

CNIDARIA: SCYPHOZOA AND NON-COLONIAL HYDROZOA

PRISCILLA LICANDRO, ASTRID FISCHER, AND DHUGAL J. LINDSAY

1 Introduction

The Phylum Cnidaria (in old classification grouped with Porifera and Ctenophora as Coelenterata) assembles highly diverse primitive invertebrates that carry stinging cells called *cnida*. The presence of cnida, which are organized in specialized structures called *cnidocysts* (or *nematocysts*), makes the organisms of this group venomous to varying degrees. Cnidarians are aquatic, mostly marine invertebrates, that are characterized by a great variety of forms and sizes; they may live as free-living plankton or settle as sessile generally benthic forms, being either solitary or colonial. They are ubiquitous, occurring at all latitudes and depths. Cnidarian populations are characterized by a regular seasonal cycle, but they also undergo interannual fluctuations, with much larger populations in some years than in others. Due to the plasticity of their physiological response, cnidarians may quickly achieve extremely high abundances (up to ten-hundred individuals per cubic metre of water) with favourable environmental conditions (Mills, 2001; Purcell et al., 2007; Boero et al., 2008). During such events, called *outbreaks*, swarms of Cnidaria can be spread over large regions of the sea (Pitt and Lucas, 2014). This chapter is focused on pelagic non-colonial cnidarians, while siphonophores, which are pelagic colonial hydrozoans, have been described in a separate chapter.

2 Life cycle

Cnidaria Medusozoa are typically dimorphic, i.e. they may assume completely different morphologies at different stages of their life cycle (Bouillon et al. 2006) (Fig. 66). In meroplanktonic species (Fig. 66A) the ciliated free-swimming early larva (*planula*) metamorphoses into a generally benthic *polyp* (or *hydroid*) that in turn produces by budding several to many free-living immature *medusae* (called *ephyra* in Scyphozoa or *actinula* in some Hydrozoa). Polyps can be ‘thecate’, i.e. surrounded by a chitinous perisarc that may extend around hydranths (*hydrotheca*), reproductive organs (*gonotheca*), and dactylozooids (*dactylotheca*), which serve the colony for both defense and food capture. Normally the polyp and the medusa are, respectively, the asexual and sexual stages.

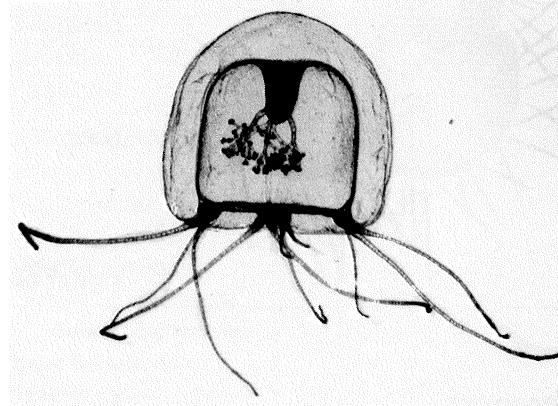


FIGURE 65: Hydrozoa Anthoathecata *Bougainvillia muscus*. Photo courtesy of C. Carré.

In holoplanktonic species (Fig. 66B) the planula directly develops in an ephyra or actinula-like stage. Sexual reproduction is usually external, with male and female medusae releasing sperm and eggs into the water where the fertilization occurs. It is only in some Cubomedusae that the fertilization is mainly internal, with the male using the manubrium to directly transfer its *spermatophore* (i.e. packed sperm) to a tentacle of the female that, in turn, transfers it into the *gastric cavity* (Lewis and Long, 2005). Some Hydromedusae may reproduce asexually, either by direct budding of young medusae or by longitudinal fission. In most Scyphozoa and Cubozoa the medusa phase is shorter than the polyp phase. Cnidaria are able to adjust their life cycle entering into dormancy to survive when resources are limiting; with favourable environmental conditions the resting stage or cyst will hatch, releasing a larva that will restart the reproductive cycle, leading to a new peak in the population.

3 Ecology

Cnidarians are essentially carnivorous and, depending on their size, can eat a variety of prey (Purcell, 1991; Purcell and Arai, 2001). Hydrozoans eat mainly copepods but also ostracods, molluscs, chaetognaths, euphausiids, and early fish larvae and eggs, with the exception of the Narcomedusae, which prey on

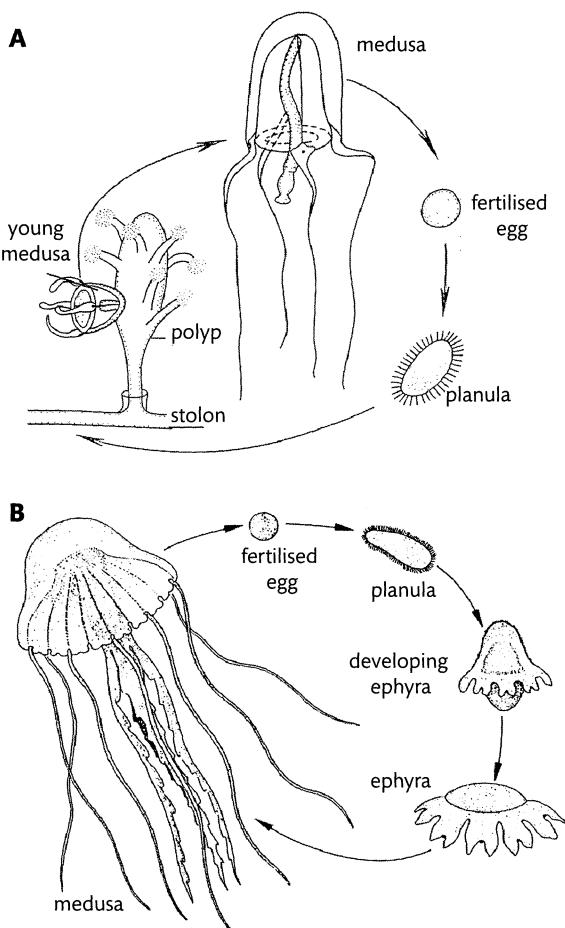


FIGURE 66: Life cycle of Cnidaria. Examples of life cycles in meroplanktonic Anthomedusae (A) and holoplanktonic Scyphomedusae (B). After Naumov (1960).

other gelatinous organisms. Big Scyphozoa can also prey on smaller cnidarians and small fish. There are a few examples of Cnidaria (e.g. *Cassiopea* and *Mastigias*) hosting symbiotic zooanthellae algae, which can take up dissolved organic matter. Although different species may peak at different times of the year, generally Cnidaria tend to be more abundant between spring and autumn. High densities of medusae with calm seas and no wind tend to remain aggregated in swarms.

Meroplanktonic Cnidaria are mainly distributed in coastal waters. On the contrary, holoplanktonic medusae can be distributed inshore and offshore. In medusae the rhythmic contraction of the umbrella empties the water from beneath the subumbrella and allows the animal to move by jet-propulsion. Cnidarians are able to adjust their buoyancy through osmoregulation to some degree. Due to the difficulty in their cultivation, basic information on their physiology and environmental preferences are not yet available for most cnidarian species.

4 General morphology

The main morphological traits of the three pelagic groups of Medusozoa and of the main orders of Hydrozoa are summa-

rized in Tables 1 and 2. Pelagic cnidarians are characterized by a relatively simple structure (Fig. 67) consisting of an ectodermal *epidermis* and an endodermal *gastrodermis* separated by gelatinous, mainly acellular, *mesoglea*. Free-swimming medusae are mainly characterized by a tetramerous radial symmetry, typically bell- or lens-shaped, with a swimming bell (*umbrella*) of variable thickness and height. The outer aboral surface of the umbrella (*exumbrella*) of ectodermal origin is usually convex while the inner oral surface (*subumbrella*) is concave and delimits the internal gastrovascular cavity (or *coelenteron*) that serves for circulation, as well as digestion and distribution of food.

Most Hydromedusae have a *velum*, i.e. a thin membrane of ectoderm and mesoglea that, within the bell margin, partially closes the space under the subumbrella. The velum is absent in the Scyphomedusae, whereas in the Cubomedusae it is replaced by a *velarium*, which has a similar function but different origin. The subumbrella is extended in an appendix called a *manubrium* containing the gastric cavity, which in some species is mounted upon a gelatinous *gastric peduncle*; the mouth, which often carries lobes called *lips*, is either suspended at the end of the *manubrium* or in the centre of the subumbrella. Manubria greatly vary in shape and size. In some species of Hydrozoa (e.g. *Leuckartiara octona*) the manubrium is perradially attached to the subumbrella through a layer of tissue called *mesentery*. In most Scyphomedusae the manubrium is tubular and ends in four elongated structures, i.e. *oral arms*, which in some Rhizostomeae are covered by strapped structures named *epaulettes* (or *scapulettas*) (Fig. 68N). In Hydromedusae the coelenteron ramifies radially along the bell to the margin into *radial canals*, which in most Hydromedusae join a *ring canal* lying within the rim of the bell. In some species radial canals are branched in other *centripetal canals* (Fig. 68K) that rise upwards from the circular canal without reaching the gastrovascular cavity. In Scyphomedusae and Cubomedusae, the coelenteron is divided by four longitudinal oral–aboral mesenteries and the pattern of radial canals is often complex. As in the Hydromedusae, the four mouth lips are perradial and there are four interradii and eight adradii. In some Hydrozoa (e.g. Narcomedusae) and in the Scyphomedusae the umbrella margin is interrupted by notches forming separate marginal lobes called *lappets* (Fig. 67E). In Hydromedusae and Scyphomedusae, tentacles armed with nematocysts, sometimes grouped in knobs or specialized capsules (i.e. *cnidophores*) (Figs 68G and I) are typically located at the margin of the umbrella (*marginal tentacles*) and sometimes around the mouth (*oral* or *gastric tentacles*). In some Hydromedusae (e.g. Narcomedusae) they are inserted on the exumbrella. Tentacles and similar organs called *cirri* (Fig. 68A,B,F) that are placed between marginal tentacles, greatly vary in shapes and numbers. The margin of the bell may be provided with specialized sense organs (Figs 67A,B,F and 68A–E). Those include: (i) *cordyli*, minute club-shaped structures situated between the tentacles; (ii) gravity receptors containing one or more statoliths called *statocysts*; and (iii) *rhopalia*, i.e. club-shaped sensory centres, each containing a statocyst,

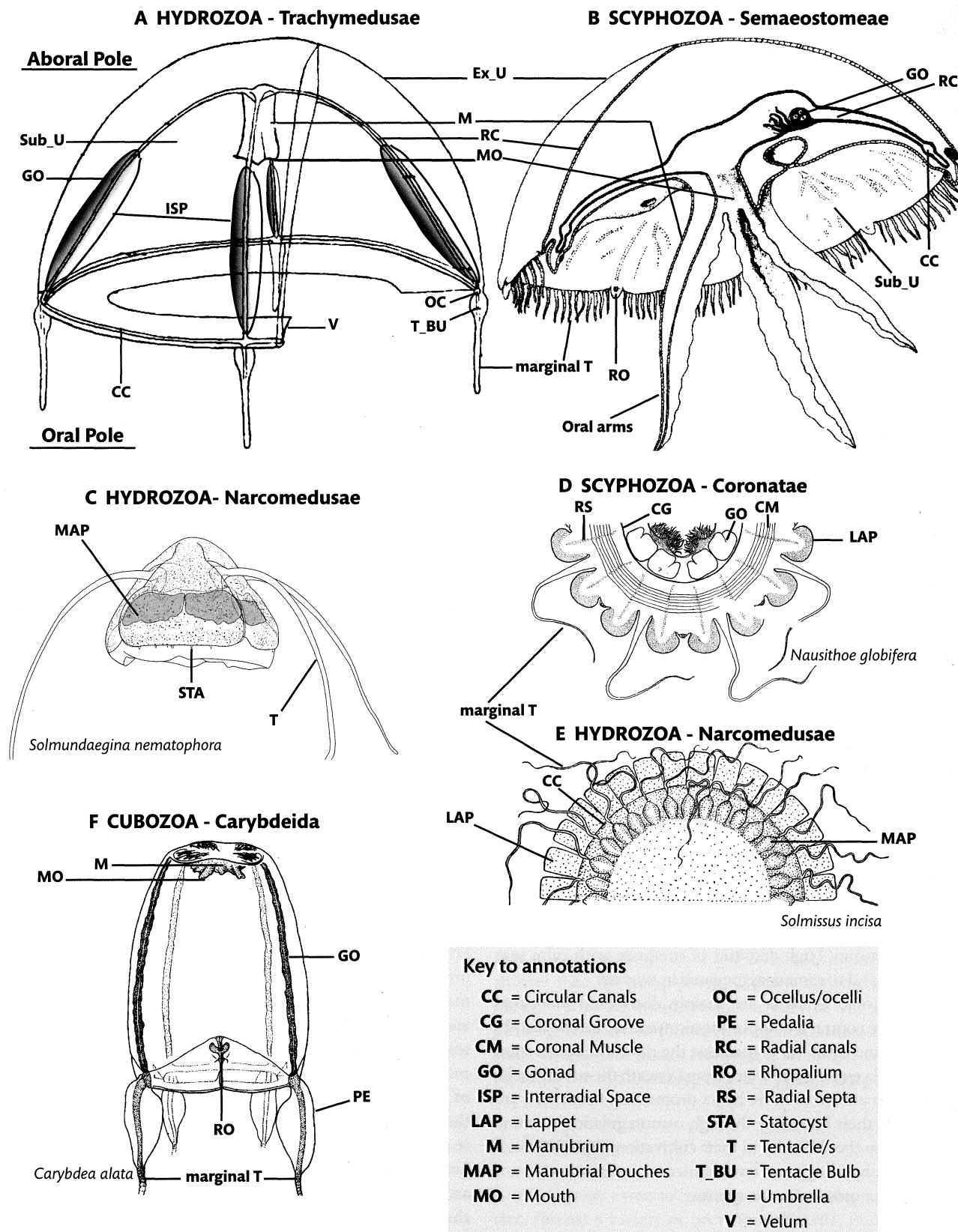
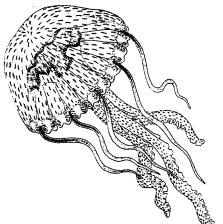
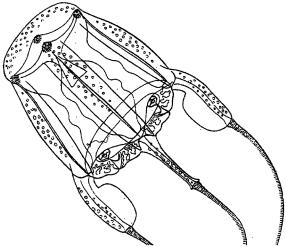


FIGURE 67: General morphology of Cnidarian medusae. A, Hydrozoa Trachymedusae, lateral view. B, Scyphozoa Semaeostomeae, lateral view. C, Hydrozoa Narcomedusae *Solmundaegina nematophora*, lateral view. D, Scyphozoa Coronatae *Nausithoe globifera*, ventral view. E, Hydrozoa Narcomedusae *Solmissus incisa*, ventral view. F, Cubozoa Carybdeida *Carybdea alata*, lateral view. A, Modified from Trégouboff and Rose (1957); B, modified from Naumov (1960); C, Lindsay et al. (in press); D and E, Russell (1970); E, edited from Fewkes, 1886; F, © Corbera in Pagès et al. (1992).

TABLE 1: Main morphological traits and life cycles in Medusozoa. *Pelagia noctiluca* after Mayer (1910); *Carybdea marsupialis* after © Corbera, in Mianzan & Cornelius (1999); *Liriope tetraphylla* after Russell (1953).

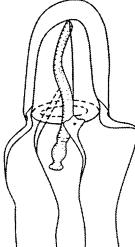
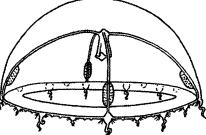
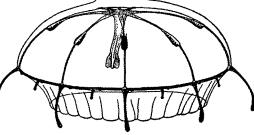
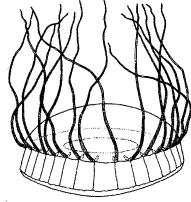
Scyphozoa 'true jelly'		Cubozoa 'sea wasps and box jelly'	Hydrozoa
	<i>Pelagia noctiluca</i>		<i>Carybdea marsupialis</i>
Known Species	200	45	3700
MEDUSA (sexual pelagic stage)			
Umbrella	Big (up to 2 m in diameter); saucer-shaped or hemispherical (except Coronatae) Without velum: distinct pigmentation and thick mesoglea	Fairly small (up to 25 cm tall), cubic With velarium: colourless Lower edge of umbrella extended in a 'pedalium' that supports tentacles	Mostly small (up to 10 cm in diameter) though siphonophore colonies can reach 40m length With velum: transparent
Gastrovascular cavity	Divided by four mesenteries	Divided by four longitudinal oral-aboral septa	Undivided
Sense organs	Endodermal origin. Eight aradial (Coronatae) and four interradial (Semaeostomeae and Rhizostomeae)	Endodermal origin	Ectodermal origin, if present
Origin	Strobilation if not holoplanktonic, i.e. transverse fission of the polyp (scyphistoma)	Polyp directly metamorphoses into one medusa	Asexual budding, sometimes by longitudinal fission
Reproduction	External	Internal	External
POLYP (asexual benthic stage)			
Structure	Usually small and simple, mainly solitary. Sometimes absent (e.g. in <i>Pelagia</i> , <i>Atolla</i> , and <i>Peryphylla</i>)	Usually small and simple	Usually colonial, with individual specialized polyps. Male and female colonies are usually separated

epidermal neurons, a pair of sensory pits and often a photoreceptor (*ocellus*). The number and shape of statocysts is often used to separate different groups of Hydromedusae: ectodermal statocysts, open or closed, are small marginal pockets or open pits that develop in the velum and can be found in the Antho/Leptomedusae (Fig. 68A,B,D); endodermal statocysts are sensory clubs, small tentacle-like structures hanging freely out of the umbrella margin or enclosed in the umbrella (Fig. 68C,D), that characterize Limnomedusae, Trachymedusae, and Narcomedusae. The shape of the manubria, types of tentacles (Fig. 68M), position of the gonads, as well as the presence of distinctive canals (Fig. 68K–L) and of other structural characters, such as cirri, *otoporpae*, *warts*, and *gelatinous papillae* (Fig. 68A,B and F–J) are also used for taxonomic identification.

