known

Corymorpha intermedia Schuchert, 1996

Corymorpha januarii Steenstrup, 1854 = eumedusoid.

Corymorpha nutans M. Sars, 1835

*Corymorpha sagamina* Hirohito, 1988 = only medusa buds known *Corymorpha* sp. Uchida, 1947

# Genus Eugotoea Margulis 1989:

Corymorphidae with exumbrella divided in 4 prominent leaf-shaped facets separated by 4 longitudinal large and deep grooves; without marginal bulbs; with only one marginal tentacle with a terminal cnidocyst knob; «gonads» surrounding manubrium.

Hydroid: Unknown. Eugotoea petalina Margulis, 1989

### Genus Euphysora Maas, 1905:

Corymorphidae usually with 3 short or rudimentary tentacles and one long principal tentacle that differs from others not only in size, but also in structure. Hydroid: Where known (*E. bigelowi*), with the general characteristics of the family; hydranths vasiform, with 35 oral tentacles more or less distinctly capitate, with scattered cnidocyst batteries and, set in irregular rows on hypostome; with 15-20 aboral elongated non contractile filiform tentacles; a parenchymatic diaphragm separates the hypostome from the polyp body; hydrocaulus with thin perisarc, with cavity filled by parenchymatic endoderm with a limited number of simple peripheral endodermal canals, with anchoring rootlets; medusa buds borne in clusters on slightly branched inflated pedicels arising above aboral tentacles.

Euphysora abaxialis Kramp, 1962 Euphysora annulata Kramp, 1928 Euphysora bigelowi Maas, 1905 Euphysora furcata Kramp, 1948 Euphysora gemmifera Bouillon, 1978 Euphysora gigantea Kramp, 1957 Euphysora gracilis (Brooks, 1882) Euphysora normani (Browne, 1916) Eyphysora pseudoabaxialis Bouillon, 1978

Euphysora russelli Hamon, 1974 Euphysora valdiviae Vanhöffen, 1911 Euphysora verrucosa Bouillon, 1978

## Genus Gotoea Uchida, 1927:

Corymorphidae with 4 radial canals, with one bulb bearing a well developed, hollow tentacle, ending in a cnidocyst knob and three marginal bulbs without tentacles, clasping exumbrella; manubrium with interradial sausage-like gastric pouches; mouth simple, without lips; «gonads» encircling manubrium and extending along the gastric pouches; without ocelli. Hydroid: Unknown. *Gotoea similis* Kramp, 1959 *Gotoea typica* Uchida, 1927

**Genus** *Paragotoea* Kramp, 1942 (after Kramp, 1961, not Ralph, 1959): Corymorphidae without exumbrellar cnidocyst tracks; with 4 radial canals, without gastric pouches; with circular mouth; with 1 well developed tentacle terminating in large cnidocyst knob and 3 very large marginal bulbs without tentacles but with cnidocyst spurs, proximal part of tentacle hollow, distal part solid; with simple gonad, annular in mature specimens; without ocelli. Hydroid: Unknown.

Paragotoea bathybia Kramp, 1942 Paragotoea elegans = Paragotoea bathybia

### Genus Vannuccia Brinckmann-Voss, 1967:

Corymorphidae with usually a slightly asymmetrical umbrellar margin, with or without apical process; without exumbrellar tracks of cnidocysts; with small, simple marginal bulbs; with 1 swollen marginal tentacle, hollow for half its length and ending in long, large, oval to cylindrical swelling armed with cnidocysts.

Hydroid: Hydroids solitary, hydrocaulus long, cylindrical, slightly enlarged at its two extremities, aboral third of hydrocaulus with papillae and, more aborally,

numerous rooting anchoring filaments; hydrocaulus filled with parenchymatic endodermal cells presenting numerous peripheral longitudinal canals; hydrocaulus surrounded by a flexible perisarc extending slightly below hydranth; hydranth vasiform, with 12-14 oral moniliform tentacles carrying 4-6 cnidocyst clusters, with 16 to 20 very long aboral filiform tentacles with a more or less developed terminal swelling; with a parenchymatic diaphragm; medusa buds borne naked in clusters on short blastostyles just above aboral whorl of tentacles; asexual reproduction by transverse constriction of the basal part of the hydrocaulus.

*Vannuccia cargoi* (Vargas-Hernandez and Ochoa-Figuera, 1991) *Vannuccia forbesii* (Mayer, 1894)

## Genus Yakovia Margulis, 1989:

Corymorphidae with 4 radial canals but with only one marginal bulb bearing a single long marginal tentacle with numerous short terminal ramifications, each ending in capitate cnidocyst clusters; manubrium large extending beyond umbrella margin? (see above); «gonads» encircling central part of manubrium. Hydroid: Unknown.

Yakovia polinae Margulis, 1989

## Corymorphidae: conspecifics:

Altairina cargoi Vargas-Hernandez and Ochoa-Figueros, 1990 = Vannuccia cargoi

Altairina forbesi (Mayer, 1894) = Vannuccia forbesii

### Family Eleutheriidae Russell, 1953 (16):

Anthomedusae with usually a thickened continuous or broken ring of cnidocysts around umbrellar margin; with a circular mouth, simple or armed with cnidocysts knobs; with a variable number of radial canals, which may or not branch; «gonads» on manubrium, or on subumbrellar surface or in specialised dorsal brooding pouches; marginal tentacles hollow, variable in number, bifurcating in an upper branch armed with one or several cnidocysts clusters or

knobs and a lower unarmed branch terminating in an adhesive pad; with abaxial ocelli.

Hydroid: Stolonal reptant colonies; hydroids almost sessile, with an oral whorl of capitate tentacles; with or without aboral whorl of filiform tentacles; mouth with oral mucus gland cells forming a preoral cavity.

1.- upper tentacular branches with one cnidocyst knob = *Eleutheria* 1a.- upper tentacular branches with more than one cnidocyst knob = *Staurocladia* 

### Genus Eleutheria Quatrefages, 1842:

Eleutheriidae with a brood pouch above manubrium; with a thickened cnidocyst ring around umbrellar margin; manubrium simple; «gonads» reduced, hermaphroditic; with bifurcated tentacles, lower branch with adhesive disk, upper branch with only one terminal cluster of cnidocysts; asexual reproduction by budding from circular canal either from subumbrellar side (*E. claparedei*) or from exumbrellar side (*E. dichotoma*).

Hydroid: Hydranths with oral tentacles only.

Eleutheria claparedei Hartlaub, 1889

Eleutheria dichotoma Quatrefages, 1842

Genus Staurocladia Hartlaub, 1917:

Eleutheriidae adapted for crawling and walking; without brood pouch above manubrium; «gonads» around manubrium or developed in ectodermal manubrial pockets; with 6-11 radial canals some bifurcating shortly distal to manubrium; mouth circular with or without enidocyst knobs; with up to 60 marginal tentacles, dichotomous, upper branch with several enidocyst clusters, lower with adhesive organ; often asexual reproduction by medusa budding or by fission.

Hydroid: Hydranths with an oral whorl of capitate tentacles and with or without aboral filiform tentacles.

Staurocladia acuminata (Edmondson, 1930)

Staurocladia alternata (Edmondson, 1930) Staurocladia bilateralis (Edmondson, 1930) Staurocladia capensis (Gilchrist, 1918) Staurocladia charcoti Bedot, 1908 Staurocladia haswelli Briggs, 1920 Staurocladia hodgsoni (Browne, 1910) Staurocladia kerguelensis (Gilchrist, 1918) Staurocladia oahuensis (Edmonson, 1930) Staurocladia portmanni Brinckmann, 1964 Staurocladia schizogena Bouillon, 1978 Staurocladia ulvae Bouillon, 1978 Staurocladia vallentini (Browne, 1902) Staurocladia wellingtoni Schuchert, 1996

# Family Dicyclocorynidae Petersen, 1979 (1):

Only newly liberated medusa known; umbrella evenly rounded; manubrium stout; with simple circular mouth; 4 marginal tentacular bulbs of sarsiid type; 4 short marginal tentacles somewhat flattened with series of minute projections on each side and prominent, flattened spherical terminal knob of cnidocysts; without ocelli.

Hydroid: Colonies more or less branched, monopodial; hydranth with an oral whorl of 4-7 capitate tentacles and 1-3 close-set aboral whorls of 6-20 amphicoronate aboral tentacles; with free medusae or fixed sporosacs borne on hydranths.

Genus Dicyclocoryne Annandale, 1915:

With characters of the family.

*Dicyclocoryne filamenta* Annandale, 1915 = only newly liberated medusa known

Family Euphysidae Haeckel, 1879 (13):

Anthomedusae generally with an evenly rounded umbrella; without apical canal; without exumbrellar cnidocyst tracks; manubrium stoutly cylindrical, not extending beyond umbrella margin; mouth simple, circular; with 1-4 marginal tentacles, either unequally developed or of similar length, all of same structure; «gonads» encircling almost all length of manubrium.

Diagnoses after Bouillon (1995a) slightly emended, the Euphysidae comprise the following genera: *Cnidocodon* Bouillon, 1978; *Euphysa* Forbes, 1848 (= *Hypolytus* Murbach, 1899; *Hetaractis* Almann, 1864); *Euphysilla*, Kramp, 1955; *Euphysomma* Kramp, 1962; *Meiorhopalon* Salvini-Plawen, 1987; *Pinushydra*, Bouillon and Grohmann, 1990; *Siphonohydra* Salvini-Plawen, 1966. Only *Cnidocodon, Euphysa, Euphysilla* and *Euphysomma* have medusa stages.

Petersen (1990) recognised only two genera with medusae within the family Corymorphidae: *Corymorpha* and *Euphysa*. The *Euphysa* medusae being defined by him as follow: "Medusa with evenly rounded umbrella, without apical canal; with one to four tentacles unequally developed, but all of same structure, moniliform or modified moniliform; manubrium stout, cylindrical, with small round mouth, shorter than bell cavity:" The following genera were put in conspecificy with *Euphysa* by Peteresen: *Hypolytus*; *Heteractis*; *Meiorhopalon*; *Euphysomma*. Petersen's definition appears not well founded: *Euphysa flammea*, *Euphysa japonica*, *Euphysomma brevia*, for instance, have four identical tentacles and not unequally developed ones.

Hydroid: Where known, solitary, hydrocaulus without parenchymatic endoderm and peripheral canals; hydranth without parenchymatic diaphragm, with an oral whorl of short moniliform, capitate or filiform tentacles; with aboral tentacles moniliform or filiform in one or three close-set whorls or dispersed; often with an irregular whorl of 4-16 short papillae each with an endodermal statocyst-like structure or with an adhesive mucus organ; hydrocaulus surrounded by a reduced perisarc often of more or less gelatinous consistency or naked; with free medusa or fixed sporosacs.

1.- with 1- 4 marginal tentacles, either unequally developed or of similar length, usually moniliform or modifid moniliform = *Euphysa* 

1a.- with 4 marginal tentacles equally developed, not moniliform = 2

2.- marginal tentacles elongated, with one row of cnidocyst clusters along all their length and with a terminal knob = 3

2a.- marginal tentacles very short, each dividing in 3-5 short capitate branches = *Cnidocodon* 

3.- manubrium with quadrate base, «gonads» circular along all lenght of manubrium; marginal tentacles with numerous adaxial (8-11) or abaxial (6-9) transverse cnidocyst claps pending the species and 1 small terminal cluster = *Euphysilla* 

3a.- base of manubrium circular; «gonads» circular but leaving aboral part of manubrium free; manubrium with short rounded apical chamber; marginal tentacles with 2 to 4 abaxial shortly pedunculated cnidocyst knobs and a terminal cluster = Euphysomma

# Genus Cnidocodon Bouillon, 1978:

Corymorphydae with dome-shaped umbrella, without apical projection or apical canal; exumbrella with dispersed cnidocysts; 4 radial canals, with circular canal; 4 large marginal bulbs with an adaxial cnidocyst cushion; 4 short marginal tentacles ending in a cluster of 3-5 capitate branches, manubrium cylindrical, shorter than umbrella; «gonads» surrounding manubrium, leaving only most oral part free.

Hydroid: Unknown. *Cnidocodon leopoldi*, Bouillon, 1978 *Cnidocodon (Ramus) xiamenensis* Zhang and Wu, 1981 = *C. leopoldi*?

#### Genus Euphysilla Kramp, 1955:

Corymorphydae, with evenly rounded umbrella; manubrium with quadratic base; circular mouth; with four equally developed tentacles with adaxial or abaxial clasps and a terminal cnidocyst cluster; without gatric peduncle; mature «gonads» circular, surrounding all manubrium; without ocelli.

Hydroid: Unknown. Euphysilla peterseni Allwein, 1967 Euphysilla pyramidata Kramp, 1955

# Genus Euphysa Forbes, 1848:

Umbrella evenly rounded; without apical canal; 1-4 marginal tentacles often unequally developed but all of the same structure, tentacles usually moliniform. Hydroid: When known solitary, with hydrocaulus about twice as long as hydranth, embedded in a soft, sticky perisarc covered by mud and detritus; hydranth almost cylindrical, with rounded hypostome, with 3-10 oral capitate tentacles and up to 20 aboral moniliform tentacles; with an irregular whorl of papillae, each with an endodermal statocyst-like structure below aboral whorl of tentacles; asexual reproduction by constriction of the distal end of hydrocaulus and of budding of new hydranths with reversed polarity on lower part of mother hydranth; medusa buds borne singly or in clusters just above the aboral tentacles.

Euphysa aurata Forbes, 1848 Euphysa australis von Ledenfeld, 1884 = doubtful species Euphysa flammea (Linko, 1905) Euphysa japonica (Maas, 1909) ?Euphysa problematica Schuchert, 1996 = perhaps Dipurena ophiogaster (Schuchert in preparation.) Euphysa monotentaculata Zamponi, 1983 Euphysa ruthae Norenburg and Morse, 1983 Euphysa sp. Uchida, 1947 Euphysa tentaculata Linko, 1905 Euphysa tetrabrachia Bigelow, 1904 Euphysa vervoorti Brinckmann-Voss and Arai, 1997

Genus Euphysomma Kramp, 1962:

Euphysidae with broad manubrium, surrounded by a ring-like gonad leaving aboral part free; manubrium with a short apical chamber; mouth rim simple,

studded with cnidocysts; 4 short, hollow, identical, tentacles provided with abaxial shortly pedunculated cnidocyst knobs and a terminal cnidocyst cluster; without ocelli.

Hydroid: Unknown.

Euphysomma brevia Uchida, 1947

# Family Margelopsidae Uchida, 1927 (6):

Anthomedusae without apical projection; without cnidocyst tracks; with simple circular mouth; with «gonads» surrounding manubrium; with 4 radial canals; with solid, generally moniliform tentacles in marginal clusters, or at different levels on exumbrella; without ocelli; eggs may develop into actinulae on manubrium or into encysted resting stages.

Hydroid: Pelagic, solitary, hydranth vasiform, with one or several whorls of solid, filiform oral tentacles; with either two or three close-set, alternating whorls of aboral tentacles, or with numerous scattered aboral tentacles; hydrocaulus absent or reduced to a button-like processs; medusa buds on short blastostyles.

1.- umbrella with pairs of tentacles at several levels = *Climacocodon*1a.- umbrella with 4 perradial clusters of tentacles = 2
2.- tentacles all alike = *Margelopsis*2a.- tentacles of different size in a special arrangement; only juvenile medusae kown = *Pelagohydra*

Genus Climacocodon Uchida, 1924:

Margelopsidae with pairs of solid perradial tentacles at several levels on exumbrella; with actinulae on manubrium. Hydroid: As in *Margelopsis* but without vestige of hydrocaulus.

Climacocodon ikarii Uchida, 1924

Genus Margelopsis Hartlaub, 1897:

Margelopsidae with four perradial rounded tentacular bulbs on bell margin, each with two to six stiff solid tentacles irregularly distributed; with actinulae on manubrium.

Hydroid: With vasiform hydranth; without parenchymatic endodermal specializations; with one whorl of oral tentacles with cnidocysts in diffuse rings around all length and concentrated in small terminal knob (moniliform-like); with two or three close-set, altenating whorls of aboral tentacles with cnidocysts arranged as on oral tentacles; with a short, button-like vestige of hydrocaulus. *Margelopsis australis* Browne, 1910 *Margelopsis gibbesi* (McCrady, 1859)

Margelopsis haeckeli Hartlaub, 1897

Margelopsis hartlaubi Browne,1903

### Genus Pelagohydra Dendy, 1902:

Only known as medusa buds, not seen free; umbrella bell-shaped to quadrangular, mesoglea rather thick, with apical canal; exumbrella with many scattered cnidocycts; manubrium cylindrical with quadratic base; mouth simple; no «gonads» visible; with 4 radial canals and a circular canal; four large perradial marginal bulbs each with 6-7 slightly capitate, solid tentacles in a special arrangement: the most abaxial pair points sideways, the next pair projects downwards and is followed adaxially by a single median tentacle which also projects downwards and then 1-2 small tentacles projecting adaxially. Hydroid: Pelagic freely floating solitary hydranth without trace of hydrocaulus up to 35 mm long; hydranth body divided into a larger oval part (float) and a smaller, tubular oral part (proboscis); the float bears up to 150 scattered, tapering tentacles; the oral part of the hydranth is provided with up to 80 tentacles scattered over the distal three-quarters of its length; adnate to the proboscis wall; along the mouth rim are some very short, differently coloured tentacles; all tentacles filiform with slight terminal capitation; the float has a complicated internal anatomy consisting in an intricate structure of mesogleal lamellae and endodermal chambers which open in the gastric cavity of the proboscis; gonophores develop on branched blastostyles dispersed between the

aboral tentacles, up to 300 per animal; the blastostyles may bear up to 5 gonophores which develop into free medusae. *Pelagohydra mirabilis* Dendy, 1902

# Family Pennariidae McCrady, 1859 (2):

Anthomedusae reduced to short living eumedusoids; with manubrium not extending beyond umbrella margin; with a simple circular mouth or without mouth; with four radial canals; with «gonads» completely surrounding manubrium; with four permanently rudimentary tentacles, usually reduced to mere bulbs, with or without ocelli. Many of the reduced medusa species described in this family could be eumedusoids belonging to several Tubulariida or Zancleida families; only the few species which have their cycle known can be considered belonging really to the Pennariidae.

Hydroid: When known, arising from a network of creeping stolons and forming large, pinnate, feather-like colonies; hydrocaulus monosiphonic giving rise alternately from opposite sides to two series of numerous unbranched hydrocladia lying in one plane; longest hydrocladia in the middle of the colonies, gradually decreasing in length upwards and downwards; perisarc thick, firm; hydrocaulus and hydrocladia with terminal hydranths (monopodial); numerous hydranths on short pedicels originating on upper side of the hydrocladia; hydranths spindle or pear-shaped, with dome-shaped hypostome; with a whorl of 4-6 oral capitate tentacles, up to 18 capitate tentacles scattered or in more or less regular whorls on hydranth body and an aboral whorl of up to 16 semifiliform to slightly capitate aboral tentacles, 3-5 eumedusoids arising on short stalks just above aboral tentacles; sexes are separated per colony; eumedusoids free or not.

**Genus** *Pennaria* Goldfuss, 1820: Eumedusoid. Hydroid: With characters of the family. *Pennaria adamsia* von Lendenfeld, 1884? *Pennaria armata* Vanhöffen, 1911= generic position unclear

Pennaria disticha Goldfuss, 1820 Pennaria grandis Kramp, 1928? Pennaria pauper Kramp, 1959? Pennaria rosea von Lendenfeld, 1884? Pennaria vitrea Agassiz and Mayer, 1899 = doubtful species Pennaria wilsoni Bale 1913

# Family Tubulariidae Fleming, 1828 (18):

Anthomedusae usually with exumbrellar cnidocyst tracks; with 4 radial canals; usually with a circular mouth; with «gonads» encircling completely the manubrium; with 1-4 marginal tentacles; sexual reproduction often through actinula larvae; without ocelli.

Hydroid: Where known, solitary or colonial; hydranths vasiform with two sets of tentacles, oral tentacles capitate, moniliform, filiform or pseudofiliform in one to several close-set whorls (oral tentacles often slightly capitate or capitate in juvenile stages); with one whorl of long pseudofiliform or filiform aboral tentacles, with a more or less developed parenchymatic cushion under aboral tentacles whorl; hydrocaulus divided into a distal neck region covered by thin perisarc, and a proximal region which may be short and thick with tuber-like aboral processes, or long, cylindrical, or cone-shaped with basal disc or stolons covered by thicker perisarc; free medusae or sporosacs.

1.- with tentacular marginal bulbs = 2

1a.- without tentacular marginal bulbs = *Rhabdoon* 

2.- with normal, symmetrical umbrella = 3

2.a.- with asymmetrical umbrella, bell margin obliquely set to the vertical axis = *Hybocodon* 

3.- with longitudinal exumbrellar cnidocyst tracks or rows = Ectopleura

3a.- exumbrellar cnidocysts scattered singly or in clumps = *Plotocnide* 

Genus Ectopleura L Agassiz, 1862:

Tubulariidae with normal, symmetrical, rounded or pyriform umbrella; exumbrella with 8 longitudinal exumbrellar cnidocyst rows, issuing in pairs from tentacular bulbs; manubrium short at most reaching bell margin; with 2 opposite or 4 equally developed, simple perradial marginal tentacles, moniliform or with abaxial cnidocyst clusters; with 4 radial canals. Hydroid: Where known, solitary or colonial hydroids with high stems; hydranth vasiform with oral tentacles in one whorl; perisarc originates from collar on neck region and does not cover whole neck, hydrocaulus simple, with two rarely up to five internal longitudinal endodermic ridges. With free medusae, eumedusoid or fixed sporosacs.

*Ectopleura americana* Petersen, 1990 = only medusa buds in blastostyle known *Ectopleura bethae* (Warren, 1908) = only medusa buds known

Ectopleura dumortieri (van Beneden, 1844)

*Ectopleura grandis* Fraser 1944 = only medusa buds known ; perhaps eumedusoid?

*Ectopleura guangdongensis* Xu, Huang and Chen Xu, 1991 = *E. minerva*? *Ectopleura indica* Petersen, 1990 = only newly liberated medusa known *Ectopleura latitaeniata* Xu and Zhang, 1978

*Ectopleura mayeri* Petersen, 1990 = only medusa buds in blastostyle known *Ectopleura minerva* Mayer, 1900

*Ectopleura obypa* Migotto and Marques, 1999 = only immature medusa known *Ectopleura octagona* Thiel,1938 = crumpled specimen, probably *E. dumortieri Ectopleura pacifica* Thornely, 1900 = only medusa buds known

Ectopleura sacculifera Kramp, 1957

Ectopleura sp. Schuchert, 1996

*Ectopleura wrighti* Petersen, 1979 (description in Petersen 1990) *Ectopleura xiamenensis* Zhang and Lin, 1984

Remarks: Many nominal species of *Ectopleura* have recently been described only by their larval hydroid stage (see above) the medusae being known either as just liberated juveniles or as medusa buds, on the other hand some adult medusae have their cycle unknown and could correspond to some of those



hydroids. Rearing experiments seem thus necessary to elucidate the life cycles of those hydroids before assigning them a specific name.

## Genus Hybocodon L. Agassiz, 1862:

Tubulariidae bilaterally symmetrical, with umbrella margin at oblique angle to vertical axis; without pointed apical process; with or without exumbrellar cnidocyst tracks; manubrium cylindrical on short peduncle not extending beyond umbrellar margin; 4 radial canals, 1 short, 2 medium sized and one longer; with 1 simple or compound marginal bulb with 1-3 moniliform tentacles corresponding to the longest radial canal; with the 3 remaining perradial bulbs rudimentary.

Hydroid: Solitary, with high stems; oral tentacles in two whorls; perisarc originating just below hydranth and covering the whole neck region; eight or more longitudinal endodermic ridges.

