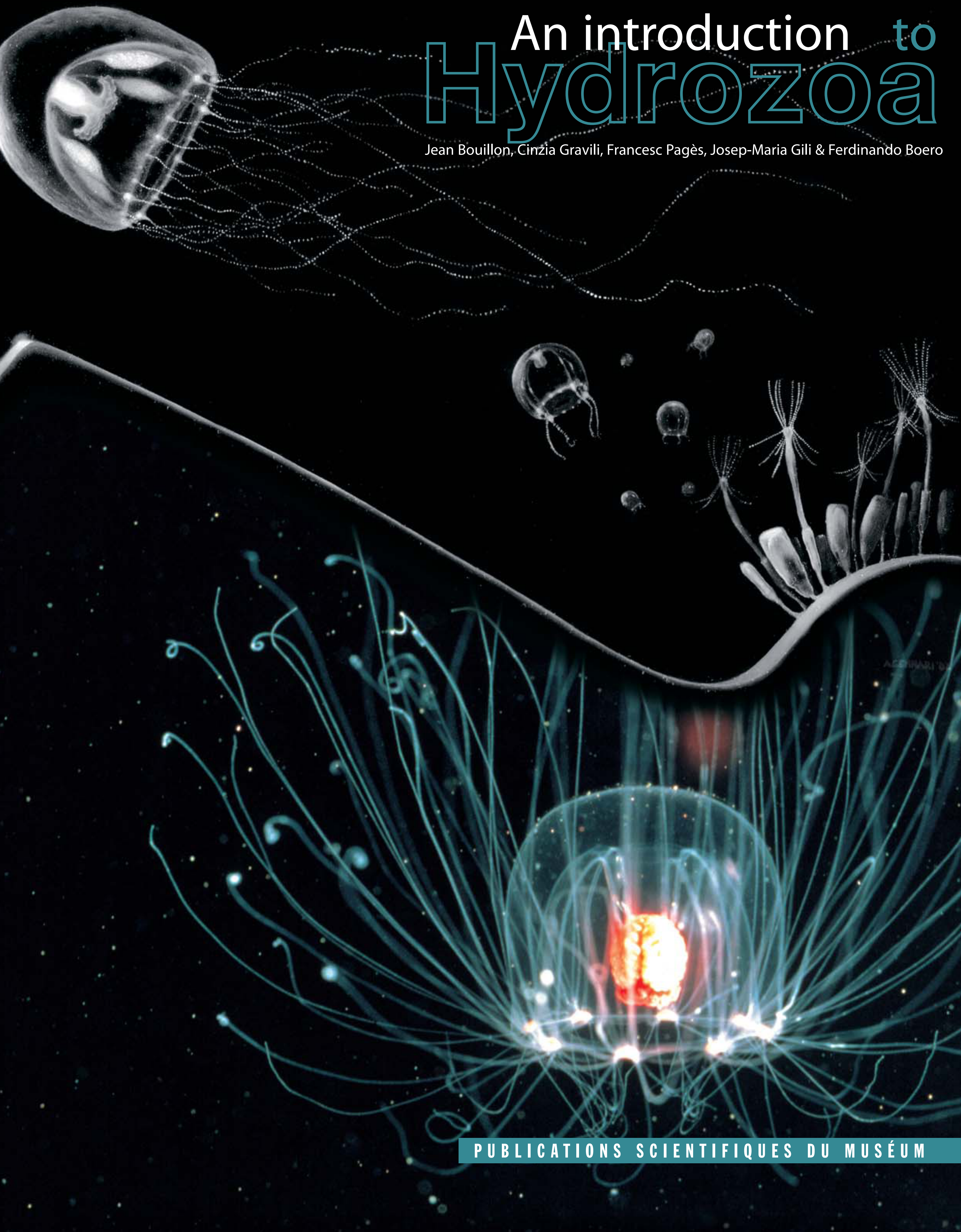
An introduction to Hydrozoa

Jean Bouillon, Cinzia Gravili, Francesc Pagès, Josep-Maria Gili & Ferdinando Boero



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Jean BOUILLON (1), Cinzia GRAVILI (2)
Francesc PAGÈS (3), Josep-Maria GILI (3)
& Ferdinando BOERO (2)

(1) Laboratoire de Biologie Marine
Université Libre de Bruxelles
50 avenue F. D. Roosevelt
1050 Bruxelles - Belgium

(2) Dipartimento di Scienze e Tecnologie Biologiche ed Ambientali
Stazione di Biologia Marina
Università di Lecce
73100 Lecce - Italy

(3) Institut de Ciències del Mar
CMIMA-CSIC
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ABSTRACT

BOUILLON J., GRAVILI C., PAGÈS F., GILI J.-M. & BOERO F. 2006 – An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle* 194: 1-591. Paris ISBN: 2-85653-580-1.

The superclass Hydrozoa of the phylum Cnidaria comprises 3,702 species currently regarded as valid, ascribed to three heterogeneous classes. The 134 species of the class Automedusa have simple life cycles with medusae and no polyp stage, and are divided into three subclasses: Actinulidae, Narcomedusae, Trachymedusae. The 3,567 species of the class Hydroidomedusa have complex life cycles with polyps producing medusae through a medusary nodule, and are divided into five subclasses: Anthomedusae, Laingiomedusae, Leptomedusae, Limnomedusae, Siphonophorae. The single species of the class Polypodiozoa has a complex life cycle, involving endocellular parasitism. Diagnoses and keys are presented for all supraspecific taxa, and lists of included species are given for each genus. The diagnostic characters and character states in the superclass are described. A glossary summarizes definitions of all technical terms referred to in the superclass. References to all original species descriptions are given.
Zhangiella nom. nov. pro Platystoma Zhang, 1982, non Meigen, 1803
Pseudosolanderiidae Bouillon & Gravier-Bonnet, fam. nov.

RÉSUMÉ

BOUILLON J., GRAVILI C., PAGÈS F., GILI J.-M. & BOERO F. 2006 – An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle* 194: 1-591. Paris ISBN: 2-85653-580-1.

Cette monographie couvre l'ensemble de la super-classe des Hydrozoa, celle-ci appartient à l'embranchement des Cnidaires, un des plus simples parmi les Eumétazoaires, et caractérisé essentiellement par la présence de cellules urticantes ou cnidocystes, de structure extrêmement complexe et variée, d'où l'embranchement tire son nom.
La super-classe des Hydrozoa est divisée en trois classes : les Automedusa, les Hydroidomedusa et les Polypodioza. Les Automedusa sont constituées par les sous-classes des Actinulidae, des Narcomedusae et des Trachymedusae. Les Hydroidomedusa comprennent les sous-classes des Anthomedusae, des Laingiomedusae, des Leptomedusae, des Limnomedusae et des Siphonophorae. L'unique espèce formant la classe des Polypodioza a un cycle de vie complexe comprenant une phase de parasitisme endocellulaire des œufs de certains poissons appartenant aux Acipenseridae (esturgeons) et de Polyodontidae, sa position taxonomique est encore hypothétique et sujette à discussions. La biodiversité et l'écologie des espèces constituant ce groupe, généralement constitué de forme de taille discrète, sont peu connues des taxonomistes non spécialisés.

RÉSUMÉ DÉVELOPPÉ

BOUILLON J., GRAVILI C., PAGÈS F., GILI J.-M. & BOERO F. 2006 – An introduction to Hydrozoa. *Mémoires du Muséum national d'Histoire naturelle* 194: 1-591. Paris ISBN: 2-85653-580-1.

La super-classe des Hydrozoa comprend environ 3 702 espèces actuellement considérées comme valides. Seulement cent trente quatre de ces espèces appartiennent à la classe des Automedusa qui sont majoritairement marins, solitaires et pélagiques exception faite des Actinulidae ayant une vie interstitielle dans les sables marins côtiers. Les autres espèces forment la classe des Hydroidomedusa dont la majeure partie des espèces est marine mais qui renferme également des formes d'eau saumâtre et d'eau douce, et dont le cycle de vie complexe fait généralement alterner un stade fixé benthique, les polypes, et un stade pélagique libre, la méduse. Les cycles biologiques des hydrozoaires sont en réalité parmi les plus variés et complexes du règne animal et sont dans l'ensemble peu connus.

On peut toutefois distinguer quatre types de cycles majeurs :

– celui propre aux Automedusa où les embryons ou planula n'acquièrent jamais de stade benthique et se développent soit directement ou par l'intermédiaire de larves actinuloïdes pélagiques en une méduse adulte sexuée ;

– celui de la plupart des Hydroidomedusa où les planula se développent en un stade larvaire, les polypes essentiellement benthiques, soit solitaires ou modulaires, qui vont engendrer ultérieurement par reproduction asexuée, via un nodule médusaire, le stade méduse adulte pélagique, solitaire et sexué. Ce cycle bien que globalement caractéristique des Hydroidomedusa souffre toutefois de nombreuses modifications qui sont décrites en détail dans le présent travail et dont la plus significative est la suppression de la phase sexuée ou méduse libre que l'on observe chez à peu près la moitié des espèces d'Hydroidomedusa. Chez celles-ci, le stade méduse est réduit à des degrés variables et n'est plus représenté que par des sporosacs restant fixés en permanence aux polypes et au sein desquels se différencient les gamètes. Les larves polypes deviennent ainsi par pédogenèse le stade adulte sexué, ces sporosacs étant parfois restreints à de simples gonades ;

– chez les Hydroidomedusa Siphonophorae les planula ne se fixent jamais et se développent en des colonies majoritairement pélagiques, extrêmement polymorphes intégrant différents types polypoïdes et des méduses réduites à des flotteurs ou à des organes propulseurs ;

– celui Polypodiozoa où des stades parasites (ou polypoides?) endocellulaires produisent des medusoïdes tentaculés libres. Les Polypodiozoa ne sont représentés que par un genre et une espèce : *Polypodium hydriforne* Ussov, 1885.