5 Systematics

The classification of the Cnidaria has seen many changes over the years, with recent updates following the advent of molecular phylogenetic analyses. Here we adopt the classifications proposed by Schuchert (2012), Daly et al. (2007), and Mianzan and Cornelius (1999) that revised previous classifications from Bouillon et al (2006) and Kramp (1959a and 1961). As the focus of this book is the North Atlantic plankton, the taxonomic list and keys are limited to the families of cnidarian medusae. Key morphological features of the main medusa species and of the planktonic hydroid colony of the Porpitidae *Velella velella* are also included. Considering the recent changes in their systematics (Lindsay et al., in press), the taxonomic key of hydrozoan Narcomedusae has been detailed up to the genus level.

TABLE 2: Main morphological traits in non-colonial Hydrozoa. *Sarsia tubulosa* after Naumov (1960); *Lovenella clausa* after Russell (1963); *Rhopalonema velatum* after Mayer (1910); *Solmaris corona* after Pagès et al. (1992).

Anthomedusae <i>Sarsia tubulosa</i>		Leptomedusae <i>Lovenella clausa</i>	Trachymedusae <i>Rhopalonema velatum</i>	Narcomedusae <i>Solmaris corona</i>
				
Umbrella	Bell-shaped, higher/ as high than wide	Lens-shaped, wider/ as wide than high	Hemispherical, quite high	Flat with lobes
Circular canals	Yes. Can have centripetal canals (e.g. <i>Timoides</i>)	Yes	Yes. Can have centripetal canals	Absent or looped into the marginal lappets
Radial canals	Yes	Yes	Yes	No
Position of gonads	On/around manubrium, might be attached to subumbrella by mesenteries	On radial canals, sometimes extending into manubrium	On radial canals	On manubrium and/or on manubrial pouches
Marginal tentacles	Hollow/solid, mainly tentacular bulbs	Usually hollow, with tentacular bulbs	Solid or solid and hollow, with no real tentacular bulbs	If present, solid. Primary tentacles on exumbrella. No tentacular bulbs, only solid roots
Sense organs	No statocysts/cordyls, might have ocelli	Might have ectodermal statocysts, cordyls, and/or ocelli	Endodermal statocysts, generally free but also enclosed. No ocelli/cordyls	Mostly free ecto-/endodermal statocysts. Can have otoporae. No ocelli or cordyls
Life cycle	Meroplanktonic	Meroplanktonic	Holoplanktonic	Holoplanktonic
Polyp	Athecata polyp	Thecata polyp	No polyp stage	No polyp stage but can have parasitic stolon phase

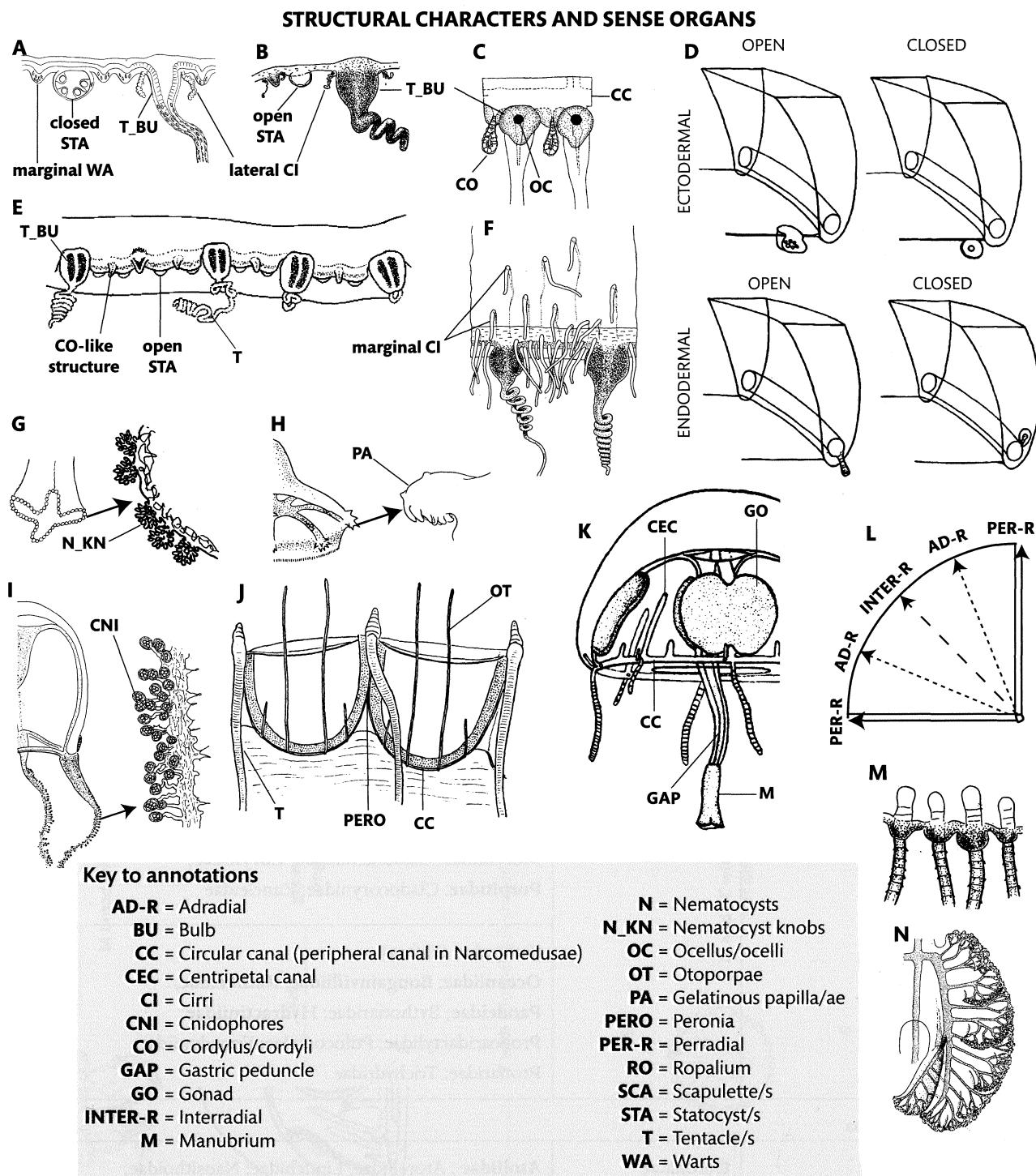


FIGURE 68: Structural characteristics of cnidarian medusa. Part of the marginal bell of **A**, *Eutima coerulea*; **B**, *Eucheilota maculata*; **C**, *Laodicea* spp.; **E**, *Paratectaria norvegica*; and **F**, *Cosmetira pilosella*. **D**, Types of statocysts; **G**, *Turritopsis nutricula*, mouth and detail of mouth margin with nematocyst knobs; **H**, *Halicreas minimum*, detail of umbrella and of gelatinous papilla; **I**, *Zanclea costata*, lateral view and detail of cnidophores; **J**, *Pegantha rubiginosa*, marginal lappets; **K**, *Liriope tetraphylla*, some details; **L**, diagram to define the radii of a medusa; **M**, *Obelia* spp., portion of umbrella margin, showing bases of solid marginal tentacles and their endodermal roots; **N**, *Rhizostoma pulmo*, scapulette. All lateral views. A, K and M, Mayer (1910); B, D, F, G, I, and L, Russell (1953); C, Kramp (1919); E, Hosia and Pagès (2007); H (detail of umbrella), Vanhöffen (1902); H (detail of gelatinous papilla), Bigelow (1909); J, Kramp (1959a); N, Russell (1970).

TABLE 3: Outline classification of marine cnidarian medusa. Families in bold are those treated in more detail.

Phylum Cnidaria	Orders	Suborders and families
Class: Cubozoa		
	Carybdeida	Alatinidae; Carukiidae; Carybdeidae; Tamoyidae; Tripedaliidae
	Chirodropida	Chirodropidae; Chiropsalmidae; Chiropsellidae
Class: Hydrozoa		
Subclass: Trachylinae	Trachymedusae	Geryoniidae; Halicreatidae; Petasidae; Ptychogastriidae; Rhopalonematidae
	Narcomedusae	Aeginidae; Cuninidae; Solmarisidae; Solmundaeginidae; Pseudaeginidae
Subclass: Hydroidolinae	Leptothecata	Aequoreidae; Barcinidae; Blackfordiidae; Campanulariidae; Cirholoveniidae; Dipleurosomatidae; Eirenidae; Hebellidae; Laodiceidae; Lovenellidae; Malagazziidae; Melicertidae; Mitrocomidae; Orchisotomatidae; Octocannoidae; Phialellidae; Phialuciidae; Sugiuridae; Teclaiidae; Tiarannidae; Tiaropsidae
	Siphonophorae*	* group described in separate chapter
	Anthoathecata	[Suborder: Aplanulata] Tubulariidae; Corymorphidae; Margelopsidae; Aplanulata incerta sedis
		[Suborder: Capitata sensu stricto] Moerisiidae; Cladonematidae; Corynidae; Porpitidae; Cladocorynidae; Zancleidae
		[Suborder: Filifera] Oceaniidae; Bougainvilliidae; Rathkeidae; Pandeidae; Bythotiaridae; Hydractiniidae; Proboscidactylidae; Ptilocodiidae; Eucodonidae; Protiaridae; Trichydridae
Class: Scyphozoa		
	Coronatae	Atollidae ; Atorellidae; Linuchidae; Nausithoidae; Paraphyllinidae; Periphyllidae
Subclass: Discomedusae	Semaeostomae	Cyaneidae; Drymonematidae; Pelagiidae; Ulmaridae
	Rhizostomeae	[Suborder: Kolpophorae] Cassiopeidae; Cepheidae; Mastigiidae; Thysanostomatidae; Versurigidae
		[Suborder: Daktyliophorae] Lychnorhizidae; Catostylidae; Lobonematidae; Rhizostomatidae ; Stomolophidae

TRACHYMEDUSAE

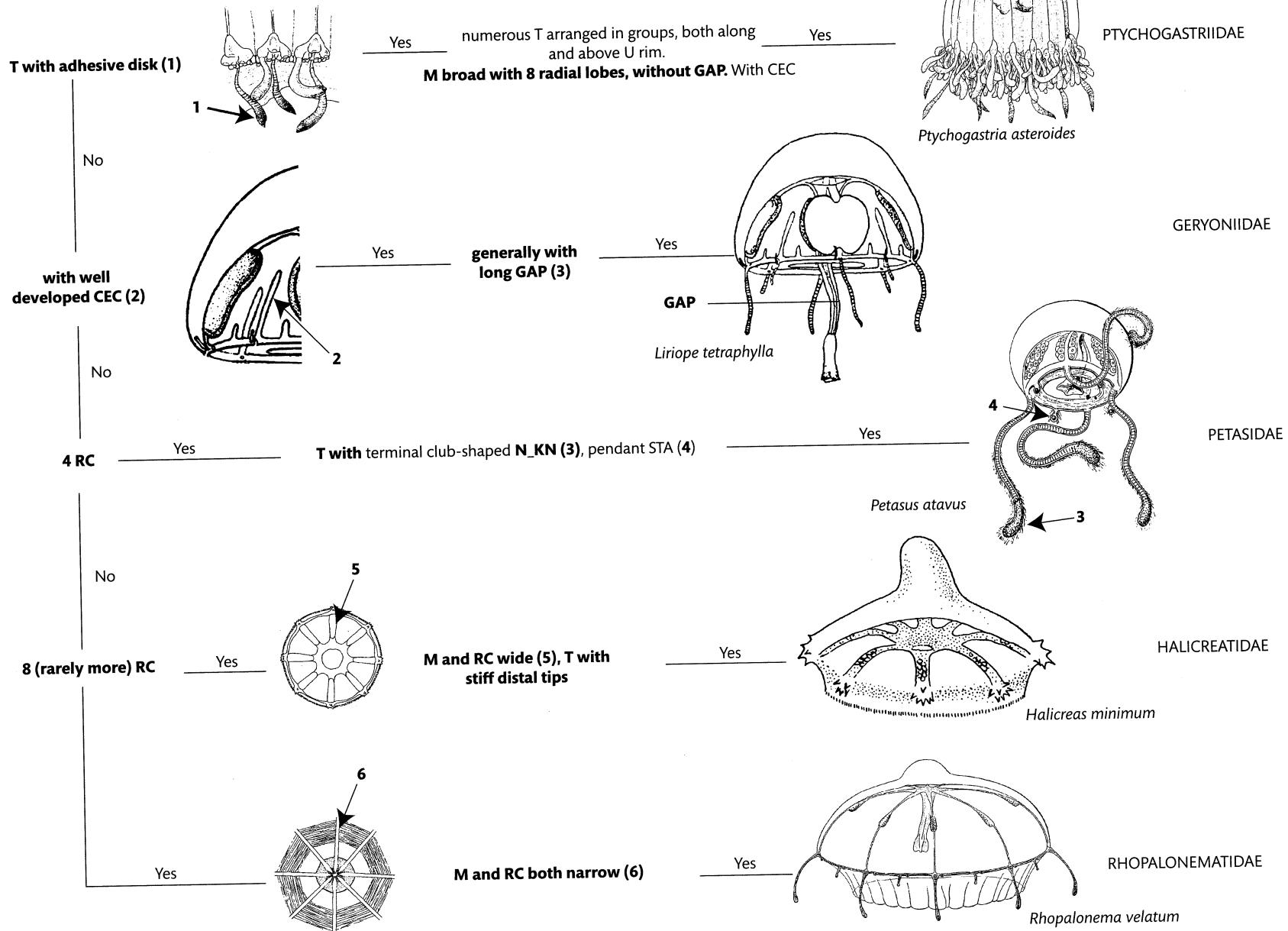


FIGURE 69: Trachymedusae: *Ptychogastria asteroides*, whole figure and detail of umbrella margin (1), after Gili et al. (1999); *Liriope tetraphylla*, whole figure and detail of umbrella margin (2), after Trégouboff and Rose (1957); *Petasus atavus* and *Rhopalonema velatum* after Mayer (1910); *H. minimum* after Vanhöffen (1902); *H. minimum*, ventral view (5), after Kramp (1947); *Pantachogon haeckeli*, ventral view (6), after Russell (1953). All lateral views, unless noted otherwise.

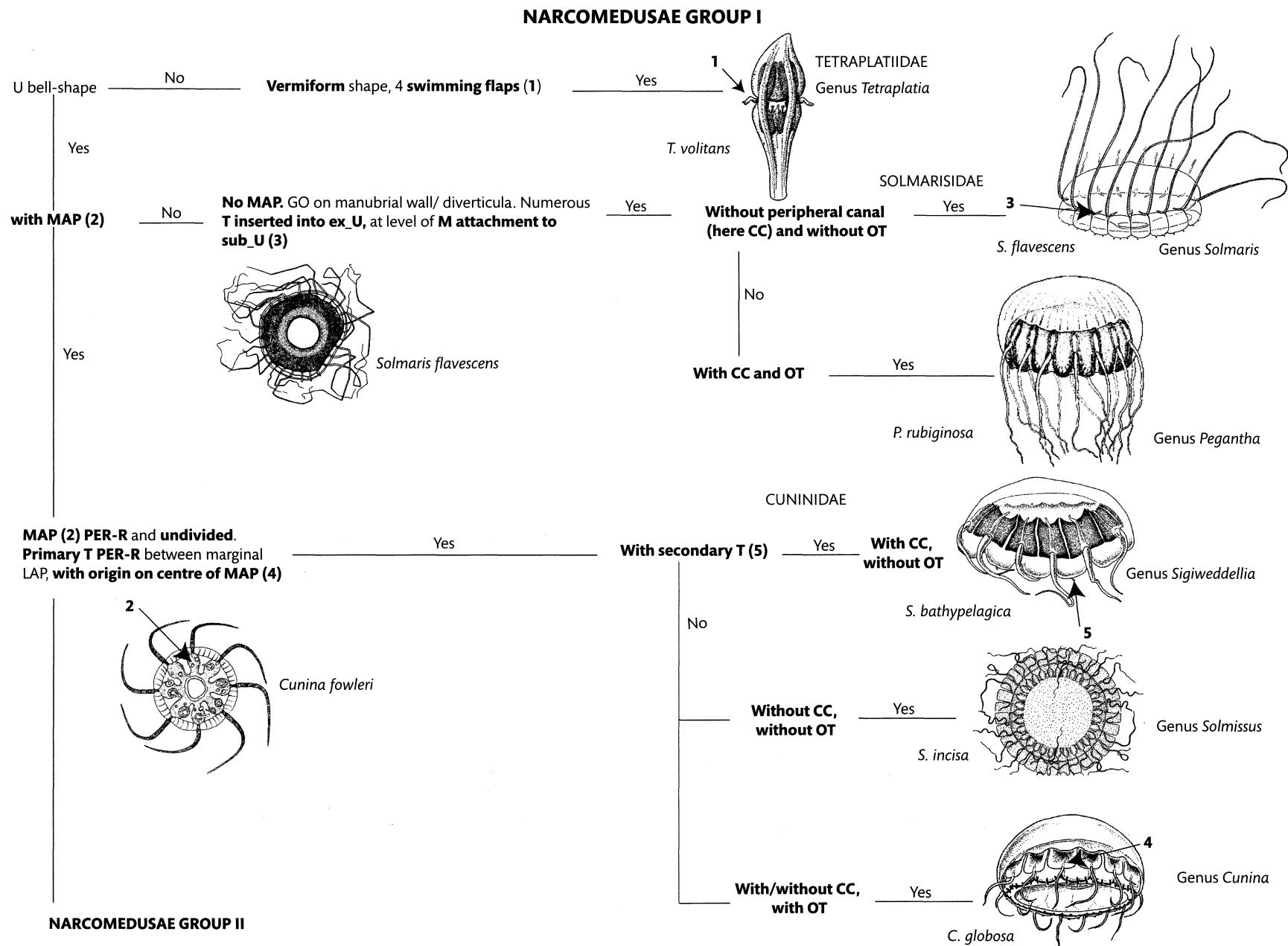


FIGURE 70: Narcomedusae group I: *Tetraplatia volitans* after Russell (1970); *Solmaris flavescens* after Mayer (1910); *S. flavescens*, ventral view, after Russell (1953); *Pegantha rubiginosa* after Pagès et al. (1992); *Sigiweddellia bathypelagica* after Bouillon et al. (2001); *Solmissus incisa*, ventral view, modified after Kramp (1959a); *Cunina globosa* after Bigelow (1909); *Cunina fowleri*, ventral view, after Browne (1906); All lateral views, unless noted otherwise.