Hybocodon atentaculata Uchida, 1947

*Hybocodon cryptus* Watson, 1984 = short lived eumedusoids

Hybocodon pendulus (L. Agassiz, 1862)

Hybocodon prolifer L. Agassiz, 1862

Hybocodon octopleurus Kao, 1958

Hybocodon unicus (Browne, 1902)

### Genus Plotocnide Wagner, 1885:

Tubulariidae with exumbrellar cnidocysts scattered singly or in clumps; with a dome-shaped apical chamber lined with vacuolated endodermal cells. Hydroid: Unknown.

Remarks: The systematic position of the single, rare, arctic species is doubtful. Mayer (1910) described a short gastric peduncle (see also Hartlaub, 1907) and considered it as a Protiara. For Uchida (1933) it could be conspecific with *Sarsia inabai* Uchida, 1933. An opinion shared by Kramp (1942) who considered that Uchida erroneously described ocelli in *Sarsia inabai* and expressed "no doubts "about the conspecificity of the two species. Kramp underlined the relationship of *Plotocnide* with the genus *Eucodonium*, including

both in the Tubulariidae sensus lato (Kramp, 1959a, 1961, 1968). Arai and Brinckmann-Voss (1980) and Bouillon, (1985a, 1995a) assigned also Plotocnide to the Tubulariidae. Bouillon (1978a, 1980) rediscovered Sarsia inabai twice, confirming Uchida's statement about the presence of abaxial ocelli, Sarsia inabai appears thus to be a valid species. For Naumov (1960, 1969) the genus *Plotocnide* is congeneric with *Eucodonium*. Petersen (1990) awaiting the discovery of their hydroid stage put *Plotocnide* in the Tubulariida incertae sedis. The cnidome of this species contains desmonemes and stenoteles (Hand and Kan, 1961) which agrees with its belonging to the Capitata Tubulariidae. They have no relationships with the genus Eucodonium whose cnidome contains euryteles and desmonemes and which has been rightly classified in a new family of Filifera, the Eucodoniidae, by Schuchert (1996). We tentatively maintain *Plotocnide* in the Tubulariidae awaiting more informations about their cycle, the presence in adult specimens of scattered or clumps of exumbrellar cnidocysts could perhaps correspond to reduced exumbrellar cnidocyst tracks.

Plotocnide borealis Wagner, 1885

? *Plotocnide incertae* (Linko, 1900) = doubtful position, belongs to an other genus

Genus Rhabdoon Keferstein and Ehlers, 1861:

Tubulariidae with single hollow marginal tentacle ending in large, complex knob of cnidocyst clusters; without marginal tentacular bulbs; manubrium occupying almost entire bell cavity; with vacuolated cells containing refractive droplets along 4 radial canals, at manubrium apex and bell margin; «gonads» surrounding distal 2/3 of manubrium.

Hydroid: Unknown.

Rhabdoon singulare Keferstein and Ehlers, 1861

### Tubulariidae with eumedusoids:

Genus Ralpharia Watson, 1980:

Only free or fixed eumedusoids known.

Hydroid: Solitary or colonial; hydranth with two or more whorls of filiform oral tentacles and one whorl of long aboral filiform tentacles; filmy perisarc around neck region secreted from groove between hydranth base and neck; cylindrical hydrocaulus filled with parenchymatic endoderm with 10-20 peripheral canals one of which is larger than the rest; hydrorhiza long, branched or unbranched buried in octocoral; medusa buds or fixed gonophores carried on dichotomously blastotyles with or without terminal cluster of nematophores. *Ralpharia coccinea* Watson, 1984 = free? eumedusoid *Ralpharia magnifica* Watson, 1980 = free eumedusoids *Ralpharia parasitica* (Korotneff, 1887) = free eumedusoid similar to *Propachycordyle* (see Wedler and Larson, 1986)

### Suborder Zancleida Russell, 1953 (29):

Capitata medusae with flask-shaped manubrium with quadrate or octogonal base and cylindrical mouth tube; usually interradial «gonads»; with exumbrellar cnidocyst pouches or tracks; with 0-2 or 4 marginal tentacles with or without abaxial cnidophores; marginal tentacles developed only at junction between radial and circular canals; with or without ocelli.

Hydroid: Floating or fixed colonies; fixed colonies arising either from simple creeping stolonal tubes, from an encrusting basal mat, from upright branched hydrorihza consisting of a central axis of perisarc covered by coenosarc, or from a calcified exoskeleton; hydranths monomorphic or polymorphic, with capitate or moniliform oral tentacles and with aboral tentacles either capitate, moniliform, ramified capitate, reduced or without tentacles; free medusae, eumedusoids or sporosacs.

1.- marginal tentacles without cnidophores = Porpitidae
 1a.- marginal tentacles usually with cnidophores = 2
 2.- medusae with 2 exumbrellar cnidocyst pouches on non-tentaculate perradial bulbs; pouches with macrobasic euryteles = Cladocorynidae
 2a.- medusae with 0 or 4 exumbrellar cnidocyst pouches with stenoteles = 3

3.- medusae with ocelli = Teissieridae

3a.- medusae without ocelli = Zancleidae

The Asyncorynidae and Rosalindidae are not included in the key having only undeveloped medusae known. The diagnosis of those families will however be given below.

## Family Asyncorynidae Kramp, 1949 (1):

Only newly liberated medusae known, with 4 tentacles with cnidophores; with exumbrellar cnidocyst pouches containing stenoteles.

Hydroid: Colonies with club-shaped hydranths with one oral whorl of four to six solid capitate tentacles and numerous solid moniliform aboral tentacles scattered over hydranth body; hydrocaulus short rising from creeping stolons; perisarc of both hydocaulus and hydrorhiza lamellar, complex, made up of numerous distinct inflated layers, with intracoenosarcal perisarcal tubular connections; with stolonal coenosarc locally divided by several longitudinal endodermal canals; medusa buds borne on lower third of hydranth.

Genus Asyncoryne Warren, 1908

See family characters.

Asyncoryne philippina Hargitt, 1924 = only medusa bud known Asyncoryne ryniensis Warren, 1908 = only juvenile immature medusa known

Family Cladocorynidae Allman, 1872 (2):

With only two exumbrellar pouches, containing macrobasic euryteles on non tentaculate perradial marginal bulbs; tentaculate perradial marginal bulbs very large, without cnidocyst pouches; tentacles with cnidophores; «gonads» interradial on manubrium.

Hydroid: With club-shaped hydranth, with moniliform or capitate oral tentacles in one whorl and moniliform or branched capitate aboral tentacles scattered or in several whorls; with cnidocysts on body wall arranged in conspicuous rounded patches; stem simple or slightly branched, rising from a creeping

stolon; gonophores carried singly or on short, branched pedicels, on lower or middle part of hydranth; with cryptomedusoids or free medusae.

# Genus Pteroclava Weill, 1931:

Cladocorynidae with 4 radial canals; with two big perradial tentaculate bulbs clasping the exumbrellar margin, without cnidocyst pouches, tentacles with about a hundred of abaxial cnidophores and with two small non-tentaculate perradial bulbs with cnidocyst pouches containing macrobasic euryteles; manubrium conical, slightly extruding from velar opening; «gonads» interradial over two thirds of manubrium, leaving oral region free. Hydroid: colonies growing on alcyonaceans and gorgonians, with perisarccovered hydrorhiza embedded in host tisssues; hydranth with up to 30 quasi moniliform tentacles scattered on an elongated body; one to four patches of big cnidocysts on the lower part of hypostome, under oral tentacles; gonophore as medusae borne singly or in groups in the mid region of hydranth. *Pteroclava crassa* (Pictet, 1893) = only medusa buds known *Pteroclava krempfi* (Billard, 1919)

### Family Porpitidae Goldfuss, 1818 (2):

Anthomedusae with umbrella presenting 4 or 8 tracks of cnidocysts issued from marginal bulbs and containing stenoteles; with 4 four or 8 radial canals and a circular canal; manubrium short, conical; with quadrate or octogonal base; with a circular mouth; «gonads» perradial or irregularly arranged perradially and interadially; with 2 opposite, perradial, capitate marginal tentacles and with or without 2 additional smaller capitate tentacles adaxial to the first, tentacles with macrobasic euryteles; zooxanthellae generally present. Hydroid: see below.

1.- with four radial canals; manubium with quadrate base; with four capitate tentacles = *Velella* 

1.a.- with eight radial canals; manubrium octogonal; with two capitate tentacles = *Porpita* 

#### Genus Porpita Lamarck, 1801:

Porpitidae with eight radial canals; with conical manubrium, with octagonal base; with two opposite marginal capitate tentacles and six non tentaculate bulbs; «gonads» 8, perradial; short exumbrellar cnidocyst tracks above each bulb.

Hydroid: Floating colonies, dark blue, diameter up to 30 mm, mostly smaller, with disk-shaped mantle and internal float, margin soft, flexible; central region firm, slightly convex, with a central pore and numerous stigmata; mantle with radiating endoderm canals; with an internal chitinous float consisting of a series of concentric chambers; a disks-shaped reservoir of cnidocysts lying between float and central gastrozooid; undersurface with one large central gastrozooid, a median circle of gastro-gonozooids, and a peripheral circle of dactylozooids; central gastrozooid short and broad with a terminal mouth, without tentacles or prominent cnidocyst clusters; gastro-gonozooids clavate, lacking tentacles but with prominent cnidocyst clusters scattered over body, medusae develop near base in clusters; dactylozooids with a distal whorl of 4 capitate tentacles, body with varying number of short, small capitate tentacles in 3 vertical rows. *Porpita porpita* (Linnaeus, 1758)

### Genus Velella Lamarck, 1801:

Porpitidae with 4 exumbrellar cnidocyst rows, with 4 radial canals; with two pairs of opposite, perradial tentacles, one short adaxial and one long abaxial, each tentacle with a large terminal cnidocyst cluster; two perradial marginal bulbs without tentacles; manubrium conical with quadrate base; with tubular mouth; «gonads» irregularly arranged perradially and interradially. Hydroid: Colonies floating on water surface, with flattened oval, elliptical float and a triangular sail; up to 40 mm long and 20 mm wide higher in the centre than at the edges; there are two mirror images of the animal (left and right sailing); float and sail are kept rigid by a chitin support covered by mantle tissue; margin of float soft and flexible; chitin float oval to slightly S-shaped with concentric air chambers; mantle tissue with network of endoderm canals;
in centre of underside a single large gastrozooid or "siphon" encircled by a ring of medusa producing gastro-gonozooids and a peripheral band of dactylozooids; central feeding zooid broadly oval with an elongated hypostome, without tentacles or medusa buds; gastro-gonozooids spindle-shaped with a swollen mouth region, lacking tentacles but with warts of cnidocyst clusters concentrated in distal half; on proximal half of hydranth numerous medusa buds growing in groups from short blastostyles; dactylozooids long and tapering, oval in cross section, with cnidocysts concentrated in two lateral bands on the narrow sides, mouth lacking; colours: float deeply blue when alive, medusa buds yellow-olive from symbiotic algae.

The prevalence of one form in one region may be due to sorting by prevailing winds (Edwards, 1966a).

Velella velella (Linnaeus, 1758)

### Family Rosalindidae Bouillon, 1985 (1):

Only non-liberated medusae known in one species (*Rosalinda naumovi*, see below), with two tentacles apparently provided with cnidophores. Hydroid: Colonies with plump, sausage-shaped hydranth with 30-50 scattered capitate tentacles, almost sessile, arising from a crust-like stolonal plate consisting of a thin perisarcal sheet covered by coenosarc and an external peridemal film, the whole supported by perisarcal spines and trabeculae forming a more or less thick framework of meshes; medusa buds or fixed gonophores carried singly or on short pedicels among proximal tentacles.

Genus Rosalinda Totton, 1949:

See above, one species with medusa: *Rosalinda naumovi* Antsulevich and Stepanjants, 1985 = only non liberated medusa buds known

Family Tessieridae Bouillon, 1974 (3):

With or without apical projection; with 4 radial canals; with four perradial exumbrellar cnidocyst pouches on base of radial canals, containing stenoteles; with only two perradial opposite marginal bulbs bearing tentacles with abaxial cnidophores; non tentaculate perradial bulbs small or absent; «gonads» interradial; one ocellus in the most apical part of the exumbrellar pouches. Hydroid: Polymorphic colonies, with broad sausage-shaped gastro-gonozooids with scattered capitate tentacles, with or without a clear whorl of oral tentacles; with one or two types of dactylozooids; with a basal hydrorhizal incrusting plate provided with spines penetrating the overlaying coenosarc; medusa buds carried single or in small groups among the tentacles of gastro-gonozooids.

Genus Teissiera Bouillon, 1974: With the characters of the family. Teissiera australe Bouillon, 1978 Teissiera medusifera Bouillon, 1978 Teissiera macrocystae Xu, Huang and Chen Xu, 1991= insufficient description and illustration, a Zanclea? Teissiera milleporoides Bouillon, 1974 Teissiera polypofera Xu, Huang and Chen Xu, 1991 = insufficient description and illustration = Zanclea medusopolypata?

#### Family Zancleidae Russell, 1953 (25):

Anthomedusae with bell-shaped umbrella; with 4 perradial exumbrellar cnidocyst pouches, either oval, clavate, elongate or linear, usually containing stenoteles; with a simple circular mouth, without oral tentacles (except in *Oonautes*, of uncertain family affinity; see Capitata incertae sedis); with 4 radial canals (exceptionally bifurcated in *Ctenaria*, of uncertain family affinity; see Capitata incertae sedis); marginal tentacles 0, 2 or 4 hollow, each bearing numerous abaxial cnidophores, with macrobasic euryteles; «gonads» usually interradial, rarely in a single mass around manubrium; without ocelli. Hydroid: Colonial; with creeping, stolonal, hydrorhiza, hydrocaulus unbranched; polyps monomorphic or polymorphic; gastrozooids either with oral

and aboral capitate tentacles, or with reduced capitate tentacles, or without tentacles; gonozooids and dactylozooids when present varied in expression; perisarc enveloping hydrocaulus and hydrorhiza not lamellar; stolonal coenosarc a simple tube.

1.- umbrella laterally compressed in tentacular plane = Zanclella\*
1a.- umbrella not laterally compressed= Zanclea and Halocoryne\*
\*Most of the various Zancleidae are actually not identifiable without a detailed study of the structure of the macrobasic euryteles cnidocysts of the polyp stage and the knowledge of their complete life cycle.

#### Genus Halocoryne Hadzi, 1917:

Either eumedusoids with no tentacles and no mouth; with 4 radial canals; with four perradial bulbs and four cnidocyst exumbrellar pouches; «gonads» surrounding manubrium; or medusae either *Zanclea*-like or with very elongated tentacular bulbs bearing short tentacles armed with short and stiff cnidophores. Hydroid: Stolonal, living in association with bryozoans; polymorphic; gastrozooids reduced, without tentacles; hypostome armed or not with cnidocysts; dactylozooids columnar, slender, usually with one or two terminal cnidocyst knobs, sometimes with lateral rows of cnidocysts as well, without mouth; reproduction by eumedusoids or free medusae. *Halocoryne epizoica* Hadzi, 1917 = eumedusoid *Halocoryne frasca* Boero, Bouillon and Gravili, 2000 = free medusae *Halocoryne pirainoid* Boero, Bouillon and Gravili, 2000 = free medusae

## Genus Zanclea Gegenbaur, 1857:

Zancleidae with bell-shaped umbrella, lateral walls evenly thin, mesoglea slightly thicker at the apex; with 4 exumbrellar perradial cnidocyst patches or tracts, with stenoteles; mouth simple, circular; with 4 simple radial canals; marginal tentacles 0, 2 or 4, with numerous abaxial extensile cnidophores with macrobasic euryteles; «gonads» interradial, no ocelli.

Hydroid: Colonial, stolonal with creeping hydrorhiza; hydrocaulus unbranched; often associated with bryozoans, bivalves and corals; polyps monomorphic or polymorphic; polymorphic colonies with gastrozooids, dactylozooids, gonozoids; gastrozooids on unbranched short pedicels, often almost sessile, elongated, cylindrical or claviform with an oral whorl of capitate tentacles and numerous aboral capitate tentacles scattered or in several whorls over the body; gonozooids and dactylozooids, when present, varied in expression. Zanclea alba (Meyen, 1834) Zanclea bomala Boero, Bouillon and Gravili, 2000 Zanclea divergens Boero, Bouillon and Gravili, 2000 Zanclea costata Gegenbaur, 1857 Zanclea dubia Kramp, 1959 Zanclea fanella Boero, Bouillon and Gravili, 2000 Zanclea giancarloi Boero, Bouillon and Gravili, 2000 Zanclea gilii Boero, Bouillon and Gravili, 2000 Zanclea hirohitoi Boero, Bouillon and Gravili, 2000 Zanclea medusapolypata Boero Bouillon and Gravili, 2000 Zanclea orientalis Browne 1916 = Halocoryne orientalis Zanclea polymorpha Schuchert, 1996 Zanclea retractilis Boero, Bouillon and Gravili, 2000 Zanclea sessilis (Gosse, 1853) Zanclea spp.

### Genus Zanclella Boero and Hewitt, 1992:

Either eumedusoids bearing exumbrellar cnidocyst chambers; with no tentacular bulbs, no mouth or tentacles; with «gonads» in a single mass encircling manubrium, or medusae with 2 tentacles with stiff cnidophores; with umbrella laterally compressed in the tentacular plane; with four radial canals and circular canal when adult; with exumbrellar cnidocyst chambers; «gonads» interradial on manubrium; medusae with only two radial canals and without circular canal at liberation.

Hydroid: Colonies living in association with bryozoans; polymorphic with gastrozooids usually with reduced number of tentacles and with dactylozooids. *Zanclella bryozoophila* Boero and Hewitt, 1992 = eumedusoid *Zanclella diabolica* Boero, Bouillon and Gravili, 2000 = free medusae *Zanclella glomboides* Boero, Bouillon and Gravili, 2000 = free medusae

## Capitata incertae sedis:

### Genus Ctenaria Haeckel, 1879:

With an apical cavity above manubrium; with 4 bifurcated radial canals; with two feathered marginal tentacles and simple unbranched oral tentacles; with eight adradial, meridional lines of cnidocysts on exumbrella and a cnidocyst track above the base of each marginal tentacle. Hydroid: Unknown.

?Ctenaria ctenophora Haeckel, 1879?

## Genus Oonautes Damas, 1936:

Exumbrella with 8 lines of cnidocysts which join to form 4 perradial tracks near the apex; manubrium very thick, narrowing in the bell cavity and distally expanded again; broad apical chamber; manubrium with with 3 separated rings of short tentacles, the two most oral ones somewhat larger; no marginal tentacles.

Hydroid: Unknown. ?*Oonautes hanseni* Damas, 1936 = doubtful species, observed only once.

### Genus Pteronema Haeckel, 1879:

Medusa with a brood-sac above manubrium; without meridional cnidocyst tracks upon exumbrella; manubrium spindle-shaped; mouth with 4 simple lips; with 4 marginal tentacles with an abaxial row of side branches with terminal cnidocyst knobs; without ocelli.

Hydroid: Unknown.

Pteronema darwini Haeckel, 1879 = Asyncoryne philippina Hargitt, 1924?

Tetraralphia Pagès and Bouillon, 1997:

Umbrella with scattered cnidocysts, with 4 stiff marginal tentacles terminating in a disc-shaped cnidocyst cluster, with four marginal bulbs with cnidocyst pads; manubrium quadrate; with four manubrial pouches and simple circular mouth, without ocelli.

Hydroid: Unknown.

Tetraralphia hypothetica Pagès and Bouillon, 1997?

## **ANTHOMEDUSAE INCERTAE SEDIS** (3):

### Genus Mitrocampana Fewkes, 1889:

Anthomedusae with an apical canal; with 6 radial canals; with 6 radially placed marginal tentacles, 5 of which are rudimentary and one well developed, club-shaped; manubrium conical to spindle-shaped, as long as bell cavity. Hydroid: Unknown. *Mitrocampana conica* Fewkes, 1889

# Genus Propachycordyle Thiel, 1931:

Anthomedusae with a bell-shaped body; manubrium short, spherical; gonads in the ectoderm; 4 radial canals; ring canal and velum present; tentacles, tentacular bulbs and ocelli are lacking.

Hydroid: Unknown.

*Propachycordyle canalifera* Thiel, 1931= perhaps eumedusoid of *Ralpharia parasitica*?

## Genus Thamnostylus Haeckel, 1879?:

Anthomedusae with two opposite hollow moniliform perradial tentacles; manubrium prismatic, very long extending largely from velar opening; mouth quadratic with 4 simple lips armed with cnidocysts; gonads folded adradial on aboral part of manubrium; four large, perradial, oral tentacles, several times dichotomously branched, with capitate ends, issued far away from mouth

opening, just under the gonads; with 4 radial canals; ring canal conspicuous; with abaxial ocelli on tentacular bulbs and on small non tentacular perradial bulbs.

Hydroid: Unknown.

? Thamnostylus dinema Haeckel, 1879 = not found since Haeckel's description

## Subclass Laingiomedusae Bouillon, 1978 (4):

Diagnosis: Medusae with an almost hemispherical umbrella divided by peronial grooves or similar structures so that umbrellar margin is lobed. Four radial canals; no typical circular canal but a solid core of endodermal cells around umbrella margin. Tentacles solid, inserted on the exumbrellar surface above margin; tentacular bulbs in contact or not with the endodermal circular core. Alternating with the tentacles there may be narrow exumbrellar cnidocyst bands or triangular ciliated fields. Manubrium simple, quadrangular, tubular or conical; mouth opening simple, quadrangular to circular. «Gonads» in four masses on the manubrium or as epidermal lining of interradial pockets of the manubrium. Marginal sense organs apparently missing. Cnidome: include macrobasic mastigophores or macrobasic euryteles. Sexual reproduction unknown. The Laingiomedusae represent the smallest group of Hydroidomedusa, two of the four species presently include in this subclass, Kantiella enigmatica and Laingia jaumotti present medusa budding with formation of a medusary nodule. This character and the presence of marginal tentacular bulbs allow their inclusion in the Hydroidomedusa. They present a mosaic of characters of Narcomedusae and Hydroidomedusa, more informations about their life cycle are needed to precise their affinities with the other subclasses of the last group.

#### Family Laingiidae Bouillon, 1978 (4):

Laingiomedusae with umbrella divided by peronial grooves or similar structures so that umbrellar margin is lobed; four radial canals; no typical circular canal but a solid core of endodermal cells around umbrella margin; tentacles solid, inserted on the exumbrellar surface above bell margin; alternating with the

tentacles there may be narrow exumbrellar cnidocysts bands or triangular ciliated fields; manubrium simple, quadrangular, tubular or conical; mouth opening quadrangular to circular; «gonads» in four masses on the manubrium or as epidermal lining of interradial pockets of the manubrium; marginal sense organs apparently missing. Cnidome include macrobasic mastigophores or macrobasic euryteles.

Hydroid: Unknown.

 1.- without exumbrellar cnidocyst bands = 2
 1a. with exumbrellar cnidocyst bands; marginal tentacular bulbs largely separated from marginal circular strand = *Kantiella* 2. with interradial ciliated fields; marginal bulbs only somewhat displaced towards exumbrella = *Fabienna* 2a.without interradial ciliated fields, marginal bulbs largely displaced towards exumbrella forming peronial-like structures= *Laingia*

## Genus Fabienna Schuchert, 1996:

Laingiidae with slightly lobed umbrellar margin; with four perradial tentacles with origin somewhat displaced towards the exumbrella; interradial triangular ciliated fields; larger cnidocysts confined to tentacle tips in one terminal cluster immediately followed proximally by an adaxial cluster; the two clusters may fuse in older individuals; cnidome includes macrobasic euryteles; «gonads» develop on manubrium only, in an interradial position.

Hydroid: Unknown.

*Fabienna oligonema* (Kramp, 1955) *Fabienna sphaerica* Schuchert, 1996

### Genus Kantiella Bouillon, 1978:

Laingiidae with exumbrellar cnidocyst bands; «gonads» on walls of four manubrial interradial pouches; 4 short marginal tentacles with terminal cluster of cnidocysts, above peronia-like structures. Hydroid: Unknown.