Ce travail n'est pas une révision systématique des hydrozoaires mais se veut un manuel de référence pour l'étude de ce groupe. Il est divisé en plusieurs parties. La première partie couvre de façon extensive et illustrée la morphologie et la structure histologique des principaux stades du cycle biologique des hydrozoaires, à savoir le stade adulte, – la méduse –, et les stades larvaires – les hydroïdes –, ainsi que les divers stades de leur reproduction sexuée de l'œuf à la gastrula ou planula. Chez les hydrozoaires les processus de gastrulation, c'est-à-dire ceux qui conduisent à la mise en place de l'ectoblaste et de l'endoblaste, sont remarquables et parmi les plus variés du monde animal.

Les Hydrozoa possèdent également de multiples formes et possibilités de reproduction asexuée, cette forme de reproduction étant même une de leur caractéristique la plus marquante. Les divers aspects de ces différents types de reproduction (bourgeonnement polypodiaux et médusaires ; fission ; formation de podocystes ; frustulation ; enkystement et régénération) sont analysés en détail et illustrés. La formation des méduses à partir d'éléments larvaires ou du bourgeonnement médusaire des formes adultes s'effectue de façon totalement différente chez les Automedusa et les Hydroidomedusa : ce ne sont que des phénomènes analogues. Chez les premières, la cavité sous-ombrellaire, le velum et leurs dérivés se forment à partir d'un simple repli de l'ectoderme larvaire ou de la zone bourgeonnante de l'adulte ; chez les derniers le bourgeonnement médusaire s'effectue toujours par l'intermédiaire d'un nodule médusaire, structure complexe, conférant à la méduse adulte une origine de type triploblastique.

Les kystes ou stades dormants, représentent un stade extrêmement important dans la plupart des cycles d'hydrozoaires. Beaucoup d'espèces sont en effet saisonnières ou disparaissent même de leur biotope traditionnel pendant plusieurs années. L'étude de cette forme particulière de survie est malheureusement encore peu avancée. Il faut noter toutefois que parmi les Automedusa, seules les Narcomedusae présentent une forme de reproduction asexuée: le bourgeonnement médusaire ; les Trachymedusae et les Actinulidae ne présentent aucun type de reproduction asexuée. Un tableau illustré résume les principaux caractères cytologiques distinguant les différentes catégories de cnidocystes, éléments souvent indispensables à la détermination des hydrozoaires.

La seconde partie du travail est consacrée principalement à l'aspect systématique de la super-classe des Hydrozoa. Une nomenclature unifiée est utilisée pour l'ensemble des hydroïdes et des méduses, elle est résumée, ci-après, page 15.

En premier lieu, les divers caractères systématiques utilisés pour la distinction des taxa sont donnés tant pour les stades polypes que pour les stades méduses. Des clefs d'identification et des diagnoses comprenant les principaux caractères distinctifs sont ensuite établis pour l'ensemble des Hydrozoa, à des niveaux taxonomiques allant de la super-classe aux différents genres reconnus actuellement. Pour chaque genre une série de références utiles et la liste la plus actualisée possible des espèces nominales qui le compose est fournie avec l'indication du nom de leur auteur initial. Des dessins illustrent au moins une espèce pour chaque genre valide cité. Dans le texte, les catégories supra-familiales sont classées par affinités phylogénétiques et dans chacune de ces catégories les familles et les genres qui les composent sont agencés par ordre alphabétique.

Il faut toutefois réaliser qu'étant donné le nombre de nouvelles informations ajoutées quasi journellement à nos connaissances, un pareil travail n'est jamais terminé ni complètement à jour.

Des renseignements techniques concernant les diverses méthodes de récolte et les moyens de fixation et de préservation des spécimens font l'objet de deux sections couvrant l'ensemble des stades benthique et pélagique des hydrozoaires.

La liste des références bibliographiques citées dans la monographie est présentée en fin de travail et constitue une partie importante de celui-ci.

Enfin, un glossaire extensif des termes scientifiques utilisés dans le présent travail a été établi afin de faciliter la compréhension des diagnoses.

INTRODUCTION

All general invertebrate zoology textbooks, implicitly or explicitly, treat the phylum Cnidaria as a monophyletic taxon characterised by a convincing diagnostic character: the presence of cnidocysts. It is traditionally divided into four classes: Anthozoa (with the polyp stage only), Scyphozoa (with polyps giving rise to medusae via strobilation), Cubozoa (giving rise to medusae through polyp metamorphosis) and Hydrozoa (giving rise to medusae through budding). Cornelius (1995) raised the Hydrozoa to superclass rank. Bouillon & Boero (2000) proposed the same taxonomic rank for the Hydrozoa, recognising three classes: the Automedusa, producing medusae via direct development of the planula or through an “actinula” stage (see below for the differences between actinula-like morphs in the Hydrozoa), the Hydroidomedusa, producing medusae via a medusary nodule, and the Polypodiozoa, with a much modified, parasitical developmental pattern (see below). Bouillon and Boero (2000) provided diagnoses and species lists of the hydrozoan genera with free medusae. In this paper, intended to be a “textbook” for the Hydrozoa, the diagnoses for all hydrozoan genera and suprageneric taxa are given, and also a list of all the nominal species. The future task of taxonomists will be to revise genera and families, so to clear out synonymies and provide unambiguous descriptions for all species. This is currently being done by some specialists, their work has been widely used to build the diagnoses of the taxa they revised. Under each genus, we list the species curreclty accepted as valid, and give only those synonyms that are still being used in the recent literature; unused synonyms are not listed.

DEFINITION OF THE SUPERCLASS HYDROZOA

Cnidaria with either tetramerous, polymerous or, exceptionally, biradial symmetry; gastrovascular system simple, deprived of stomodeum (pharynx, actynopharynx), septa or gastric tentacles; mesoglea acellular; sexes generally separated; gametes, with few exceptions, ectodermal in origin (endodermal in the Polypodiozoa, Actinulidae, *Protohydra leuckarti*, *Nannocoryne mammylia*, *Pegantha clara* and *Solmaris flavescens*), ripening usually in the ectoderm and shed directly to the outside, never into the gastrovascular cavity (except *Polypodium* ?); medusae with velum (except *Obelia*), a muscular membrane projecting inwards from the umbrellar margin and partially occluding the umbrellar opening; polyps, when present, solitary or, most often, colonial, modular, with interconnected coelenterons, often polymorphic, with chitinous exoskeleton (perisarc), some secreting extensive calcium carbonate exoskeletons (coenosteum); cnidocysts of about 24 major types, generally restricted to the ectoderm; atrichous isorhizas are the only cnidocyst type found throughout the Hydrozoa, never very common, but present at least in some species of all subclasses, they occur also in Anthozoa, Cubozoa and Scyphozoa; life cycles involving:

– planulae developing directly into medusae, or into intermediate “actinula”-like stages (Automedusa);
– planulae developing indirectly into either solitary or modular, asexual polyps, generating planktonic, individual, sexual medusae usually by budding via a medusary nodule; many paedomorphic species with various degrees of medusa reduction, reduced medusoids generally producing gametes without breaking away from polyp colony, sometimes functioning for the propulsion of planktonic colonies (Hydroidomedusa);

– planulae developing into pelagic, swimming or floating, highly polymorphic, integrated colonies composed of several modified types of polyps and reduced medusae (formed via a medusary nodule) attached to a stem;
– endocellular parasitic (polypoid?) stages producing free-living (medusoid?) tentacled stages (Polypodiozoa).

The Hydrozoa are a wide and heterogeneous group, comprising 3,702 nominal species that share few derived features, namely the velum, absent only in *Obelia* (see Boero *et al.* 1996 for a detailed treatment of the peculiarities of this medusa and on its possible origin), and the ectodermal "gonads". The superclass Hydrozoa comprises three classes: the Automedusa (134 nominal species), the Hydroidomedusa (3,567 nominal species) and the Polypodiozoa (1 nominal species) (see Bouillon & Boero 2000).

The Hydrozoa are typically carnivores; they are among the most important planktonic and benthic predators; when abundant, they are actually major consumers of fish larvae, crustaceans and other planktonic and benthic organisms. Some species may feed on bacteria, protozoans, phytoplankton and even dissolved organic matter, other species harbour symbiotic intracellular algae from which they may derive some nutrients. Hydromedusae have been used as biological indicators to detect movements of oceanic waters. Several species are known as indicators of upwelling systems.