NARCOMEDUSAE GROUP II

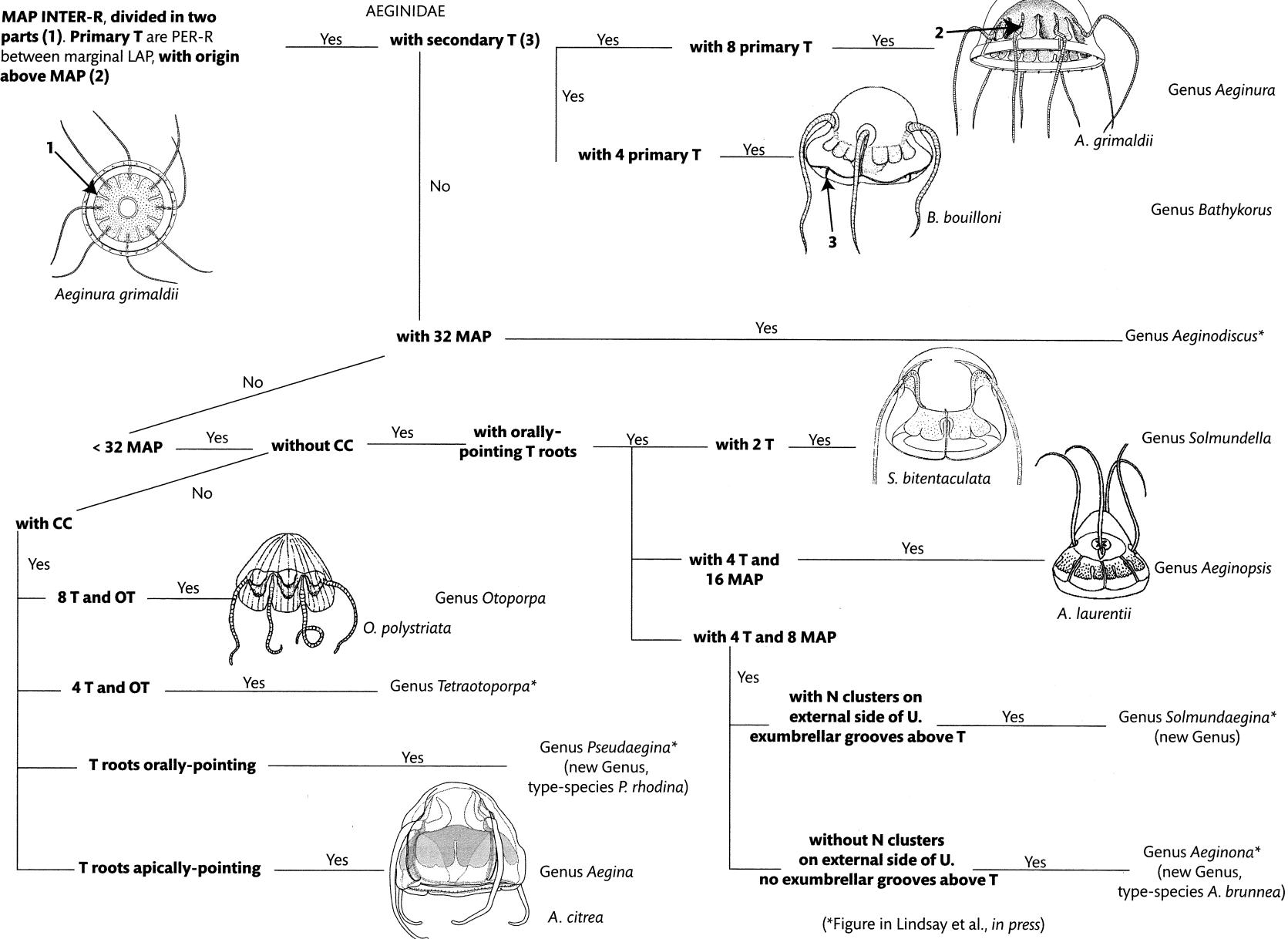
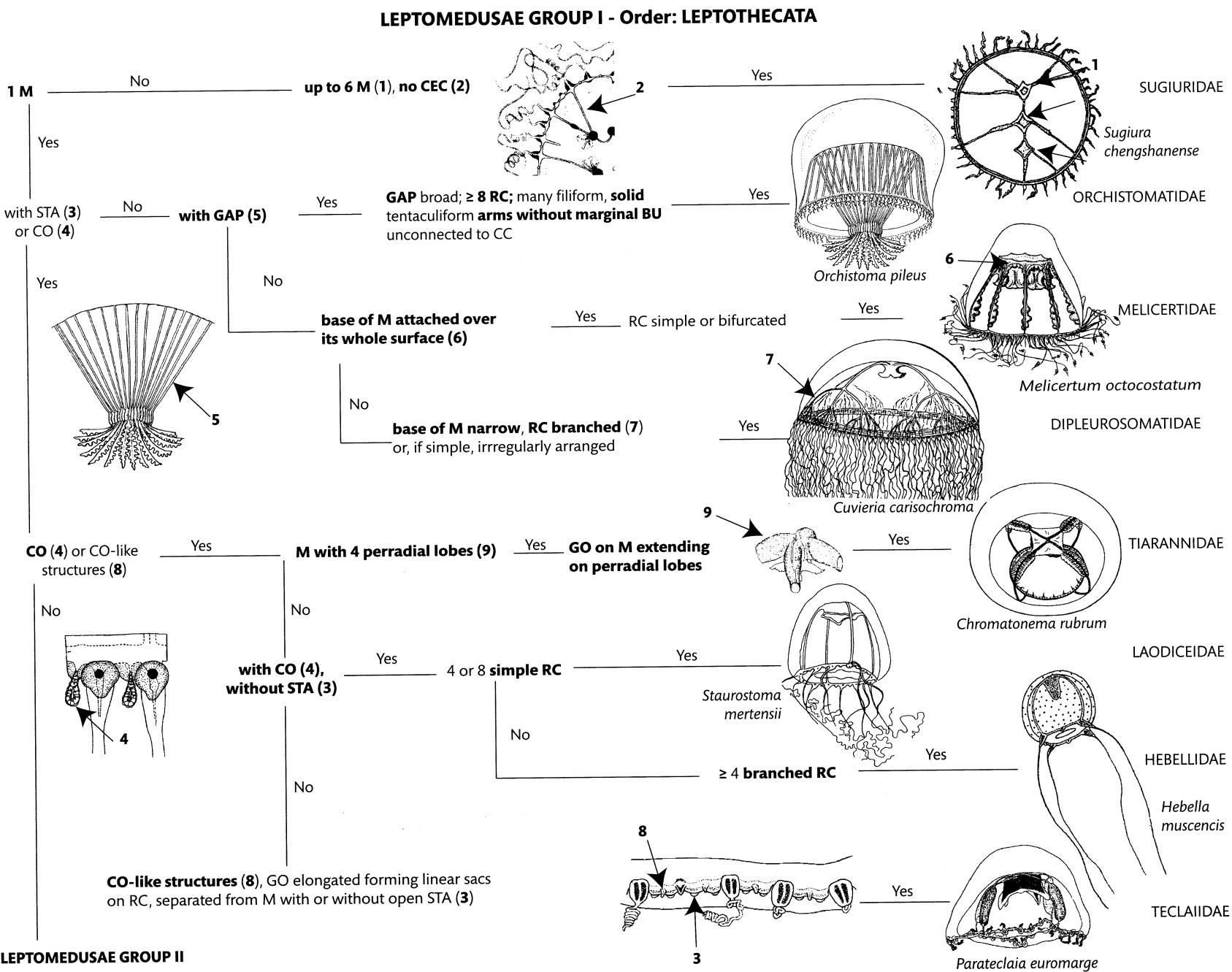


FIGURE 71: Narcomedusae group II: *Aeginura grimaldii*, ventral (1) and lateral views, after Maas (1905); *Bathykorus bouilloni* after Wang et al. (2014); *Solmundella bitentaculata* and *Aeginopsis laurentii* after Mayer (1910); *Otoporpa polystriata* after Xu and Zhang (1978); *Aegina citrea* after Lindsay et al. (*in press*). All lateral views, unless noted otherwise.



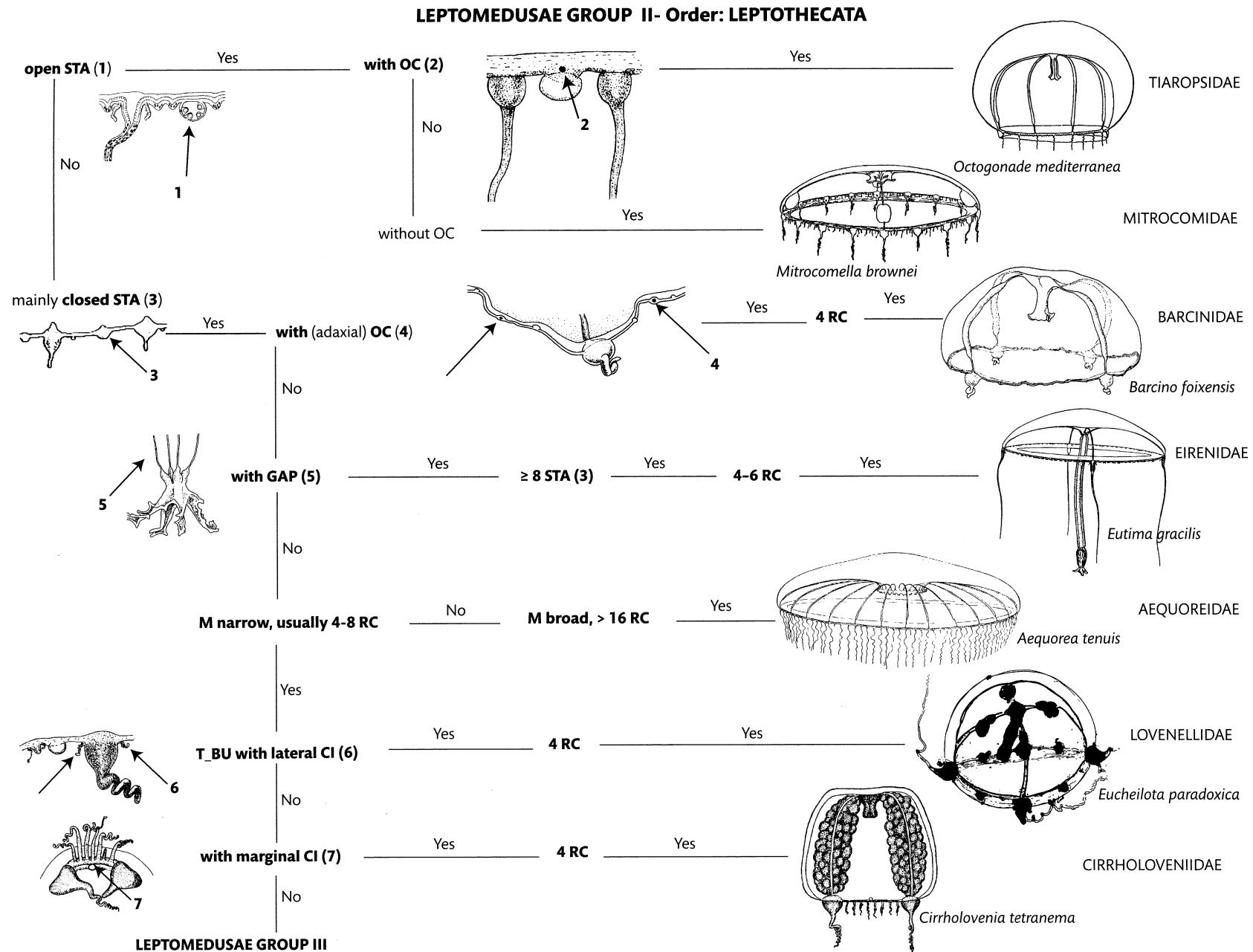


FIGURE 73: Leptomedusae group II-Leptothecata: *Octogonade mediterranea*, *Aequorea tenuis* and detail of umbrella margin of *Eutima coerulea* (1), after Mayer (1910); details of umbrella margin of *Tiaropsis multicirrata* (2), *E. viridula* (3) and of *Eucheilota maculata* (6), after Russell (1953); *Mitrocomella brownii* and *Eutima gracilis* after Kramp (1959a); *Barcino foixensis*, whole figure and detail of umbrella margin (4), after Gili et al. (1999); *Eucheilota paradoxica* after Carré and Carré (1990); detail of manubrium of *Eirene viridula* (5), *Cirrholovenia tetraneura*, whole figure and detail of umbrella margin (7), after Kramp (1959b). All lateral views.

LEPTOMEDUSAE GROUP III- Order: LEPTOTHECATA

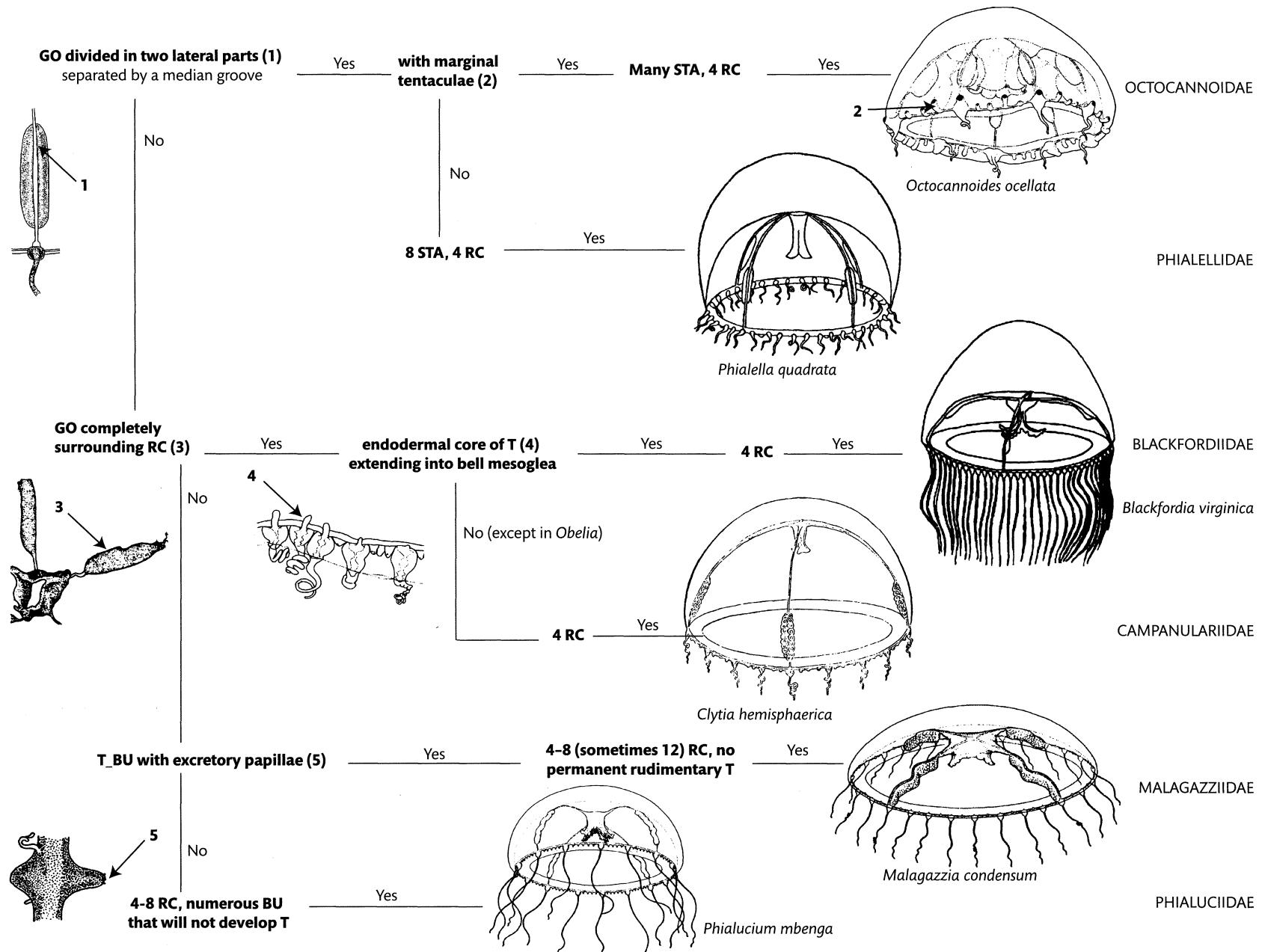


FIGURE 74: Leptomedusae group III-Leptothecata: *Octocnoides ocellata* after Bouillon et al. (1991); *Phialella quadrata* after Kramp (1959a); detail of gonads of *P. quadrata* (1) and tentacle bulb with excretory papillae of *Eutima gegenbauri* (5), after Russell (1953); *Blackfordia virginica* and *Clytia hemisphaerica* after Mayer (1910); detail of gonads (ventral view) of *C. hemisphaerica* (3) after Pagès et al. (1992); detail of umbrella margin of *B. virginica* (4) after Moore (1987); *Malagazzia condensum* after Bouillon (1984a); *Phialium mbenga* after Bouillon (1984b). All lateral views, unless noted otherwise.