## Kantiella enigmatica Bouillon, 1978

### Genus Laingia Bouillon, 1978:

Laingiidae without exumbrellar cnidocyst tracks; «gonads» on manubrium in 4 interradial pouches; marginal bulbs largely displaced towards exumbrella, forming peronial-like structures; tentacles bent shortly after their point of origin. Hydroid: Unknown.

Laingia jaumotti Bouillon, 1978

### Subclass Leptomedusae Haeckel, 1866 (1879) (294 valid species).

Diagnosis: Medusae flatter than bell-shaped, typically with hemispherical or flattened umbrella. «Gonads» confined to the radial canals, exceptionally extending onto the proximal part of the 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*), with tentacular bulbs. Cnidome: often microbasic mastigophores and merotrichous isorhizae. Reproduction through a complex planula stage with cnidoblasts, interstitial cells, neural cells and usually two types of embryonic glandular cells.

Hydroid: "Thecata" hydroids; all parts of the colonies generally protected by rigid perisarc: hydrotheca, nematotheca and gonotheca; rarely with naked hydranths

## Order Conica Broch, 1910 (253 valid species).

Diagnosis: Hydranths with a simple, generally conical or rounded-conical hypostome, without a "buccal cavity" beneath mouth opening; medusa varied in expression.

1.- with only one manubrium = 2
1a.- with up to six manubria; without centripetal canals = Sugiuridae\*
2.- without statocysts or cordyli = 3
2a.- with statocysts or cordyli = 5

3.- with large, broad, gastric peduncle, with numerous filiform, solid tentaculiform structures without marginal bulbs and not in connection with circular canal = Orchistomatidae 3a- without a gastric peduncle = 44.- with base of manubrium attached over its whole surface; radial canals simple or bifucated = Melicertidae 4a.- with base of manubrium narrow; radial canals either branched or, if simple, irregularly arranged = Dipleurosomatidae 5.- with cordyli or cordyli-like structures = 55a.- with statocysts = 75.- manubrium with 4 perradial lobes connected with subumbrella; «gonads» on manubrium and extending on perradial lobes; with cordyli like structures = Tiarannidae 5.a.- manubrium without perradial lobes = 66.- with cordyli, «gonads» on radial canals usually contiguous with manubrium, without statocysts = Laodiceidae 6a.- with cordyli like structures; with «gonads» elongated forming linear sacs on radial canals, separated from manubrium; with or without open statocysts = Teclaiidae 7.- with open statocysts = 8 (see also 6a.-) 7.a.- with closed statocysts = 98.- open statocyts associated with ocelli = Tiaropsidae 8.a.- open statocysts without ocelli = Mitrocomidae 9.- with closed statocysts and adaxial ocelli = Barcinidae 9a.- with closed statocyst and without ocelli = 1010.- with distinct gastric peduncle; with 8 or many statocysts = Eirenidae 10a.- without distinct gastric peduncle = 1111.- manubrium very broad; with many (more than 16) radial canals; tentacle bulbs with excretory pores on or not on excretory papillae = Aequoreidae

11.a.- manubrium narrow; with normally 4-8 radial canals = 12

12.- tentacle bulbs with excretory pores, 4-8 radial canals (exeptionally 12) = Malagazziidae

12a.- tentacle bulbs without excretory pores = 1313.- tentacle bulbs with lateral cirri = Lovenellidae 13a.- tentacle bulbs without lateral cirri =1414.- exumbrella with marginal cirri = Cirrholoveniidae 14a.- exumbrella without marginal cirri = 1515.- with «gonads» divided in two lateral parts separated by a median groove = 16 15a.- «gonads» completely surrounding radial canals = 17 16.- with 8 marginal statocysts; without marginal tentaculae; with 4 radial canals = Phialellidae 16a.- with numerous statocyst; with marginal tentaculae; with 8 radial canals = Octocannoidae 17.- endodermal core of tentacles extending inwards from bell margin into bell mesoglea = Blackfordiidae 17a.- no endodermal tentacular expansions: Campanulariidae (see under Proboscoida)

Several paedomorphic Leptomedusae families, namely Aglaopheniidae, Haleciidae, Plumulariidae, Sertulariidae, with free medusa stage normally totally suppressed from their life cycle, being reduced to fixed sporosacs, may exceptionally present some secondarily pelagic reproductive and dispersive structures or swimming gonophores. Those structures are all of very uniform morphology and are consequently not included in the key. The Clathrozoidae with eumedusoids and the Lafoeidae with either eumedusoids or swimming gonophores or with no mature medusae known are not include in the above key either. The diagnosis of those families will however be found in the text.

\*See also *Gastroblasta*, Campanulariidae with numerous manubria but with centripetal canal.

Family Aequoreidae Eschscholtz, 1829 (24):

Leptomedusae with very wide, circular manubrium; usually without gastric peduncle; with many simple or branched radial canals; with «gonads» on radial canal separated from manubrium; with hollow marginal tentacles; usually with excretory pores or papillae; without marginal or lateral cirri; with closed statocysts; without ocelli.

Hydroid: Where known, colonies stolonal or, when erect, only little and sympodially branched; hydrothecae delicate, tubular, elongated, radially symmetrical, with an operculum formed by several triangular convergent segments being a continuation of the hydrothecal wall and not delimited basally by crease-line; hydranth contractile, with basal intertentacular web; no nematophores; gonothecae pedicellate, giving one or two medusae.

1.- radial canals branched or bifurcated =Zygocanna

1a.- radial canals simple, undivided = 2

2.- manubrium with circular rows of papillae in same number as radial canals = *Gangliostoma* 

2a.- manubrium without papillae = 3

3.- subumbrella with radial rows of gelatinous papillae = *Rhacostoma* 

3a.- subumbrella without rows of gelatinous papillae = Aequorea

Genus Aequorea Péron and Lesueur, 1810:

Acquoreidae with numerous simple radial canals; subumbrella without rows of gelatinous papillae.

Hydroid: when known, with the characters of the family. The hydroids are inadequate for diagnosis (see Cornelius, 1995).

Aequorea albida L.Agassiz, 1862

Aequorea australis Uchida, 1947

Aequorea coerulescens (Brandt, 1838)

Aequorea conica Browne, 1905

Aequorea cyanea de Blainville, 1834 = unidentifiable species

Aequorea floridana (L. Agassiz, 1862)

Aequorea forskalea Péron and Lesueur, 1810

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Aequorea globosa Eschscholtz, 1829 Aequorea krampi Bouillon, 1984 Aequorea macrodactyla (Brandt, 1834) Aequorea minima Bouillon, 1985 Aequorea papillata Huang and Xu, 1984 Aequorea parva Browne, 1905 Aequorea pensilis (Eschscholtz, 1829) Aequorea sp. Menon,1945 Aequorea tenuis (L. Agassiz, 1862) Aequorea victoria (Murbach and Shearer, 1902) Aequorea vitrina Gosse, 1853

### Genus Gangliostoma Xu, 1983:

Aequoreidae with very broad manubrium, with a basal circular row of papillae which are in same number as radial canals; without subumbrellar gelatinous papillae. Hydroid: Unknown.

Gangliostoma guangdongensis Xu, 1983

#### Genus Rhacostoma L. Agassiz, 1850:

Aequoreidae with numerous simple radial canals; subumbrella with radial rows of gelatinous papillae. Hydroid: Unknown. *Rhacostoma atlantica* L. Agassiz, 1850

#### Genus Zygocanna Haeckel, 1879:

Aequoreidae with numerous radial canals, branched or bifurcated; exumbrella sometimes with radial rows of gelatinous papillae. Hydroid: Unknown. Zygocanna buitendijki Stiasny, 1928 Zygocanna diploconus (Haeckel, 1879) Zygocanna pleuronota (Péron and Lesueur, 1810)

*Zygocanna purpurea* (Péron and Lesueur, 1810) *Zygocanna vagans* Bigelow, 1912

Family **Aglaopheniidae** Marktanner-Turneretscher, 1890 (2): Gonophores: as fixed sporosarcs, medusa stage totally suppressed from life cycle except exceptionally as swimming gonphores. Hydroid: with branched or unbranched upright monosiphonic or polysiphonic colonies; hydrothecae uniseriate, usually completely adnate, with or without marginal cusps, absent from hydrocaulus except in basalmost segment; nematophores with nematothecae; hydrothecae flanked with one or more pairs of lateral nematothecae, and typically with an unpaired median inferior nemathothea that may be doubled or have two terminal apertures, nemathothecae at least partially fused to hydrothecae, one chambered (monothalamic) and immovable; gonothecae usually as fixed sporosacs or exceptionally as swimming gonophores, unprotected or surrounded by recurved branches in phylactocarp, or nearly completely enclosed within corbula; gonothecae lacking nematothecae.

#### Genus Gymnangium Hincks, 1874:

Gonophores: usually fixed sporosacs, exceptionally one species with swimming gonophores

Hydroid: with characters of family, hydrocladia unbranched, alternate or opposite, giving off from oposite sides of hydrocaulus, hydrothecae only on hydrocladia; intrathecal septum present or absent; margin with or without cusps; each hydrotheca with a pair of lateral nemathotecae and a single adnate median inferior nematotheca conspicuously longer than hydrothecae and having more than one opening; gonotheca solitary, not protected by phylactocarps or corbulae.

Gymnangium ferlusi Billard, 1901 = swimming gonophores

Genus Macrorhynchia Kirchenpauer, 1872:

Gonophores: usually fixed sporosacs, exceptionally one species with swimming gonophores.

Hydroid: with characters of family, but hydrocladia unbranched and arranged pinnately; hydrothecae only on hydrocladia; margin dentate; abcauline or adcauline intrathecal septum present; cauline internodes with triangular nemathotheca; each hydrotheca with a pair of lateral nemathotecae and a single partly adnate median inferior nematotheca; gonothecae on unbrached phylactocarps occuring single or aggregated in pseudocorbula. *Macrorhynchia philippina* Kirchenpauer, 1872 = swimming gonophores

Family **Barcinidae** Gili, Bouillon, Pagès, Palanques and Puig, 1999 (1): Leptomedusae with closed marginal vesicles and adaxial ocelli; manubrium narrow; with no peduncle; with four simple radial canal; with four marginal tentacles with large, globular tentacular bulbs; without cirri or excretory pores; «gonads» linear, ribbon-like, surrounding radial canals. Hydroid: Unknown.

**Genus** *Barcino* Gili, Bouillon, Pages, Palanques and Puig, 1997: With the characters of the family. *Barcino foixensis* Gili, Bouillon, Pagès, Palanques and Puig, 1999

#### Family Blackfordiidae Bouillon, 1984 (4):

Leptomedusae with narrow, short manubrium; mouth with 4 long, fluted lips; without gastric peduncle; with numerous hollow tentacles; endodermal core of tentacles extends inwards from bell margin into bell mesoglea; with 4 radial canals; «gonads» completely surrounding radial canals; without permanent rudimentary tentacles; without marginal and lateral cirri; with numerous closed statocysts.

Hydroid: Where known, forming reptant, rarely slightly ramified colonies; hydrothecae with a diaphragm; operculum consisting of numerous triangular flaps meeting centrally and showing no clear demarcation from the hydrothecal margin; hydranth with a whorl of 12-16 filiform tentacles, intertentacular

membranous web present; gonothecae developing on stem or on stalk of the hydranths, one medusa at a time in each gonophore.

Genus Blackfordia Mayer, 1910: Medusae and hydroids with characters of family. Blackfordia manhattensis Mayer, 1910 Blackfordia polytentaculata Hsu and Chang, 1962 Blackfordia sp. Bouillon, 1988 Blackfordia virginica Mayer, 1910

## Family Cirrholoveniidae Bouillon, 1984 (2):

Leptomedusae with small manubrium; without peduncle; without excretory pores; with 4 simple radial canals; with «gonads» on radial canals separated from manubrium; with hollow marginal tentacles; with marginal cirri; without lateral cirri; with 4 or more closed statocysts; without ocelli. Hydroid: Where known, colonies stolonal, of «*Cuspidella*» type; hydrothecae sessile, tubular, closed by a pyramidal operculum formed by numerous flaps meeting centrally and not clearly demarcated from the hydrothecae; no intertentacular membranous web; gonothecae unknown.

Genus Cirrholovenia Kramp, 1959:

Cirrholoveniidae with 4-40 marginal tentacles; 7-8 marginal cirri between successive marginal tentacles. Hydroid: Only known in *C. tetranema*. *Cirrholovenia polynema* Kramp, 1959 *Cirrholovenia teranema* Kramp, 1959

Family **Clathrozooidae** Stechow, 1921 emend. Hirohito, 1967 (1): Hydroid: colonies arborescent, with a skeleton of complexly anastomosing chitinous stolons; hydrothecae tubular, wholly or largely embedded in skeleton; hydranths cylindrical, deeply retractile in hydrothecae, with a single whorl of filiform tentacles around hypostome; nemathothecae tubular scattered on

surface of skeleton; gonophores developed in anastomoses of stolons, giving or fixed sporosacs or free eumedusoids.

**Genus** *Clathrozoon* Spencer, 1891: As free eumedusoid Hydroid: With the characters of the family. *Clathrozoon wilsoni* Spencer, 1891

### Family **Dipleurosomatidae** Russell, 1953 (6):

Leptomedusae with manubrium with narrow base; with 3, 4 or more radial canals either branched or, if simple irregularly arranged; with «gonads» on radial canals separated from manubrium; with hollow or solid? marginal tentacles; without marginal or lateral cirri; without statocysts or cordyli, ocelli may be present.

Hydroid: "Cuspidella"-like, only known from rearing in Dipleurosoma typicum.

1.- radial canal regularly arranged and branched, all branches reaching circular canal = 2

1a.- radial canals irregularly arranged, simple or irregularly branched = *Dipleurosoma* 

2.- the 4 main canals not continued perradially to circular canal, but each divided into two canals with lateral branches; «gonads» adjacent to manubrium = *Dichotomia* 

2a.- the 4 main canals continued perradially to ring canal giving rise to lateral branches; «gonads» on distal parts of the canals = 3

3.- each of the 4 canals with one pair of simple unbranches lateral branches = *Cannota* 

3a.- main canals as well as lateral branches repeatedly branched = Cuviera

Genus Cannota Haeckel, 1879:

Dipleurosomatidae with 4 radial canals, each giving rise to two simple unbranched side branches; which join circular canalon either side of the main canal; 12 «gonads» on the four main canals and side branches. Hydroid: Unknown. *Cannota dodecantha* Haeckel, 1879

### Genus Cuviera Péron, 1807:

Dipleurosomatidae with 4 main radial canals, which branch repeatedly, all branches joining circular canal; «gonads» on terminal branches of canals. Hydroid: Unknown. *Cuviera carisochroma* Péron, 1807 *Cuviera huxleyi* (Haeckel, 1879)

## Genus Dichotomia Brooks, 1903:

Dipleurosomatidae with 4 main radial cannals once bifurcating into two diverging branches, each of which gives rise to lateral branches all reaching circular canal; «gonads» adjacent to manubrium, extending outwards along the canals and their branches. Hydroid: Uknown. *Dichotoma cannoides* Brooks, 1903

### Genus Dipleurosoma Boeck, 1866:

With 5 or more main radial canals some or all of which branch iregularly; radial canals originate from manubrium or branching at short distance of manubrium and normally join circular canal; with numerous tentacles; with adaxial ocelli; with or without club-shaped bodies.
Hydroid: See family characters *Dipleurosoma collapsum* (Mayer, 1900) = Orchistoma collapsa
?Dipleurosoma gemmifera Thiel, 1938 = Gastroblasta?
Dipleurosoma ochraceum Mayer, 1910 = Wuvula ochracea
Dipleurosoma pacificum Agassiz and Mayer, 1902
Dipleurosoma typicum Boeck, 1886

#### Family Eirenidae Haeckel, 1879 (63):

Manubrium small, usually on rather well differentiated gastric peduncle; 4-6 simple radial canals running from circular canal across underside of bell and along peduncle to manubrium; with or without excretory papillae or pores; with hollow tentacles; with or without cirri or marginal warts; «gonads» on radial canals separated from manubrium, in each species on well defined part(s) of radial canal; 8 to many statocysts; without ocelli.

Hydroid: Colonies either stolonal, erect, ramified, or parasitic on bivalves, or comprising a single polyp budding totally into a single medusa (*Eirene hexanemalis*); young colonies of erect forms with cylindrical hydrothecae with diaphragm and folded pleated operculum formed by convergent flaps not demarcated from the hydrothecal rim (*Campanulina* type), in older colonies of this type, the operculum is generally lost and the hydotheca is reduced to a perisarcal collar, looking like a haleciid hydrotheca; in stolonal colonies also the hydrotheca is usually reduced or absent, the hydranths, naked, being borne directly on hydrorhiza or on short pedicels (*Campanopsis* type); commensal species lack totally perisarc, they are affixed to host by a pedal disc, in all forms the hydranths are elongated, with filiform tentacles in a single amphicoronate whorl; intertentacular web present; nematophores absent; gonophores on hydranths, hydrocaulus, or hydrorhiza, naked or more usually at least initially in a gonotheca.

1.- with more than 8, typically with indefinite number of statocysts = 2 1a.- with usually 8 statocysts, rarely 12; without excretory papillae = 6 2.- without cirri; with or without excretory papillae = 3

2a.- with cirri = 4

3.- «gonads» only on subumbrellar part of radial canals; without marginal warts *= Eirene* 

3a.- «gonads» along all length of radial canals; with marginal warts = Tima 4.- with lateral cirri at base of some or all marginal tentacles = 5

4a.- with marginal cirri ; «gonads» only on subumbrellar part of radial canals =Phialopsis 5.- with «gonads» restricted to subumbrellar parts of radial canals = *Helgicirrha* 5a.- with «gonads» on entire length of radial canals = Irenium 6.- reduced medusae without marginal tentacles = Eugymnanthea6a.- normal medusae, with marginal tentacles = 77.- without cirri = 97a.- with cirri = 88.- with lateral cirri on marginal warts and usually also on marginal tentacles = Eutima 8a.- with marginal cirri; with very long lips = Eutimalphes 9.- without cirri and marginal warts, «gonads» restricted to subumbrella = Eutonina 9a.- without cirri, with marginal warts, with «gonads» along entire length of radial canals = *Neotima* Genus Eirene Eschscholtz, 1829:

Eirenidae with distinct gastric peduncle; without marginal or lateral cirri or marginal swellings; with or without excretory pores; 4- 6 simple radial canals; «gonads» on subumbrellar part of radial canals, not extending onto gastric peduncle; numerous statocysts. Hydroid: *Campanopsis* or *Campanulina* type, see family characters. *Eirene brevigona* Kramp, 1959 *Eirene brevistylis* Huang and Xu, 1994 *Eirene ceylonensis* Browne, 1905 *Eirene chiaochowensis* Kao, Li Fung-Lu , Chang and Li Hien-Lun, 1958 = *E. lactea Eirene elliceana* Agassiz and Mayer,1902 *Eirene fexanemalis* (Goette, 1886) *Eirene kambara* Agassiz and Mayer, 1899 *Eirene lactea* (Mayer,1900)

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*Eirene lacteoides* Kubota and Horita, 1992 *Eirene menoni* Kramp, 1953 *Eirene mollis* Torrey, 1909 *Eirene palkensis* Browne, 1905 *Eirene parvitentaculata* Bouillon, 1984 *Eirene proboscidea* Bouillon and Barnett, 1999 *Eirene pyramidalis* (L. Agassiz, 1862) *Eirene sp.* Calder, 1991 *Eirene tenuis* (Browne, 1905) *Eirene viridula* (Péron and Lesueur, 1810)

#### Genus Eugymnanthea Palombi, 1935:

Eumedusoids with 8 marginal statocysts containing 1 to 4 statoliths pending the species, «gonads» on radial canals; with or without manubrium; without marginal tentacles

Hydroid: Hydroids living in the mantle cavity of mollusc bivalves; hydranth tubular, without hydrotheca, with a conical hypostome; with a single whorl of about 20-24 filiform tentacles; with an intertentacular membranous web, fixed to the host by a basal disc; often young hydranths budding from the middle part of the primary hydranth body; 1-2 medusa buds at the basal part of the hydranth.

Eugymnanthea inquilina Palombi, 1935 Eugymnanthea japonica Kubota, 1979

#### Genus Eutima McCrady, 1859:

Eirenidae with distinct gastric peduncle; with lateral cirri (difficult to observe and often destroyed after fixation); with marginal swellings or warts; without excretory pores; 4 simple radial canals; «gonads» on radial canals, either beneath subumbrella or on gastric peduncle or on both; with 8 (exceptionally 12) statocysts.

Hydroid: Campanulinid colonies formed either by single hydranths or by erect colonies arising from creeping stolons or by epizoic naked polyps; in non

epizoic forms, hydrocaulus with smooth perisarc, young colonies with cylindrical hydrothecae with diaphragm and a folded pleated operculum formed by convergent flaps not demarcated from the hydrothecal rim (Campanulina type), in older colonies of this type, the operculum is generally lost and the hydotheca is reduced to a perisarcal collar looking like a haleciid hydrotheca; tentacles usually connected basally by a membranous web. Eutima (Eutimalphes) brownei Torrey, 1909 Eutima cirrhifera Kakinuma, 1964 = Eutima japonica Eutima coerulea (L. Agassiz, 1862) Eutima commensalis Santhakumari, 1970 *Eutima cuculata* Brooks, 1883 = doubtful species; systematic position doubtful Eutima curva Browne, 1905 Eutima gegenbauri (Haeckel, 1864) Eutima gentiana (Haeckel, 1879) Eutima gracilis (Forbes and Goodsir, 1851) Eutima hartlaubi Kramp, 1958 Eutima japonica Uchida 1925 Eutima levuka (Agassiz and Mayer, 1899) Eutima longigonia Bouillon, 1984 Eutima mira McCrady, 1859 Eutima modesta (Hartlaub, 1909) Eutima mucosa Bouillon, 1984 Eutima neucaledonia Uchida, 1964 *Eutima orientalis* (Bowne, 1905) = *E. mira*? Eutima ostrearum Mattox and Crowell, 1951 Eutima sapinhoa Narchi and Hebling, 1975 Eutima suzannae Allwein, 1967 Eutima variabilis McCrady, 1859

Genus Eutymalphes Haeckel, 1879:

Eirenidae with broad gastric peduncle; mouth with complexly folded, very large lips; with eight adradial statocysts; with numerous marginal tentacles; with marginal cirri; with a few marginal warts. Hydroid: Unknown.

*Eutimalphes pretiosa* Haeckel, 1879 = observed only once.

#### Genus Eutonina Hartlaub, 1897:

Eirenidae with 8 statocysts; without cirri; without marginal warts; «gonads» restricted to subumbrella, not extending onto peduncle.

Hydroid: Where known, of campanulinid erect type, hydrotheca very delicate, in young specimens cylindrical, with a diaphragm and a conical operculum formed by convergent sharp flaps not demarcated from the hydrothecal rim by crease-line; in old specimens the hydrotheca disintegrates, leaving just a crumpled membranous collar sheath around the basal part of the hydranth; hydranth very long, with up to 20 amphicoronate tentacles linked by a basal web; gonotheca cylindrical, tapered below, squarely-truncate above, arising from stem just under a hydranth.

*Eutonina indicans* (Romanes, 1876) *Eutonina scintillans* (Bigelow, 1909)

#### Genus Helgicirrha Hartlaub, 1909:

Eirenidae with lateral cirri at the base of some or all marginal tentacle bulbs; with excretory papillae.