GENERAL CLASSIFICATION

Class AUTOMEDUSA
(includes Actinulidae, Narcomedusae, Trachymedusae)

Hydrozoa with usually direct development and entirely pelagic life cycle, planulae never settle and acquire a benthic habit, each usually transforming into a single young medusa, except in parasitic forms; sexes separate; sex cells generally ripening in the ectoderm, each fertilised egg giving rise to a single medusa, except in some Narcomedusae where parasitic stages issued from the egg may give rise to several medusae by asexual budding; medusa formation without medusary nodule, subumbrellar cavity and velum formed by folding and deepening of the oral embryonic ectoderm, so being analogous to the subumbrellar cavity and velum of the Hydroidomedusa; primary marginal tentacles always formed before subumbrellar cavity and gastrovascular system; marginal tentacles deprived of tentacular bulbs (see peronia); sensory organs as ecto-endodermal statocysts, with an endodermal axis, growing out from circular canal, with sensory cells characterised by numerous kinocilium-lacking rootlets, surrounded by stereocilia, innervated by the upper nerve ring; lithocytes and statoliths of endodermal origin; asexual reproduction present only in "actinula"-like larvae and adults of Narcomedusae; frustules and cysts unknown.

REMARKS. – Intermediate tentaculated post-embryonic stages of Narcomedusae have been inappropriately called "actinulae", and considered identical with the actinula of the Anthomedusae. However, the two are not homologous, due to differences in development: those of Automedusa immediately possess medusan features, whereas those of Anthomedusae are polypoid. The Automedusa planulae have a simple didermic cellular organisation, lacking the specialised neural and glandular cells characterising Hydroidomedusan planulae. With the exception of the interstitial Actinulidae, the Automedusa are all oceanic, mainly represented by deep sea or open sea species. Their typically diploblastic "bauplan" limited their evolution so that, although having a wide geographical distribution, the Automedusa show a limited generic and specific diversity.

Class HYDROIDOMEDUSA
(includes Anthomedusae; Laingiomedusae; Leptomedusae; Limnomedusae; Siphonophorae)

Hydrozoa usually undergoing indirect development through a succession of distinct stages. The "planula", a ciliated motile gastrula, typically developing into a benthic, modular, larval stage, the polyp (except in the Porpitidae, *Margelopsis* and *Pelagohydra* where the hydroid is floating). Polyps giving rise, by asexual budding, to planktonic, free-swimming and solitary hydromedusae, representing the sexual adult. Medusae often reduced to sporosacs (fixed gonophores), so that hydroids, 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) (Siphonophorae).

Besides extreme cases of medusa reduction (e.g., *Hydra* and *Rhysia*), medusa budding occurs via a medusary nodule or entocodon, forming a coelom-like cavity, the subumbrellar cavity, lined by striated muscle cells; primary marginal tentacles always develop after subumbrellar cavity and gastro-vascular system. Both embryonic and larval stages, the planula and the polyp, typically diploblastic; adult sexual stages, the hydromedusae, acquiring a "triploblastic" kind of organisation during the second step of embryonic development (medusary nodule formation) (Boero *et al.*, 1998).

REMARKS. – Hydroids can be solitary, but generally form modular colonies by simple budding. The colonies often produce polyps specialised for different functions, all having an interconnected coelenteron (defensive dactylozooids, reproductive gonozooids, nutritive gastrozooids, etc.). The sense organs of pelagic hydroidomedusae, when present, are ocelli (Anthomedusae, some Leptomedusae), or statocysts (Leptomedusae, Limnomedusae); sometimes cordyli of unknown function are also present (Leptomedusae); the Siphonophorae have no visible sense organs. Statocysts can have different origins and structures: closed or open velar ectodermal statocysts are formed by the subumbrellar epithelium or by the velum epithelium (all Leptomedusae); ecto-endodermal closed statocysts are located in the mesoglea, near the ring canal or in the velum (Limnomedusae). The sensory cells of velar ectodermal statocysts are innervated by the lower nerve ring (= inner or subumbrellar) and, lacking stereocilia, are morphologically distinct from those of the sensory clubs of the Automedusa; lithocytes and statoliths are ectodermal in origin. Only the Limnomedusae, among the Hydroidomedusa, have ecto-endodermal statocysts, similar to those of the Automedusa. In both groups, statocysts are innervated by the upper nerve ring and lithocytes and statoliths are of endodermal origin. The sensory cells of Limnomedusae statocysts are devoid of stereocilia. They present, thus, intermediate features between Leptomedusan and Automedusan statocysts. The presence of both a medusary nodule and of colonial modular hydroids suggests inclusion of the Limnomedusae within the Hydroidomedusa (see Collins 2000, 2002 for alternative phylogenies).

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

Class POLYPODIOZOA

Life cycle as a succession of a free-living stage and of a stage parasitizing the eggs of some Acipenseridae and Polyodontidae (Pisces).

The earliest known stage is a binucleate cell, parasitizing previtellogenetic fish oocytes. Further development may last several years, leading to a convoluted didermic stolonal structure, with inverted germ layers, forming numerous inverted buds. Before fish spawning, eversion takes place and the germ layers take their normal position (ectoderm outside, endoderm inside). The stolon becomes free and fragments into individual buds, each giving rise to a free creeping globular stage that multiplies by longitudinal fission. Globular stages can move and feed, having an oral mouth-cone and 24, 12 or 6 tentacles, according to season. Germ cells are endodermal. So-called females with two kinds of "gonads", each with a gonoduct opening in the gastral cavity. So-called males deprived of gonoducts, their "gonads" forming gametophores carrying cnidocysts.

REMARKS. – It is not known how the parasites get into young previtellogenic fish oocytes. The free-living stages are presumably homologous to sexual medusae, the parasitic stages to polyps. By their stolonal parasitic budding stage and their cnidome, the Polypodiozoa seem to present some affinities with the Narcomedusae, to which they were previously assigned. This class comprises only *Polypodium hydriforme* Ussov, 1885, which was until recently the only known metazoan adapted to an intracellular parasitic life.

Siddall *et al.* (1995) provided some evidence that the Myxozoa are related to *Polypodium*, proposing their demise as a phylum of protists and suggesting their inclusion in the Cnidaria, Hydrozoa. The taxonomic status of *Polypodium* with respect to the Myxozoa is still rather controversial (see Siddall *et al*,. 1995; Monteiro, Okamura & Holland, 2002; Okamura *et al.* 2002; Zrzavy, 2001; Zrzavy & Hypsa, 2003) and we will refrain from including the Myxozoa in this work.

GENERAL MORPHOLOGY AND HISTOLOGY OF POLYPS AND MEDUSAE

(see Thomas & Edwards 1991; Bouillon 1995a; Carré & Carré 1995) (FIGS 1-35)

HYDROIDS

GENERAL APPEARANCE OF COLONIES (FIGS 1-3)

Hydroids are generally colonial, bearing numerous individual polyps; some are solitary. Typically, they are permanently attached to their substrate but, exceptionally, they can be pelagic: *Climacocodon*, *Margelopsis*, *Pelagohydra*, *Porpita*, *Velella*. Solitary hydroids settling on hard substrates have a basal disc fixing them to their support, those settling on soft substrates have a pointed base and filamentous rootlets; both types of basal structures support a pedicel or hydrocaulus bearing a body, or hydranth, with an apical mouth normally surrounded by tentacles. In colonial forms, the basal area usually develops a system of hollow tubes, the stolons or hydrorhizae, which fix the colonies to the substrate and from which arise, from place to place, either sessile polyps, or polyps supported by a short pedicel, or large, erect, often branched stems bearing numerous polyps, either sessile or pedicellate. Main stems and pedicels form the hydrocaulus, the hydrocladia are lateral branches bearing hydranths. Stolons, hydrocauli and hydrocladia are formed by ecto-endodermal tubular prolongations of the hydranths' gastric cavities, enveloped by a protective chitinous layer, or perisarc. The living ecto-endodermal part of the tubes is the coenosarc. It is by this common tubular system of coenosarc that all the hydranths making up a colony communicate with each other allowing, for instance, food circulation. The coenosarc represents the bulk of the living material of the colony.

New hydranths are always formed by asexual budding, this commonly leading to colony formation and growth. Hydranth budding rarely occurs on the hydranths, except in solitary forms, where lateral budding is a way of asexual reproduction leading to separate individuals. In colonial forms, budding usually occurs on stems and stolons. The medusae and their reduced equivalents bud off from hydranths, hydrorhizae, hydrocauli or hydrocladia.

Hydroidomedusae colonies are mostly quite small, with few of them exceeding a few centimetres or decimetres (i.e. *Cladocarpus lignosus* 70 cm); the hydranths are usually tiny, seldom exceeding a few millimetres, but there are exceptions (i.e. *Hydrocoryne miurensis*: 6 cm; *Corymorpha nutans*: 12 cm; *Monocoryne gigantea*: 40 cm; *Candelabrum penola*: 85 cm; *Branchiocerianthus imperator*: more than 2 m).