ANTHOMEDUSAE GROUP I - Suborders: CAPITATA *sensu stricto* (*), FILIFERA

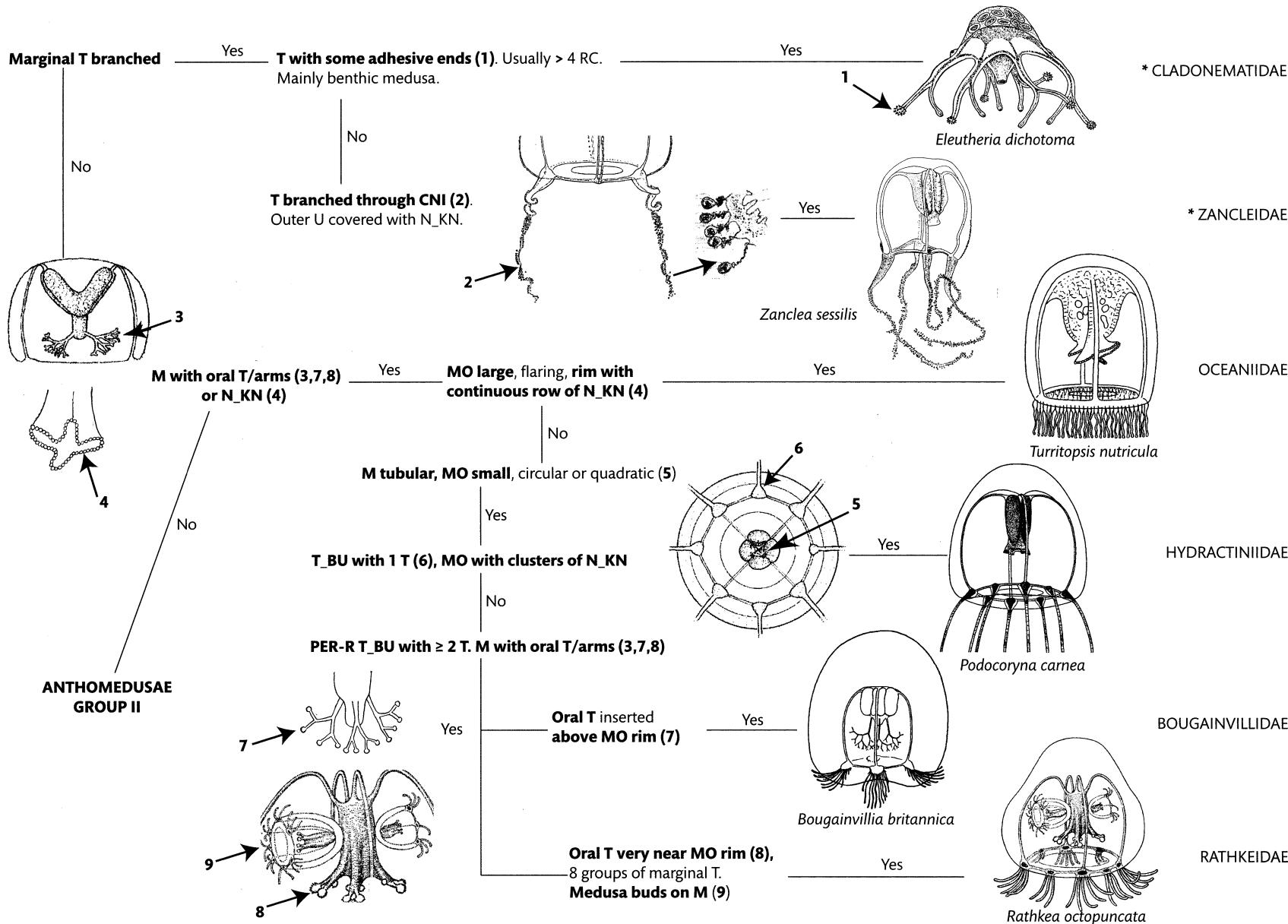


FIGURE 75: Anthomedusae group I-Suborder Capitata *sensu stricto*: *Eleutheria dichotoma* after Hincks (1868); *Zanclea sessilis* (whole figure), detail of mouth of *Turritopsis nutricula* (4) and of *Bougainvillia britannica* (7), after Russell (1953); particular of tentacles of *Z. sessilis* (2), mouth of *Bougainvillia pyramidata* (3), mouth (ventral view) of *Podocoryna carneae* (5 and 6) after Schuchert (2012); *T. nutricula* and *B. britannica* (whole figures) after Kramp (1968); *P. carneae* after Edwards (1972); *Rathkea octopunctata*, whole figure and detail of manubrium and mouth (8 and 9), after Naumov (1960). All lateral views, unless noted otherwise.

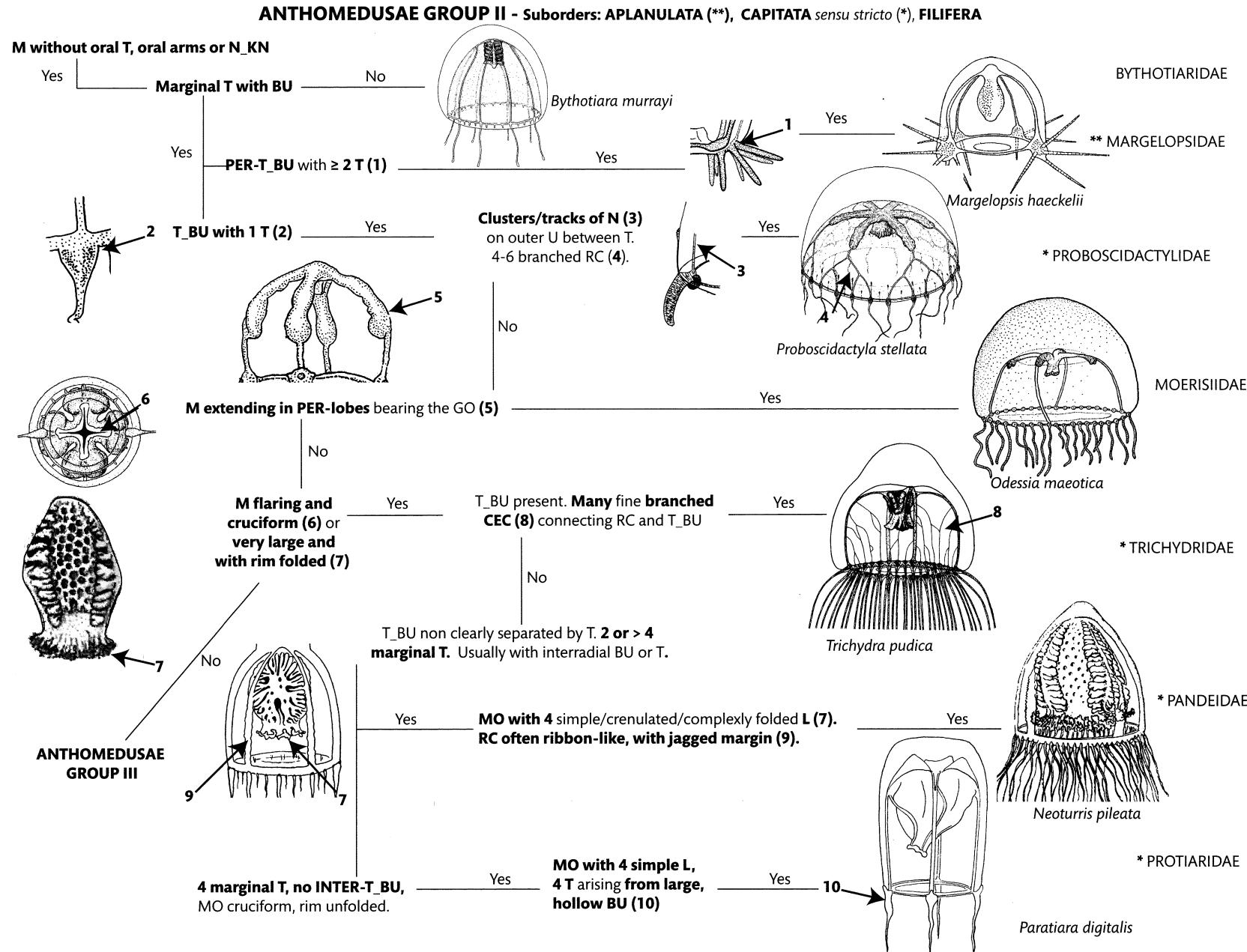


FIGURE 76: Anthomedusae group II-Suborders Aplanulata, Capitata sensu stricto, Filifera: *Marellopsis haeckeli* after Werner (1954); *Bythotiera murrayi* and *Proboscidactyla stellata* after Pagès et al (1992); particular of tentacles of *Climacocodon ikarri* (1) after Kubota (1993); detail of umbrella margin of *P. stellata* (3) after Russell (1953); detail of tentacle of Phialellidae (2) after Russell (1963); *Odessa maeotica* after Morri (1981); detail of umbrella of *Moerisia lyonsi* (5) after Boulenger (1908); *Trichydra pudica* after Edwards (1973); *Neoturris pileata*, whole figure and detail of umbrella (7 and 9), after Hartlaub (1914); *Amphinema rugosum*, ventral view (6) and detail of gonads and manubrium of *N. pileata* (7), after Schuchert (2012); *Paratiara digitalis* after Kramp (1959a). All lateral views, unless noted otherwise.

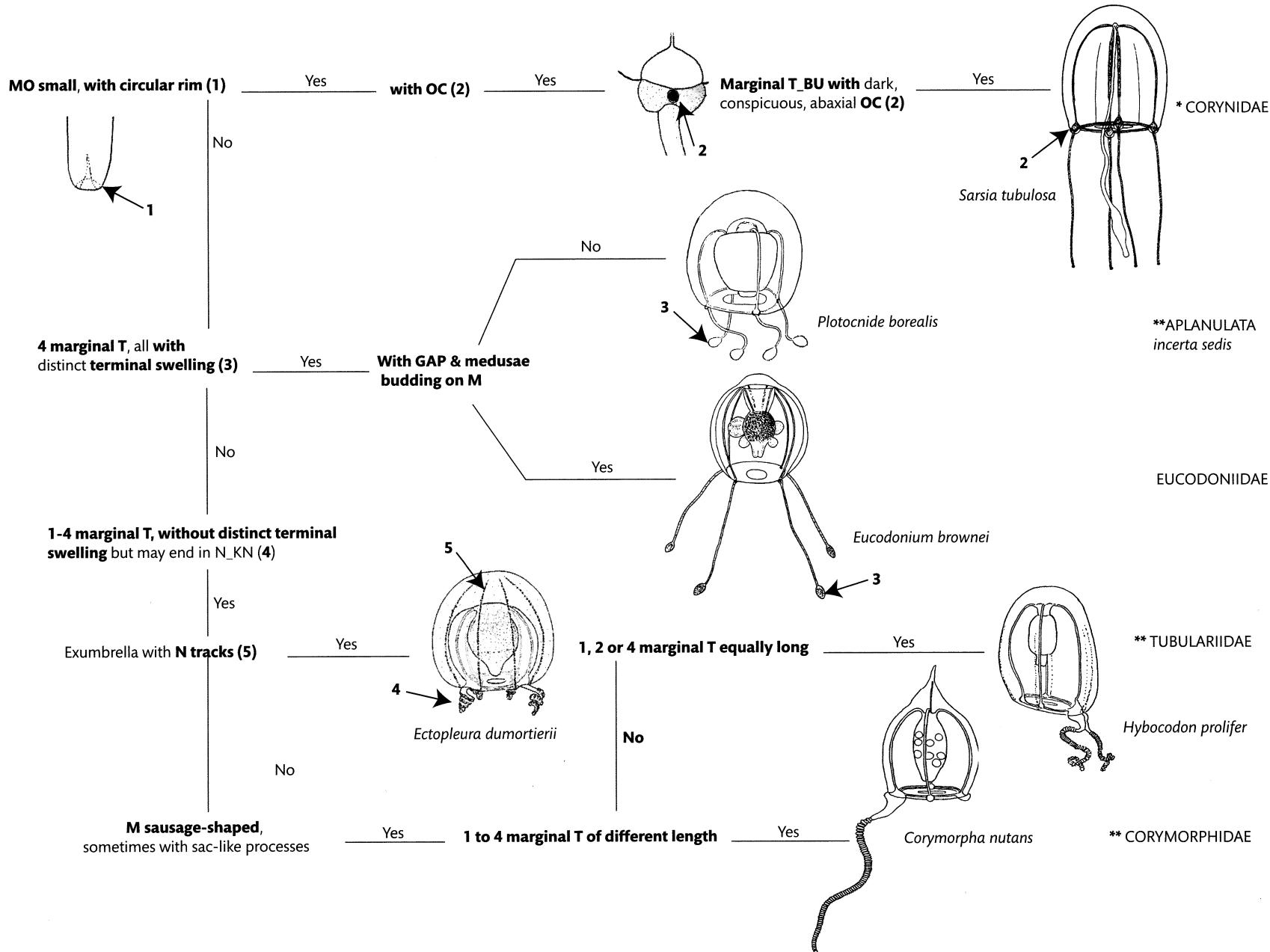


FIGURE 77: Anthomedusae group III-Suborders Aplanulata, Capitata *sensu stricto*, Filifera: *Sarsia tubulosa* after Edwards (1978); *Plotocnide borealis*, *Ectopleura dumortierii*, *Hybocodon prolifer* and *Corymorphpha nutans* after Kramp (1959a); detail of manubrium and mouth of *Sarsia* spp. (1) and *Eucodonium brownei* after Russell (1953); detail of tentacle bulb of *Codium proliferum* (2) modified after Schuchert (2012). All lateral views.

SCYPHOMEDUSAE GROUP I - Order: CORONATAE

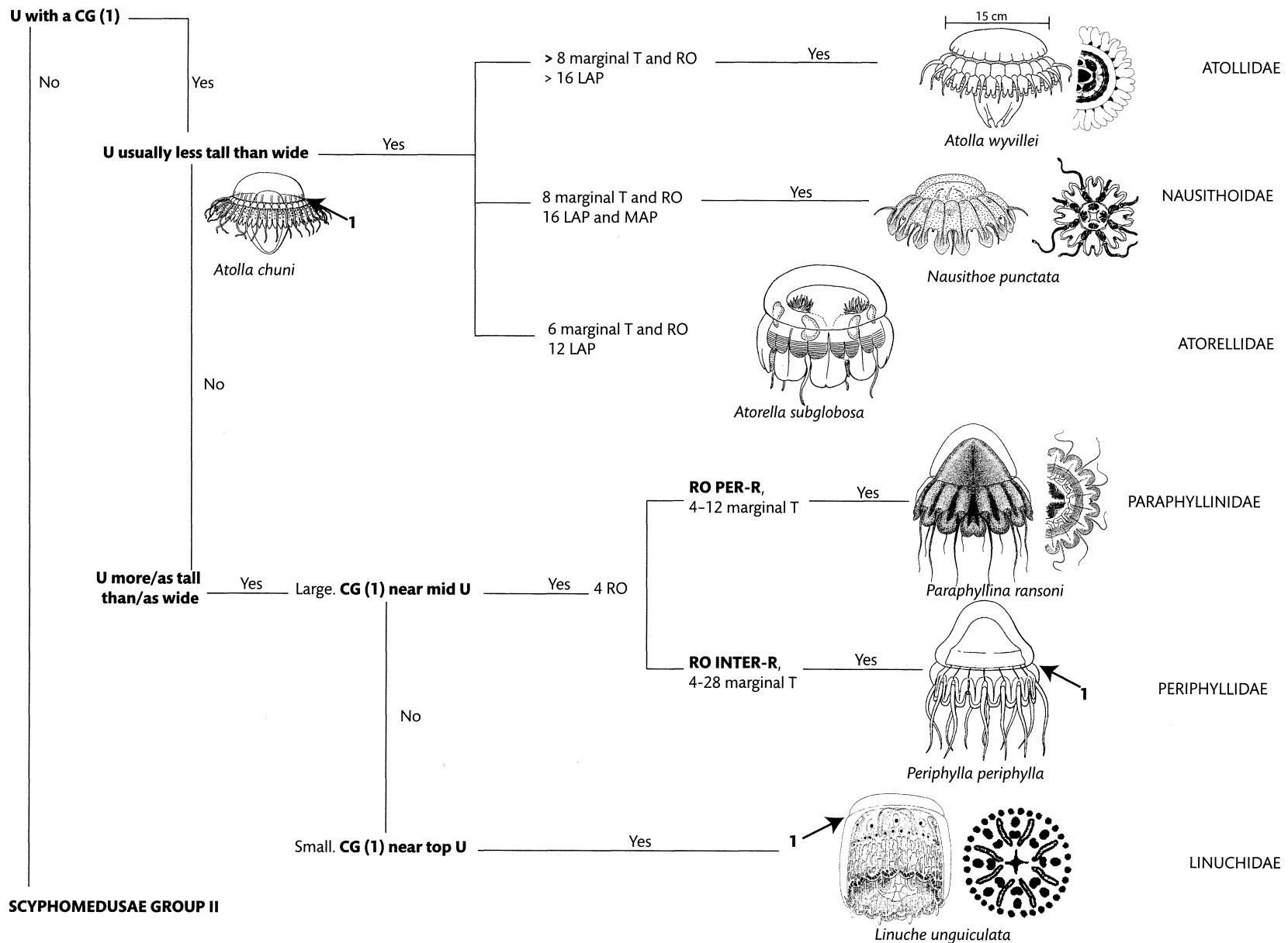


FIGURE 78: Scyphomedusae group I- Order Coronatae: *Atolla chuni* (lateral view), *Atolla wyvillei* (lateral view), *Nausithoe punctata* (lateral and ventral views), *Atorella subglobosa* (lateral view), *Paraphyllina ransonii* (detail of ventral view), *Periphylla periphylla* (lateral view) and *Linuche unguiculata* (lateral and ventral views) after Mayer (1910); *Atolla wyvillei* (detail of ventral view) after Russell (1970); *P. ransonii* (lateral view), modified after Russell (1970).