Hydroid: Where known, a campanopsid; colonies with a net like hydrorhiza giving rise to unbranched upright hydranths; hydrorhiza and base of hydranths enclosed in a thin and sticky perisarc; hydranth club-shaped, with a conical hypostome surrounded by 26 to 30 amphicoronate filiform tentacles linked by a small basal intertentacular membranous web; medusa buds borne in the middle of hydranth or sometimes even higher, single or up to three per hydranth. *Helgicirrha brevistyla* Xu and Huang, 1893 *Helgicirrha cari* (Haeckel, 1864) *Helgicirrha cornellii* Bouillon, 1984

Helgicirrha danduensis (Bigelow, 1904) Helgicirrha gemmifera Bouillon, 1984 Helgicirrha irregularis Bouillon, Boero and Seghers, 1988 Helgicirrha malayensis (Stiasny, 1928) Helgicirrha medusifera (Bigelow, 1909) Helgicirrha schulzei Hartlaub, 1909 Helgicirrha weaveri Allwein, 1967

### Genus Irenium Haeckel, 1879:

Eirenidae with numerous statocysts; with numerous marginal warts; marginal tentacles and warts with lateral cirri; mature «gonads» along entire radial canals. Hydroid: Unknown. *Irenium alabiatum* Zamponi, Suárez-Morales and Gasca, 1999 = manubrium missing, incomplete specimens? *Irenium labiatum* Zamponi, Suárez-Morales and Gasca, 1999 *Irenium quadrigatum* Haeckel, 1879 *Irenium teuscheri* (Haeckel, 1879)

Genus Neotima Petersen 1962: Eutimidae with 8 statocysts, without cirri; with marginal warts; with «gonads» on entire length of radial canals. Hydroid: Unknown. Neotima lucullana (Delle Chiaje, 1822) Neotima peterseni Bouillon, 1984

#### Genus Phialopsis Torrey, 1909:

Eirenidae with short gastric peduncle; with marginal cirri; without excretory pores; with «gonads» restricted to subumbrellar portion of radial canals; with numerous statocysts. Hydroid: Unknown. *Phialopsis diegensis* Torrey, 1909

### Genus Tima Eschscholtz, 1829:

Eirenidae with distinct gastric peduncle; without cirri; with marginal warts; «gonads» upon entire lenght of radial canals; with numerous statocysts. Hydroid: Poorly known, probably of "*Campanulina*" type. *Tima bairdi* (Johnston, 1833) *Tima flavilabris* Eshscholtz, 1829 *Tima formosa* L.Agassiz, 1862 *Tima saghalinensi* Bigelow, 1913

### Family Haleciidae Hincks, 1868 (1):

Gonophore: As fixed sporosarcs, medusa stage totally suppressed from life cycle except exceptionnally as swimming gonophores. Hydroid: stolonal or erect colonies arising from a creeping hydrorhiza; hydrothecal rim usually even, sometimes recurved, lacking operculum; renovation common; hydrothecal desmocytes large often birefringent; hydrothecal pedicel often lacking; hydrotheca shallow; hydranth much larger than hydrotheca, often robust, with or without intertentacular web; nematophores, nematothecae and nematodactyls present or absent; gonothecae solitary or grouped into a glomulus; typically sexually dimorphic, infrequently with naked gonophores.

Genus Nemalecium Bouillon, 1986:

Gonophore: As swimming gonophores.

Hydroid: with characters of the family, but hydrothecae given off alternatively in two opposite rows from hydrocaulus and from branches when present; intertentacular web absent, base of tentacles enveloped by gland cells; nematophores absent, usually with a pair nematodactyls situated between tentacular whorl and curving over hypostome; gonophores giving short lived swimming gonophores; gonothecae solitary urn to cone-shaped. *Nemalecium lighti* Hargitt, 1924 = short lived swimming gonophores

Remarks: for the genera Campalecium and Hydranthea see Lovenellidae.

#### Family Lafoeidae Hincks, 1868 (5):

When known, either swimming gonophores with a velum; 4 radial canals; 4 atentaculate marginal bulbs; «gonads» on manubrium, or liberable eumedusoids with mature «gonads» on radial canal, or free but only immature medusa known, various in expression, with 2 to 8 tentacles; with or without ocelli; with short manubium; with or without oral lips; with 4 or more radial canals. Hydroid: Colonial, stolonal or erect, arising from a creeping hydrohiza, hydrothecae varying from tubular to campanulate in shape; radially or bilaterally symmetrical, adherent or pedicellate; margin entire; operculum usually absent; diaphragm present or absent; hydranth with a conical hypostome surrounded by a whorl of filifom tentacles; abcauline diverticulum present or absent; nematophores present or absent; gonophores see above; gonothecae either solitary or aggregated into coppinia or scapus.

1.- with swimming gonophores = *Anthohebella* 1a.- with eumedusoids or free medusae = *Hebella* 

**Genus** *Anthohebella* Boero, Bouillon and Kubota, 1997: As swimming gonophores with a velum; 4 radial canals; 4 atentaculate marginal bulbs; «gonads» on manubrium. Hydroid: see family characters. *Anthohebella brevitheca* (Leloup, 1938) = swimming gonophores *Anthohebella najimaensis* (Hirohito, 1995) = swimming gonophores *Anthohebella parasitica* (Ciamician, 1880) = swimming gonophores *Anthohebella tubitheca* (Millard and Bouillon, 1975) = swimming gonophores

#### Genus Hebella Allman, 1888:

Either liberable eumedusoids with mature «gonads» on radial canals, or medusa already mature at liberation with 4 radial canals, each with a proximal gonad; 4 perradial atentaculate bulbs and 4 small interradial atentaculate bulbs; manubium short; mouth and gastric cavity present; during life span some

tentacles and more marginal bulbs may grow, or free but only immature medusa known, various in expression, with 4 or more radial canals; with 2 to 4 perradial tentacles, sometimes with 4 developing interradial marginal tentacles and adradial atentaculate bulbs; with or without ocelli; with short cruciform manubium; with or without oral lips Hydroid: see family characters. *Hebella calcarata* (L. Agassiss, 1862) = only juvenile medusa known Hebella crateroides Ritchie 1909 = only medusa buds kown *Hebella contorta* Marktanner-Turneretscher, 1890 = eumedusoids *Hebella cylindrica* (Von Lendenfeld, 1885) = only medusa buds known *Hebella dissymetrica* Billard, 1933 = medusae mature at liberation *Hebella furax* Millard, 1957 = only young medusae known Hebella muscensis Millard and Bouillon, 1975 = only medusa buds known Hebella plana Ritchie, 1907 = only medusa buds known Hebella scandens (Bale, 1888) = only juvenile medusae known; perhaps a Staurodiscus Haeckel, 1879 medusa? Hebella striata Allman, 1888 = only medusa buds known

### Family Laodiceidae Agassiz, 1862 (36):

Leptomedusae with marginal cordyli with or without cnidocysts; with 4, 8, or more simple or branched radial canals; marginal tentacles hollow; «gonads» on radial canals, on radial canals and lobes of the manubrium or into manubrial pouches; with or without marginal cirri; with or without adaxial ocelli; without statocysts.

Hydroid: Where known, "*Cuspidella*" type; colonies stolonal; hydrotheca tubular, sessile, sometimes with basal constriction at origin, or exceptionally a poorly delimited pedicel (*Ptychogena*); hydrotheca often with transversal growth-rings; operculum conical comprising several pleated flaps meeting centrally, with visible crease-line basally; no intertentacular web, tentacles amphicoronate; no nematophores; gonothecae where known resembling hydrothecae but larger.

1.- cordyli with zooxanthellae = Wuvula 1a.- cordyli without zooxanthellae = 22.- radial canals closed = 32a.- radial canals open grooves forming large cruciform mouth = *Staurophora* 3.- with four radial canals = 53.a.- with 6 or more radial canals = 44.- with eight simple, unbranched radial canals = *Melicertissa* 4a.- some or all of the radial canals dichotomously branched, all branches joigning ring canal but primary radial canals not proceeding to ring canal = *Toxorchis* 5.- radial canals with one or a few pairs of lateral branches, primary radial canals proceeding straight to ring canal = *Staurodiscus* 5a.- radial canals simple = 66.- manubrium with perradial lobes or pouches = 76a.- manubrium without marginal perradial pouches; «gonads» simple, wavy along radial canals, sometimes adjacent to manubrium; usually some or all tentacular bulbs with adaxial ocelli = Laodicea 7.- manubrium with funnel-shaped lobes; radial canals with lateral diverticulae in which the «gonads» are placed; without cirri and ocelli = Ptychogena 7a.- with well developed manubrial perradial pouches; «gonads» on proximal part of manubrium and in manubrium pouches, germ cells developing on numerous lateral lamellar folds of the proximal part of the radial canals included in the pouches; with ocelli, with marginal cirri = Guillea

**Genus** *Guillea* Bouillon; Pages; Gili; Palanques; Puig and Heussner (in press): Laodiceidae with well developed manubrial perradial pouches; with complex «gonads» on proximal part of manubrium and in manubrial pouches, germ cells developing in manubrial pouches on numerous lateral lamellar folds of the proximal part of the radial canals; with marginal cirri and ocelli. Hydroid: Unknown.

Guillea canyonincolae Bouillon Gili and Pagès, 2000

Genus Laodicea Lesson, 1843:

Laodiceidae with small manubrium, sometimes with small perradial lobes; with four radial canals, simple or with short lateral diverticula; with simple wavy «gonads»; with or without marginal cirri; with or without adaxial ocelli. Hydroid of "Cuspidella" type, see family characters; hydrothecae sessile. Laodicea brevigona Allwein, 1967 Laodicea chapmani Günther, 1903 = doubtful species ?Laodicea eucope (Haeckel, 1879) = systematic position doubtful Laodicea fertilis (von Lendenfeld, 1884) Laodicea fijiana Agassiz and Mayer, 1899 *Laodicea indica* Browne, 1905 = *L. undulata*? Laodicea marama Agassiz and Mayer, 1899 Laodicea minuscula Vannucci, 1957 *Laodicea neptuna* Mayer, 1900 = doubtful species Laodicea ocellata Babnik, 1948 = doubtful species Laodicea pulchra Browne, 1902 Laodicea undulata (Forbes and Goodsir, 1851)

#### Genus Melicertissa Haeckel, 1879:

Laodiceidae with 8 simple radial canals; with adaxial ocelli; with or without cirri.

Hydroid: Unknown.

Melicertissa adriatica Neppi, 1915

Melicertissa clavigera Haeckel, 1879

Melicertissa malayica (Maas, 1905)

Melicertissa mayeri Kramp, 1959

Melicertissa orientalis Kramp, 1961

Melicertissa platygastra Nair, 1951

Melicertissa rosea Bouillon, 1984

Melicertissa sp. Kramp, 1965

Genus Ptychogena A. Agassiz, 1865:

Laodiceidae with four radial canals giving rise to lateral diverticula, in which the «gonads» are located; manubrium with funnel-shaped perradial lobes; without cirri; without ocelli. Hydroid: Unknown. *Ptychogena antarctica* Browne, 1907 *Ptychogena aurea* Vanhöffen, 1912 = *Chomatonema rubrum*? *Ptychogena californica* Torrey, 1909 *Ptychogena crocea* Kramp and Damas, 1925 *Ptychogena hyperborea* Kramp, 1942 *Ptychogena lactea* A Agassiz, 1865 *Ptychogena longigona* Maas, 1893 = *Laodicea undulata*?

## Genus Staurodiscus Haeckel 1879:

Laodiceidae with four radial canals, each giving rise to one or more pairs of lateral branches which may or not communicate with the circular canal; primary radial canals proceeding straight to the circular canal; «gonads» on the main 4 radial canals and branches; with adaxial ocelli; without marginal cirri. Hydroid: Perhaps a hebellid (see Paes De Andrade and Migotto, 1997). *Staurodiscus brooksi* (Mayer, 1910) *Staurodiscus gotoi* (Uchida, 1927) *Staurodiscus heterosceles* Haeckel,1879 *Staurodiscus nigricans* Agassiz and Mayer, 1899 *Staurodiscus quadristoma* Bouillon, 1984 *Staurodiscus tetrastaurus* Haeckel, 1879 *Staurodiscus vietnamensis* Kramp, 1962

## Genus Staurophora Brandt, 1834:

Laodiceidae with unusual cross-shaped manubrium; mouth opening extending along the 4 radial canals transformed for a long distance into open grooves, only most distal parts remaining free and closed; mouth arms slit-like, with strongly folded lips; «gonads» on diverticula in lateral walls of cruciform, enlarged, mouth-radial canal complex; without cirri; with adaxial ocelli.

Hydroid: A typical cuspidellid, hydrotheca sessile; gonothecae unknown. *Staurophora mertensii* Brandt, 1834 *Staurophora purpurea* Foerster, 1923 = *Foersteria purpurea* 

### Genus Toxorchis Haeckel, 1879:

Laodiceidae with 4, 6, or more main radial canals, some or all branching dichotomously one or more times, all branches reaching circular canal, primary radial canals not extending to circular canal; «gonads» on outermost branches; numerous tentacles and cordyli; with or without cirri; with or without ocelli. Hydroid: Unknown *Toxorchis arcuatus* Haeckel, 1879 *Toxorchis kellneri* Torrey, 1909 *Toxorchis milleri* Bouillon, 1984 *Toxorchis polynema* Kramp, 1959 *Toxorchis thalassinus* (Péron and Lesueur, 1810)

### Genus Wuvula Bouillon, Seghers and Boero, 1988:

Laodiceidae with more than 4 radial canals, sometimes partially ramified; with numerous cordyli modified in vesicles enclosing a great number of zooxanthellae; with adaxial papillae on the marginal tentacular bulbs, on the cordyliform vesicles and the rudimentary bulbs when present; no ocelli. Hydroid: Unknown. *Wuvula fabietti* Bouillon, 1988

Wuvula ochracea (Mayer, 1910)

### Family Lovenellidae Russell, 1953 (31):

Leptomedusae with short manubrium; without gastric peduncle; without excretory pores; with 4 simple radial canals; marginal tentacles hollow, with lateral cirri; without marginal cirri; «gonads» on radial canals, not reaching manubrium; without or with 8 (exceptionally 4 or 12) or indefinite number of statocysts, 16 or more when adult; no ocelli.

Hydroid: Colonies stolonal or erect, sympodial; hydrotheca pedicellate, elongate, everted-conical to bell-shaped; operculum conical, formed either by many triangular plates on embayements in shallowly cusped hydrothecal margin and well demarcated from hydrothecal wall by noticeable crease line, or formed by a folded continuation of the hydrothecal wall, lacking hinge-like base; hydrothecae often collapsing, disintegrating in developed specimens, in some species just a crumpled collar-shaped sheath is left around the base of the hydrants; diaphragm present; with or without intertentacular web; no nematophores; gonothecae pedunculate. Like in many Haleciids the hydrothecae of the Lovenellidae may renovate. Remarks: The family Lovenellidae was created by Russell (1953) for Leptomedusae with lateral cirri, with four radial canals, without marginal cirri, without peduncle, without excretory pore. Where known, the hydroids being

without peduncle, without excretory pore. Where known, the hydroids being Lovenella-like with a well demarcated operculum and hydrothecal margin embayements. Russell (1953) made a distinction between the genus Lovenella with an indefinite number of statocysts and Eucheilota where the number of statocyst is usually eight. Kramp (1959a) adopted these views and later (Kramp, 1959b; 1961; 1968) added the genus Cirrholovenia with marginal cirri, so modifying Russell's original definition. Calder (1971, 1975) observed that the hydroid of Lovenella gracilis lacks the opercular embayements typical of the genus Lovenella having an operculum in continuation with the hydrothecae and consequently resurrected the genus Dipleuron for this species (Calder, 1991). Bouillon (1985a) considering the impossibility to integrate the diagnostic characters of the polyps and the medusa phases separated Kramp's Lovenellidae in three families: the family Cirrholoveniidae having medusae with marginal cirri and "cuspidellid" hydroid; the Eucheilotidae with medusae with lateral cirri, 8 statocysts and "campanulinid" hydroids with a well demarcated operculum but without hydrothecal embayements, and the Lovenellidae with lateral cirri, an indefinite number of statocysts and a "Lovenella" type of hydroid presenting a well demarcated opeculum with embayements of the hydrothecal margin. The study of "Lovenellidae" life cycles shows however that if the medusa phase of this family present clear characters allowing their

separation from the other leptomedusan medusae families, their hydroids are puzzling, all belong to a "campanulinid" type but their opercular structures presenting differences even at the generic level. It is thus hopeless to refer with confidence one or another type of opercular structure to a family group taxon, particularly to a family established originally for the medusa phase. After Kramp (1919, 1932b) a too great importance has been given to the opercular structures of the Campanulinida. The operculum can show differences in structure in a same family (among others the Tiaropsidae) or even in the same genus, in Phialella for instance some species have opercular flaps demarcated from hydrothecae and other species have not (Boero, 1987). This type of structure is evidently inconstant and cannot be used to distinguish families or even genera. The more, in many campanulinids the operculum can completely disappear with the apical part of the hydrotheca during normal growth of the colonies as shown by Werner (1968 a and b) in Eucheilota maculata and Eutonina indicans or can even not exist in some species of a normal operculate genus (many Eirenidae), only a little more than a collar remain at the base of the hydrothecae of fully developed hydranths, looking like a haleciid thecae (see for instance Werner, 1968, fig.14). The family Eucheilotidae is consequently suppressed and the genera Eucheilota and Lovenella are again included in the Lovenellidae, being defined as above for the medusa stage, the hydroid stage being characterised by "campanulinid polyps" with an operculum well or not well demarcated from the hydrothecae, with hydrothecae having or not marginal embayement or with hydrothecae reduced to a basal collar; usually with an intertentacular web; cnidome generally with merotrichous haplonemes. The family Cirrholoveniidae with marginal cirri and "cuspedelliid" type of hydroids being kept separated.

1.- without statocyst = *Paralovenia*1a.- with statocysts = 2
2.- with usually no more than 8 statocysts = *Eucheilota*2.a- with an indefinite number of statocysts (16-32) = *Lovenella*

Remarks: Two genera, *Hydranthea* which releases free eumedusoids and *Campalecium* from which only medusa buds or newly released medusae are known, pending the species are here tentatively included in the Lovenellidae. They were formerly considered as Haleciidae due to the collar shape of their hydrothecae, in our opinion they are campanulinid hydroids with reduced thecae. This point of view is discussed in the remarks concerning *Lovenella cirrata*.

## Genus Campalecium Torrey 1902:

Only juvenile medusae or medusa buds known pending the species. Hydroid: Colonies typically stolonal, pedicels of varied length bearing terminal hydranth, often secondary pedicels forming sympodial branches; hydrothecae shallow, often regenerated, with a distinct diaphragm, large desmocytes; hydranths relatively large, elongated, cylindrical, not retractable into hydrothecae; up to 30 amphicoronate tentacles with an intertentacular web, endodermal epithelium differentiated into distinct part the upper digestive, the basal part formed by chordal cells; gonophores with free medusae, gonothecae clavate arising from hydrothecal pedicels beneath hydrothecal pedicel, each with several medusa buds.

Campalecium medusiferum Torrey, 1902

? Campalecium cirratum "Millard and Bouillon, 1975"; not Haeckel, 1879

#### Genus Eucheilota McCrady, 1859:

Lovenellidae with usually 8 statocysts.

Hydroid: Colonies of "campanulinid" type; with a well developed operculum not demarcated from the rest of the hydrothecae by a basal crease line; hydrothecae often reduced to a collar shaped sheath around base of the hydranth.

Eucheilota bakeri (Torrey, 1909) Eucheilota birabeni Tundisi, 1962 Eucheilota comata (Bigelow, 1909) Eucheilota diademata Kramp, 1959

Eucheilota duodecimalis A.Agassiz, 1862 Eucheilota flevensis van Kampen, 1922 Eucheilota foresti Goy, 1979 Eucheilota intermedia Kubota, 1984 = Eutima japonica Eucheilota maasi Neppi and Stiasny, 1911 Eucheilota macrogona Zhang and Lin, 1984 Eucheilota maculata Hartlaub, 1894 Eucheilota menoni Kramp, 1959 Eucheilota minima Bouillon, 1984 Eucheilota multicirris Xu and Huang, 1990 Eucheilota sp. Bouillon and Barnett, 1999 Eucheilota sp. Kramp, 1959 Eucheilota paradoxica Mayer, 1900 Eucheilota taiwanensi Xu and Huang, 1990 = Eucheilota paradoxica? Eucheilota tropica Kramp, 1959 Eucheilota ventricularis McCrady, 1859

## Genus Hydranthea Hincks, 1868:

Only short-lived male free eumedusoids known; without tentacles; with four radial canals; «gonads» on radial canals, eight statocysts. Hydroid: Colonies stolonal, hydrothecae short, collar-shaped, shortly pedicellate, borne singly; hydranth elongated, large, with an intertentacular web with merotrichous haploneme cnidocysts; gonophores as eumedusoid attached to the stolon; gonothecae reduced or absent. *Hydranthea margarica* (Hincks 1862).

## Genus Lovenella Hincks, 1868:

Lovenellidae with an indefinite number of statocysts.

Hydroid: Where known, colonies of "*Lovenella*" type; stolonal or upright and sympodial; hydrothecae pedicellate, elongate, everted-conical to bell-shaped; operculum conical, formed either by many triangular plates with embayements of the hydrothecal margin and well demarcated from hydrothecal wall by

noticeable crease line, or formed by a folded continuation of the hydrothecal wall, lacking hinge-like base, (= L. gracilis see below); diaphragm present; without intertentacular web; no nematophores.

Remarks: Some *Lovenella* hydroids have been described without their mature medusa stage known, their systematic validity will only be established after their whole life cycle will be elucidated.

Lovenella annae (von Lendenfeld, 1884) = doubtful species? Lovenella assimilis (Browne, 1905) Lovenella bermudensis (Fewkes, 1883) Lovenella chiquitita Millard, 1957 Lovenella cirrata (Haeckel, 1879) Lovenella clausa (Lovèn, 1836) Lovenella corrugata Thornely, 1908 = only juvenile medusa known Lovenella gracilis (Clarke, 1882) Lovenella haichangensis Xu and Huang, 1983

### Genus Paralovenia Bouillon, 1984:

Lovenellidae with 2 opposite perradial tentacles issued from two large marginal bulbs without cirri; 2 small non-tentacular bulbs with 6 lateral cirri; without rudimentary bulbs; without statocysts. Hydroid: Unknown. *Paralovenia bitentaculata* Bouillon, 1984

# Family Malagazziidae Bouillon, 1984 (16):

Leptomedusae with small manubrium; without gastric peduncle; with 4-8, sometimes up to 12 radial canals; «gonads» completely surrounding radial canals and separated from manubrium; with adaxial excretory papillae; with not permanent rudimentary marginal bulbs (all bulbs potentially transforming into tentacles); with closed statocysts; without ocelli; without cirri. Hydroid: Where known, of "campanulinid" type; colonies stolonal; hydrotheca shortly pedicellate, with a conical operculum formed by numerous convergent
segments not clearly demarcated from the hydrothecal wall; hydranths with an intertentacular web; gonothecae claviform, arising from the stolons.

1.- normally with 4 radial canals (sometimes up to 10, but then asymmetrically arranged) = 3
1a.- normally with 8 or more symmetrically arranged radial canals = 2
2.- mouth with 4 lips = *Octocanna*2a.- mouth with 8 lips = *Octophialucium*3.- with rounded «gonads»; without excretory papillae = *Tetracanna*3a.- with linear «gonads»; with excretory papillae = *Malagazzia*

Genus Malagazzia Bouillon, 1984: Malagazziidae normally with 4 radial canals; manubrium with four lips; gonad linear or ribbon-like Hydroid: See family characters. Malagazzia carolinae (Mayer, 1900) Malagazzia condensum (Kramp, 1953) Malagazzia curviductum (Xu and Zhang, 1978) Malagazzia cyphogonia (He and Xu, 1982) Malagazzia multitentaculatum (Menon, 1932) Malagazzia taenogonia (Chow and Huang, 1958)

Genus Octocanna Haeckel, 1879:

Malagazziidae with 8 radial canals; 8 «gonads» on radial canals; 4 hollow marginal tentacles and 4 small, non-tentacular marginal bulbs; mouth with 4 long lips; excretory pores on small adradial papillae. Hydroid: Unknown. *Octocanna haeckeli* Vannucci and Soares Moreira, 1966

**Genus** *Octophialucium* Kramp, 1955: Malagazziidae with normally 8 radial canals; with 8 «gonads» on radial canal; mouth with 8 lips.