MORPHOLOGY OF POLYPS (FIGS 4-11)

THE HYDRANTH

The hydranth, or feeding polyp, may have various shapes (urn-shaped, conical, club-shaped, cylindrical, etc.), with specialized zones:

Hypostome or proboscis. The apex of hydranths, above the tentacles when these are present, is differentiated into a hypostome or proboscis. Hypostomes are mostly either conical or dome shaped, rarely peduncled (Eudendriidae, Campanulariidae), always bearing a terminal mouth. The hypostome and the surrounding tentacles play an important

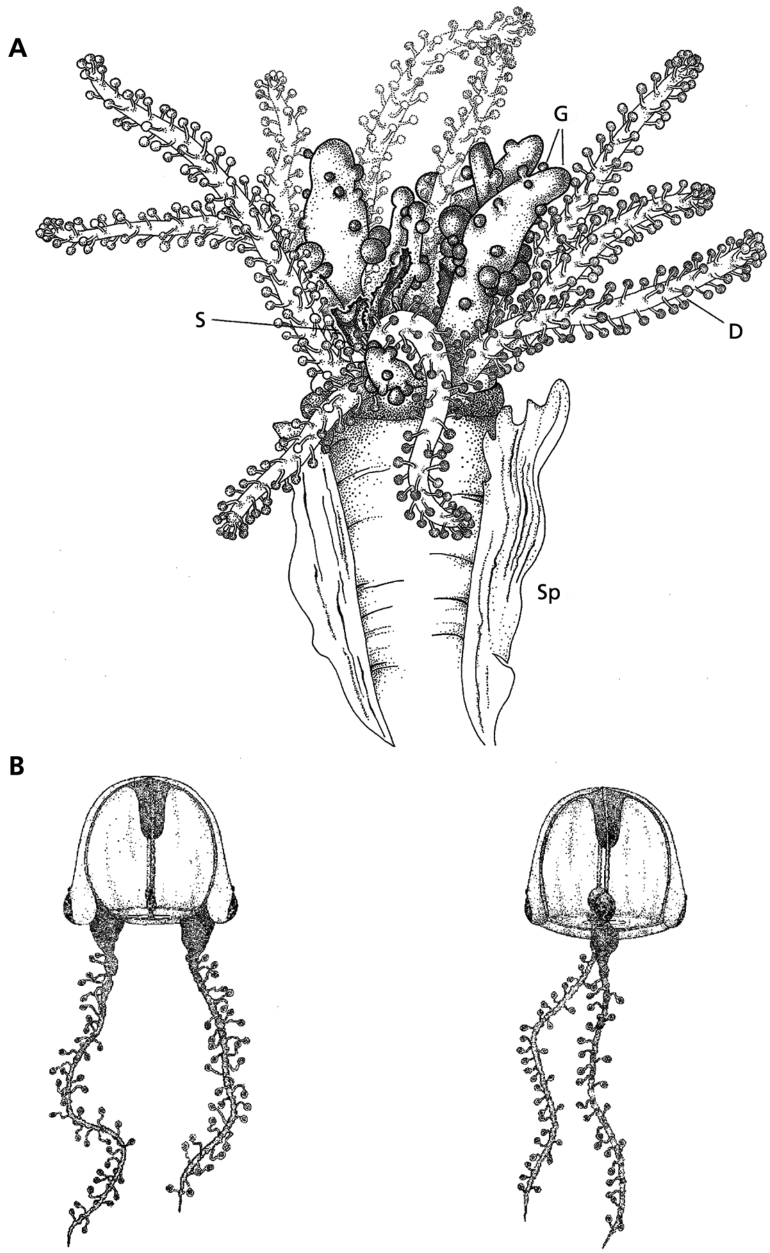


FIG. 1. Morphology of hydroids, general types and cycles. A-B, Anthomedusae, Teissieridae. (= *Teissiera milleporoides*). A, polymorphic colony with gastrozooids, dactylozooids, gonozooids and spines; B, young medusae. (after Bouillon, 1974). BM = medusary bud; D = dactylozooid; E = spine; G = gono-gastrozooid; S = spine; Sp = *Spirobranchus.*

FIG. 1. *Morphologie des hydroïdes, types généraux et cycles. A-B, Anthomedusae, Teissieridae. (=* Teissiera milleporoides*). A, colonie polymorphique avec gastérozoïdes, dactylozoïdes, gonozoïdes et épines ; B, jeune méduse. (d'après Bouillon, 1974). BM = bourgeon médusaire ; D = dactylozoïdes ; E = épine ; G = gono-gastérozoïdes ; Sp =* Spirobranchus.

role in feeding and in the first stages of prey ingestion. In the Cladonematidae, the ectoderm of the hypostome is glandular and furrowed by a preoral cavity. A preoral cavity of very different origin is also observed in the Bonneviellidae, certain Tubulariidae and some species of *Bimeria*.

Gastric column. The gastric column is the main part of the hydranth. Internally, the gastric cavity is simple and not divided by septa, as in the other cnidarian superclasses, but in certain species the endoderm may present folds and villosities increasing the absorption surface (i.e. *Bonneviella*, *Candelabrum*, *Clava*, *Koellikerina*). It bears tentacles in some groups. Anthomedusae, Limnomedusae, and some Leptomedusae often differentiate medusary buds and gonophores at this level. The different steps of extracellular digestion and, according to species, intracellular digestion, take place in this zone too. In certain species, the contracted gastric column presents a lateral expansion opposite the hydrocaulus (see section below) forming the abcauline sac or abcauline caecum. In the Haleciidae, Plumulariidae, and Syntheciidae, the gastric endoderm is differentiated into two zones, an oral digestive region rich in glandular cells and digestive vacuoles, and an aboral non-digestive region lacking such structures.

Sphincter. The sphincter is a muscular ring at the base of the hydranth. In the Anthomedusae polyps and in some Leptomedusan ones (e.g., Haleciidae, Eirenidae, etc.) the sphincter is usually represented by a zone at the base of the hydranth, deprived of tentacles, rich in muscular elements, whose endoderm, deprived of digestive inclusions, is formed by chordal cells. This region of reduced metabolic activity divides the gastric column from the pedicel; its function is to isolate the column to the rest of the gastrovascular system to allow localised digestion of prey