SCYPHOMEDUSAE GROUP II - Orders: SEMAEOSTOMEAE, RHIZOSTOMAE (Scapulatae)

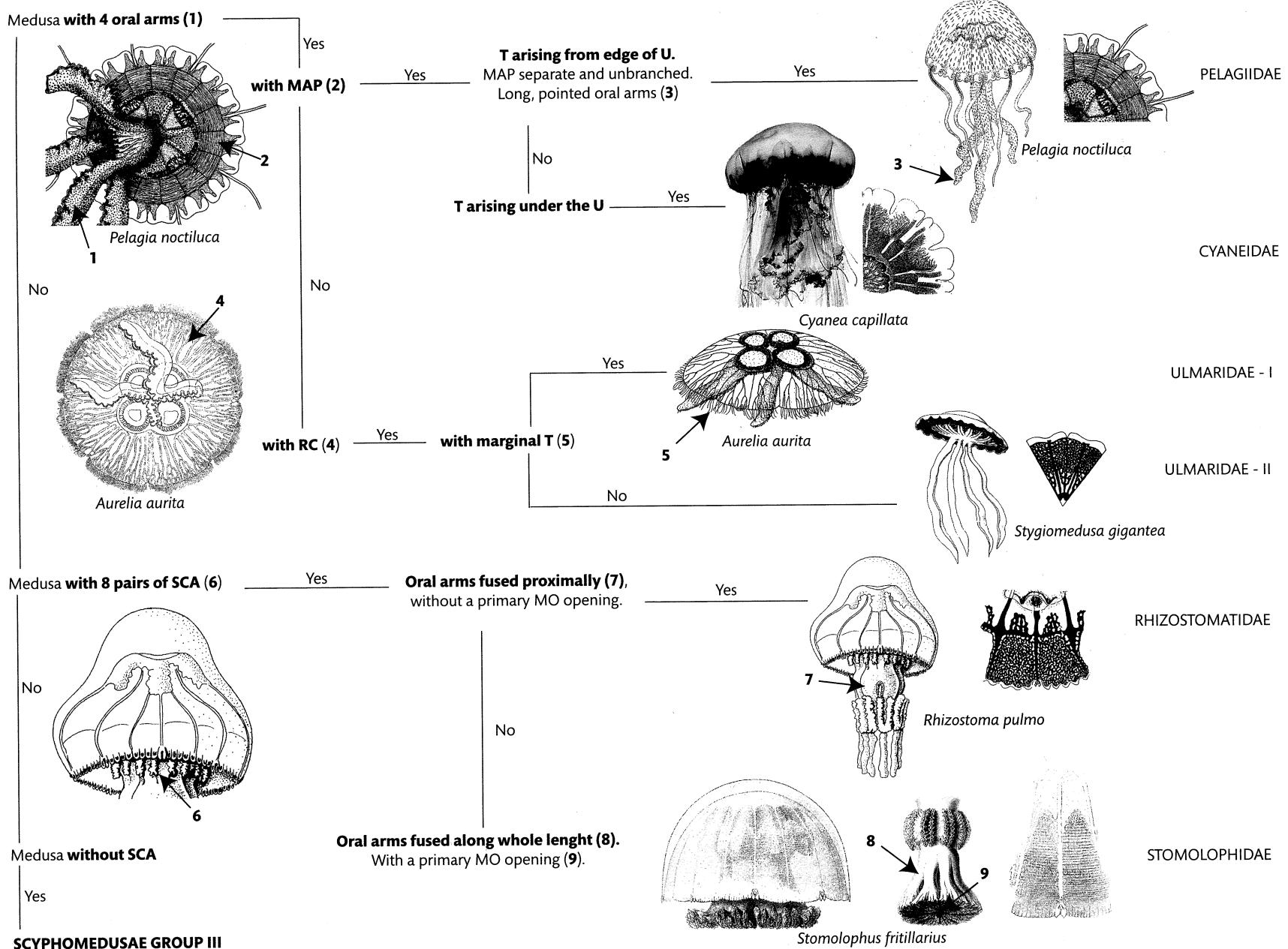


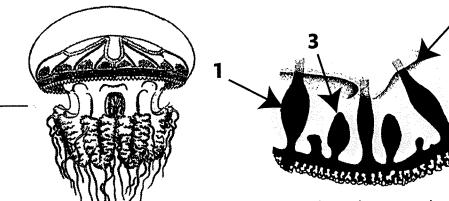
FIGURE 79: Scyphomedusae group II-Orders Semaeostomeae, Rhizostomae (Scapulatae): *Pelagia noctiluca*, *Rhizostoma pulmo*, whole figure and detail of umbrella (6), detail of umbrella margin of *Cyanea capillata* (ventral view) and *Stomolophus fritillarius*, whole figure and details of manubrium (8 and 9) and of umbrella margin (ventral view), after Mayer (1910); *P. noctiluca*, ventral view (1 and 2) and detail of umbrella margin (ventral view), after Russell (1970); *C. capillata* (whole figure) modified from picture of © Jason Gregory, www.britishmarinelifepictures.co.uk; *Aurelia aurita* and detail of umbrella margin of *R. pulmo* (ventral view), after Stiasny (1923); *A. aurita* ventral view (4), after Russell (1968); *Stygiomedusa gigantea* (whole figure and detail of umbrella margin, ventral view), composite by Elias after Mianzan and Cornelius (1999). All lateral views, unless noted otherwise.

SCYPHOMEDUSAE GROUP III - Order: RHIZOSTOMAE (Inscapulatae)

**Network of RC (1)
arising from CC (2)**

 Yes

**CEC (3) between 16 RC, usually blindly ending and
NOT anastomosing. Broad, much folded oral arms**

 Yes

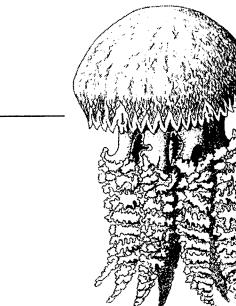
LYCHNORHIZIDAE

*Lychnorhiza lucerna**Lychnorhiza arubae*

No

No

**Network of anastomosing circular CEC (4),
communicating with CC (2). Pyramidal oral arms**

 Yes

CATOSTYLIDAE

Catostylus tagi

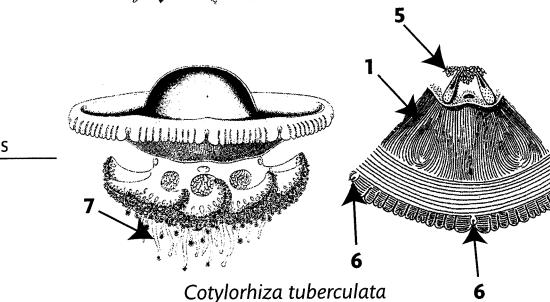
**Network of RC (1)
arising from MO area (5)**

 Yes

**Numerous RC between RO (6).
Ex-U smooth, oral arms
with long filaments (7)**

 Yes

No CC

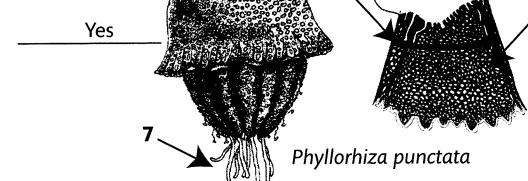
 Yes

CEPHEIDAE

Cotylorhiza tuberculata

No

**With CC (8). Ex-U finely
granular and dome-shaped**

 Yes

MASTIGIIDAE

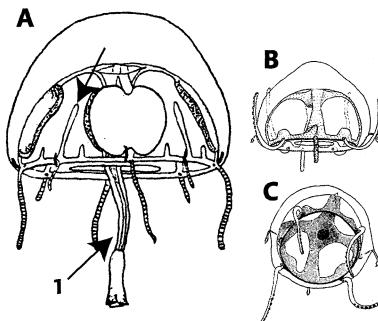
Phyllorhiza punctata

FIGURE 80: Scyphomedusae group III-Order Rhizostomae (Inscapulatae): *Lychnorhiza lucerna* whole figure and *Cotylorhiza tuberculata*, whole figure and detail of umbrella margin (1, 5 and 6, ventral view), after Mayer (1910); detail of umbrella margin of *Lychnorhiza arubae* (1, 2 and 3, ventral view), after Stiasny (1921); *Catostylus tagi* whole figure, after Grenacher and Noll (1876); *Phyllorhiza punctata*, whole figure and detail of umbrella margin (1, 5 and 8, ventral view) and detail of umbrella margin (2 and 4, ventral view) of *C. tagi*, after Stiasny (1923). All lateral views, unless noted otherwise.

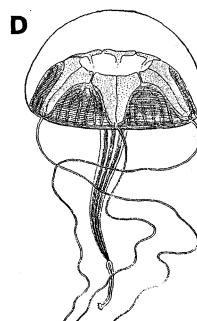
Trachymedusae Family Geryoniidae

4-6 (sometimes more) RC; With CEC. M with GAP, GO flat and leaf-shaped on RC. Marginal T solid and hollow. Ecto-endodermal STA enclosed in mesoglea.

Distribution and ecology: *L. tetraphylla* is a cosmopolitan neritic species that performs daily vertical migrations. The sting of *G. proboscidalis* is considered highly irritating for humans.

***Liriope tetraphylla***

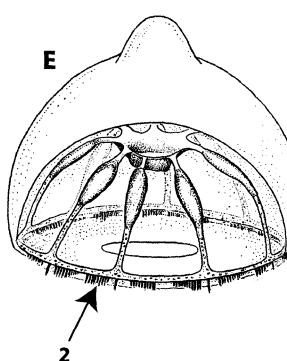
(Chamisso & Eysenhardt, 1821)

Size: 10–30 mm W**RC:** 4**GO:** 4, midway on RC**CEC:** 1–3 per ISP**GAP:** twice the M length (1)**T:** 4 long and 4 short**STA:** 8**Note:** juveniles have GAP reduced/absent and more T**Distrib:** epipelagic in CNRY, GFST, NASE, NASW, NECS, NWCS***Geryonia proboscidalis***

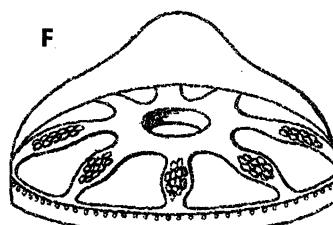
(Forsskål, 1775)

Size: 35–80 mm W**RC:** 6**GO:** 6**CEC:** up to 7 per ISP**GAP:** twice the size of M**T:** 6 long and 6 short**STA:** 12**Distrib:** epipelagic in CNRY, NASE, NASW**Trachymedusae Family Halicreatidae**

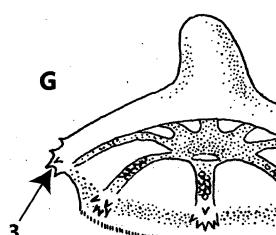
Usually ≥ 8 broad RC; without CEC. M broad and circular, without GAP. MO without distinct lips. Numerous marginal T, different in size but all structurally alike, i.e. flexible proximally and stiff distally. T that can be arranged in a continuous row (e.g. in *Halicreas* and *Haliscera*) or in groups (e.g. in *Botrynema*). Might have PA on exumbrella (genus *Halicreas*). Free ecto-endodermal STA.

***Botrynema brucei***

Browne, 1908

Size: up to 25 mm W**U:** wide, ends in a distinct knob**RC:** 8**GO:** midway on RC**M:** short and wide**T:** arranged in 16 groups of 11–12 (2) + 8 solitary perradial**STA:** 3 per ISP +1–2 on either side of perradial T**Distrib:** meso-bathypelagic in ARCT, NADR, NASE, NASW, NECS***Haliscera conica***

Vanhöffen, 1902

Size: up to 18 mm W**U:** wide, with conical projection**RC:** 8**GO:** midway on RC**M:** short and wide**T:** 8–9 per ISP**STA:** 2 in each ISP**Distrib:** meso-bathypelagic in NASE, CNRY, NASW***Halicreas minimum***

Fewkes, 1882

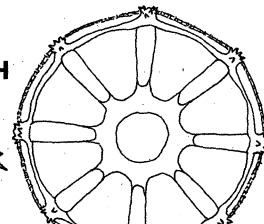
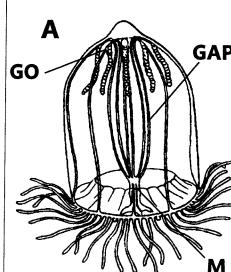
Size: 30–40 mm W**U:** wide, with conical projection**RC:** 8**PA:** 8 (3)**GO:** flat, along greater part of RC**M:** short and wide**T:** Very numerous, up to 640**STA:** 3 in each ISP +1–2 on either side of the perradial T**Distrib:** meso-bathypelagic in ARCT, GFST, NADR, NASE, NASW, NECS

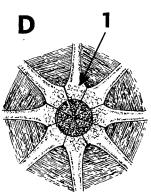
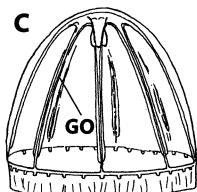
FIGURE 81: *Liriope tetraphylla*: A, adult, lateral view; B, C, juvenile, lateral and latero-ventral views. *Geryonia proboscidalis*: D, adult, lateral view. *Botrynema brucei*: E, adult, lateral view; *Haliscera conica*: F, adult, lateral view; *Halicreas minimum*: G, H, adult, lateral and ventral views. A and D Mayer (1910); B, C and E Russell (1953); F and G, Vanhöffen, (1902); H, Kramp (1947).

Trachymedusae Family Rhopalonematidae

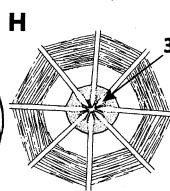
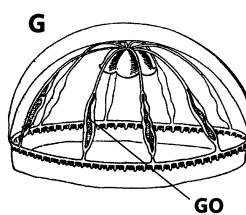
8 (rarely more) RC; no CEC. M narrow, with distinct lips, might have GAP. GO globular, linear or pendent on RC or as a ring around M, extending on RC. Marginal T evenly distributed, sometimes of two kinds, generally of uniform structure throughout. STA are free, or rarely enclosed in the U.

***Aglantha digitale***

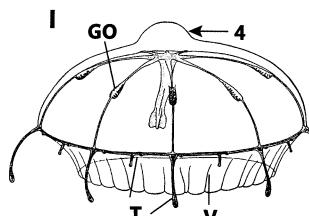
(O. F. Müller, 1776)

Size: 10-40 mm H**RC:** 8**GO:** 8 sausage-shaped pendent from sub-U portion of RC, at the base of GAP**GAP:** slender, as long as U**T:** ≥ 80 solid, all alike**STA:** 8 free, club-shaped**Note:** U twice higher than wide, with small conical projection**Distrib:** epipelagic in ARCT, GFST, NADR, NASE, NASW, NECS, NWCS, SARC***Colobonema sericeum***

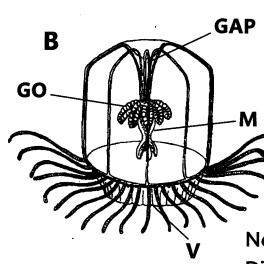
Vanhöffen, 1902

Size: 35 mm H, 45 mm W**RC:** 8**GO:** 8 linear, extending on whole RC**GAP:** absent**T:** 32 all alike, developing in succession**STA:** free, club-shaped**Note:** sub-U with muscular fields typically star-shaped (1). Broad V**Distrib:** bathypelagic in ARCT, NADR, NASE***Pantachogon haekeli***

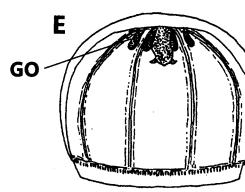
Maas, 1893

Size: 20 mm H/W**RC:** 8**GO:** linear, on 2/3 of RC**GAP:** absent**T:** 64 solid, all alike**STA:** 64 free, club-shaped**Note:** sub-U with circular muscular fields at the apex (3)**Distrib:** epi-bathypelagic in ARCT, NASE, NADR, NASW***Rhopalonema velatum***

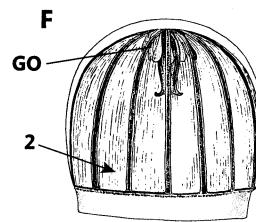
Gegenbaur, 1857

Size: 6 mm H, 8-10 mm W**RC:** 8**GO:** 8 oval, mid- of RC**GAP:** absent**T:** 8 PER-R long, club-shaped, up to 24 AD-R short, cirrus-like**STA:** 8 enclosed, beside T**Note:** U with apical knob (4) and very broad V**Distrib:** epipelagic in NADR, NASE, NASW, NECS, NWCS, SARC***Aglaura hemistoma***

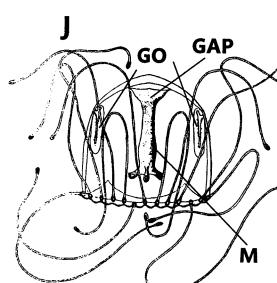
Péron & Lesueur, 1810

Size: 4-6 mm H, 3-4 mm W**RC:** 8**GO:** 8 sausage-shaped on GAP**GAP:** shorter than U and slender**T:** 48-85, all alike**STA:** 8 free, club-shaped**Note:** U with flat apex. Broad V**Distrib:** epipelagic in NASE, NWCS***Crossota rufobrunnea***

(Kramp, 1913)

Size: 10 mm H, 22 mm W**RC:** 8**GO:** 8 sausage-shaped on RC, at the base of M**GAP:** absent**T:** up to 350**STA:** number unknown**Note:** Ex_U of *Crossota* spp. with numerous meridional furrows (2). Red-brown U, M, GO and T in alive specimens.**Distrib:** bathypelagic in ARCT, NADR, SARC***Crossota norvegica***

Vanhöffen, 1902

Size: 18 mm H, 20 mm W**RC:** 10-14**T:** 200-250**GO, GAP, STA, Note:** see *Crossota rufobrunnea***Distrib:** bathypelagic in ARCT, SARC***Persa incolorata***

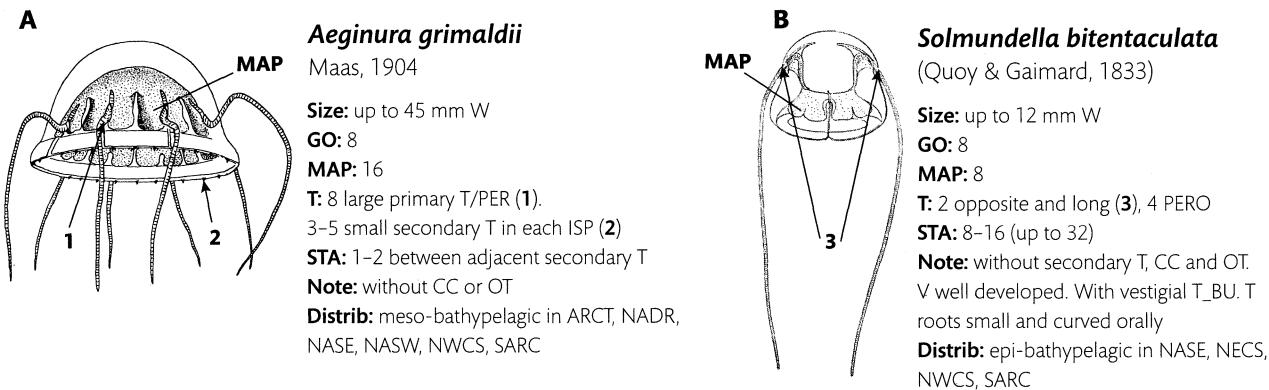
McCrady, 1857

Size: 4 mm H, 3 mm W**RC:** 8**GO:** 2 oval/sausage-shaped pendent from sub-U mid of opposite RC**GAP:** small**T:** 48 long, ending with N_KN**STA:** 8 free, club-shaped**Distrib:** epi-bathypelagic in NASE, NWCS

FIGURE 82: *Aglantha digitale*: A, adult, lateral view; *Aglaura hemistoma*: B, adult, lateral view. *Colobonema sericeum*: C, D, adult, lateral and ventral views. *Crossota rufobrunnea*, E, and *C. norvegica*, F: adults, lateral views. *Pantachogon haekeli*: G, H, adult, lateral and ventral views. *Rhopalonema velatum*: I, adult, lateral view. *Persa incolorata*: J, adult, lateral view. A, B, I and J Mayer (1910); C, G, Vanhöffen (1902); D, H Russell (1953); E, Kramp (1913); F, Kramp (1959a).