Hydroid: Where known, of "campanulinid" type, see family characters. Octophialucium aphrodite (Bigelow, 1919) Octophialucium bigelowi Kramp, 1955 Octophialucium funerarium (Quoy and Gaimard, 1827) Octophialucium indicum Kramp, 1958 Octophialucium krampi Bouillon, 1984 Octophialucium medium Kramp, 1955 Octophialucium mollis Bouillon, 1984 Octophialucium solidum (Menon, 1932)

# Genus Tetracanna Goy, 1979:

Malagazziidae with 4 radial canals; 8 marginal tentacles; mouth with 4 long lips; «gonads» voluminous, rounded on almost entire length of radial canals; 1-3 statocysts between successive tentacles. (Family assignment doubtful; no excretory pores have been mentioned.) Hydroid: Unknown. *Tetracanna octonema* Goy, 1979

## Family Melicertidae Agassiz, 1862 (5):

Leptomedusae with base of manubrium attached over its whole surface; with eight simple or bifurcated radial canals; with hollow marginal tentacles; without marginal or lateral cirri; without statocysts and cordyli, with or without ocelli. Hydroid: Where known, stolonal colonies with branching stolons and erect shoots bearing one, sometimes two, hydranths; perisarc thinning away completely below base of the hydranths, no hydrotheca; hydranth large, fat in the middle, attenuate below, tapering gently above, with narrow, amphicoronate tentacles; without intertentacular web; gonophores borne on the column of hydranth, no gonothecae (hydroid known only in *Melicertum*).

1.- radial canals bifurcated = *Netocertoides*1a.- radial canals simple = 2

2.- eight radial canals, four of which developed centripetally from the circular canal = *Melicertoides* 

2a.- all radial canals arise from manubrim = 3

3.- with 8 large marginal tentacles and a few rudimentary bulbs = *Orchistomella*3a.- with numerous marginal tentacles = *Melicertum* 

# Genus Melicertoides Kramp, 1959:

Melicertidae with eight simple radial canals, four primary and four secondary, the latter developed centripetally from circular canal; with «gonads» adjacent to manubrium.

Hydroid: Unknown.

*Melicertoides centripetalis* Kramp, 1959 *Melicertoides octolabialis* Xu, Huang and Chen Xu, 1991 = juvenile of any medusae with 8 radial canals

# Genus Melicertum L.Agassiz,1862:

Melicertidae with eight simple radial canals, four primary and four secondary, all arising from manubrium; with «gonads» on the radial canals separated from manubrium; without ocelli?

Hydroid: See family characters.

Melicertum georgicum A. Agassiz, 1862

Melicertum octocostatum (M. Sars, 1835)

*Melicertum panocto* (Haeckel, 1879)?

## Genus Netocertoides Mayer, 1900:

Melicertidae with eight main radial canals bifurcating once, all arising from manubrium; «gonads» on main radial canals adjacent to manubrium. Hydroid: Unknown. *Netocertoides brachiatus* Mayer, 1900

Genus Orchistomella Kramp, 1959:

Melicertidae with eight or more radial canals, all of which arise from manubrium; with or without ocelli, «gonads» unknown. Hydroid: Unknown. Orchistomella applanata Kramp, 1959 Orchistomella graeffei (Neppi and Stiasny, 1911) = juvenile Aequorea? Orchistomella tentaculata (Mayer, 1900) = juvenile Aequorea?

Family **Mitrocomidae** Haeckel, 1879 (part); Torrey, 1909 (21): Leptomedusae with bases of manubrium attached to subumbrella along continuation of radial canals; with 4 or more simple radial canals; marginal tentacles hollow; marginal cirri present in some genera; with «gonads» oval or linear, only on radial canals; with open statocysts; without ocelli. Hydroid: Usually poorly known, most of "*Cuspidella*" type; hydrotheca tubular, sessile; with pyramidal operculum made either of several triangular flaps, or of pleats in the continuation of hydrothecal tube, all not well demarcated from hydrothecal wall, lacking a crease-line at base of flaps or pleats; hydranth extensile, with a single usually amphicoronate whorl of filiform tentacles; no intertentacular web; no nematophores; gonophores where known scarcely pedicellate, on hydrorhiza.

1.- with radial canals in an "S" = *Cyclocanna* 1a.- with straight radial canals = 2 2.- with 4 radial canals = 3 2a.- with 12 to 16 radial canals = *Halopsis* 3a.- without marginal cirri = 4 3.- with marginal cirri = 5 4.- with numerous open statocysts = *Foersteria* 4a.- with only 8 open statocysts = *Cosmetirella* 5.- with flexile cirri, with cnidocyst throughout their length, with 8 marginal statocycts = *Cosmetira* 5a.- with spiral marginal cirri with terminal clusters of cnidocysts = 6 6.- with 8-16 open statocysts = *Mitrocomella* 

6a.- with numerous (20-160) open statocysts = Mitrocoma

Genus Cosmetira Forbes, 1848:

Mitrocomidae with 4 radial canals; with 8 open statocysts; without ocelli; with flexile cirri provided with numerous cnidocysts throughout their length, usually straight, exceptionally, in young specimens, spirally coiled. Hydroid: See family characters. *Cosmetira pilosella* Forbes, 1848

Genus Cosmetirella Browne, 1910:

Mitrocomidae with 4 radial canals; with 8 open statocysts; without marginal cirri; without ocelli. Hydroid: Unknown. *Cosmetirella davisi* (Browne, 1902)

**Genus** *Cyclocanna* Bigelow, 1918: Mitrocomidae with 4 radial canals each bent like an S; with 8 open statocysts; without ocelli. Hydroid: Unknown. *Cyclocanna welshi* Bigelow, 1918

Genus *Foersteria* Arai and Brinckmann-Voss, 1980: Mitrocomidae with 4 radial canals; with numerous open statocysts; without marginal cirri. Hydroid: Unknown.

*Foersteria antoniae* Gili, Bouillon, Pagès, Palanques, Puig and Heussner, 1998 *Foersteria araiae* Gili, Bouillon, Pagès, Palanques and Puig, 1999 *Foersteria bruuni* (Navas, 1969) *Foersteria purpurea* (Foerster, 1923)

**Genus** *Halopsis* A. Agassiz, 1863: Mitrocomidae with more than 8 radial canals; with marginal spirally coiled cirri; with numerous (about 80) statocysts.

Hydroid: Unknown. Halopsis ocellata A. Agassiz, 1863

# Genus Mitrocoma Heackel, 1864:

Mitrocomidae with 4 radial canals; with numerous open statocysts; with marginal cirri. Hydroid: Colonies, where known, of "*Cuspidella*" type, operculum with numerous sharp pointed, triangular flaps meeting centrally and presenting no clear limits with the hydrothecal margin. *Mitrocoma annae* Haeckel, 1864 *Mitrocoma cellularia* (A.Agassiz, 1865) *Mitrocoma discoidea* Torrey, 1909 *Mitrocoma minervae* Haeckel, 1879 = doubtful species

# Genus Mitrocomella Haeckel, 1879:

Mitrocomidae with 4 radial canals; with marginal cirri which may or not be spirally coiled; with 8, 12 or 16 (exceptionally up to 19) statocysts. Hydroid: Where known, colonies of "*Cuspidella*" type; with pleated operculum, presenting no clear limits with the hydrothecal margin; see family characters. *Mitrocomella brownei* (Kramp, 1930) *Mitrocomella cruciata* A Agassiz, 1865 *Mitrocomella frigida* (Browne, 1910) *Mitrocomella fulva* Browne, 1903 *Mitrocomella grandis* Kramp, 1965 *Mitrocomella millardae* Pagès, Gili and Bouillon, 1992 *Mitrocomella niwai* Bouillon and Barnett, 1999 *Mitrocomella polydiademata* (Romanes,1876) *Mitrocomella sinuosa* (Foerster, 1923)

Family **Octocannoidae** Bouillon, Boero and Seghers,1991 (1): Leptomedusae with eight simple radial canals; with eight marginal tentacles; with 16-32 short club-shaped "tentaculae", all marginal structures with black

pigmented spots; with short manubrium; mouth with 8 simple lips; without gastric peduncle; without excretory papillae; «gonads» consisting of two lateral halves; with numerous statocysts, no ocelli. Hydroid: Unknown.

**Genus** *Octocannoides* Menon, 1932 With the characters of the family. *Octocannoides ocellata* (Menon, 1932)

#### Family Orchistomatidae Bouillon, 1984 (5):

Leptomedusae with very short manubrium; with large gastric peduncle; mouth with 8-30 sinuous or crenulated lips; with 8 or more radial canals, simple, ramified, or in clusters of 4; up to 64 marginal tentacles, laterally compressed; no marginal cirri, but numerous filiform tentaculiform structures devoid of marginal bulbs, not in contact with circular canal, in each intertentacular space; «gonads» usually on proximal parts of radial canals; numerous (up to 800) adaxial ocelli; no statocysts or cordyli; without excretory pores or papillae. Hydroid: Unknown.

Genus Orchistoma Haeckel, 1879: With the characters of the family. Orchistoma agariciforme Keller, 1884 Orchistoma collapsa (Mayer, 1900) Orchistoma manam Bouillon, 1984 Orchistoma nubiae Bouillon, 1984 Orchistoma pileus (Lesson, 1843)

#### Family Phialellidae Russell, 1953 (6):

Leptomedusae with small manubrium; without gastric peduncle; with 4 radial canals; with «gonads» on radial canals, separated from manubrium and divided into two lateral parts by a median groove; with hollow tentacles; without

excretory pores; without lateral or marginal cirri; with 8 closed statocysts, each on a bulbous-like swellings; without ocelli.

Hydroid: Colonies stolonal or erect, sympodial; hydrotheca pedicellate, tubular, persistent, with operculum formed by separate triangular flaps demarcated or not from the hydrothecal margin by a basal crease line, gonothecae usually stolonal, sometimes on erect shoots.

Genus Phialella Browne, 1902:

Medusa and hydroids with the characters of the family. *Phialella annulata* (von Lendenfeld, 1884) = doubtful species *Phialella dissonema* (Haeckel, 1879) = doubtful species *Phialella falklandica* Browne, 1902 *Phialella fragilis* (Uchida, 1938) *Phialella hyalina* (von Lendenfeld, 1884) = doubtful species *Phialella macrogona* Xu, Huang and, Wang Wenqiao, 1985 *Phialella parvigastra* (Mayer, 1900) *Phialella quadrata* (Forbes, 1848) *Phialella turrita* (Hincks, 1868) = only medusa buds known *Phialella zappai* Boero, 1987

Family Plumulariidae McCrady, 1859 emended Hincks, 1868 (2):

Gonophore: As fixed sporosacs; medusa stage totally suppressed from life cycle except exceptionally as swimming gonophores.

Hydroid: With upright monosiphonic or polysiphonic colonies with hydrocauli branched or unbranched, hydrocladia alternate, opposite or in verticils; hydrotheca uniseriate, usually at least partially adnate occuring only on hydrocladia, with usually even margin; nematophores with nematothecae; with paired lateral nematothecae present or absent, not fused with hydrothecae; all nematothecae usually two-chambered (bithalamic) and movable, mesial hydrothecae not fused with hydrothecae; gonothecae solitary, without nematothecae; with or without phylactocarps.

# Genus Denthitheca Stechow, 1919:

Gonophore: As fixed sporosacs, exceptionally with swimming gonophore Hydroid: Unbranched, unfascicled colonies, pinnate, bearing alternate hydrocladia; hydrocladia bearing hydrothecae on anterior surface, hydrothecae with strong perisarc, adnate, margin with two large triangular lateral lobes and an acauline lobe; three nematothecae on each apophysis; gonothecae arising from axils of hydrocladia, inverted conical with truncated apex, smooth. *Denthitheca bidentata* (Jäderholm, 1920) = swimming gonophores

#### Genus Monotheca Nutting, 1900:

Gonophore: As fixed sporosacs, exceptionally with swimming gonophore. Hydroid: Colonies with minute, erect, unbranched or sparingly branched stems; hydrocladia alternate, unbranched, short, not extending beyond hydrotheca, each with two internodes: a basal one and second bearing the terminal hydrotheca; hydrothecae large only on hydrocladia, margin more or less entire, sinuous; hydrothecate internode with a single median inferior nematotheca and a terminal pair of lateral nematothecae above hydrothecae; gonothecae solitary at base of first hydrocladium, truncated distally and tapering at base, lacking nematothecae, not protected.

Monotheca obliqua (Johnston, 1847) = short-lived swimming gonophores.

Remarks: Allman (1871) reported reduced medusoids in *Nemertesia antennina* (L., 1758) but his observation has not been confirmed by futher studies (see Millard, 1975; Hughes, 1977).

#### Family Sertulariidae Lamouroux, 1812:

Gonophore: as fixed sporosacs; medusa stage totally suppressed from life cycle except exceptionally as swimming gonophores

Hydroid: Colonies erect, exceptionally stolonal; hydrothecae bi- or multiseriate, exceptionally secondarily apparently uniseriate, sessile through adnate to wholly sunk within perisarc, or exceptionally pedicellate, radially to bilaterally symmetrical, rim usually cusped, with operculum of 1-4 flaps; with diaphragm

in few pedicellate forms, others having a clearly defined basal floor pierced by narrow and eccentric hydropore; hydranth completely retractable in hydrotheca, in some species with an abcauline gastric caecum; nematophores absent; gonothecae solitary, usually sexually dimorphic.

# Genus Amphisbetia L. Agassiz, 1862:

Gonophore: Fixed, exceptionally swimming gonophore. Hydroid: See family characters, with opposite and biseriate hydrothecae; with two abcauline marginal cusps and sometimes a small adcauline one; operculum of two unequal valves a larger adcauline one and a smaller abcauline one; hydranth with abcauline blind caecum.

Amphisbetia operculata (L., 1758) = swimming gonophores

# Genus Sertularia L.,1758:

Gonophore: Fixed, exceptionally swimming gonophore. Hydroid: See family characters, hydrothecae sessile, sub-alternate to alternate in two longitudinal rows, with two marginal cusps between abcauline and adcauline edges and in some species, a third adcauline one, operculum non pyramidal, two-valved, adcauline valve smaller than abcauline; hydranth with abcauline blind caecum.

Sertularia marginata Kirchenpauer, 1864 = swimming gonophores

## Family Sugiuridae Bouillon, 1984 (1):

Leptomedusae with up to six manubria, usually with 4 radial canal per well developed manubrium all joining circular canal; no centripetal canals; 2-6 ovoid «gonads» on some of the canals, ovoid; marginal tentacles numerous; numerous statocyst; asexual reproduction by fission.

Hydroid: Stolonal colonies; hydrotheca cylindrical tapering apically, on a short pedicel; with a pyramidal operculum formed by numerous convergent flaps not demarcated by a basal crease line; hydranth with one row of tentacles surrounding a conical hypostome, tentacles with an intertentacular basal web; gonophores unknown.

**Genus** *Sugiura* Bouillon, 1984: With the characters of the family. *Sugiura chengshanense* (Ling, 1937)

Family **Teclaiidae** Bouillon, Pages, Gili, Palanques, Puig and Heussner 1999 (3):

Leptomedusae with 4 simple radial canals; with hollow tentacles; with 4 simple lips; with elongated «gonads» forming linear sacs on radial canals, separated from manubrium; with one to three cordyliform structures between successive tentacles; without ocelli; without cirri; with or without open statocysts. Hydroid: Unknown.

1.- medusae with open statocysts = *Parateclaia* 1.a- medusae without statocysts = *Teclaia*

**Genus** *Parateclaia* Bouillon, Pagès and Gili, 2000: Teclaiidae with open statocyst. Hydroid: Unknown. *Parateclaia euromarge* Bouillon, Pagès and Gili, 2000

**Genus** *Teclaia* Gili, Bouillon, Pagès, Palanques and Puig, 1998: Teclaiidae without statocyst. Hydroid: Unknown. *Teclaia recincolae* Gili, Bouillon, Pagès, Palanques and Puig, 1999

## Family Tiarannidae Russell, 1940 (5):

Leptomedusae without apical projection; without gastric peduncle; with wide, cross-shaped manubrium, with 4 perradial pouches joined to subumbrella; mouth with 4 simple or crenulated lips; with 4 simple radial canals; «gonads» folded on interradial walls of manubrium and/or on the perradial manubrial pouches; marginal tentacles numerous, hollow; with hollow cordyli-like structures bearing cnidocysts; without ocelli.

Hydroid: Where known, colonies stolonal of "*Stegopoma*" type; hydrotheca pedicellate or sessile, deep, asymmetric-tubular; operculum formed by two pleated membranes which meet one another like a gabled roof, with straight ridges above and on the sides of hydrotheca, continuing up at each end, the all imparting a bilateral symmetry to the distal part of the hydrotheca; hydranths where known lacking intertentacular web; gonothecae resembling hydrothecae but larger, with free medusae or fixed sporosacs.

1.- «gonads» on perradial manubrial pouches only = 2
1a.- «gonads» on manubrium and perradial gastric pouches = *Modeeria*2.- «gonads» widely split longitudinally = *Krampella*2a.- «gonads» not split longitudinally = 3
3.- 4 simple, smooth, «gonads» on walls of perradial manubrial pouches = *Margalefia*3a. «gonads» in eight adradial rows of 10-16 sac-like invaginations on each side of perradial manubrial pouches = *Chromatonema*

# Genus Chromatonema Fewkes, 1882:

Tiarannidae with «gonads» represented by 8 (10-16) series of sac-like invaginations from the surface of perradial pouches, separated in interradi; 20-24 marginal tentacles; 1-2 cordylus-like structure between successive tentacles. Hydroid: Unknown.

*Chromatonema erythrogonon* (Bigelow, 1909) = *C. rubrum? Chromatonema hertwigi* (Vanhöffen, 1911) = *C. rubrum? Chromatonema rubrum* Fewkes, 1882

# Genus Krampella Russell, 1957:

Tiarannidae with 4 perradial manubrial pouches extending almost to circular canal; «gonads» oval to bean-shaped on distal 2/3 of the radial pouches, widely divided longitudinally; 8 marginal tentacles; up to five cirrus-like tentaculae between successive marginal tentacles. Hydroid: Unknown.

Krampella dubia Russell, 1957 Krampella tardenti Gili, Bouillon, and Pagès, 1998

# Genus Margalefia Pagès, Bouillon and Gili, 1991:

Tiarannidae with 4 long and large perradial manubrial pouches extending almost to circular canal; with simple, smooth, undivided «gonads» on all the surface of perradial manubrial pouches; up to 150 marginal tentacles; one cordylus-like structure between every three marginal tentacles. Hydroid: Unknown. *Margalefia intermedia* Pagès, Bouillon and Gili, 1991

## Genus Modeeria Forbes, 1848:

Tiarannidae with «gonads» transversally folded on interradial walls of manubrium and extending outwards along both sides of the perradial pouches; 16-28 marginal tentacles; 2-3 spindle-shaped cordylus-like appendages between successive tentacles.

Hydroid: see family characters.

Modeeria formosa Forbes, 1848 = doubtful species, perhaps *M. rotunda*? Modeeria rotunda (Quoy and Gaimard, 1827) Modeeria sagamina Uchida, 1947 = doubtful species, perhaps *M. rotunda*?

# Tiarannidae incertae sedis or conspecifics:

*Tiaranna ducalis* (Forbes and Goodsir, 1853) = doubtful species *Tiaranna globulosa* (Forbes, 1848) = doubtful species *Tiarnana ikarii* Uchida, 1927 = *Pandeopsis ikarii Tiaranna sagamina* Uchida, 1948 = *Mooderia rotunda*?

# Family **Tiaropsidae** Boero, Bouillon and Danovaro, 1987 (9): Leptomedusae with 4 or 8 radial canals (exceptionally up to 16); with one or two types of marginal tentacles (long and rudimentary, both with marginal bulbs); without marginal cirri; sense organs compound, comprising an ectoendodermal ocellus and an open velar statocyst.

Hydroid: Where known, colonies "*Cuspidella*" like; hydrothecae tubular, sessile or with reduced pedicel; with operculum comprising numerous flaps demarcated or not from the rest of the hydrothecae by a crease line; hydranth without intertentacular web; gonotheca, where known, tubular or rounded, laterally compressed, operculate or not, with short peduncle, growing singly from hydrorhiza.

1.- with numerous (50-60) compound sense organs; mouth with eight lips = Octogonade1a.- with 8 or 16 (exceptionally 48) compound sense organs; mouth with four

 $\frac{1}{10} = 2$ 

2.- with two kinds of marginal tentacles = *Tiaropsidium*2a.- with one kind of tentacles = *Tiaropsis* 

# Genus Octogonade Zoja, 1896:

Tiaropsidae with 8 radial canals; mouth with 8 lips; with numerous compound statocysts; with two kind of tentacles; without marginal cirri. Hydroid: Unknown. *Octogonade mediterranea* Zoja, 1896

# Genus Tiaropsidium Torrey, 1909:

Medusa:Tiaropsidae with 4 or more (up to 16) simple radial canals; mouth with four lips; with 8 or 16 (rarely 48) compound sense organs; with two kinds of tentacles; without marginal cirri. Hydroid: Where known, colonies of "*Cuspidella*" type; operculum formed by several flaps sharply demarcated from the hydrothecal margin by a crease line; gonothecae ellipsoid, without operculum. *Tiaropsidium atlanticum* Russell, 1956 *Tiaropsidium japonicum* Kramp, 1932 *Tiaropsidium kelsey* Torrey, 1909 *Tiaropsidium mediterraneum* (Metschnikoff, 1886) *Tiaropsidium polyradiatum* Kramp, 1965

# Tiaropsidium roseum (Maas, 1905)

# Genus Tiaropsis Agassiz, 1849:

Tiaropsidae with 4 radial canals; with 8 compound sense organs; with only one kind of marginal tentacle; without marginal cirri.

Hydroid: Where known, colonies of "*Cuspidella*" type; operculum formed by several flaps not sharply demarcated from the rest of the hydrothecae by a crease line; gonothecae tubular, smooth, operculate. *Tiaropsis gordoni* Bouillon and Barnett, 1999

Tiaropsis multicirrata (M. Sars, 1835)

## **Conica of uncertain systematic position** (1):

## Genus Tripoma Hirohito, 1995

Eumedusoid described from inside gonothecae, not seen free; with radial canals; with ring canal; 4 hollow marginal tentacles; no statocysts observed; with a velum; position of gonads unclear.

Hydroid: Colonies with fascicled stem and branches, not divided distinctly in internodes; hydrotheca tubular, bending or not, embedded in rhizocaulus, with an annulated short pedicel, without diaphragm; hydrotheca with three inconspicuous marginal teeth; with operculum composed by three distinct flaps; gonothecae tubular embedded in rhizocaulus, containing one eumedusoid. *Tripoma arboreum* Hirohito, 1995

## Order Proboscoida Broch, 1910 (41 valid species).

Diagnosis: Hydranths having a complex flared to globose hypostome, forming a "buccal cavity" beneath the mouth .

Medusa varied in expression, with closed statocysts; never with cordyli, open statocysts, excretory pores, cirri or ocelli.

1.- without permanent tenon-like rudimentary marginal bulbs = Campanulariidae

1.a.- with triangular, tenon-like permanent rudimentary marginal bulbs = Phialuciidae

# Family Campanulariidae Johnston, 1836 (40):

Leptomedusae with short manubrium; without gastric peduncle; typically with 4 radial canals (except in *Gastroblasta* and *Pseudoclytia*); with or without velum (without in *Obelia*); with «gonads» on radial canals, completely surrounding them and separated from manubrium; with hollow tentacles (except in *Obelia* where they are solid and with a short prolongation of endoderm into bell mesoglea); with or without tenon-like rudimentary bulbs; without marginal or lateral cirri; without excretory papillae or pores; numerous (16-200) closed velar marginal statocysts (only 8 in *Obelia*, each situated on underside of the basal bulb of some marginal tentacles); no ocelli.