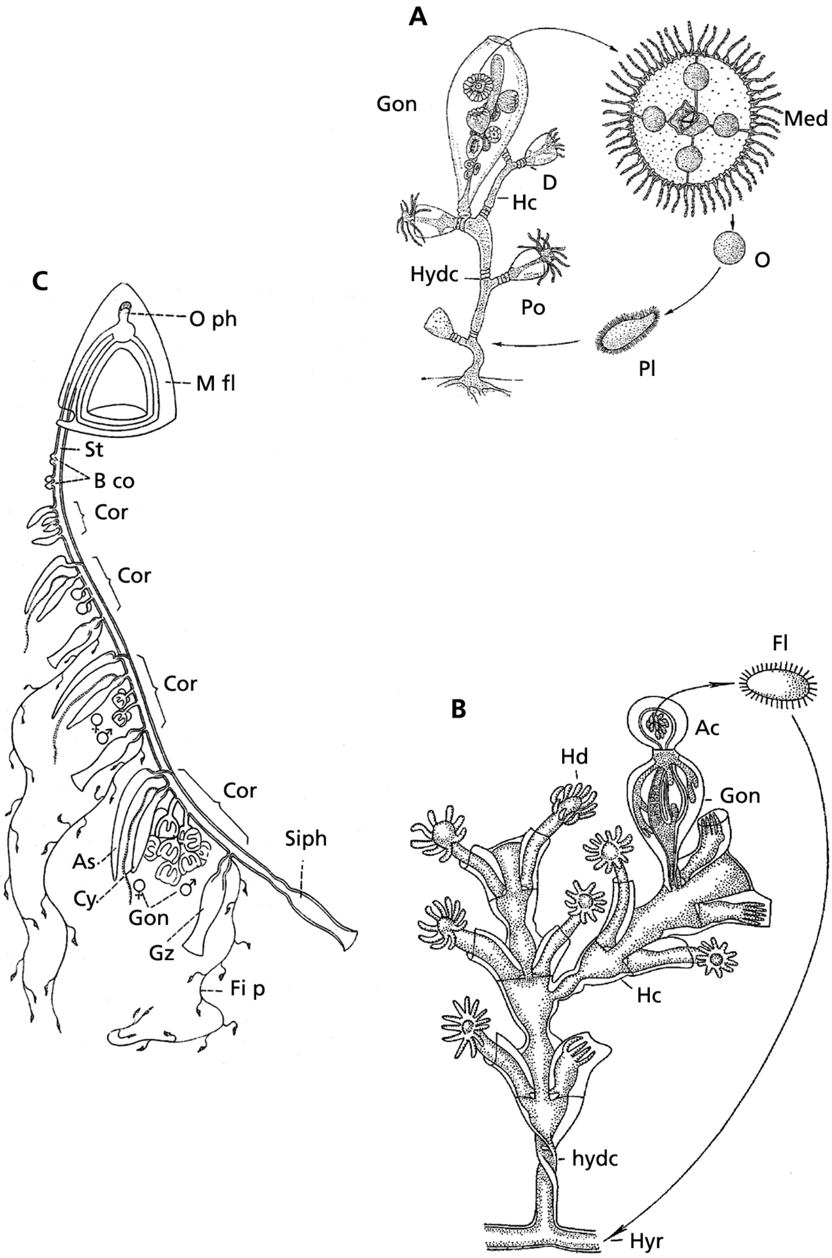


FIG. 2. Morphology of hydroids, general types and cycles. A-B, Leptomedusae. A, life cycle comprising a medusae stage: *Obelia geniculata* (Campanulariidae); B, paedomorphic life cycle reduced to hydroid stage and fixed sporosac: *Dynamena pumila* (Sertulariidae). C, Siphonophorae. Schema of the general structure of a Calycophoran. (A-B after Naumov, 1969 modified; C after Brien, 1963); Ac = acrocyst; As = bract; Bco = budding part of the stolon; Cor = cormidia; Cy = dactylozooid; D = diaphragm; Fip = fishing tentacle with tentilla; Gon = gonozooid; Gz = gastrozooid; Hc = hydrocladium; Hd = hydranth; Hydc = hydrocaulus; hyr = hydrorhiza; Med = medusa; Mfl = nectophore or swimming bell; O = egg; Oph = somatocyst; Pl = planula; Po = polyp; Siph = siphon or terminal gastrozooid; St = stolon.

FIG. 2. *Morphologie des hydroïdes, types généraux et cycles. A-B, Leptomedusae. A, cycle vital comprenant un stade médusae :* Obelia geniculata *(Campanulariidae); B, cycle paedomorphique ou la colonie est réduite au stade hydroïde et au stade sporosac fixé :* Dynamena pumila *(Sertulariidae). C, Siphonophorae. Schéma général de la structure d'un Calycophore. (A-B d'après Naumov, 1969 modifié ; C d'après Brien, 1963) ; Ac = acrocyste ; As = bractée ; Bco = partie bourgeonnante du stolon ; Cor = cormidie ; Cy = dactylozoïde ; D = diaphragme ; Fip = tentacule pêcheur avec tentille ; Gon = gonozoïde ; Gz = gastérozoïde ; Hc = hydroclade ; Hd = hydranthe ; Hydc = hydrocaule ; Hyr = hydrorhize ; Med = méduse ; Mfl = nectophore ou cloche natatoire ; O = oeuf ; Oph = somatocyste ; Pl = planula ; Po = polype ; Siph = siphon du gastérozoïde terminal ; St = stolon.*

and avoid introduction of too large food items into the lumen of the stolonal system. In the Tubulariidae, a cushion of special endodermal cells projects into the basal part of the gastral cavity, functioning like a sphincter.

Tentacles. Tentacles are the most characteristic hydranth structures; they vary in type and structure according to the mode of distribution of cnidocysts on their surface.

The main types are:

– acnide: sensory, deprived of cnidocysts (e.g., certain proximal tentacles of the Corynidae and Cladonematidae).

– capitate: with a distinct large capitation (a knobbed end, or acrosphere), richly armed with cnidocysts (e.g., the Capitata).

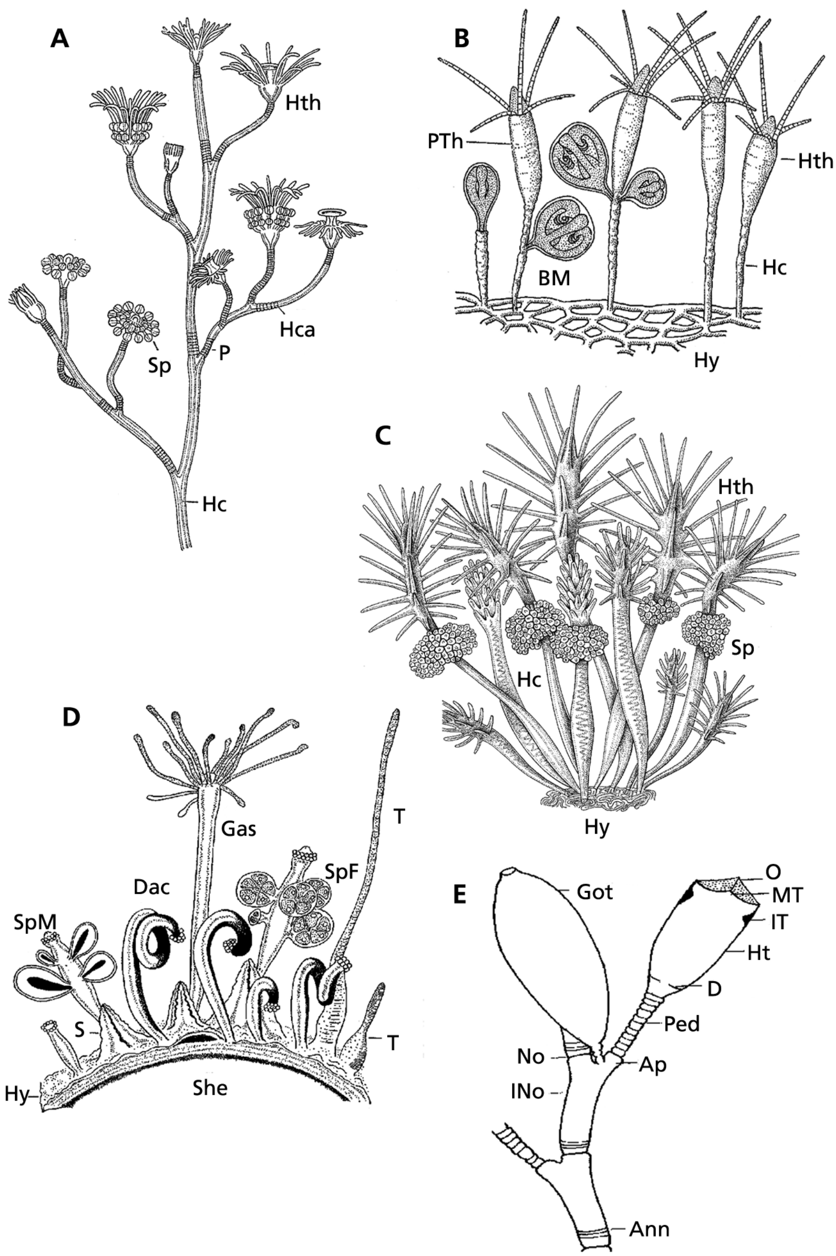


FIG. 3. Morphology of hydroids, general types and cycles. Anthomedusae. A, C-D, paedomorphic life cycle reduced to hydroid stage and fixed sporosac: A, Eudendriidae, *Eudendrium ramosum*; C, Clavidae, *Clava multicornis*; D, Hydractiniidae, *Hydractinia echinata*. B, life cycle comprising a medusa stage: Pandeidae, *Neoturris pileata*, morphology. E, Leptomedusae, part of skeleton of a pedicellate and symmetrical hydrothecae. (A & C after Allman, 1871; B after Edwards, 1965; D after Stokes, 1974; E after Millard, 1975). Ann = annulations; Ap = apophysis; BM = medusa bud; D = diaphragm; Dac = dactylozooid; Gas = gastrozoooid; Got = gonotheca; Hc = hydrocaulus; Hca = hydrocladium; Ht = hydrotheca; Hth = hydranth; Hy = hydrorhiza; INo = internode ; IT = internal tooth; MT = marginal tooth; No = node; O = operculum; P = perisarc; Ped = pedicel; Pth = pseudohydrotheca; She = shell; S = spine; Sp = fixed sporosac; SpF = female sporosac; SpM = male sporosac; T = tentaculozooid.

***FIG. 3.** Morphologie des hydroïdes, types généraux et cycles. Anthomedusae. A, C-D, cycle vital paedomorphic avec des colonies réduites aux stades hydroïdes et aux stade sporosacs fixés : A, Eudendriidae,* Eudendrium ramosum *; C, Clavidae,* Clava multicornis *; D, Hydractiniidae,* Hydractinia echinata*. B, cycle vital comprenant un stade méduse libre : Pandeidae,* Neoturris pileata*, morphologie. E, Leptomedusae, partie d'un hydroclade montrant une hydrothèque pédicellée et symétrique. (A & C d'après Allman, 1871 ; B d'après Edwards, 1965 ; D d'après Stokes, 1974 ; E d'après Millard, 1975). Ann = annulations ; Ap = apophyse ; BM = bourgeons médusaire ; D = diaphragme ; Dac = dactylozoïde ; Gas = gastérozoïde ; Got = gonothèque ; Hc = hydrocaule ; Hca = hydroclade ; Ht = hydrothèque ; Hth = hydranthe ; Hy = hydrorhize ; INo = internode ; IT = dent interne ; MT = dent marginale. No = node ; O = opercule ; P = périsarc ; Ped = pédicelle ; Pth = pseudohydrothèque ; She = coquille ; S = épine ; Sp = sporosac fixé ; SpF = sporosac femelle ; SpM = sporosac mâle ; T = tentaculozooide.*

– cateniform: with cnidocysts in a distinct large terminal capitation and with numerous small, spirally arranged cnidocyst clumps (e.g., *Margelopsis* and some Leptomedusae).
– filiform: thread-like, with straight sides of relatively uniform or tapering diameter, lacking prominent cnidocyst clusters, the cnidocysts appearing more or less evenly distributed (e.g., the Filifera and the majority of Leptomedusae polyps).
– monilifiliform: with dispersed small isolated clusters of cnidocysts on the adoral side and with a continuous band of cnidocysts along the aboral side (e.g., aboral tentacles of Tubulariidae).
– moniliform: with cnidocysts arranged in a terminal capitation and in rather regularly spaced conspicuous clumps or bands of tall epidermal cells bearing cnidocysts (e.g., *Asyncoryne*, *Euphysa*).