Narcomedusae Families Aeginidae and Solmundaeginidae

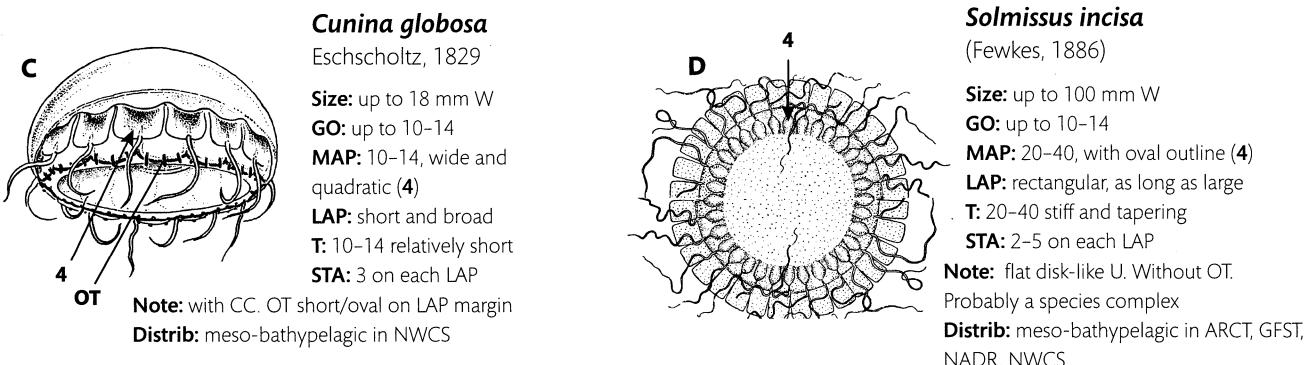
Following the recent revision of Lindsay et al. (in press) some genera previously attributed to the family Aeginidae have now been assigned to the new family Solmundaeginidae, which comprises the species of *Solmundaeginina*, *Solmundella*, *Aeginopsis* and *Solmundus*. Aeginidae might have CC, while CC are absent in Solmundaeginidae. Both families have MAP INTER-R bearing the GO, undivided or divided into two to four parts; PER-R primary T on ex-U, inserted above MAP and between marginal LAP. Aeginidae might have secondary T, while Solmundaeginidae have only secondary T_BU. Only Aeginidae might have OT.



Narcomedusae Family Cuninidae

Might have CC. MAP PER-R, undivided and bearing the GO. PER-R primary T on ex-U, inserted on to the central margin of each MAP. Might have secondary T. Might have OT.

Distribution and ecology: *S. incisa* preferably prey on gelatinous plankton, particularly on ctenophores, cnidarians and salps.



Narcomedusae Family Solmarsidae

Might have CC. Without MAP. GO on M wall/diverticula. Numerous T on U at level of periphery of M. Might have OT.

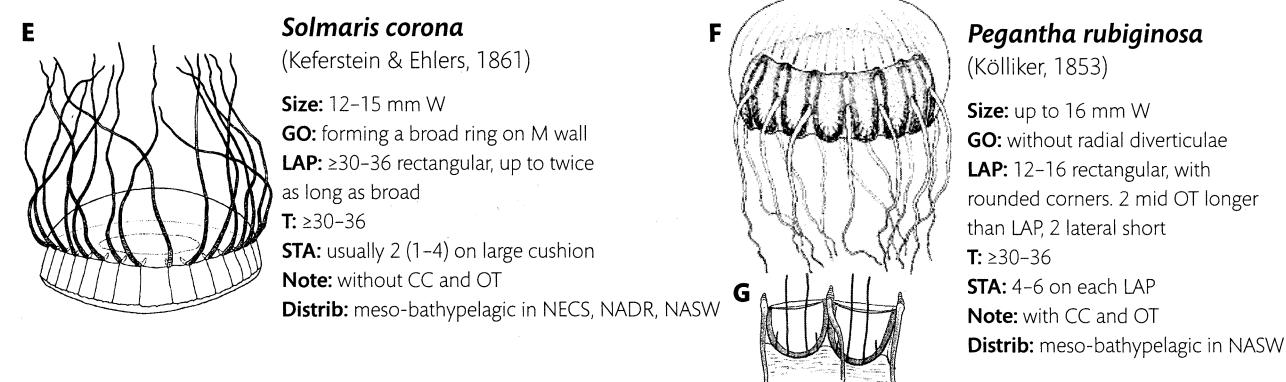


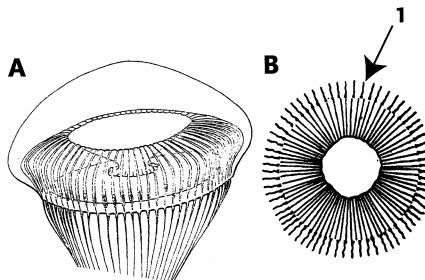
FIGURE 83: *Aeginura grimaldii*: A, adult, lateral view. *Solmundella bitentaculata*: B, adult, lateral view. *Cunina globosa*: C, adult, lateral view. *Solmissus incisa*: D, adult, ventral view. *Solmaris corona*: E, adult, lateral view. *Pegantha rubiginosa*: F, adult, lateral view; G, detail of umbrella margin showing otoporae and CC. A, Maas, (1905); B and F, Mayer (1910); C, Bigelow (1909); D, edited from Fewkes (1886); E, Pagès et al., (1992); G, Kramp (1959).

Leptomedusae Family Aequoreidae

Many simple or branched RC. M very wide, circular, usually without GAP. GO on RC, separated from M and divided longitudinally. Marginal T hollow, fine, about 1/2 to 3 times the number of RC. No CI. With excretory pores, might have PA and OC. STA closed.

Note: *Aequorea* spp. have simple and undivided RC and no PA.

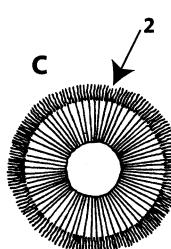
Distribution and ecology: *Aequorea* spp. eat mainly soft-bodied prey.



Aequorea forskalea

Péron and Lesueur, 1810

Size: 175 mm W
RC: usually 60–80, sometimes fewer or up to 160
GO: along whole length of RC
T: generally less than RC, can be 1/2 or twice the number of RC (1).
STA: 5–10 between successive T
Distrib: neritic in NECS, NWCS, SARC



Aequorea vitrina

Gosse, 1853

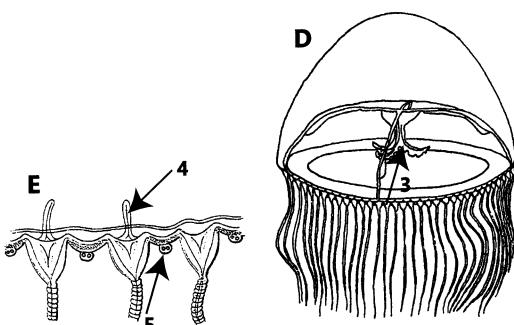
Size: 100–170 mm W
RC: 60–100
GO: along whole length of RC
T: >3 times than RC (2)
STA: 1–2 between successive T

Distrib: neritic in NECS, NWCS

Leptomedusae Family Blackfordiidae

4 simple RC. M narrow and short, without GAP. MO with 4 long curved lips (3). GO completely surround RC. 80–250 hollow marginal T, with endodermal core extending from margin into bell mesogela. Numerous closed STA.

Distribution and ecology: *B. virginica* preys not only on zooplankton but also on phytoplankton, ciliates and detritus.



Blackfordia virginica

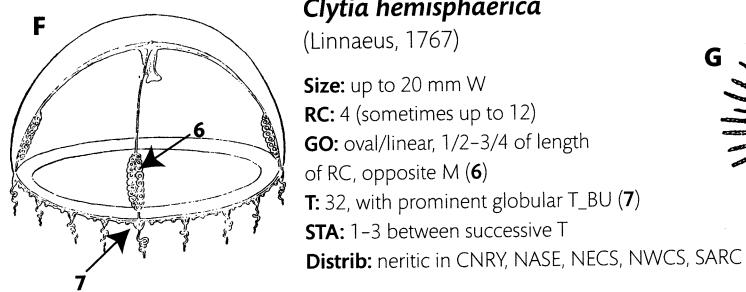
Mayer, 1910

Size: 14 mm W
RC: 4
GO: linear, >1/2 length of RC from M
T: 80, long, with diverticula into U margin (4)
STA: 1 (rarely 2) between successive T (5)
Note: introduced species from the Black Sea
Distrib: neritic in NASE, NWCS

Leptomedusae Family Campanulariidae

Usually 4 RC. Might have V. M short, without GAP. GO separated from M, completely surrounding RC. Marginal T usually hollow (except in *Obelia*). Without excretory pores, PA, CI (except in *Paralovenia*) and OC. 16–200 closed STA.

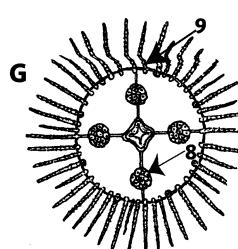
Note: the classification of this family is unsatisfactory. Divisions are not always well defined.



Clytia hemisphaerica

(Linnaeus, 1767)

Size: up to 20 mm W
RC: 4 (sometimes up to 12)
GO: oval/linear, 1/2–3/4 of length of RC, opposite M (6)
T: 32, with prominent globular T_BU (7)
STA: 1–3 between successive T
Distrib: neritic in CNRY, NASE, NECS, NWCS, SARC



Obelia spp.

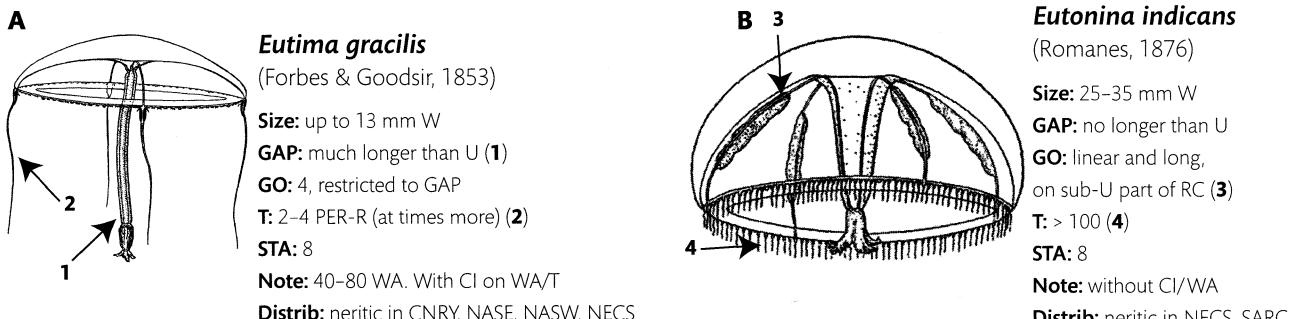
Péron & Lesueur, 1810

Size: 2.5–6 mm W
RC: 4
GO: sac-like, on middle-end of RC (8)
T: numerous short, stiff solid, with diverticula into U margin (9)
STA: 8, under T_BU
Note: very flat, no V
Distrib: neritic in CNRY, NASE, NECS, NWCS, SARC

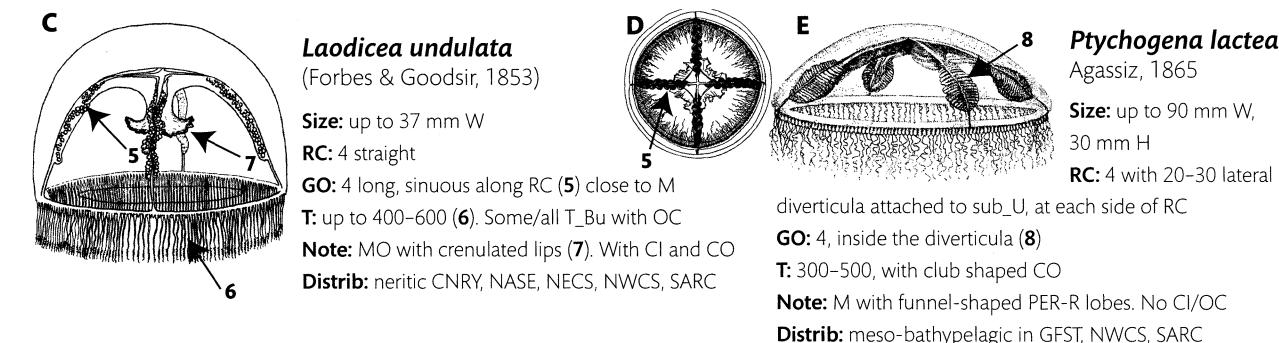
FIGURE 84: *Aequorea forskalea*: A–B, adult, lateral and ventral views. *Aequorea vitrina*: C, adult, ventral view. *Blackfordia virginica*: D, adult lateral view; E, detail of umbrella margin showing endodermal diverticula of tentacle bulbs and statocyst. *Clytia hemisphaerica*: F, adult lateral view. *Obelia* spp.: G, adult dorsal view. A, D, E and F, Mayer (1910); B, C, Russell (1953); G, Kramp (1933).

Leptomedusae Family Eirenidae

4–6 simple RC. M small, usually on well-developed GAP. GO separated from M, in each species on well-defined part(s) of RC. Hollow marginal T (except in *Eugymnanthea*). Might have marginal WA or CI, excretory pores or PA. Without OC. 8 or more closed STA.

**Leptomedusae Family Laodiceidae**

4 or 8 simple RC. M might have lobes or pouches, without GAP. GO on RC, on RC and M-lobes, or into M-pouches. Hollow marginal T. With marginal CO. Might have CI and OC. Without STA.

**Leptomedusae Family Lovenellidae**

4 simple RC. M small, without GAP. GO on RC, separated from M. Hollow marginal T with lateral CI*. Without marginal CI, OC and excretory pores. With closed STA. (*Except in *Paralovenia*).

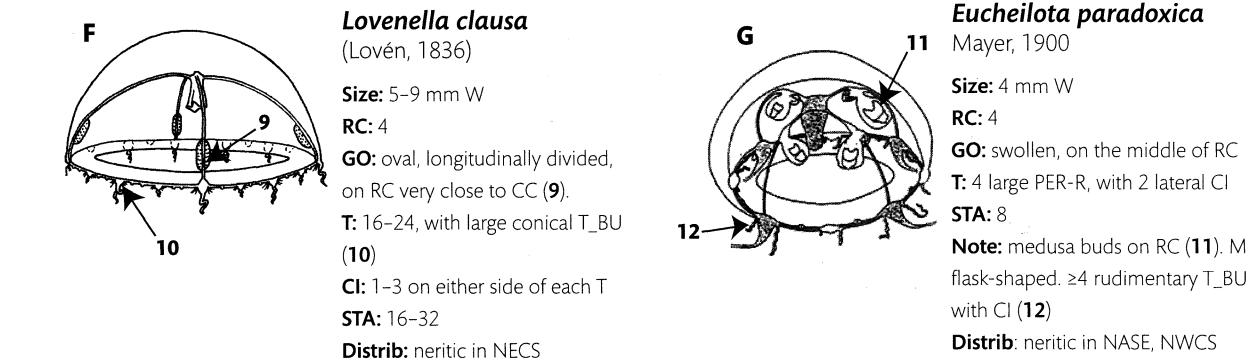
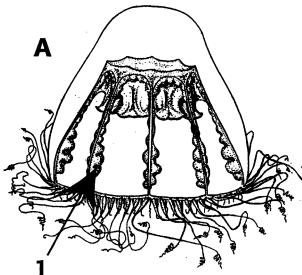


FIGURE 85: *Eutima gracilis*: A, adult, lateral view. *Eutonina indica*: B, adult, lateral view. *Laodicea undulata*: C, adult, lateral view. *Ptychogena lactea*: D, adult, ventral view; E, adult, lateral view. *Lovenella clausa*: F, adult, lateral view. *Eucheilota paradoxica*: G, adult, lateral view. A, B, and D, Kramp (1959a); C, Hyman (1940); E, Naumov (1960); F, Russell (1963); G, Carré and Carré (1990).