Hydroid: Hydroids forming erect or stolonal colonies; hydrothecae bell-shaped or campanulate, radially or, secondarily, bilaterally symmetrical; pedicellate, rim cusped or not, lacking operculum, with basal diaphragm or inward annular projection of perisarc; nematophores absent, hydranth when known generally tubular with flared or globose hypostome delimiting a "buccal cavity", with one whorl of filiform tentacles, gastric endoderm of uniform structure; hydrothecal spherules present or not; free medusae, eumedusoids or sporosacs.

1.- with more than four radial canals = 2

1a.- normally with four radial canals = 3

2.- with up to 20 radial and centripetal canals; with numerous manubria each with 4 lips = Gastroblasta

2a.- with up to seven radial canals; with one manubrium and as many lips as radial canals = *Pseudoclytia* 

3.- with reduced medusae; without manubrium; without tentacles = Orthopyxis 3.a.- with normally developed medusae; with one manubrium with 4 lips; with tentacles = 4

4.- with hollow marginal tentacles and normal velum = *Clytia*4a.- with solid marginal tentacles; without velum = *Obelia* 

Genus Clytia Lamouroux, 1812:

Campanulariidae with a short manubrium; with normal velum; with hollow marginal tentacles; without tenon-like permanent rudimentary bulbs; with numerous statocysts.

At the medusa level, very few species of *Clytia* are known with certainty, most of the morphological characters used to distinguish them falling in the range of variations that can be expected in a single species and having little or no taxonomic value. The genus needs a careful revision.

Hydroid: Hydroids with reptant, branched but not anastomosing hydrorhiza, colonies unbranched stolonal or erect branched; hydrothecal rim sinuous or deeply indented, with clefts between the round to sharply-pointed cusps; hydrothecae with true hydrothecal diaphragm; usually without subhydrothecal spherules (present in *C. hummelincki*).

Remarks: Several species of *Clytia* are cited hereunder being known only by their larval hydroid stage, solely medusa buds or juvenile immature medusa having been observed. Their list is far from exhaustive, many more species of *Clytia* hydroids having been described without their mature medusa stage known. The future systematic validity of all this species will only be established after their whole life cycle will be elucidated.

Clytia ambiguum Agassiz and Mayer, 1899 = only immature medusa known Clytia arborescens Pictet, 1893 = only medusa buds known Clytia bicophora L. Agassiz, 1862 Clytia brunescens (Bigelow, 1904) Clytia delicatula (Thornely, 1900) = only medusa buds known Clytia discoida (Mayer, 1900) Clytia folleata (Mc Crady, 1859) Clytia gardineri (Browne, 1905) Clytia gelatinosa (Mayer, 1900) Clytia globosa (Mayer, 1900)

Clytia gracilis (Sars, 1851) *Clytia gravieri* (Billard, 1904) = only medusa buds known Clytia gregaria (L.Agassiz, 1862) Clytia hemisphaerica (Linnaeus, 1767) Clytia hexanemalis Xu, Huang and Chen Xu, 1991 = doubtful species Clytia hummelincki (Leloup, 1935) = only immature medusae known Clytia iridescens Maas, 1906 Clytia islandica Kramp, 1919 Clytia languida (L. Agassiz, 1862) *Clytia latitheca* Millard and Bouillon, 1973 = only medusa buds known Clytia linearis (Thornely, 1900) Clytia lomae (Torrey, 1909) Clytia mccradyi (Brooks, 1888) Clytia macrogonia Bouillon, 1984 Clytia malayense Kramp, 1961 Clytia multiannulata Hirohito, 1995 = only medusa buds known *Clytia noliforme* (McCrady, 1859) = only immature medusae known Clytia obliqua (Clarke, 1907) = only medusa buds known *Clytia ovale* (Mayer, 1900) = abnormal *Clytia*? Clytia pacifica (Agassiz and Mayer, 1899) *Clytia phosphoricum* (Péron and Lesueur, 1810) = name covering several species of Clytia medusae Clytia paulensis (Vanhöffen, 1910) Clytia rangiroae (Agassiz and Mayer, 1902) *Clytia serrulata* (Bale, 1888) = only medusa buds known; perhaps *C*. hemisphaerica or C.gracilis? Clytia simplex (Browne, 1902) Clytia singularis (Mayer, 1900) Clytia uchidai Kramp, 1961 Clytia viridicans (Leuckart, 1856) Clytia warreni (Warren, 1908) = only medusa buds known

# Genus Gastroblasta Keller 1883:

Campanulariidae with several manubria; with up to 20 radial and centripetal canals; with normal velum; with hollow marginal tentacles; without tenon-like permanent rudimentary bulbs; with numerous statocysts.

Hydroid: When known, *Clytia* like, living embedded in sponges. *Gastroblasta raffaelei* Lang, 1886 *Gastroblasta timida* Keller,1883

Genus Obelia Péron and Lesueur, 1810:

Campanulariidae with short quadrangular manubrium; without velum; with numerous solid, stiff, not extensile tentacles, with short endodermal roots extending into bell mesoglea; 8 statocysts situated on underside of basal bulbs of some marginal tentacles.

Hydroid: Hydroids with erect hydrocauli forming branched or unbranched, fascicled or unfascicled, upright colonies, variably flexuose; stolons not anastomosing; internodes annulated proximally, hydroclades with distal hydrothecae; hydrothecae bell-shaped to campanulate, radially symmetrical, with toothed or untoothed margin, with true hydrothecal diaphragm, without sub-hydrothecal spherule; hydranth with globose hypostome forming a " buccal cavity"; gonothecae inverted conical, usually with raised terminal aperture but sometimes simply truncated.

Remarks: Various nominal species of *Obelia* hydroids have been described throughout the world, the medusae of this genus are however all very similar in morphology so that their connecting with their hydroid stage is almost impossible and often not reliable.

According to Zamponi and Genzano (1990), the medusae of *Obelia dichotoma* (L., 1758) and *Obelia longissima* (Pallas, 1766) can be distinguished by their cnidome, composed of atrichous isorhizas, atrichous anisorhizas and basitrichous isorhizas in *O. dichotoma*, and by microbasic mastigophores and macrobasic mastigophores in *O. longissima*. However, macrobasic mastigophores seem improbable in the genus *Obelia*, although they have been

found in other Leptomedusae. Östman, (1982, 1983) by scanning electron microscopy has found minute differences in the cnidocyst fine morphology of newly liberated medusae of *O. dichotoma*; *O. longissima* and *O. geniculata*. Unfortunately the above techniques is laborious, expensive in equipment and requires fresh material.

*Obelia bicuspidata* Clarke, 1875 *Obelia dichotoma* (L., 1758) *Obelia fimbriata* (Dalyell, 1848) *Obelia geniculata* (L., 1758) *Obelia longissima* (Pallas, 1766) *Obelia spp.* 

Genus Orthopyxis L. Agassiz, 1862:

Campanulariidae with eumedusoids, either free, facultatively retained, or never released; without manubrium and tentacles but with 8 statocysts. Hydroid: Colonies stolonal or with short unbranched uprights; stolons anastomosing; hydrothecae fundamentally radially symmetrical but often asymmetrically thickened; without true hydrothecal diaphragm; eumedusoids (the species with unknown gonothecal content are not listed). *Orthopyxis crenata* (Hartlaub, 1901) = eumedusoid *Orthopyxis everta* Clarke, 1875 = eumedusoid *Orthopyxis compressa* (Clark, 1876) (see Arai and Brinckmann-Voss, 1980 and Antsulevich, 1987) *Orthopyxis fujianensis* Huang and Xu, 1994 = eumedusoid. *Orthopyxis integra* (Macgillivray, 1842) = eumedusoid. *Orthopyxis platycarpa* (Bale, 1914) = eumedusoid (see Antsulevich, 1987). *Orthopyxis sargassicola* (Nutting, 1915) = short lived eumedusoid, perhaps *O. crenata*?

Genus Pseudoclytia Mayer, 1900:

Campanulariidae medusae with more than 4 radial canals and with a corresponding number of manubrial lips. Hydroid: Unknown. *Pseudoclytia pentata* (Mayer, 1900)

# Campanulariidae nomen nudum:

## Genus Zelounies Gravier-Bonnet, 1992:

Life cycle described from rearing but generic diagnoses never given by the author.

*Zelounies estrambordi* Gravier-Bonnet, 1992: life cycle described from rearing but species diagnosis or formal description never given by the author.

# Family Phialuciidae Kramp, 1955 (1):

Leptomedusae with small manubrium; without peduncle; with 4 simple radial canals; with «gonads» on radial canals, completely surrounding them and separated from manubrium; with hollow marginal tentacles; with triangular tenon-like permanent marginal rudimentary bulbs; without marginal or lateral cirri; no excretory pores; with closed statocysts.

Hydroid: Not known from field, of "Campanulariid" type; hypostome peduncled; stem long, not annulated; hydranth with 10-14 filiform tentacles (Bouillon, 1984).

**Genus** *Phialucium* Maas, 1905: With the characters of the family. *Phialucium mbenga* (Agassiz and Mayer, 1899)

# Subclass Limnomedusae Kramp, 1938 (38 valid species).

Diagnosis: Medusae with «gonads» either on manubrium or along radial canals. Marginal tentacles peripheral, hollow, without true basal bulb, tentacles' base usually with a parenchymatic endodermal core embedded in the umbrellar mesoglea. Marginal sense organs as internal enclosed ecto-endodermal

statocysts embedded in the mesoglea near ring canal or in the velum. Exceptionally reduced medusoids (*Monobrachium*). Planulae, when known, with cnidoblasts but without embryonic glandular cells. Hydroid: When known, very simple, solitary or colonial; small, sessile; with or without tentacles; often close to planula structure and budding planula-like structures or frustules. Hydroids' body plans range from: forms without mouth and permanent gastric cavity = feeding planula (Microhydrulidae, *Olindias*) to forms with an hypostome, but without tentacles, forming transitory colonies or definitive colonies with a limited number of individuals: *Craspedacusta, Limnocnida*; to forms with hypostome and tentacles : *Calpasoma, Gonionemus, Scolionema, Vallentinia*. No perisarcal thecae, but cysts and stolons covered by chitin

The Limnomedusae are a small group of Hydroidomedusa with a dimorphic benthic-pelagic cycle; the hydroid stages are small, poorly developed, rarely really modular; medusa production is comparatively much reduced; many of the present-day Limnomedusae inhabit fresh-or brackish-waters and their medusae are often seasonal, whereas the hydroids and the resting stages are perennial, resisting adverse conditions: *Craspedacusta* cysts can survive 40 years while completely desiccated.

reduced medusae, creeping burrowed in coarse sand sediments; without radial canals, statocysts and nerve system = Armorhydridae
 free swimming medusae, with radial canals, statocysts and nerve system = Olindiidae

Family Armorhydridae Swedmark and Teissier, 1958 (1):

Reduced Limnomedusae creeping within the interstices in coarse sand sediments; umbrella margin with a whorl of two kind of solid tentacles, filiform and adhesive; with a voluminous manubrium linked to subumbrella by longitudinal septa containing endodermal tubes; with gonads on manubrium; with a velum pierced by a narrow central opening; without radial canals, nerve system, statocysts or any other visible sense organ; with separate sexes.

Cycle not completely known (Lacassagne, 1973).

**Genus** *Armorhydra* Swedmark and Teissier, 1958: See family diagnosis. *Armorhydra janowiczi* Swedmark and Teissier, 1958

Family Olindiidae Haeckel, 1879 (37):

Limnomedusae with or without centripetal canals; with internal ecto-

endodermal statocysts; with simple, unbranched radial canals; with «gonads» on radial canals or on manubrium; without ocelli.

Hydroid: Where known, hydroids usually solitary, seldom colonial; generally reduced, minute, either without tentacles or with one tentacles, or with a few tentacles in a single ring, sometimes with dactylozooids; with no theca; with very active asexual reproduction by buds or frustules; usually with free medusae, exceptionally with free or fixed eumedusoids.

1.- statocysts in elongated vesicles enclosed in velum; «gonads» on radial canals = *Craspedacusta* 

1a.- statocysts spherical, enclosed in mesoglea of umbrellar margin = 2

2.- with centripetal canals = 3

2.a- without centripetal canals = 5

3.- with tentacles of one kind = 4

3a- with primary tentacles projecting above umbrellar margin and with terminal adhesive pads, secondary tentacles on umbrellar margin, without adhesive pads *= Olindias* 

4.- with tentacles situated on exumbrella at different height above bell margin; without adhesive pads = *Eperetmus* 

4a.- with all tentacles on umbrellar margin and without adhesive pads = *Meaotias* 

5.- tentacles in groups on bell margin = Gossea

5a.- tentacles not in groups = 6

6.- with 6 radial canals = *Nuarchus* 

6a.- with 4 radial canals = 7

7.- «gonads» on manubrium = *Limnocnida*7a.- «gonads» on radial canals = 8
8.- all tentacles without adhesive pads = *Aglauropsis*8a.- some or all tentacles with adhesive pads = 9
9.- with one type of tentacle, with a terminal adhesive pad = 10
9a.- with two kinds of tentacles with and without adhesive pads = 11
10.- with numerous statocysts = *Gonionemus*10a.- with no more than 16 statocysts = *Scolionema*11.- adhesive pads terminal = *Vallentinia*11a.- adhesive pads at some distance from outer end of tentacles = *Cubaia*

#### Genus Aglauropsis F. Müller, 1865:

Olindiidae with four radial canals; without centripetal canals; numerous tentacles of one kind on bell margin, not arranged in groups, without adhesive pads; numerous statocysts. Hydroid: Unknown. *Aglauropsis aeora* Mills, Rees and Hand , 1976 *Aglauropsis agassizi* Fr. Müller, 1865 = inadequately described, probably similar to *A. kawari Aglauropsis conanti* Browne, 1902 *Aglauropsis edwarsii* Pagès, Bouillon and Gili, 1991 *Aglauropsis jarli* Kramp, 1955 *Aglauropsis kawari* Moreira and Yamashita, 1972 *Aglauropsis vannucci* Thomas and Chlapgar, 1975

## Genus Craspedacusta Lankester, 1880:

Olindiidae without peduncle; with four simple radial canals; without centripetalcanals; with «gonads» only on radial canal, hanging, pouch-like; with evenly distributed marginal tentacles all of one kind, without organs of adhesion; with closed ecto-endodermal statocysts situated in the velum. Hydroid: Solitary or forming small reptant colonies of 2 to 4, rarely 7 polyps; hydranths without tentacles, cylindrical, with apical mouth (hypostome)

surrounded by cnidocysts forming a spherical capitulum under which the polyp is slightly tapering, forming a distinct neck; basal portion of hydranths with periderm covering, attaching colonies to substrate; medusa buds lateral, on the middle or lower part of the bodycolumn, often becoming terminal by hydranth reduction; asexual reproduction by frustules, transversal division and resting stages (cysts).

Craspedacusta chuxiogensis He, Xu & Nie, 2000 Craspedacusta kuoi Shieh and Wang, 1959 = Craspedacuta sowerbyi Craspedacusta iseana (Oka and Hara, 1922) Craspedacusta sichuanensis He and Kou, 1984 = Craspedacuta sowerbyi Craspedacusta sinensis Gaw and Kung, 1939 Craspedacusta sowerbyi Lankester, 1880 Craspedacusta vovasi Naumov and Stepanjants,1971 Craspedacusta ziguiensis He and Xu, 1985 = Craspedacuta sowerbyi

Remark: Numerous species of *Craspedacusta* have been described, mainly from China. It cannot be exclude that they represent nothing more than variations of a single species. The same remark can be applied to the *Limnocnida* from India.

## Genus Cubaia Mayer, 1894:

Olindiidae with 4 simple radial canals; without centripetal canals; with 2 series of tentacles: one series (20) issuing from exumbrella above bell margin, with terminal adhesive disks and about 8 cnidocyst rings, the other series (50-60) without adhesive disks, with 25-30 cnidocyst rings arising from bell margin; numerous statocysts.

Hydroid: Unknown. Cubaia aphrodite Mayer, 1894

## Genus Eperetmus Bigelow, 1915:

Olindiidae with 4 radial canals and several blind centripetal canals, oral lips with cnidocyst knobs; with numerous tentacles of one kind, not in-groups but

situated at different heights above exumbrella margin, with rings of cnidocysts, without adhesive pads, with numerous statocysts.

Hydroid: Small, with a single elongated filiform tentacle, issued of a creeping stolon covered by perisarc.

Eperetmus typus H.B. Bigelow, 1915

# Genus Gonionemus, A. Agassiz, 1862:

Olindiidae without or with slight peduncle; with 4 simple radial canals; without centripetal canals; with folded «gonads» on radial canals only; with evenly distributed marginal tentacles all of one kind, with organs of adhesion; with numerous statocysts enclosed in mesoglea.

Hydroid: small, solitary, devoid of hydrorhiza, with a conspicuous conical hypostome and a circlet of 4-6 very long tentacles; medusa buds, frustules, cysts formed by intensive asexual budding.

*Gonionemus chekiangensis* Kao, Li, Chang and Li, 1958 = *G. vertens*?

Gonionemus conanti Browne, 1902 = G. vertens?

Gonionemus hamatus Kramp, 1965

Gonionemus oshoro Uchida, 1929 = G. vertens

Gonionemus vertens A. Agassiz, 1862

Gonionemus vindobonensis Joseph, 1918 = G. vertens

Genus Gossea L.Agassiz, 1862:

Olindiidae with four simple radial canals; with or without gastric peduncle; without centripetal canals; with folded ribbon-like «gonads» only on radial canals; with one kind of tentacles, some of which are arranged in groups; without adhesive pads; with statocysts enclosed in exumbrellar mesoglea. Hydroid: Unknown.

Gossea brachymera Bigelow, 1909 Gossea corynetes (Gosse, 1853) Gossea faureae Picard, 1952 Gossea indica Bouillon, 1978

Genus LimnocnidaGünther, 1893: Olindiidae with circular flat manubrium, with large, simple circular mouth, with 4 simple radial canals; with «gonads» on manubrium only, with enclosed marginal statocysts. Hydroid: Similar to *Craspedacusta*. *Limnocnida biharensis* Firoz-Ahmad, Sen, Mishra and Bharti, 1986 = perhaps *L. indica*? *Limnocnida congoensis* Bouillon, 1958 *Limnocnida indica* Annandale, 1912 *Limnocnida nepalensis* Dumont, 1976 = *Limnocnida indica*? *Limnocnida rhodesiae* Boulenger, 1912 = perhaps *L. tanganyicae*? *Limnocnida tanganyicae* Günther, 1893

Remark: see under Craspedacusta.

# Genus Maeotias Ostroumoff, 1896:

Olindiidae with centripetal canals; with numerous tentacles with tightly packed cnidocyst rings, all on umbrellar margin and without adhesive pads; with «gonads» on radial canals.

Hydroid: Unknown (see below)

Remarks: Mills and Sommer (1995) described the polyp and the newly released medusae of this species; they could not detect statocysts in the adult medusae and reclassified *Maeotias* in the Moerisiidae. Mills (pers. Comm.), however, thinks that the polyp and newly medusa they described as *Maeotias* were actually Moerisiids. Furthermore, the examinations of living specimens of mature *Maeotias* showed her the unquestionable presence of numerous marginal statocysts. She came to the conclusion that the Limnomedusae may at this point remain the most appropriate location for this species until more is known. *Maeotias inexspectata* Ostroumoff, 1896

Genus Nuarchus Bigelow, 1912:

Olindiidae with six radial canals, without centripetal canals, mouth simple, circular; «gonads» leaf-like, on radial canals; statocysts at base of tentacles. Hydroid: Unknown.

Nuarchus halius Bigelow, 1912

# Genus Olindias Müller, 1861:

Olindiidae with 4 radial canals and numerous centripetal canals; numerous tentacles of two kinds: primary ones issuing above bell margin, with distal adhesive pads and cnidocysts in transverse clasps, secondary ones on bell margin, without adhesive pads, with cnidocysts in rings; «gonads» with papilliform processes; numerous marginal clubs which may transform into tentacles, statocysts usually in pairs at base of primary tentacles. Hydroid: Only known in *Olindias phosphorica* as small solitary hydranth without tentacles, enclosed in a perisarcal tube. *Olindias formosa* (Goto, 1903) *Olindias malayensis* Maas, 1905 *Olindias sambaquiensis* Müller, 1861 *Olindias singularis* Browne, 1905 *Olindias tenuis* (Fewkes, 1882) = probably *O. phosphorica* ? *Olindioides formosa* Goto, 1903 = *Olindias formosa* 

## Genus Scolionema Kishinouye, 1910:

Olindiidae without or with slight peduncle; with 4 simple radial canal; without centripetal canals; with folded «gonads» extending along 1/3 to 1/2 of distal part of radial canals only; with evenly distributed marginal tentacles all of one kind, with rudimentary organs of adhesion; with never more than 16 statocysts enclosed in mesoglea.

Hydroid: Solitary, small, discoidal; with not well defined hypostomial region, with up to 5 tentacles; presenting varied and intensive lateral asexual budding: medusa buds, frustules, cysts.

Scolionema suvaense (Agassiz and Mayer, 1899)

# Genus Vallentinia Browne, 1902:

Olindiidae with 4 radial canals, without centripetal canals; with 4 to 8 hollow tentacles with terminal adhesive pads, and numerous tentacles without adhesive pads but with numerous rings of cnidocysts; with 16 or more statocysts. Hydroid: Solitary, small, conical, with one apical ring of tentacles, asexual reproduction by frustules. *Vallentinia adherens* Hyman, 1947 *Vallentinia falklandica* Browne, 1902 *Vallentinia gabriellae* Mendes, 1948

# Olindiidae incertae sedis; with eumedusoids; only known by juvenile meduses; or insufficiently described:

## Genus Astrohydra Hashimoto, 1981:

Only juvenile medusae known; with up to 29 hollow marginal tentacles without marginal bulbs, each tentacle bearing many unicellular long and straight bristlelike expansions with one to three cnidocysts on apices; manubrium quadrangular; mouth with 4 small lips; radial canals usually 4; up to 15 spherical statocyst, no gonads formed (Hashimoto, 1985).

Hydroid: Polyp solitary, barrel-shaped, with 10-30 very fine, filiform tentacles, irregularly strewn over hydranth; with frustules and medusa buds on hydranth body.

Astrohydra japonica Hashimoto, 1981

#### ?Genus Keralica Khatri, 1984:

Umbrella with 128 marginal tentacles; 4 radial canals; mouth circular with 6 lobes; with statocysts; only juvenile specimens with weakly developed gonads on radial canals known, some specimens also with eggs on manubrium(?). Hydroid: Unknown.

*Keralica idukkensis* Khatri, 1984 = insufficient diagnosis, doubtful systematic position; needs confirmation.

Genus Mansariella Malhotra, Duda and Jyoti, 1976:

with about 160 marginal tentacles; one statocyst per tentacle; manubrium short, mouth circular; gonads unkown; with medusa buds.

Hydroid: Unknown.

*Mansariella lacustris* Malhotra, Duda and Jyoti, 1976 = immature specimen of a *Limnocnida* species?

Genus Monobrachium Mereshkowsky, 1877:

Only eumedusoids known.

Hydroid: Creeping colonies living on bivalve shells; hydrorhiza reticulated or incrusting or both reticulated and incrusting; hydranths sessile, claviform, with only one oral filiform tentacle; hypostome large, club-shaped; sometimes dactylozooids in form of pedunculated cnidocyst knobs; gonophores pedunculated on hydrorhiza giving fixed or free eumedusoids, with or without statocysts.

*Monobrachium antarctica* Robins, 1972 = fixed eumedusoid? *Monobrachium drachi* Marche-Marchad, 1963 = ree eumedusoid. *Monobrachium parasiticum* Mereschkowsky, 1877 = probably free eumedusoid.