– pseudofiliform: with cnidocysts scattered in a relatively low epidermis along the adoral side and a concentration of cnidocysts in tall epidermis on the aboral side (e.g., oral tentacles of Tubulariidae).
– ramified capitate: branched, with a capitation on each branch (e.g., *Cladocoryne*).
– semifiliform: with a capitation stretched towards the aboral side (e.g., *Pennaria*, *Paracoryne*).
– semimoniliform: with a large capitation and numerous small cnidocyst clusters on the adoral side (e.g., *Odessia*).

A single polyp sometimes possesses different tentacle types (*Cladonema*, capitate and filiform; *Euphysa*, capitate and moniliform; *Cladocoryne*, capitate and ramified capitate; *Pennaria*, capitate and semifiliform).

Almost all hydranths have an oral tentacle circlet. Exceptions are atentacled hydranths (e.g., *Craspedacusta*, *Halocoryne*, *Limnocnida*, *Protohydra*, *Rhaptapagis*) and those with a proboscis (e.g., *Sphaerocoryne*). Aboral tentacles, when present, can be either scattered or in one or several whorls. In exceptional cases, tentacle arrangement is asymmetrical (e.g., *Monobrachium*, *Proboscidactyla*, *Zanclella*). The number of tentacles varies greatly, mostly oscillating between 8 and 50, sometimes less; exceptionally the number of tentacles is much higher, as in some solitary polyps (e.g., *Monocoryne* 110; *Branchiocerianthus imperator* 480; *Candelabrum capensis* 400 to 600; *Candelabrum penola* 330.000!). In some Leptomedusan hydroids, the bases of the tentacles are connected by an intertentacular web (or umbrellula).

STOLONAL SYSTEM

The hydrorhiza. Colonial forms are attached to the substrate by coenosarcal tubes usually contained in a perisarc sheath: the hydrorhiza. The stolonary gastric cavity is usually simple but is sometimes divided into several canalicules limited by endodermal cells (i.e. Asyncorynidae). The hydrorhizal stolons grow on the substrate, increasing the colony surface

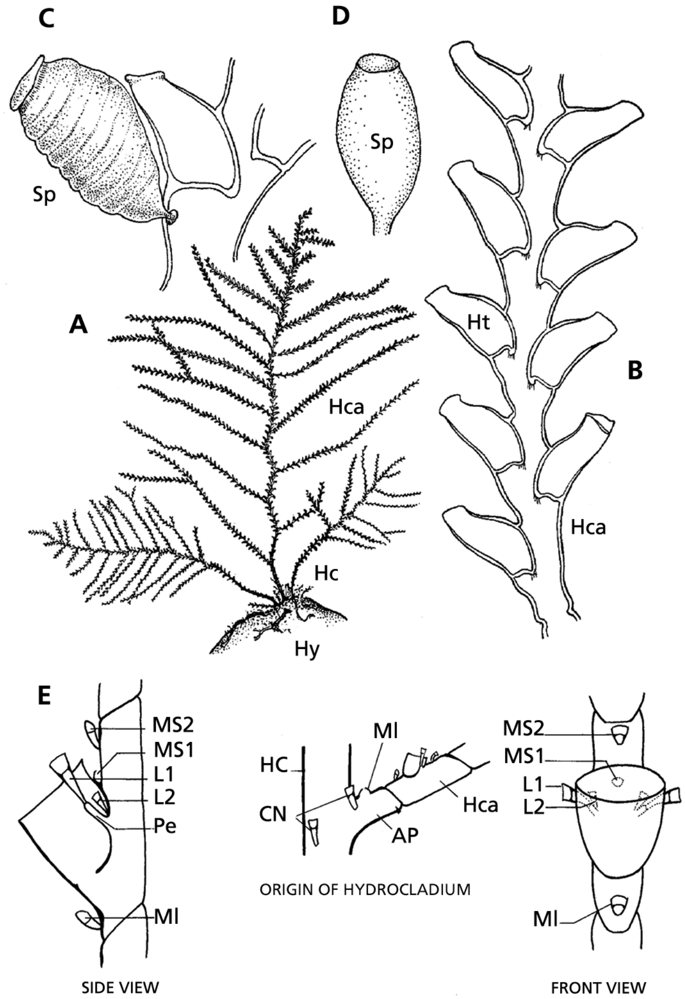


FIG. 4. Morphology of the hydroids, Leptomedusae. A-D, Sertulariidae: *Abietinaria abietina*. A, whole colony; B, part of hydrocladium; C, detail of hydrotheca and gonotheca; D, gonotheca. E, Plumulariidae, position of nematothecae: side view (left), origin of hydrocladium (middle), front view (right) (A-D after Leloup,1952; E after Millard, 1975). Ap = apophysis; CN = cauline nematotheca; Hc = hydrocaulus; Hca = hydrocladium; Ht = hydrotheca; Hy = hydrorhiza; L1 = first lateral nematotheca; L2 = second lateral nematotheca; MI = median inferior nematotheca; Ml = mamelon; MS1 = first median superior nematotheca; MS2 = second median superior nematotheca; Pe = pedicel; Sp = fixed sporosac.

FIG. 4. *Morphologie des hydroïdes, Leptomedusae. A-D, Sertulariidae :* Abietinaria abietina. *A, colonie entière ; B, partie d'un hydroclade ; C, détail d'une hydrothèque et d'une gonothèque ; D, gonothèque. E, Plumulariidae, position des nématothèques : vue latérale (à gauche), origine d'un hydroclade (au milieu), vue frontale (à droite) (A-D d'après Leloup,1952 ; E d'après Millard, 1975). Ap = apophyse ; CN = nématothèque caulinaire ; Hc = hydrocaule ; Hca = hydroclade ; Ht = hydrothèque ; Hy = hydrorhize ; L1 = première nématothèque latérale ; L2 = seconde nématothèque latérale ; MI = nématothèque mediane inférieure ; Ml = mamelon ; MS1 = première nématothèque mediane supérieure ; MS2 = seconde nématothèque médiane supérieure ; Pe = pédicelle ; Sp = sporosac fixé.*

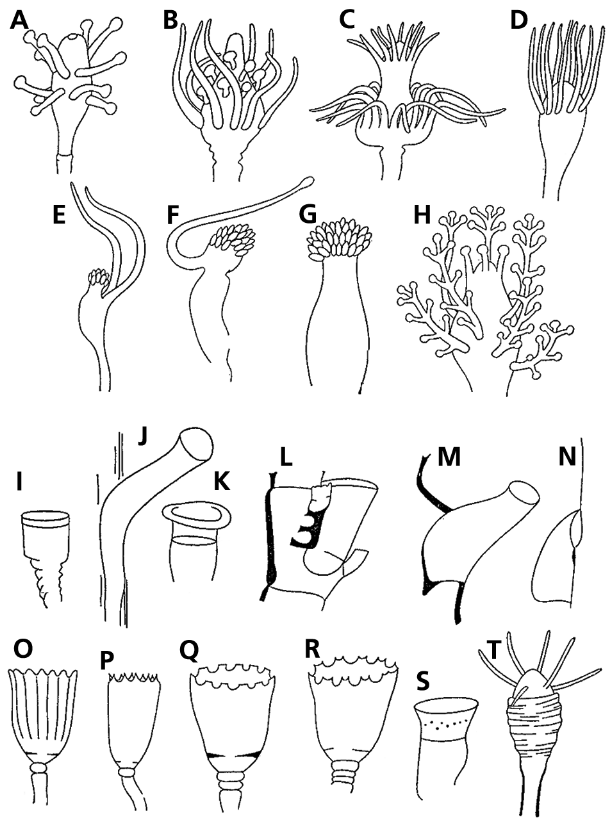


FIG. 5. Morphology of the hydroids. A-H, some of the different forms, arrangement and number of tentacles occurring in hydrozoan hydranths: A, *Coryne* with capitate tentacles; B, *Pennaria* with semifiliform and capitate tentacles; C, *Tubularia* with filiform and monilifiliform tentacles; D, *Hydractinia* with filiform tentacles; E, *Proboscidactyla* with two filiform tentacles and a hypostomial capitulum of cnidocysts; F, *Monobrachium* with one filiform tentacle and a hypostomial capitulum of cnidocysts; G, *Craspedacusta* without tentacles, with only a hypostomial capitulum of cnidocysts; H, *Cladocoryne* with ramified capitate tentacles. I-T, various forms of hydrothecae found in hydrozoan hydranths: I, J, K & S, tubular; O-R, bell-shaped; L-M, adnate; N, sunk; T, pseudohydrotheca; I, *Halecium speciosum*; J, *Grammaria stentor*; K, *Halecium labrosum*; L, *Cladocarpus formosus*; M, *Abietinaria abietina*; N, *Thuiaria laxa*; O, *Campanularia groenlandica*; P, *Clytia gracilis*; Q, *Gonothyraea loveni*; R, *Hartlaubella gelatinosa;* S, *Halecium halecinum*; T, Bougainviliidae or Pandeidae sp. (all after Naumov, 1969 modified).