Leptomedusae Family Meliceridae

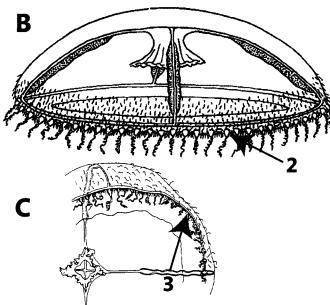
8 simple/bifurcated RC. Base of M attached over its whole surface, without GAP. GO on RC. Hollow marginal T. Without STA, CI and CO. Might have OC.

***Melicertum octocostatum***

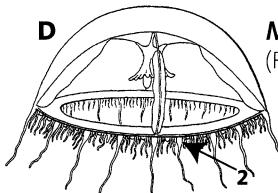
(M. Sars, 1835)

Size: 10–14 mm W/H**GO:** 8 sinuous separated from M, covering almost whole length of RC and thicker near U (1)**T:** up to 88 large T, alternating with small ones**OC:** None**Note:** 3–7 fine lines of N in each ISP on sub-U**Distrib:** neritic in ARCT, GFST, NASE, NECS, NWCS**Leptomedusae Family Mitrocomidae**

≥ 4 simple/S-shaped RC. Base of M attached to Sub-U along edges of RC. GO linear/oval on RC only. Hollow marginal T. Open STA. Might have CI. Without OC.

***Cosmetira pilosella***

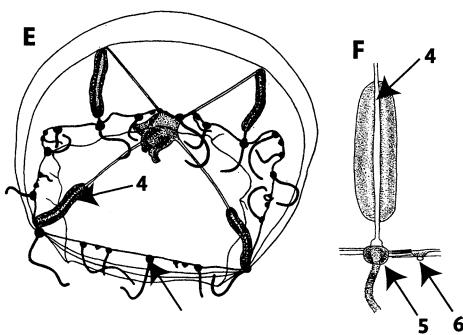
Forbes, 1848

Size: 20–48 mm W**RC:** 4 straight**GO:** 4 linear with median division, along 1/2–3/4 of RC**T:** 64–100 with large T_BU (2)**STA:** 8**Note:** 6–10 CI between adjacent T (3)**Distrib:** neritic in NECS, SARC***Mitrocomella polydiademata***

(Romanes, 1876)

Size: 12–30 mm W**RC:** 4 straight**GO:** 4 straight, along 2/3–4/5 of RC**T:** usually 36–48 with large T_BU (2)**STA:** 16**Note:** 5–9 spiral CI with terminal CNI, arranged between adjacent T**Distrib:** neritic in NWCS, NECS, SARC**Leptomedusae Family Phialellidae**

4 simple RC. M small, without GAP. GO divided in the middle by a median groove (4), placed on RC, separated from M. Hollow marginal T smooth/moniliform. Without marginal/lateral CI, excretory pores or OC. 8 closed STA, usually each on a bulbous-like swelling.

***Phialella quadrata***

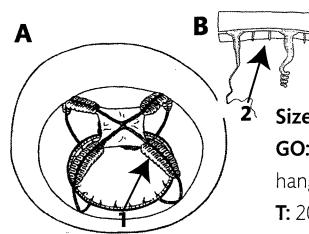
(Forbes, 1848)

Size: up to 13 mm W**RC:** 4**GO:** elongated, on the outer third of RC**T:** 16–32, with globular T_BU (5)**CI:** 1–3 on either side of each T**STA:** 16–32 (6)**Note:** V well developed**Distrib:** neritic in NASE, NECS

FIGURE 86: *Melicertum octocostatum*: A, adult, lateral view. *Cosmetira pilosella*: B, adult, lateral view; C, detail of umbrella and gonads, ventral view. *Mitrocomella polydiademata*: D, adult, lateral view. *Phialella quadrata*: E, adult, ventro-lateral view. F, adult, detail of umbrella margin, radial canal and gonad. A, Kramp (1933); B, Cornelius (1995); C, Hartlaub (1909); D, Mayer (1910); E and F, Russell (1953).

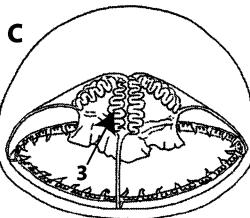
Leptomedusae Family Tiarannidae

4 simple RC. M wide, cross-shaped, with 4 PER-R lobes attached to Sub-U, without GAP. MO with 4 simple/crenulated lips. GO folded on M, extending on PER-R lobes. Numerous hollow marginal T. Hollow CO-like structures. Without OC.

***Chromatonema rubrum***

Fewkes, 1882

- Size:** up to 27 mm W/ 22 mm H
GO: 10–16 sac-like, separated and hanging on each side of PER-R lobes (1)
T: 20–24, with conical T_BU
Note: 2 CO among adjacent T (2)

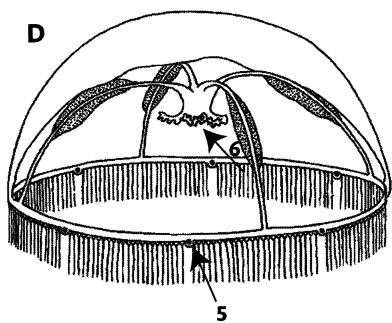
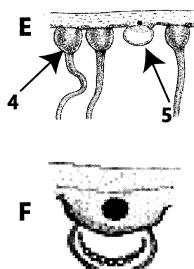
Distrib: meso-bathypelagic in ARCT, NADR, NASE, NWCS***Modeeria rotunda***

(Quoy & Gaimard, 1827)

- Size:** 20 mm W
GO: transversally folded (3), on M and connected with PER-R lobes
T: 16–28, with conical T_BU
Note: 2–3 CO among adjacent T

Distrib: neritic-bathypelagic in ARCT, NASE, NADR, NECS, NWCS, SARC**Leptomedusae Family Tiaropsidae**

4–8 (exceptionally 16) simple RC. Marginal T long and rudimentary of 1 or 2 types, with T_BU. Open STA associated with OC.

***Tiaropsis multicirrata***

M. Sars, 1835

- Size:** about 20 mm W
RC: 4 straight
GO: 4 kind of sinuous, along 1/2–2/3 of RC
T: about 300 of one kind only, with swollen T_BU (4)
OC: 8
STA: 8 ecto-endodermal (5)
Note: MO with long, much folded and crenulated lips (6). Broad and flat GAP. Without CI
Distrib: neritic in ARCT, NWCS, NECS, SARC

Anthomedusae Family Aplanulata incerta sedis

The polyp of *Plotocnide* was recently identified as *Boreohydra simplex* (Pyataeva 2016). Even though the medusa of this genus has been previously associated with Tubulariidae or Corymorphidae, following Schuchert (2012) we do not assign *Plotocnide* to any particular family.

Plotocnide borealis

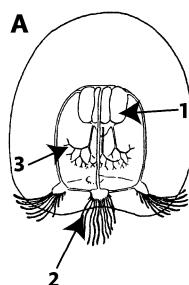
Wagner, 1885

- G**
Size: 1.5–3.5 mm H
RC: 4 narrow and straight
GO: ringlike encircle M (7) leaving lips and top portion of M free
M/GAP: M 1/2 length of sub-U, with broad apical chamber with vacuolated endodermal cells
T: 4 solid PER-R, up to twice U length. Each T has a small round T_BU and ends with an oval/swollen N_KN (8)
OC: round, on T_BU, near origin of T
Note: U with very thick mesoglea at the apex (9). N scattered on ex-U. No OC.
Distrib: ARCT, NECS, SARC

FIGURE 87: *Chromatonema rubrum*: A, adult, lateral view; B, detail of umbrella margin with marginal tentacles and cordyli. *Modeeria rotunda*: C, adult, lateral view. *Tiaropsis multicirrata*: D, adult, lateral view; E, detail of umbrella margin with marginal tentacles and statocyst; F, ecto-endodermal statocyst. *Plotocnide borealis*: G, adult, lateral view. A, Kramp (1919); B, Kramp (1933); C, Kramp (1920); D, Agassiz (1849); E and F, Russell (1953); G, Kramp (1959a).

Anthomedusae Family Bougainvilliidae

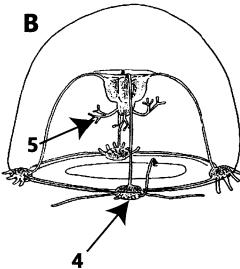
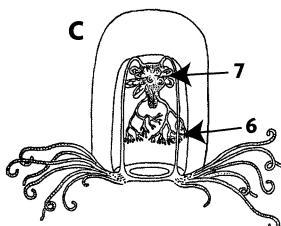
4 simple RC. MO circular with simple or dichotomously branched oral T clearly inserted above MO rim, ending with N_KN. Might have GAP. GO on M, either ring-like or in INTER/AD/PER-R position. Solid marginal T, all alike, either solitary or in groups on 4, 8 or 16 T_BU. Might have OC. 4 T_BU in PER-R position bearing ≥ 2 identical solid marginal T



Bougainvillia britannica

(Forbes, 1841)

Size: 5–8 (up to 12) mm W
GO: 8 AD-R (1) separated by PER-R cleft
T: 4 groups of 12–17 (up to 30) T on PER-R triangular T_BU (2). Oral T divided up to 4–6 times, with long basal trunks (3).
OC: oval/lenticular, at the base of T
Note: without GAP
Distrib: NECS, SARC



Bougainvillia muscus

(Allman, 1863)

Size: 1–4 mm W
GO: 4 INTER-R, at times slightly on RC
T: 4 groups of 2–8 (usually 3–4) T on PER-R T_BU (4). Oral T divided 2 times, with moderate basal trunks (5).
OC: round, on T_BU, near origin of T
Note: GAP absent or very small
Distrib: NECS, NWCS, SARC

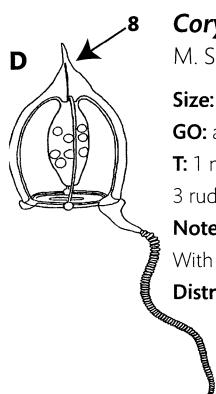
Bougainvillia niobe

Mayer, 1894

Size: 5 mm W
GO: 8 AD-
T: 4 groups of 8 T. Oral T divided 4 times, with long basal trunks (6)
OC: at the base of each T
Note: M wide, flask-shaped, 1/2 length of sub-U, often with medusa buds (7)
Distrib: NASW, NWCS

Anthomedusae Family Corymorphidae

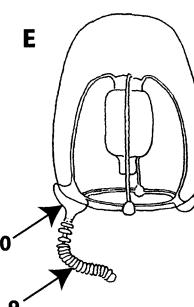
4 simple RC. M sausage-shaped generally not longer than U. Simple circular MO. GO surrounding M along its whole length. 1–4 marginal T, only 1 of which fully developed. 3–4 T_BU. Without OC.



Corymorpha nutans

M. Sars, 1835

Size: 3 mm W/up to 6 mm H
GO: around M, leaving GAP/MO free
T: 1 moniliform with 40–80 N_KN.
3 rudimentary T_BU
Note: U with pointed apex and canal (8).
With small GAP
Distrib: NECS, SARC



Euphysa aurata

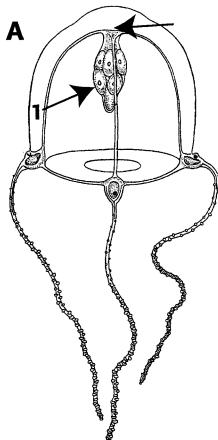
(Allman, 1863)

Size: 2.5–6 mm H
GO: around whole M
T: 1 quite short PER-R, with 6–25 N_KN (9).
3 rudimentary T_BU (10)
Note: M 2/3 or as long as sub-U, with oil drops in the upper half of M
Distrib: NECS, NWCS, SARC

FIGURE 88: *Bougainvillia britannica*: A, adult, lateral view. *Bougainvillia muscus*: B, adult, lateral view. *Bougainvillia niobe*: C, adult, lateral view. *Corymorpha nutans*: D, adult, lateral view. *Euphysa aurata*: E, adult, lateral view. A, C, D and E, Kramp (1959a); B, Russell (1953).

Anthomedusae Family Corynidae

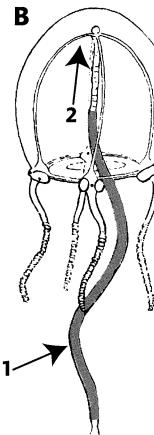
4 simple RC. M tubular, without lips. GO around M. 4 hollow marginal T. 4 T_BU with 1 OC each.

***Coryne eximia***

(Allman, 1859)

Size: 3 (up to 10) mm W**GO:** encircle M for almost entire length (1)**T:** 4, 2–3 times as long as U, with 30 N_KN**Note:** length of M about 2/3 of

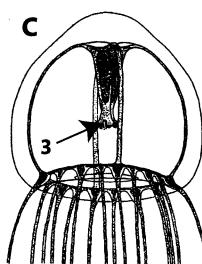
sub-U. Without medusa budding on T_BU

Distrib: NASE, NECS, NWCS***Sarsia tubulosa***

(M. Sars, 1835)

Size: 6–10 mm H**GO:** undivided, around M almost along its entire length (1), leaving both ends free**T:** 4 very long with many N_KN covering at least 1/2 of each T**Note:** length of M >2 times that of U, which is dome-shaped with mesoglea thickened at apex (2)**Distrib:** NECS, NWCS, SARC**Anthomedusae Family Hydractiniidae**

4 simple RC. M tubular/sac-shaped no longer than U, with/without GAP. MO ending with 4 N_KN, at times inserted on branched oral arms. GO on M, INTER-R, sometimes extending along basal, PER-R protrusions of the M. 4 or ≥8 marginal T ungrouped. Might have OC but not on T_BU.

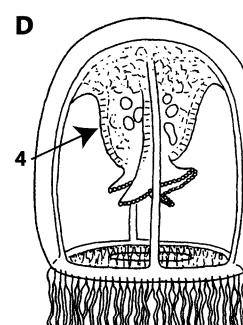
***Podocoryna borealis***

(Mayer, 1900)

Size: up to 4 mm W, 3–4 mm H**GO:** oblong, INTER-R**T:** 16–30 of different length. PER-R and INTER-R T_BU are largest.**Note:** oral arms branched 1–3 times (3). M without GAP, long about 2/3 times the length of sub-U. Without OC**Distrib:** NECS, NWCS, SARC**Anthomedusae Family Oceaniidae**

4 simple RC. MO margin fringed with numerous N_KN. GO on INTER-R walls of M. Solitary, solid T, numerous in adults. OC on AD-R side of T_BU.

Distribution and ecology: *Turritopsis* eggs develop to planulae in the sub-U. Molecular analyses have proved that *Turritopsis nutricula*, which was considered a cosmopolitan species, is only distributed in the Western Atlantic. Historical records of *T. nutricula* in the eastern Atlantic likely refer to *T. polycirrha*.

***Turritopsis nutricula***

McCrady, 1857

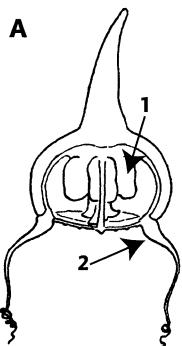
Size: up to 4–11 mm H**GO:** 4 pairs on INTER-R walls of M
T: 80–120.**Note:** pseudo-GAP formed by vacuolated endodermal cells separated in 4 blocks (4). In the congeneric species *T. polycirrha* vacuolated cells are contiguous.
Distrib: NASE, NECS, NWCS

FIGURE 89: *Coryne eximia*: A, adult, lateral view. *Sarsia tubulosa*: B, adult, lateral view. *Podocoryna borealis*: C, adult, lateral view. *Turritopsis nutricula*: D, adult, lateral view. A, Mayer (1910); B, modified from Kramp (1959a); C, Edwards (1972); D, Kramp (1959a).

Anthomedusae Family Pandeidae

4 (rarely 8) simple RC, often broadened/ribbon-like or with jagged margin. M large, with/without GAP. MO with simple/crenulated/complexly folded lips. Might have mesenteries, rarely CEC. GO AD-/INTER-R on M, have a smooth or more commonly complexly folded/pitted surface. GO might be extended on RC. 2 or >4 hollow marginal T with conical T_BU. Might have rudimentary T, i.e. small solid marginal T called *tentaculae* and OC.

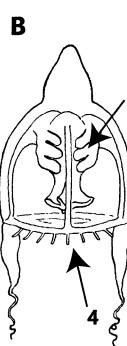
Distribution and ecology: Polyps of different species (e.g. *Pandeia conica*) settle on shells of pteropods, bivalves or in the coelom of polychaetes. Thus their medusae are widely distributed in coastal and oceanic waters.