# 3) CLASS POLYPODIOZOA Raikova 1988 (valid species 1).

This class is represented by a single species, *Polypodium hydriforme* Ussow, 1885, which is the only known metazoan adapted to intra-cellular parasitism. *Polypodium* has a unique life cycle, having a succession of a free-living stage and of an intra-cellular parasitic stage of some Acipenseridae and Polyodontidae eggs.

*Polypodium* earliest parasitic stage known, a binucleate cell, is observed in previtellogenetic fish oocytes. The further parasitic development takes place in the fish egg and may take several years, it leads to the formations of a convoluted didermic stolonal structure, with inverted germ layers, growing at

the expenses of the egg's yolk and forming numerous inverted buds. Before becoming free at the spawning of the mature fish, eversion takes place and the germ layers take their normal position (ectoderm out, endoderm inside). Free, the stolon fragments into individual buds each of which gives rise to a free creeping globular stage that can multiply by longitudinal fission. Those stages can move and feed, having an oral mouth-cone and tentacles. Specimens with 24 tentacles usually predominate but, in mid summer, 12-tentacled individuals become common whereas, in late summer, specimens with only six tentacles are found. The germ cells are endodermal in origin, the so-called females have two kinds of «gonads» each with a gonoduct opening in the gastral cavity, the socalled males are deprived of such a structure, but their «gonads» form gametophores carrying cnidocysts. It is not known how the parasites get into young fish previtellogenic oocytes. The free-living stage presumably represents the sexual medusae, the parasitic stages being considered as polypoid. By their stolonal parasitic budding stage and their cnidome, the Polypodiozoa seem to present some affinities with the Narcomedusae to which they where previously associated.

## Remarks:

This class comprise only *Polypodium hydriforme* Ussow, 1885 which, was till recently the only known metazoan adapted to an intracellular parasitic life. 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.

Family **Polypodiidae** Poche, 1914 (1): See characters of the class. **Genus** *Polypodium* Ussow, 1887: See characters of the class. *Polypodium hydriforme* Ussow, 1885

# E: GLOSSARY:

**abaxial:** away from the main axis or on a site remote from it; in a medusa marginal tentacle, the outer tentacular surface.

**abcauline:** on the side away from the caulus, the opposite is adcauline. **aboral:** away, opposite from mouth or oral end.

**actinula:** postembryonic tentacle-bearing larval stage that creeps along substratum, characteristic of some Anthomedusae, somewhat resembling a small hydranth, usually with two or more circles of tentacles and developing directly into a hydroid stage. Not homologous to the tentaculated postembryonic larvae of the Trachymedusae and Narcomedusae inappropriately called «Actinulae» which have only one aboral circle of tentacles, a different histological structure and give rise directly to a medusa stage.

**actinopharynx:** in the Anthozoa, ectoderm of the mouth rim turned in for a considerable distance as a muscular introduction to the coelenteron. In Hydrozoa, Cubozoa and Scyphozoa ectoderm and endoderm meet at the mouth rim.

**adaxial:** position opposite to abaxial, facing towards the main axis; in a medusa marginal tentacle, the inner tentacular surface.

adcauline: directed towards the caulus, see abcauline.

**adhesive pad:** in medusa adhesive structure lacking cnidocysts near tentacle tip.

**adnate:** having part or all of one side in contact with or fixed to another structure, (e. g., adaxial side of a marginal tentacle fixed to the exumbrella in *Leuckartiara adnata*; hydrothecae having part or all of one side in contact with the stem or another structure).

**adradial:** the axes or sectors lying between the perradial and interradial ones; in a medusa with 4 radial canals there are 4 perradial axes; 4 interradial axes and 8 adradial axes and 16 sectors.

**amphicoronate:** alternate up and down arrangement of a single row of oral tentacles.

**annulus:** in hydroids one in a series of rings in perisarc, typically in groups directly below hydranths, demarcating the internodes, at nodes or at point of branching of stalks.

annular thickening: see diaphragm.

**apical or umbilical canal:** during the development of a medusa bud, an opening provides continuity and exchanges between the "maternal" gastric cavity and that of the bud. Generally this opening disappears after liberation, but in some medusae it remains as a small canal or duct projecting from the manubrium into the apical mesoglea and often leading upwards to the outside (e. g. *Sarsia producta, Corymorpha nutans*).

**apical knob or chamber:** small aboral chamber at the apex of the manubrium, protruding into the apical umbrellar mesoglea (e. g., some *Sarsia; Amphinema rubra; Euphysora furcata, Plotocnide borealis,* etc.).

**apical projection or process:** a rounded or pointed, usually roughly conical mesoglear extension of the top of the umbrella (e. g., *Amphinema, Leuckartiara*).

**athecata:** the hydroids of the Anthomedusae, all lack a proper hydrotheca or chitinous cup surrounding partially or entirely their hydranths.

# **basal web = intertentacular web**

**bell:** = umbrella.

bicoronate: arrangement of oral tentacles in two whorls.

**bimucronate:** with two sharp points (e. g., the hydrothecal cusps of *Obelia bidentata*).

**blastostyle:** gonozooid or gastro-gonozooid generally reduced to a didermic axis or stalk bearing the developing gonophores: medusae or their reduced derivatives medusoids or sporosacs.

**blind canal:** centrifugal or radial canals that do not join circular canal (e. g., *Toxorchis*); centripetal canals that do not join radial canals or manubrium (e. g., some *Calycopsis*).

**butt** = **shaft:** enlarged portion of tubule in cnidocysts, may bear stylets and/or spines, either of uniform or not uniform diameter. **campanulate:** bell-shaped.

**campanulinid:** hydroids not necessarily closely related to a "*Campanulina*", but with tubular hydrotheca with conical operculum formed by several triangular, convergent pleats or cusps meeting centrally and which may be or may not be sharply demarcated from the hydrothecal margin (cuspidellid, campanopsid, eirenid, etc.).

**capitate tentacle:** tentacle with a knobbed end, richly armed with cnidocysts. **cathamnal lamella:** endodermal sheet connecting the radial canals through the umbrellar jelly and separating the outer from the inner mesoglea. **caulus:** main stem (hydrocaulus).

**centrifugal canal:** canal issued from the manubrium and directed towards umbrellar margin (= generally radial canals).

**centripetal canal:** canal issued from the circular canal and directed to the manubrium (e. g., *Calycopsis*).

**chordal or chordoid:** formed by a core of single disk-like or cylindrical cells placed end to end in a single row (e. g., solid tentacles of *Obelia*).

**circular or ring canal:** simple canal running around the umbrellar margin linking the ends of the radial canals; occasionally the circular canal is not hollow but consist in a solid core of endodermal cells (e. g., *Proboscidactyla*, Laingiomedusae). In the Narcomedusae, with umbrellar margin deeply cleft into broad flaps, a circular canal may be present or not; when present, the marginal canal follows the edge of the margin of the exumbrellar flaps and is called "peripheral canal system", the vertical parts of which are the peronial canals. **cirri:** small tentacular-like organs situated on the umbrellar margin between the true marginal tentacles, they are devoid of swollen marginal bulbs and are solid. Two types are generally found:

1° **spiral cirri:** coiling spirally, with scattered cnidocysts and a terminal cluster of cnidocysts, common (e. g., *Mitrocomella*).

**2° flexile cirri:** straight, do not coil and have cnidocysts in rings (e. g., *Cosmetira*).

Cirri may immediately be adjacent to the marginal bulbs and are then said **lateral** cirri (e. g., *Eucheilota*), they may also occur along the umbrellar margin

in the inter-spaces between marginal tentacles, they are then called **marginal** cirri (e. g., *Cosmetira, Phialopsis*).

**clasp:** part of a marginal bulb embracing the exumbrella (e. g., *Leuckartiara*) (see exumbrellar spur).

**cladium:** in a hydroid, a **branchlet** off the main stem or caulus (hydrocladium). **cnidae:** a general term for the stinging or adhesive cells characteristic of the Cnidaria: cnidocysts, spirocysts and ptychocysts.

**cnidoblast:** developing cnidocyte, often used synonymously with cnidocyte. **cnidocil:** bristle-shaped projection adjacent to operculum at the distal end of a cnidocyte; serves as trigger to discharge the cnidocyst.

**cnidocyst (nematocyst or stinging cell):** stinging organelle characteristic of the Cnidaria, it consists of a double-walled capsule, secreted by a particular cell called cnidocyte, containing a refringent fluid, a distal opeculum, and a coiled and folded tubule (shaft, thread or internal tube) which everts and straightens on discharge. Following the structure of the internal tube different types of cnidocysts are recognised, they are of great use in taxonomy. Cnidocyst are used for prey capture, defence, and attachment.

**cnidocyst marginal ring = nettle ring:** in Trachymedusae, a dense band of cnidocysts encircling the exumbrellar margin.

**cnidocyte:** specialised cell type, located usually in the ectoderm. It consists of a basal nucleus, a distal cnidocil and contains the cnidocyst; cell walls with supporting roots. Typically concentrated in the tentacles.

cnidome: entire complement of cnidocyst types in a given taxon.

**cnidophore:** cnidocyst-filled cellular capsules covered by numerous long cilia and attached to tentacles by elongated, filiform and very contractile stalks of special structure (e. g., *Zanclea*), not to be confounded with branched tentacles. **compound sense organ:** marginal sense organ formed by an ecto-endodermal ocellus and an open ectodermal statocyst (in the Tiaropsidae).

coenosarc: the living tissue of a hydroid colony.

**coppinia:** a close aggregation of numerous gonothecae together in a muff-like structure (e. g., in the Lafoeidae).

**corbula:** protective basket-like group of modified hydrocladia protecting several gonothecae loosely fused together (Aglaopheniidae).

**cordylus:** minute, marginal club-shaped structures situated on the umbrellar margin between the tentacles. With a narrow peduncle and a thick distal portion, either hollow or completely filled by endoderm, with cnidocysts or not, function unknown, probably sensory (e. g., Laodiceidae, Tiarannidae).

**crenulated**: having low rounded cusps or lobes separated by sharp but shallow notches (e. g., of mouth lips).

cruciform: cross-shaped.

cryptomedusoid: strongly reduced medusae; seldom with free pelagic life (swimming gonophores); without radial canals but with an endodermal lamina lining the exumbrellar ectoderm: the umbrella endoderm (homologous to the cathamnal lamella); still provided with a reduced subumbrellar cavity or with the subumbrellar cavity represented only by an ectodermal layer: the internal ectoderm, germ cells on spadix (= manubrium), in eccentric position. **cvst:** generally chitinous protected structure containing eggs, embryos or even portion of an organism in an inactive stage. Cysts are resting stages, usually resistant to bad or unfavourable environmental conditions. They can either be part of the normal life cycle or appear depending on circumstantial conditions. **dactylozooid** (= machozooid): defensive or protective polyp, usually highly extensible and mobile, richly armed with cnidocyst, often a reduced and modified gastrozooid; usually deprived of mouth and either without or with a reduced number of tentacles. Some with characteristic structure (see tentaculozooid, nematophore, sarcostyle and spiral zooid), some with chemioreceptors.

**desmocyte:** minute chitinous rivet anchoring the skeleton to the mesoglea (= punctae or birefringent nodules).

**diaphragm:** protrusion of the endoderm partitioning the gastric cavity in some hydroids (Corymorphidae); in many thecate hydroids, a thin inwardly projecting, circular, chitinous shelf at the base of the hydrotheca, sometimes an annular thickening of a less defined nature occupies the same position. The centre of the diaphragm is perforated by a hole, or hydropore.
**diploblastic:** being composed of two epithelia, in hydroids formed by an outer ectoderm and an inner endoderm, separated by a kind of relatively undifferentiated connective layer, the mesoglea, usually not regarded as a real tissue layer.

**direct development:** development where the medusa stage will give rise to another medusa without passing through a hydroid phase (e. g., Trachymedusae, most Narcomedusae) or where a hydroid will produce directly an other hydroid (e. g., *Hydra*).

distal: at the far end, near the end.

ectoderm: outermost cellular layer (epidermis).

**ectodermal lining:** layer of ectoderm lining the hydrotheca, arising from hydranth base and continous with the roofing plate.

**ectodermal statocyst:** marginal sense organ of orientation and equilibration developed in the velum and entirely ectodermal, formed in depressions or pockets of the velum and either remaining open (open ectodermal statocysts of, e. g., Mitrocomidae, Tiaropsidae) or being sealed by velar tissues (closed ectodermal statocysts, e. g., the other Leptomedusae). Characterised by special cells or lithocytes containing one or more tiny polygonal or spherical concretion (statolith = otolith). Closed statocysts with a basal cushion of cells with sensory cilia.

**ecto-endodermal ocelli:** photoreceptors found in the Tiaropsidae where the cup-shaped mass of pigment is formed by the endoderm of the circular canal, the nerve elements being ectodermal. The ocelli of the other Hydroidomedusa are completely ectodermal in origin. In the Tiaropsidae the ocelli are associated with open ectodermal statocysts forming a compound sense organ.

**embayement:** a rounded or pointed gap between two adjacent cusps along the rim of a hydrotheca.

**embryo:** an early developmental stage resulting from repeated cleavage and subsequent growth of a zygote. Embryological development passes through several stages, such as morula, blastula, and gastrula, this corresponding to the embryonic stage where the germ layers become established first. In the Hydrozoa the gastrula is the two-layered developmental stage in which the

rudimentary endoderm layer differentiate = planula. In contrast to larvae, embryonic stages are neither planktotrophyc nor lecythotrophic and cannot lead a long independent existence, except when encysted.

**endoderm:** innermost cellular layer, lines the gastrovascular cavities. **ecto-endodermal statocyst = tentaculocyst = sensory club:** club-like sense organ of orientation and equilibration growing out of the umbrellar margin in the fashion of a tentacle; each is formed by an endodermal axis originating from the circular canal and covered by the umbrellar ectoderm. With one or more distal, large endoderm cell (lithocytes) each containing a solid concretion (statolith). In this form they are called "free ecto-endodermal statocysts or free sensory clubs " (e. g., Narcomedusae and Trachymedusae). In some species sensory clubs are enveloped by mesoglea or by an ectodermal vesicle embedded in the mesoglea, being called "closed ecto-endodermal statocysts" (e. g., Limnomedusae, few Trachymedusae and a genus of Narcomedusae: *Sigiweddelia*).

**Entocodon = glockenkern = medusary nodule:** one of the most important and characteristic features of hydroidomedusan development, a solid multistratified nodule produced between ecto- and endoderm by an invagination of the apical budding zone during the morphogenesis of medusa buds or of fixed gonophores, later on developing a cavity: the future subumbrellar cavity. Endodermal components of buds (manubrium, gastro-vascular canals) formed by evagination of the "mother" endoderm (spadix). In few medusae, budding is exclusively ectodermic (*Bougainvillia niobe, Lizzia blondina, Podocoryna minima, Rathkea octopunctata*), the entocodon developing both ectodermal and endodermal components of the buds.

**eumedusoid:** the first step in medusa reduction, with radial canals and subumbrellar cavity, with or without manubrium; when present, manubrium not eccentric; generally without tentacles, usually with sense organs, with velum; gonads on manubrium when Anthomedusae, on radial canals when Leptomedusae. Often with short free pelagic life.

**excretory papillae:** papillae situated in some medusae either between marginal tentacles, or at base of some marginal structures (tentacular bulbs, non-

tentacular or rudimentary bulbs or marginal warts), or on the radial canals. With an opening, or excretory pore, in contact with the cavity of the bulbs or of the gastro-vascular system. Used for the elimination of undigested material. **excretory pore:** opening of the excretory papillae. Sometimes papillae are abesent and pores are simple slits.

**exumbrella:** upper, aboral convex surface of the umbrella (see umbrella). **exumbrellar cnidocyst cluster or band:** exumbrellar specialised tissue in form of oval, club-shaped, spoon-shaped, or elongated patches containing cnidocysts, localised immediately above the marginal bulbs (*Zanclea*) or on exumbrellar margin between tentacles (*Proboscidactyla*).

**exumbrellar spur:** upwards growth of marginal tentacular bulbs, clasping umbrellar margin (e. g., *Leuckartiara*).

**fascicled:** stem comprising two or many coenosarc tubes united in a composite single stem structure (= polysiphonic).

**filiform tentacle:** a throughout straight-sided tentacle, lacking prominent cnidocyst clusters, cnidocyst being evenly distributed.

**flexuose:** hydroid with hydrocauli or hydroclades with successive internodes directed alternately left and right, in a zigzag fashion.

**frustule:** little didermic portion of Hydroidomedusa tissues formed asexually either by budding or by constriction and acting as dormant and/or dispersion stages. Generally formed by polyps, exceptionally by medusae; they all develop into polyps.

**gastric peduncle = peduncle**: in some medusae, a cone-shaped thickening projecting downwards from the subumbrellar mesoglea into the subumbrellar cavity, bearing the manubrium; radial canals run down the peduncle to reach the manubrium; varied in shape and size (e. g., long and narrow in *Eutima mira*; large and pyramidal in *Bougainvillia macloviana*; very short in *Phialopsis diegensis*).

**gastric cavity:** see manubrial cavity. **gastric pouches:** see manubrial pouches.

**gastrovascular system:** the coelenteron or enteron, comprising the manubrium cavity and the gastrovascular canals (i.e., the radial and circular canals and their derivatives).

**gastrozooid:** normal feeding polyp, with mouth and normally with tentacles, without reproductive organs.

**gonad:** there are no real organs in Hydrozoa, so this term is inappropriate although largely used by specialists. We use this term in brackets, being aware that, in medusae, «gonads» indicates the place where the sex cells become mature, this may happens on manubrium walls or/and on the radial canals. The position of the germ cells has a considerable value in classification. When «gonads» are on the manubrium they may completely surround it, being cylindrical, or be in interradial, adradial or perradial position. When situated on the radial canals, they usually develop on their lateral walls but, in some medusae, they are continuous also over the ventral wall (e. g., *Clytia hemisphaerica*). Their position along the course of the radial canals is often a diagnostic character as are their shape and size.

**gonangium:** in colonial hydroids, a reproductive unit consisting of the outer gonotheca and enclosed blastostyle bearing one or many gonophores. **gonophore:** asexual reproductive structure formed by the hydroid stage, normally developing into medusa buds; in many Hydroidomedusa, however, the medusae are reduced to a varying degree and are not liberated anymore, remaining attached to the hydroid in the gonophoral structures. They are then called fixed gonophore or sporosac or fixed sporosac since they are not released anymore. The gonophores give origin to the generative elements, ova or spermatozoa (see medusa reduction)

**gonotheca:** chitinous structure with a distal opening, surrounding and protecting a gonophore.

**gonozooid:** reproductive polyp bearing gonophores; usually a modified gastrozooid with various stages of reduction and reduced or no tentacles.

**Heteromedusoid = sporosac:** highly atrophied medusa devoid of radial canals, umbrellar endoderm, tentacles and sense organs; internal ectoderm remnant of subumbrellar cavity still present.

**hollow tentacle:** tentacle either with a central cavity in continuation with the cavity of the circular canal, or without any lumen but with an endodermal core formed by several peripheral rows of cells (parenchymatic). The basal regions of such tentacles often disclose central cavities. In the Bythotiaridae the tentacles are hollow, but the mesoglea of the distal part of the tentacles is often enlarged and reduces strongly the endodermal axis.

hydranth: the feeding polyp of a hydroid colony.

**hydroclade:** lateral, hydranth-bearing branch of the main stem or hydrocaulus in an erect hydroid colony.

**hydroid:** the polypoid or prolonged and most generally sessile post-planula larva in the Hydroidomedusa life cycle.

**hydrotheca:** chitinous structure surrounding entirely or partially the hydranth in most Leptomedusae.

**hydrocaulus:** main stem of a fixed, erect hydroid colony, typically bearing branches or hydroclades with hydranths.

hydropore: see diaphragm.

**hydrorhiza:** all structures by which fixed hydroids are attached to the substratum, normally in form of a network of branching, anastomosed, creeping tubes or stolons; hydrorhizal tubes may fuse in a mat, becoming incrusting or forming other different structures.

hypostome: distal end of the hydranth, carrying the mouth at its end.

**internode:** segment often dividing the hydrocauli and hydroclades by partitions or nodes often delimited above and below by perisarc annexes (annuli).

**interradial:** the radial axis lying in between two adjacent perradii; between the radial canals.

**intertentacular web = basal web:** thin, transparent sheet, often containing cnidocysts, connecting the base of the tentacles in some thecate families. **intrathecal septum:** internal and transversal shelf or ridge of perisarc inside the hydrotheca.

**juvenile:** a developmental stage which has attained the adult body plan (i.e., symmetry, general body shape and major functional systems such as locomotion and feeding), but not sexual reproduction.

**lappet:** a lobe-like extension around umbrellar margin (some Laingiomedusae, the Narcomedusae).

lateral cirri: see cirri.

**larva:** post-embryonic intermediate developmental stage distinctly different in morphology and physiology from the sexual adult.

**lip:** lobe-like extension of manubrial margin surrounding the mouth (see mouth). Lips may be of simple or complicated structure (i. e., crenulated, folded, short or elongated, pointed or rounded) armed or not with cnidocysts distributed uniformly or in clusters. In the Rathkeidae, lips are elongated, simple or branched and armed with terminal and usually also lateral cnidocyst knobs. **lithocyte:** a cell containing a movable concretion or statolith, closely associated with sensory cells (see ectodermal statocyst and ecto-endodermal statocyst). **lithostyle:** see statocyst.

**manubrial or gastric cavity** (= **stomach**): central cavity of the manubrium in connection with the exterior by the mouth and ending in the radial canals openings, delimited by an endodermal layer histologically divided into several regions named according to function: oral, digestive, stomacal, or sexuated and cnidoblastic when the «gonads» develop on the manubrium. Structure rather uniform throughout the various subclasses, except in *Koellikerina* (Bougainvilliidae) where the endoderm of the gastric cavity presents numerous conspicuous endodermal expansions sustained by a mesoglean axis and containing excretory vacuoles (see Bouillon, 1988a).

**manubrial or gastric pouch or pocket:** lateral perradial or interradial extension of the manubrial cavity (e. g., Narcomedusae, Tiarannidae, *Gotoea*). **manubrium:** axial didermic projection of the subumbrella surrounding the gastric or stomachal cavity, distally bearing the terminal mouth and proximally leading to the radial canals. Manubria are greatly varied in shape and size, ranging from tubular to cruciform, quadratic, fusifom, barrel-shaped, flask-shaped, short, long, narrow or very large, etc. Erroneously considered as synonym with stomach (see stomach).

marginal cirri: see cirri.

marginal cnidocyst ring: see cnidocyst marginal ring.

**marginal lappet:** one in a series of lobe-like extensions around umbrellar margin (e. g., Narcomedusae).

**marginal tentacle:** a tentacle inserted on the edge of the umbrella. **marginal vesicle:** see statocyst.

**marginal wart or swelling:** small, wart-like swellings of the umbrellar margin never destined to carry tentacles (e. g., *Eutima mira*).

**medusa budding:** asexual budding of medusae. In hydroids, it occurs on the lateral wall of the polyp, on the hydrorhiza, on the hydrocauli, on the hydroclades or on specialised structures. Common also among hydromedusae; medusa buds formed either on the manubrium, the radial canals, the marginal bulbs or the subumbrellar rim.

medusa reduction: in many Hydoidomedusae, the medusa becomes reduced, abortive, not leaving the colony anymore, the hydroid becoming the paedomorphic carrier of the sexual cells. Medusa reduction to fixed gonophores or sporosacs evolved independently in many Hydrozoa families and has no phylogenetic value. Reduction may be more or less pronounced pending the species, ranging from stages similar to the adult medusa (free or fixed medusoids) to stages where all medusan structures fail to develop, the germ cells being located in the ectoderm of the polyp body. Different main morphological stages of medusa regression have been recognised and described (see: eumedusoids: cryptomedusoid: heteromedusoid: styloids), they represent the most typical stages of reduction, with intermediate grades in each type. In many species male and female fixed gonophores belong to different types of sporosac. Medusa reduction is exceptional in Limnomedusae; at the species level it is less common in the Anthomedusae than in Leptomedusae where this phenomenon is the rule in most of the families with conspicuous colonies, which never present a real free medusa stages, like the: Aglaopheniidae; Clathrozoidae; Haleciidae; Halopteridae; Plumulariidae; Sertulariidae; Syntheciidae. The small leptomedusan colonies are usually characterised by free medusae, the smallest hydroids often producing the biggest medusae! medusary nodule: see entocodon.