FIG. 5. *Morphologie des hydroïdes. A-H, quelques unes des formes différentes, des arrangements et du nombre de tentacules existant chez les hydranthes : A, Coryne avec des tentacules capités ; B,* Pennaria *avec des tentacules semifiliformes et capités ; C,* Tubularia *avec des tentacules filiformes et monilifiliformes ; D,* Hydractinia *avec des tentacules filiformes ; E,* Proboscidactyla *avec deux tentacules filiformes un capitulum hypostomial de cnidocystes ; F,* Monobrachium *avec un tentacule filiforme et un capitulum hypostomial de cnidocystes ; G,* Craspedacusta *sans tentacules, mais avec exclusivement un capitulum hypostomial de cnidocystes ; H,* Cladocoryne *avec des tentacules ramifiés capités. I-T, différentes formes d'hydrothèque occurant chez les hydranthes : I, J, K & S, tubulaire ; O-R, en forme de cloche ; L-M, adnée ; N, enfoncée ; T, pseudohydrothèque. I,* Halecium speciosum *; J,* Grammaria stentor *; K,* Halecium labrosum *; L,* Cladocarpus formosus *; M,* Abietinaria abietina *; N,* Thuiaria laxa *; O,* Campanularia groenlandica *; P,* Clytia gracilis *; Q,* Gonothyraea loveni *; R,* Hartlaubella gelatinosa *; S,* Halecium halecinum *; T, Bougainviliidae ou Pandeidae sp. (d'après Naumov, 1969 modifié).*

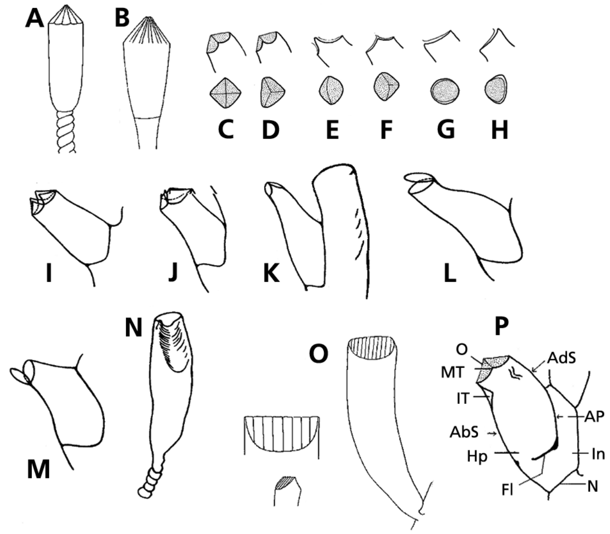


FIG. 6. Morphology of the hydroids. Leptomedusae: A-P, form and structure of operculum. A-B Campanulinidae. A, *Calycella syringa*, operculum formed by numerous flaps meeting in the centre, each flap seated in a hinged embayment and demarcated by basal prominent crease line; B, *Campanulina panicula*, operculum made by many segments which are simple inward folds of the distal part of the hydrotheca meeting centrally; C-H, Sertulariidae arrangement of marginal teeth and opercular valves (adcauline side on right). C, four valves and four teeth; D, three valves and three teeth; E, two valves and two teeth, adcauline larger; F, two valves and two teeth, abcauline larger; G, 1 valve , hinge adcauline; H, 1 valve, hinge abcauline. I-M, P, Sertulariidae; N, Lafoeidae; O, Tiarannidae. I, *Sertularella*, 4 valves; J, *Symplectoscyphus*, 3 valves; K, *Sertularia*, 2 valves; L, *Abietinaria*, 1 adcauline valve; M, *Thuiaria,* 1 abcauline valve; N, pseudo-operculum of *Lafoea dumosa*; O, gable–shaped operculum from *Stegopoma plicatile*; P, *Sertularella*: hydrothecal shape and structure (A, B & O after Cornelius, 1995; C-H after Millard, 1975; I-N after Naumov, 1969). AbS = abcauline side; Ads = adcauline side; Ap = adnate part; Fl = floor; Hp= hydropore; In = internode; It = internal tooth; MT = marginal tooth; N = node; O = operculum.

FIG. 6. *Morphologie des hydroïdes. Leptomedusae : A-P, forme et structure des opercules. A-B Campanulinidae. A,* Calycella syringa*, opercule formé par de nombreux segments triangulaires distincts convergent vers le centre, ces segments operculaires sont articulés dans des dépressions du bord marginal de la thèque avec lequel ils forment une nette ligne de démarcation ; B,* Campanulina panicula*, opercule formé de plusieurs segments qui sont de simple plis convergent de l'extrémité de la thèque et ne montrent aucune limite nette avec celle-ci ; C-H = Sertulariidae arrangement des dents marginales et des valves operculaires (côté adcaulinaire à droite). C, avec quatre valves et quatre dents ; D, avec trois valves et trois dents ; E, avec deux valves et deux dents, l'adcaulinaire la plus grande ; F, avec deux valves et deux dents, l'abcaulinaire la plus grande ; G, 1 avec une valve, charnière adcaulinaire ; H, 1 avec une valve, charnière abcaulinaire. I-M, P, Sertulariidae ; N, Lafoeidae ; O, Tiarannidae. I,* Sertularella*, 4 valves ; J,* Symplectoscyphus*, 3 valves ; K, Sertularia, 2 valves ; L,* Abietinaria*, 1 valve adcaulinaire ; M,* Thuiaria*, 1 valve abcaulinaire ; N, pseudo-opercule de* Lafoea dumosa *; O, opercule en forme de pignon de* Stegopoma plicatile *; P,* Sertularella *: forme et structure de l'hydrothèque. (A, B & O d'après Cornelius, 1995 ; C-H d'après Millard, 1975 ; I-N d'après Naumov, 1969). AbS = côté abcaulinaire ; Ads = côté adcaulinaire ; Ap = partie adnée ; Fl = plancher ; Hp= hydropore ; In = internode ; It = dent interne ; MT = dent marginale ; N = node ; O = opercule.*