Amphinema dinema

(Péron & Lesueur, 1810)

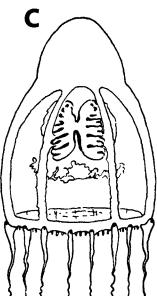
Size: 4 mm W, up to 6 mm H
RC: 4 broad
GO: 8 AD-R pads, with smooth surface (1)
M/GAP: M length 3/4 of sub-U, without GAP and with crenulated lips
T: 2 opposing PER-R with large hollow T_BU (2). Without tentaculae
Note: U with large conical apical process. 6–12 marginal WA. Without OC
Distrib: NECS, NWCS



Amphinema rugosum

(Mayer, 1900)

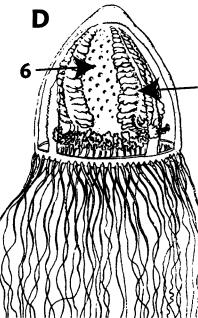
Size: 5–6 mm H
RC: 4 broad
GO: 8 AD-R pads, each one with 3–4 folds (3)
M/GAP: as in *A. dinema*
T: as in *A. dinema* but with 14–24 tentaculae (4)
Note: U with spherical/conical apical process. Without OC
Distrib: NECS, NWCS



Leuckartiara octona

(Fleming, 1823)

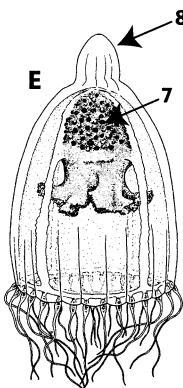
Size: usually 10 (5–20) mm H
RC: 4 broad often with jagged outline, joined to M by long mesenteries
GO: INTER-R on whole M, horse-shoe-shaped with PER-R folds and a few pits
M/GAP: M flask-shaped no longer than U, without GAP and with crenulated lips
T: Usually 16 (8–23) hollow, with T_BU clasping U to form a spur and with 1 OC. 1–3 rudimentary T_BU between adjacent T
Note: U with round/conical apical process.
Distrib: NECS, NWCS



Neoturris pileata

(Forsskål, 1775)

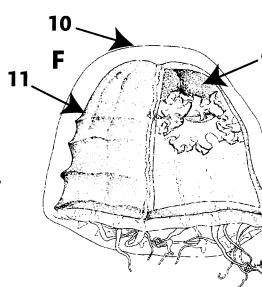
Size: up to 20–35 mm H
RC: 4 broad, with short lateral diverticula joined to M by mesenteries (5)
GO: INTER-R on whole M, with horizontal AD-R folds and with >20 isolated INTER-R pits (6)
M/GAP: M flask-shaped no longer than U, with strongly folded L. Without GAP
T: 60–90 hollow with T_BU clasping U but not forming spurs
Note: U bell/bullet-shaped with solid apical process. Without OC
Distrib: CNRY, NASE, NECS, NWCS, SARC



Pandeia conica

(Quoy and Gaimard, 1827)

Size: 10–20 mm H
RC: 4 broad with smooth/jagged outline, forming mesenteries
GO: INTER-R on 2/3 of M, separated perradially by mesenteries, forming coarse network of ridges and pits (7)
M/GAP: M long 1/2 of sub-U, mainly attached to it by mesenteries. Without GAP and with highly folded/crenulated lips
T: 16–24 (up to 45) hollow, with conical T_BU laterally compressed that clasp U forming spurs and have AD-R OC
Note: U with round/conical apex (8), with CNI tracks from each T_BU
Distrib: CNRY, NADR, NASE, NASW, NECS, NWCS, SARC



Pandeia rubra

Bigelow, 1913

Size: up to 75 mm H and W
RC: 4 very broad with jagged outline
GO: INTER-R as in *P. conica* but with close network of ridges and pits (9)
M/GAP: M large with broad base. Other characteristics as in *P. conica*.
T: As in *P. conica* but T_BU have no OC
Note: U round (10), without CNI tracks. Sub-U deeply pigmented red (11)
Distrib: meso-bathypelagic in NASW, NECS

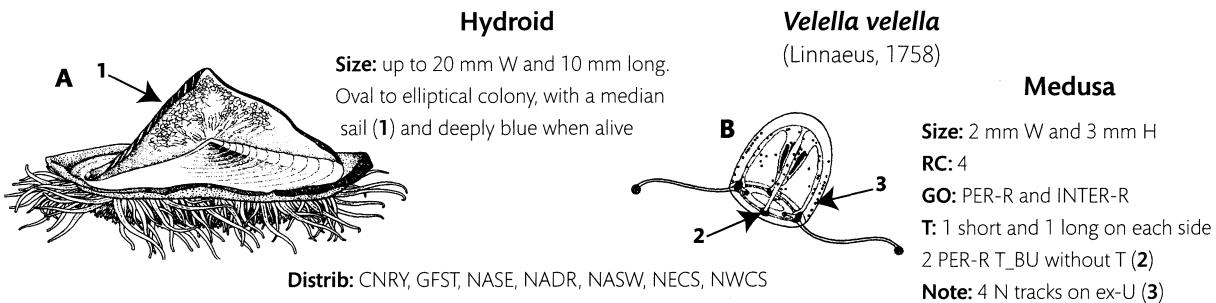
FIGURE 90: *Amphinema dinema*: A, adult, lateral view. *Amphinema rugosum*: B, adult, lateral view. *Leuckartiara octona*: C, adult, lateral view.

Neoturris pileata: D, adult, lateral view. *Pandeia conica*: E, adult, lateral view. *Pandeia rubra*: F, adult, lateral view. A, B and C, Kramp (1959a); D, Hartlaub (1914); E, Pagès et al. (1992); F, Lindsay et al. (2008).

Anthomedusae Family Porpitidae

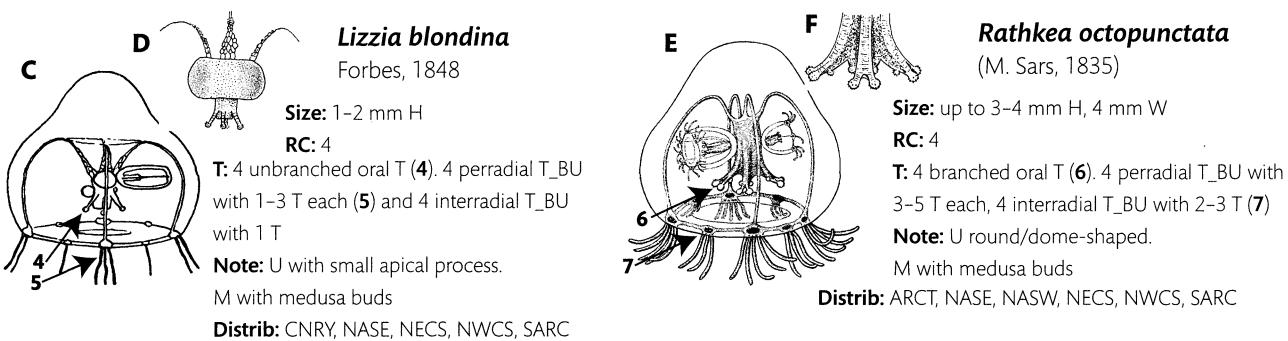
The hydroid floating colony is composed of a chitinous internal skeleton with concentric air chambers (*pneumatophore*) and covering tissue (*mantle*). Central large feeding polyp (*gastrozooid*) surrounded by gastro-gonozooids (reproductive polyps) and *dactylozooids* (defensive polyps). Medusa has 4/8 simple RC and CC. M short and MO circular. GO PER-/INTER-R. 2/4 opposite T start from T_BU and end with round N_KN. At maturity U has 4/8 N tracks issued from marginal BU.

Distribution and ecology: Hydroids float at surface while medusae are rarely seen. The hydroids of *Vevelia vevelia* prey on euphausiid larvae, copepods, fish eggs and larvae.



Anthomedusae Family Rathkeidae

4/8 RC. M cylindrical not longer than U, with GAP. MO with 4 lips elongated to form simple or branched oral arms/T armed with CNI knobs. GO completely encircling M. Mainly 8 (rarely 4) T_BU with ≥ 1 T. Without OC.



Anthomedusae Family Tubulariidae

4 simple RC. M circular. GO covering M entirely. 1-4 T. Without OC. Ex-U with N tracks.

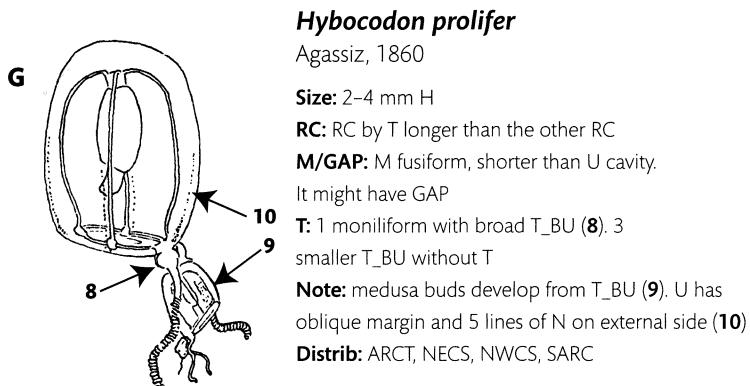


FIGURE 91: *Vevelia vevelia*: A, hydroid, lateral view; B, medusa, lateral view. *Lizzia blondina*: C, adult, lateral view; D, mouth. *Rathkea octopunctata*: E, adult, lateral view; F, mouth. *Hybocodon prolifer*: G, adult with medusa buds, lateral view. A, Pagès et al. (1992); B, Brinckmann (1964); C and G, Kramp (1959a); D and F, Russell (1953); E, Naumov (1960).

Scyphomedusae Family Atollidae

≥16 marginal LAP and >8 marginal RO alternating with an equal number of marginal T. 8 AD-R GO. *Atolla* spp. have 8 AD-R GO, 8 RO, a flat disk and a deep CG. They have a 'hypertrophied' T (HYP), larger than the others, that has a different position in different species.

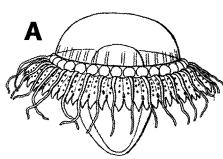
Atolla chuni

(Vanhöffen, 1902)

Size: diam. up to 70 mm

T: 24. HYP_T in line with interradius (1)

Note: 7–9 small papillae on upper surface of each LAP



1



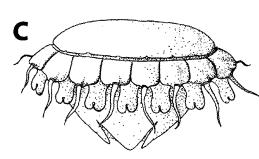
Atolla parva

Russell, 1958

Size: diam. circa 30 mm (up to 63 mm)

T: 20–26. HYP_T in line with interradius (1)

Note: RS straight, up to inner margin of CM (2)



2



Atolla vanhoeffeni

Russell, 1957

Size: diam. circa 30 mm (up to 50 mm)

T: 20. HYP_T in line with interradius (1)

Note: base of M cross-shaped (3), with 8 dark spots at outer corners (4)



4

3

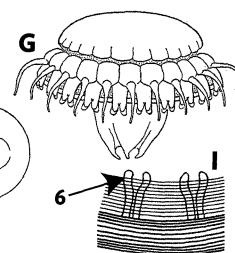
Atolla wyvillei

Haeckel, 1880

Size: diam. up to 150 mm

T: 22. HYP_T not in line with interradius (5)

Note: RS divergent and extending beyond inner margin of CM (6)



5

6



Distrib: meso- but also epipelagic, recorded across the whole North Atlantic, particularly *A. parva* and *A. wyvillei*

Scyphomedusae Family Cyaneidae

Stomach divided in MAP containing the GO, divided peripherally in numerous branching canals ending blindly in marginal LAP. Without CC. Marginal T arising from sub-U distant from U margin. 4 oral arms with much folded lips. *Cyanea* spp. have typically 8 AD-R groups of marginal T arranged on >1 row and 8 RO. For the identification of the ephyra/post-ephyra stages of *C. capillata* and *C. lamarckii* see Holst (2012).



Cyanea capillata

(Linnaeus, 1758)

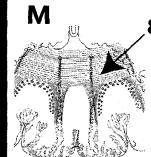
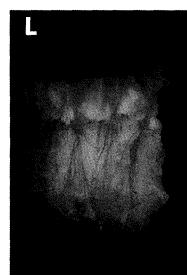
Size: diam. 300–500 mm

T: 70–150 in each AD-R group

Note: CM and RS with small pit-like intrusions (7)

Usually yellow-brown colour

Distrib: mainly recorded in NECS and NWCS



Cyanea lamarckii

Péron & Lesueur, 1810

Size: diam. 60–150 mm

T: 40–60 in each group

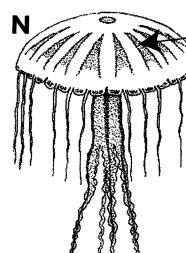
Note: CM and RS usually without small pit-like intrusions (8). Yellowish-blue colour

Distrib: mainly recorded in NECS

Scyphomedusae Family Pelagiidae

MAP separate and unbranched. Marginal T arising from U margin. Without CC. Long oral arms with frilled lips. For the identification of the ephyra/post-ephyra stages of *Chrysaora hysoscella* see Holst (2012).

Distribution and ecology: *C. hysoscella* is often found in association with young carangid fish.



Chrysaora hysoscella

(Linnaeus, 1767)

Size: diam. up to 300 mm

T: 24 in groups of 3, alternating with 8 RO

Note: Ex-U typically with 16 V-shaped radial brown markings (9). 4 long oral arms with frilled edges

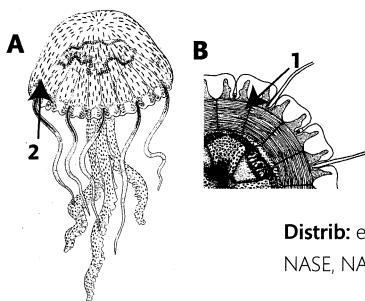
Distrib: nearshore distribution in NECS

FIGURE 92: *Atolla chuni*: A, adult, lateral view. *Atolla parva* and *A. chuni*: B, diagram showing position of hypertrophied tentacle (HYP), ventral view. *A. parva*: C, adult, lateral view; D, closeup of umbrella margin. *Atolla vanhoeffeni*: E, adult, lateral view; F, diagram showing position of HYP, ventral view. *Atolla wyvillei*: G, adult, lateral view; H, diagram showing position of HYP, ventral view; I, closeup of umbrella margin. *Cyanea capillata*: J, adult, lateral view; K, closeup of umbrella margin. *Cyanea lamarckii*: L, adult, lateral view; M, closeup of umbrella margin. *Chrysaora hysoscella*: N, adult, lateral view. A and G, Mayer (1910); B, F, H, Repelin (1965); D, K, M and N, Russell (1970); I, Russell (1959); C and E, composite by Elias, in Mianzan and Cornelius (1999); J and L, modified from pictures © Jason Gregory, www.britishmarinelifeimages.co.uk.

Scyphomedusae Family Pelagiidae

MAP separate and unbranched (1). Marginal T arising from U margin. Without CC. Long oral arms with frilled lips.

Distribution and ecology: *P. noctiluca* has no polyp stage. It preferably preys on chaetognaths and mollusc larvae but also on copepods and fish larvae. It is bioluminescent.



Pelagia noctiluca

Forsskål, 1775

Size: diam. circa 120 mm

T: 8, alternating with 8 RO

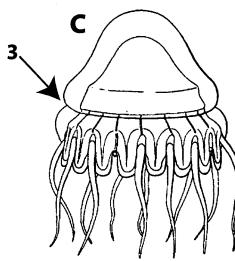
Note: Ex-U covered by red-brown stinging warts (2). 4 thick oral arms

Distrib: epi-mesopelagic in CNRY, GFST, NADR, NASE, NASW, NATR, NECS, NWCS, SARC

Scyphomedusae Family Periphyllidae

4 INTER-R RO and ≥ 4 (up to 28) marginal T

Distribution and ecology: In the last two or three decades *P. periphylla* has become very abundant in some Norwegian fjords, where it is seen as a nuisance by the local fisherman. This species performs extensive diel vertical migrations.



Periphylla periphylla

(Péron & Lesueur, 1809)

Size: diam. up to 250 mm

T: 12 stiff and tapering, 3 between each pair of RO (4 RO in total)

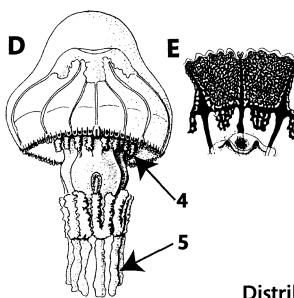
Note: U hemispherical/conical, with deep CG near mid U (3)

Distrib: meso-bathypelagic but also found in the upper layers in the whole North Atlantic

Scyphomedusae Family Rhizostomatidae

8 pairs of SCA on upper MO-arms (4), which are fused only proximally and terminate distally with a single terminal club and 3-winged appendages each (5). Without primary MO-opening. M with complex canal system.

Distribution and ecology: *R. pulmo* is mainly coastal, with hotspots in semi-enclosed areas that receive freshwater and nutrient input. It is often found in association with amphipods, crabs and young carangid fish. It is a favourite food of the leatherback turtle.



Rhizostoma pulmo

(Macri, 1778)

Size: diam. circa 400 mm

T: without marginal T

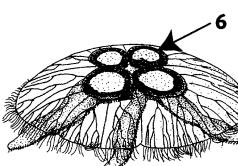
Note: U bell-shaped, translucent white-blue as the 8 thick oral arms. Edges of the 8 marginal LAP are violet. 8 RO, 16 SCA (4)

Distrib: epipelagic in NASE, NECS, SARC

Scyphomedusae Family Ulmaridae

Unbranched and/or branched RC and a CC. With or without subgenital pits. The genus *Aurelia* has, in addition to the characters of the subfamily Aureliinae (i.e. small marginal T, GO invaginated, external subgenital pits and anastomosised RC), an U with 8–16 broad and shallow marginal LAP. Molecular studies have revealed that *A. aurita*, which is characterized by high morphological variability, is a cryptic species. For the identification of the ephyra/post-ephyra stages of *A. aurita* see Holst (2012).

Distribution and ecology: In *A. aurita* the planula develops in brood pouches located on the oral arms of the female medusa.



Aurelia aurita

(Linnaeus, 1758)

Size: diam. circa 250 mm

T: filiform, very numerous (100–1000)

Note: U flat and 4 long oral arms with crenulated lips. 4 horseshoe-shaped MAP (6) and purple/violet GO. 8 marginal LAP

Distrib: cosmopolitan, usually found inshore in NASE, NECS, NWCS, SARC

FIGURE 93: *Pelagia noctiluca*: A, adult, lateral view; B, detail of umbrella margin. *Periphylla periphylla*: C, adult, lateral view. *Rhizostoma pulmo*: D, adult, lateral view; E, detail of umbrella margin. *Aurelia aurita*: F, adult, lateral view. A, C and D, Mayer (1910); B, Russell (1970); E and F, Stiasny (1923).

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