**mesentery:** in some species, a perradial tissue layer attaching the lateral walls of the manubrium to the subumbrella (see: *Leuckartiara octona*, *Neoturris papua*, *Pandeopsis ikarii*).

**mesoglea:** in Hydrozoa, a non-cellular substance lying between the ectoderm and the endoderm; The mesoglea forms the gelatinous bulk of the umbrella in the medusae stage (the jelly of jellyfish) and a lamella-likelayer (mesolamella) in polypoid forms. Synonym with extracellular matrix.

**modular:** consisting of a series of morphologically similar structural units. **moniliform tentacle:** with cnidocyts arranged in a terminal knob and in rather regularly spaced conspicuous clumps.

**mouth:** opening of the manubrium to the exterior, it can be simple and circular or may present simple or complicated lips (see lips).

**mouth arm:** expansion, dilatation of a perradial corner of the manubrial mouth rim armed with cnidocyts clusters, usually open, groove-shaped (e. g., Hydractiniidae).

nematophore: highly extensible structure, mainly known in Leptomedusan hydroids, representing a strongly reduced hydranth richly armed with cnidocysts, without mouth or tentacles, with virtual or totally absent gastric cavity, either protected (see nemathotheca) or naked (a type of dactylozooid).
nematotheca: chitinous theca of varied structure surrounding a nematophore. In the Plumularioeidea they may be either sessile, immovable and one-chambered (monothalamic), or pedicillate, mobile and two-chambered (bithalamic).
nerve ring: in the hydromedusae there are two nerve rings around umbrella margin, which lie usually on opposite sides of the velum, separated by a mesoglean lamella: a subumbrellar one, located above velum attachment (inner or upper nerve ring) and an exumbrellar one, located below velum attachment (outer or lower nerve ring). The two are connected by neurites.
nettle ring: see cnidocyst ring.

**non-tentacular marginal bulb:** marginal bulb developed on the umbrella margin without bearing tentacles. Some never develope tentacles, others can be the result of by tentacle reduction. It is necessary to distinguish between bulbs that are permanently without tentacles (permanent non-tentacular marginal



bulbs, rudimentary marginal bulbs, as in *Cirrhitiara superba*, *Aequorea macrodactyla*) and those bulbs on which a marginal tentacles will develop later on during medusan growth (developing tentacular marginal bulbs, as in *Clytia* and Malagazziidae).

node: see internode.

**ocellus (pl. ocelli):** multicellular photoreceptor found in some hydromedusae, common in Anthomedusae, usually situated on the marginal bulbs in abaxial or adaxial position. They appear as round, oblong or elongated spots, black, brown, yellow or red in colour, consisting of a small mass or cupule of pigmented cells associated with nerve cells. A lens may be present. Of ectodermal origin, except in the Tiaropsidae (see ecto-endodermal ocelli). **octant:** an eight of the umbrella; the space between the interradii in a medusa with 4 radial canals.

**operculum:** lid-like structure closing hydrothecae or gonothecae. Some comprise a single flap, others have two, three, four or many flaps meeting in the centre; opercular valves may be simple inwards folds of the distal part of the hydrothecae (pleated), or segments of the primary covering of the hydrotheca seated and hinged in embayements (prominent crease-line) of the hydrothecal margin; they may be cast away during hydranth growth or after medusa liberation. The term also refers the to lid covering the opening of cnidocysts. **oral:** near the mouth, the opposite end being aboral.

**oral tentacle:** tentacle arising above the mouth rim in some medusae with a circular mouth. Simple and located just above the mouth rim in the Cytaeididae, simple or branched and situated well above the mouth rim in the Bougainvilliidae.

**otoporpae:** in some Narcomedusae, vertical, elongated, oval or even rounded ectodermal tracts with bristles and cnidocysts running upwards from each statocyst over the exumbrella margin.

**pedicel:** stalk of a hydrotheca, a gonotheca or a hydranth (= stem, hydroclade). **peduncle**: see gastric peduncle.

**peripheral canal**: in hydroids, longitudinal peripheral canals of the hydrocaulus.

peripheral canal system: see circular canal.

**periderm:** mucoproteinic coating (= glycocalyx or cuticle) of the exposed surface of hydroids and medusae.

**perisarc:** the chitinous exoskeleton surrounding the coenosarc of most hydroids. In the Anthomedusae the polyps are never surrounded by perisarc, in the Leptomedusae they usually are (see hydrothecae, gonothecae and nematothecae).

**peronia:** in Narcomedusae and some Laingiomedusae the tentacles originate at some distance from the margin, just above the clefts separating the marginal lappets. At the edges of the clefts, the subumbrellar and exumbrellar ectoderm fuse without interposition of mesoglea ,forming grooves invaded by tentacular ectoderm making up together an ectodermal strand rich in cnidocysts, muscles and nerves: the peronia. At the base of the peronia the margin of the umbrella lappets remains curved, giving the umbrella its lobed appearance. The peronia and the exumbrellar position of the tentacles result from developmental circumstances. During Narcomedusae development, the endodermal core of the tentacles is issued from the manubrium; during umbrella growth the tentacles remain attached close to the manubrium and the tentacular ectoderm, maintaining its connection with the umbrella margin, forms the peronia (see also tentacular roots).

**peronial canal:** in Narcomedusae the part of the peripheral canal system running vertically along the peronia (see circular canal).

**perradial:** the main radial axes of a medusa, corresponding in most species to the radial canals. **pharynx:** embryologically the pharynx is a stomodeum and, as such, is lined by an integument of ectodermal origin. A real pharynx does not exist in Hydrozoa, where ectoderm and endoderm meet at the mouth rim, but is present in Anthozoa (see actynopharynx).

**phylactocarps**: in some Aglaopheniidae hydrocladia forming a protective structure around gonothecae, similar to corbula hydrocladia, but not fused. **pinnate:** stem resembling a feather.

**planula:** an embryonic free-swimming post blastula stage into which most of the Hydrozoa eggs become directly developed (= gastrula = coelogastrula or



stereogastrula). Inproperly called larva since, from a developmental point of view, it is an embryo (see embryo and larva).

**podocyst:** multicellular capsule from nipped-off portions of coenosarc, functioning as a cyst.

**polyp:** basic individual of the hydroids; may either be isolated or form colonies; represented by different types, such as hydranths, gonozooids and dactylozooids.

**primary polyp:** the hydranth formed by the metamorphic development of a newly settled planula.

propagule: any morph leading to propagation.

**polymorphic:** ability to exist in different forms (in hydroids: gastrozooids, gonozooids, dactylozooids, etc.).

**polyp reduction:** In some Campanulinida families, for instance the Eirenidae and the Eucheilotidae, only the newly developed polyps have completely developed hydrothecae, with age these become reduced, losing their operculum and apical part, and are no longer high enough to accommodate the hydranths (haleciid-like).

proximal: at the near end, at the base.

**pseudohydrotheca:** a film-like, flexible coat covering partly or entirely the hydranth body of some Anthomedusae hydroids, not homologous to the perisarcal hydrothecae but apparently similar in function (e.g., some Bougainvilliids and Pandeids).

**quadrant:** a quarter of the umbrella; the space between perradii in a medusa with 4 radial canals.

**radial canal:** canal leading from the perradial corners of the manubrium to the circular canal. Usually straight and narrow, with smooth sides. In some species large, ribbon-like (e. g., *Amphinema*) and with jagged outgrowths (e. g., *Leuckartiara*). Typically four, but more numerous in many medusae, exceeding more than 100 (e. g., *Aequorea*). Normally simple, but in certain species branched and sometimes whose branches never reach the circular canal (e. g., *Staurodiscus*). Generally growing centrifugally, from the manubrium to the

circular canal, except in a few species where they arise centripetally (e. g., *Melicertoides*; the centripetal canals).

**renovation:** a new hydrotheca developing within an old one, sometimes repeatedly, resulting in a tier of hydrothecae one within the other; sometimes only the hydrothecal margin renovates.

ring canal: see circular canal.

rudimentary bulb: see non-tentacular marginal bulb.

**sarcostyle:** specialised nematophore found mainly in the Plumularioidea and exceptionally in a few other families, naked, emerging through a hole of the perisarc or protected by a minute nematotheca, or sarcotheca. Mobile, armed with cnidocysts, some distally rich in adhesive gland cells and playing a role in phagocytosis or in cleaning the surrounding perisarc.

sensory club: see ecto-endodermal statocyst.

shaft: see butt.

**solid tentacle:** tentacle without any central cavity, with an endodermal core formed by a single row of disk-like or cylindrical vacuolated cells placed end by end (see chordal).

**spadix:** the central finger-shaped core formed by an evagination of the "mother" endoderm, covered by entocodonial ectoderm, forming the manubrium in a medusa or supporting ripe sex cells in most of the reduced gonophores (see sporosacs). Its central cavity is continuous with that of the colony.

**spermatophore:** a compact mass or packet of spermatozoa, is liberated or transferred to a female.

**spherule:** a globular region of pedicel directly beneath hydrotheca, formed by two adjacent annular constrictions.

**sphincter:** cellular or skeletal structures of the aboral part of hydranths preventing the transfer of too large prey pieces from the gastric cavity to the lumen of the stolonal system; in the Campanulariids this term is applied also to the constriction of the base of the globular hypostome.

**spiral zooid:** modified polyp without mouth, with a gastric cavity, bearing either terminal cnidocyst aggregations or stout cnidocyst knobs or very short



tentacles richly armed with cnidocysts and tending to twist or coil into spiral, characteristic of some Hydractiniidae (a type of dactylozooid).

**sporosac:** reduced type of gonophore remaining fixed to the hydroid and in which the sex cells ripen directly, of different types (see eumedusoids, cryptomedusoids, heteromedusoids and styloids).

statocyst = lithostyle = tentaculocyst = sensory club: see ectodermal statocyst
and ecto-endodermal statocyst.

**statolith = otolith:** minute concretion composed of organic material and minerals, mainly calcium carbonate, enclosed within the lithocytes of statocysts, their movement stimulates sensory receptors (see ectodermal statocyst and ecto-endodermal statocyst).

stem: any erect structure bearing hydranths.

**stolon:** in hydroids, creeping or erect hollow tube protected by perisarc and containing the same ecto-endodermal tissues of the polyps (coenosarc), generally adhering to the substrate forming a complex system, or hydrorhiza. Under adverse environmental conditions only the stolons of many colonies survive, acting as resting stages until proper conditions retourn.

**stolonal colonies:** colonies where the growth is horizontal and the hydranths arise directly or from short unbranched pedicels from a common creeping hydrorhiza.

**stomach:** internal pouch or cavity in which food is digested, name often used instead of manubrium (see manubrium).

**styloid sporosac:** the most regressed type of gonophore, without internal ectoderm and umbrellar endoderm; reduced to a single evagination of the two germ layers, between which the genital elements accumulate.

subumbrella: see umbrella.

subumbrellar cavity: see umbrella.

subumbrellar surface: see umbrella.

**swimming gonophore = swimming sporosac:** pelagic stage derived from reduced, sessile gonophores; usually without radial canals and circular canal; without tentacles; without sense organs; with sexual elements always on "manubrium" in eccentric position even in Leptomedusae. Strongly reduced

medusa stages (cryptomedusoids and perhaps heteromedusoids) developing as free gamete carriers. They can not been confused with eumedusoids, the first step of medusa reduction, still with most of the original non reproductive structure of the medusa: radial canals, circular canal, velum, sense organs, with maturation of the sexual cells according the classes (on manubrium in Anthomedusae on radial canals in Leptomedusae) and with a non eccentric position of the manubrium. The swimming gonophores are found mostly in Leptomedusae families with paedomorphic hydroids characterized by the possession of fixed and highly reduced gonophores; some are known in Anthomedusae (e. g., *Pachycordyle*).

tentacle: see marginal tentacle.

tentaculae: small solid marginal tentacles (usually without marginal bulbs) located between normal hollow tentacles (e. g., Amphinema rugosa). tentacular marginal bulb: in most Antho- and Leptomedusae, a dilated portion of the proximal part of a marginal tentacle, next umbrella margin, containing a cavity in communication with the circular canal and with the tentacular cavity of hollow tentacles. Of various shapes, most simple but in some medusae compound, originating several tentacles (e. g., Bougainvillia); performing digestive activities; centres of cnidoblast formation and, in some species, bearing ocelli. In Anthomedusae and Leptomedusae a new marginal tentacle is normally preceded by the formation of a bulb on which it will develop (see marginal bulb). In some medusae there are no true tentacular bulbs: i.e. in the Limnomedusae, Narcomedusae, Trachymedusae, in the majority of the Bythotiaridae, in the Anthomedusae Eugtoea petalina and Rhabdoon singularis. tentaculiform structure: solid marginal structure resembling to tentaculae without marginal bulb but without any contact with the circular canal (exclusively in the Orchistomatidae).

**tentacular root:** projection of the endodermal tentacular core into the umbrella mesoglea (*Blackfordia, Obelia*, some Limnomedusae, Trachymedusae and the Narcomedusae) (see peronia).

tentaculocyst: see ecto-endodermal statocyst.

**tentaculozooid:** reduced dactylozooid similar to tentacle in structure, with a solid core of chordal endoderm and no mouth, richly armed with cnidocysts and often with chemosensory receptors; very extensible and contractile. **thecate:** name for the hydroid stage of the Leptomedusae, usually with thecae protecting their hydranths and gonophores.

**theca:** chitinous extension typically protecting any kind of polyp. **thread:** hollow thin tube coiled inside cnidocyst capsule. Discharged threads may be differentiated into dilated section, or shaft, and a thinner section, or thread or tubule.

tubule: see thread.

umbilical canal: see apical canal.

**umbrella:** main body, generally resembling a bell or an umbrella, of the medusa, excluding manubrium and tentacles. The outer, generally convex, surface of the umbrella is the exumbrellar surface (exumbrella), the inner concave surface is the subumbrellar surface (subumbrella) and the cavity bounded by the subumbrellar surface is the subumbrellar cavity. The edge of the umbrella is the umbrella margin.

**vasiform:** vase-shaped, with broad base and slender top. **velar:** of the velum.

**velum:** horizontal fold projecting inwards from umbrella margin, leaving a central, circular hole, the velar opening. It consist of two layers of ectoderm separated by a thin mesoglean lamella; the inner ectoderm, of subumbrellar origin, possess striated muscles. The velum serves in the propulsion and the orientation of the medusa, it acts like a photographic diaphragm, during swimming the medusa can adjust the diameter of its aperture which can become as wide as the umbrella or almost closed.

**zooid:** in colonial hydroids, any of several types of individual polyps: dactylozooids, gastrozooids, gonozooids.

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Aegina citrea Eschscholtz, 1829 - 18,59 Aeginodiscus actinodiscus Haeckel, 1879 - 60 Aeginopsis laurentii Brandt, 1838 - 59 Aeginura beebei Bigelow, 1940 - 59 Aeginura grimaldii Maas, 1904 - 59 Aequorea albida L.Agassiz, 1862 - 166 Aequorea australis Uchida, 1947 - 166 Aequorea coerulescens (Brandt, 1838) - 166 Aequorea conica Browne, 1905 - 166 Aequorea cyanea de Blainville, 1834 - 166 Aequorea floridana (L. Agassiz, 1862) - 166 Aequorea floridana (L. Agassiz, 182) - 166 Aequorea globosa Eschscholtz, 1829 - 167 Aequorea krampi Bouillon, 1984 - 167 Aequorea macrodactyla (Brandt, 1834) - 167, 235
Aequorea minima Bouillon, 1985 - 167 Aequorea papillata Huang and Xu, 1984 - 167 Aequorea parva Browne, 1905 - 167 Aequorea pensilis (Eschscholtz, 1829) - 167 Aequorea sp. Menon, 1945 - 167 Aequorea tenuis (L. Agassiz, 1862) - 167 Aequorea victoria (Murbach and Shearer, 1902) - 167 Aequorea vitrina Gosse, 1853 - 167 Aglantha digitale (O.F.Müller, 1766) - 70 Aglantha elata (Haeckel, 1879) - 70 Aglantha ignea Vanhöffen, 1902 - 70 Aglantha intermedia Bigelow, 1909 - 70 Aglaura hemistoma Péron and Lesueur, 1810 - 11, 70, 74 Aglauropsis aeora Mills, Rees and Hand, 1976 - 214 Aglauropsis agassizi Fr. Müller, 1865 - 214 Aglauropsis conanti Browne, 1902 - 214, 254 Aglauropsis edwarsii Pagès, Bouillon and Gili, 1991 - 214 Aglauropsis jarli Kramp, 1955 - 214 Aglauropsis kawari Moreira and Yamashita, 1972 - 214, 255 Aglauropsis vannucci Thomas and Chlapgar, 1975 - 214 Allorathkea ankeli Schmidt, 1972 - 92, 258 Allorathkea macrogastrica Xu and Huang, 1990 - 93 Altairina cargoi Vargas-Hernandez and Ochoa-Figueros, 1990 - 138 Altairina forbesi (Mayer, 1894) - 138 Amphinema australis (Mayer, 1900) - 103 Amphinema dinema (Péron and Lesueur, 1810) - 103 Amphinema krampi Russell, 1956 - 103 Amphinema modernisme Bouillon, Pagès and Gili, 2000 - 103, 246 Amphinema physophorum (Uchida, 1927) - 103 Amphinema platyhedos Arai and Brinckmann-Voss, 1985 - 103, 243 Amphinema rubrum (Kramp, 1957) - 103 Amphinema rugosum (Mayer, 1900) - 103

Amphinema shantungensis Chow and Huang, 1958 - 103 Amphinema tsingtauensis Kao, Li Fung-Lu, Chang and Li Hien-Lun, 1958 - 103 Amphinema turrida (Mayer, 1900) - 103 Amphisbestia operculata (L., 1758) - 200 Amphogona apicata Kramp, 1957 - 70 Amphogona apsteini (Vanhöffen, 1902) - 70 Amphogona pusilla Hartlaub, 1909 - 70 Annatiara affinis (Hartlaub, 1913) - 103 Annatiara lempersi Bleeker and van der Spoel, 1988 - 103 Anthohebella brevitheca (Leloup, 1938) - 180 Anthohebella najimaensis (Hirohito, 1995) - 180 Anthohebella parasitica (Ciamician, 1880) - 180 Anthohebella tubitheca (Millard and Bouillon, 1975) - 180 Arctapodema ampla (Vanhöffen, 1902) - 71 Arctapodema antarctica (Vanhöffen, 1912) - 71 Arctapodema australis (Vanhöffen, 1902) 1912? - 71 Arctapodema macrogaster (Vanhöffen, 1902) - 71 Arctapodema sp. Mills, Pugh, Harbison and Haddock, 1996 - 71 Armorhydra janowiczi Swedmark and Teissier, 1958 - 213 Astrohydra japonica Hashimota, 1981 - 219, 250 Asyncoryne philippina Hargitt, 1924 - 152, 159 Asyncoryne ryniensis Warren, 1908 - 152 Australomedusa bayili Russell, 1970 - 78 Barcino foixensis Gili, Bouillon, Pagès, Palanques and Puig, 1999 - 169 Barnettia caprai Schuchert, 1996 - 104 Benthocodon pedunculata Bigelow, 1913 - 71,72 Benthocodon hyalinus Larson and Harbison, 1990 - 71, 253 Blackfordia manhattensis Mayer, 1910 - 170 Blackfordia polytentaculata Hsu and Chang, 1962 - 170 Blackfordia sp. Bouillon, 1988 - 170 Blackfordia virginica Mayer, 1910 - 170, 255 Boeromedusa auricogonia Bouillon, 1995 - 128

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Bougainvillia superciliaris (L. Agassiz, 1849) - 81 Bougainvillia trinema (von Ledenfeld, 1884) - 81 Bougainvillia vervoorti Bouillon, 1995 - 81 Bythocellata cruciformis Nair, 1951 - 97 Bythotiara capensis Pagès, Bouillon and Gili, 1991 - 97 Bythotiara depressa Naumov, 1960 - 97 Bythotiara drygalskii Vanhöffen, 1912 - 97 Bythotiara hunstmani (Fraser, 1911) - 97 Bythotiara metschnikovii Bouillon, Seghers and Boero, 1988 - 97 Bythotiara murrayi Günther, 1903 - 97 Bythotiara parasitica (Kirk, 1915) - 97 Bythotiara sp. Raskoff, 2000 - 97 Bythotiara sp. Schuchert, 1996 - 97 Bythotiara stilbosa Mills and Rees, 1979 - 97, 254 Calycopsis bigelowi Vanhöffen, 1911 - 97 Calycopsis borchgrevinki (Browne, 1910) - 97 Calycopsis borealis (Linko, 1913) - 97 Calycopsis chuni Vanhöffen, 1911 - 97 Calycopsis gara Petersen, 1957 - 97 Calycopsis krampi Petersen, 1957 - 97 Calvcopsis lipi van der Spoel and Bleeker, 1988 - 97 Calycopsis nematophora H.B. Bigelow, 1913 - 98 Calycopsis papillata Bigelow, 1818 - 98 Calycopsis simplex Kramp and Damas, 1925 - 98 Calycopsis simulans (Bigelow, 1909) - 98 Calycopsis typa Fewkes, 1882 - 98 Campalecium medusiferum Torrey, 1902 - 188 ?Campalecium cirratum "Millard and Bouillon, 1975"; not Haeckel, 1879 - 188 Campaniclava clionis Vanhöffen, 1910 - 112 Cannota dodecantha Haeckel, 1879-172 Catablema multicirratum Kishinouye, 1910 - 104 Catablema nodulosum H.B. Bigelow, 1913 - 104

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Clytia hexanemalis Xu, Huang and Chen Xu, 1991 - 208 Clytia hummelincki (Leloup, 1935) - 208 Clytia iridescens Maas, 1906 - 208 Clytia islandica Kramp, 1919 - 208 Clytia languida (L. Agassiz, 1862) - 208 Clytia latitheca Millard and Bouillon, 1973 - 208 Clytia linearis (Thornely, 1899) - 208 Clytia lomae (Torrey, 1909) - 208 Clytia mccradyi (Brooks, 1888) - 208 Clytia macrogonia Bouillon, 1984 - 208 Clytia malayense Kramp, 1961 - 208 Clytia multiannulata Hirohito, 1995 - 208 Clytia noliforme (McCrady, 1859) - 208 Clytia obliqua (Clarke, 1907) - 208 Clytia ovale (Mayer, 1900) - 208 Clytia pacifica (Agassiz and Mayer, 1899) - 208 Clytia phosphoricum (Péron and Lesueur, 1810) - 208 Clytia paulensis (Vanhoeffen, 1910) - 208 Clytia rangiroae (Agassiz and Mayer, 1902) - 208 Clytia serrulata (Bale, 1888) - 208 Clytia simplex (Browne, 1902) - 208 Clytia singularis (Mayer, 1900) - 208 Clytia uchidai Kramp, 1961 - 208 Clytia viridicans (Leuckart, 1856) - 208 Clytia warreni (Warren, 1908) - 208 Cnidocodon leopoldi Bouillon, 1978 - 142 Cnidocodon xiamenensis Zhang and Wu, 1981 - 142 Cnidotiara gotoi Uchida, 1927 - 112 Codonorchis octaedrus Haeckel, 1879 - 105 Colobonema apicatum Russell, 1961 - 71 Colobonema igneum (Vanhöffen, 1902) - 71 Colobonema sericeum Vanhöffen, 1902 - 71

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