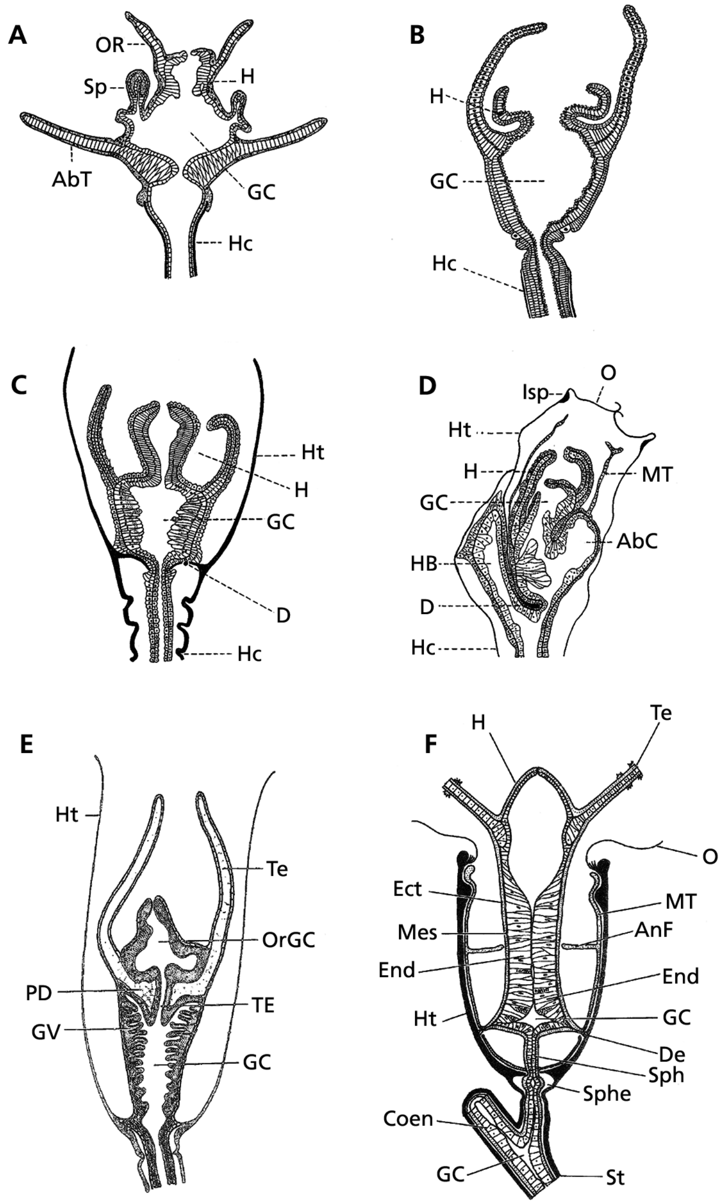


FIG. 7. Morphology of the hydroids, schematic longitudinal sections illustrating the structure of different gastrozooids. A, *Ectopleura* (*Tubularia*) *larynx*, showing the parenchymatic diaphragm or cushion under the aboral tentacle whorl, proper to most Tubulariidae. B, *Eudendrium ramosum*, pointing out the trumpet-shaped hypostome typical of the family Eudendriidae. C, *Laomedea flexuosa*, outlining the globose hypostome and buccal cavity distinctive of the Campanulariidae. D, *Sertularella crassicaulis*, a retracted hydranth showing the mantle and abcauline gastric caecum. E, *Bonneviella enterovillosa*, with an oral gastric cavity formed by an annular expansion of the tentacular bases. F, *Thyroscyphus marginatus*, presenting the mantle and its annular fold characteristic of the Thyroscyphidae. (A-B after Leloup, 1952; C-D after Kühn, 1913; E after Naumov, 1969; F after Harris, 1990: p. 233, fig. 11.6). AbC = abcauline gastric caecum; AbT= aboral tentacle; AnF = annular fold; Coen = coenosarc; D = diaphragm; De = desmocyte; Ect = ectoderm; End = endoderm; GC = gastric cavity; GV = gastric villosities; H = hypostome; HB = hydranth bud; Hc = hydrocaulus; Ht = hydrothecae; Isp = internal spine; Mes = mesoglea; MT = mantle; O = operculum; OR = oral tentacle; OrGC = oral gastric cavity; PD = parenchymatic diaphragm; Sp = sporosac; SpH = sphincter; Sphe = subhydrothecal spherule; St = stolon; Te = tentacle; TE = basal tentacular diaphragm.

FIG. 7. *Morphologie des hydroïdes, sections longitudinales schématiques illustrant la structure de différents gastérozoïdes. A,* Ectopleura *(*Tubularia*) larynx, hydranthe montrant le diaphragme parenchymatique ou coussin en-dessous des tentacules aboraux, propre à la plupart des Tubulariidae. B,* Eudendrium ramosum*, hydranthe montrant l'hypostome en forme de trompette caractéristisque de la famille des Eudendriidae. C,* Laomedea flexuosa*, hydranthe mettant en évidence l'hypostomee globuleux et la cavité buccale distinctifs des Campanulariidae. D,* Sertularella crassicaulis*, hydranthe rétracté montrant le manteau et le caecum abcaulinaire. E,* Bonneviella enterovillosa*, hydranthe présentant une cavité gastrique orale formé par l'expansion annulaire de la base des tentacules. F,* Thyroscyphus marginatus*, possédant le manteau et le plis ectodermique annulaire caractéristique des Thyroscyphidae. (A-B d'après Leloup, 1952 ; C-D d'après Kühn, 1914 ; E d'après Naumov, 1969 ; F d'après Harris, 1990 : p. 233, fig. 11.6). AbC = caecum abcaulinaire gastrique ; AbT = tentacule aboral ; AnF = plis annulaire ; Coen = coenosarc ; D = diaphragme ; De = desmocyte ; Ect = ectoderme ; End = endoderme ; GC = cavité gastrique ; GV = villosité gastrique ; H = hypostome ; HB = bourgeon d' hydranthe ; Hc = hydrocaule ; Ht = hydrothèque ; Isp = épine interne ; Mes = mésoglée ; MT = manteau ; O = opercule ; OR = tentacule oral ; OrGC = cavité gastrique orale ; PD = diaphragme parenchymatique ; Sp = sporosac ; SpH = sphincter ; Sphe = sphérule subhydrothècale ; St = stolon; Te = tentacule ; TE = diaphragme tentaculaire basal.*

and, in many species, the gonophores, and/or the nematophores develop from their surface. The hydrorhiza may or may not anastomose; internal thickenings of perisarc often occur in the hydrorhizae of some species, especially in those growing on flexible substrates such as algal thalli. Finally, under unfavourable conditions, the hydrorhizal tissues can become dormant, resorbing the soft tissues of the rest of the colony. Dormant tissues in the hydrorhizae survive until proper conditions prevail again, then regenerating new colonies.

Some hydroid species are solitary and devoid of both sphincter and hydrorhizal system; they fix to substrates by an adhesive gelatinous or glandular disk (*Hydra*, *Acaulis*, *Acauloides*, etc.) or by an anchoring system of rootlets (*Corymorpha*, *Candelabrum*, *Branchiocerianthus*, etc.).

Colonies growing horizontally, with hydranths arising separately and directly from a common hydrorhiza, with or without a pedicel, are termed stolonal, or hydrorhizal. Erect colonies grow vertically, producing upright hydrocauli bearing more than one hydranth.

Hydrocaulus. The hydrocaulus is the main stem of a hydroid colony, arising from the hydrorhiza. It is simple (often called pedicel) in solitary or stolonal forms and in some unbranched colonies (e.g., *Antennella*); in most colonial forms, stems build up complex and varied colony forms: arborescent, bushy, cymose, flabellate, flexuose, pinnate (alternate or opposite), plumose, racemose, spiral, straight (biseriate or uniseriate), whorled or verticillate etc. Hydranths can be either on the hydrocaulus (cauline hydranths) and on all the branches, or exclusively on the branches (terminal branches are called hydrocladia). The hydrocaulus perisarc is usually divided into segments, or internodes, by partitions or nodes. In some Leptomedusae polyps, each internode may give origin to nematothecae and to one or two hydrothecae or hydrocladia with great regularity, each arising from a projection shoulder or apophysis. The hydrocaulus may be composed of a single coenosarcal tube (monosiphonic) or comprising two or more coenosarc tubes (polysiphonic or fascicled) and form a composite stem structure, each tube retaining its perisarc. The coenosarcal cavity of the hydrocaulus is usually simple but it may be divided by endodermal canals in many Corymorphidae and Tubulariidae.

The form of erect colonies depends primarily on three main types of growth.

– Monopodial growth with terminal hydranth (raceme). The first hydranth on the hydrocaulus is terminal. Below this hydranth, there are a growth-zone and a budding zone. Buds are formed in the budding zone and the hydrocaulus grows above them, so that the youngest bud is at the base of the stem and the oldest at the top. Each bud then grows in a similar manner and several degrees of branching may occur, each branch topped by its oldest hydranth, e.g., most Anthomedusan colonies: *Eudendrium*, *Bougainvillia*, *Pennaria*.

– Monopodial growth with terminal growing point. There is no terminal hydranth, but the stem is topped by a growth-zone. Below the growth-zone is the budding zone, so that the oldest hydranth is at the base and the youngest one just below the tip, e.g., Plumulariidae, most Sertulariidae.

– Sympodial growth (cyme). The first hydranth is terminal, but it has no growth-zone and the stem does not elongate further. A budding zone below the hydranth produces a branch that grows beyond the first hydranth and is topped by the second hydranth. Continuation of this process produces a 'false axis' (the sympodium), which is in reality formed by successive branches (the podia), e.g., Haleciidae, Campanulinidae, and Campanulariidae. Such a stem is usually zigzag or geniculate.

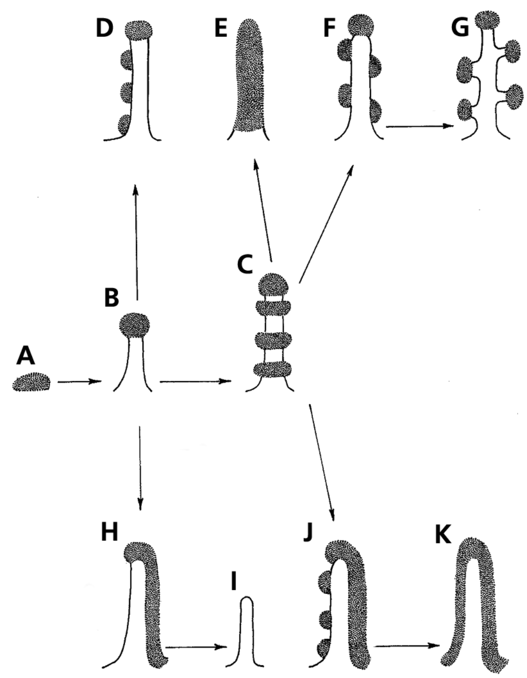


FIG. 8. Morphology of the hydroids, schema of the different types of tentacular structures and their evolution (after Prévot, 1959). A, primordial cnidocysts button. B, capitate. C, moniliform. D, semimoniliform. E, filiform. F, cateniform. G, ramified-capitate. H, semifiliform. I, acnide. J, monifiliform. K, pseudofiliform.

***FIG. 8.** Morphology des hydroïdes, schéma des différents types de structure tentaculaire et de leur évolution (d'après Prévot, 1959). A, bouton de cnidocystes primordial. B, capité. C, moniliforme. D, semimoniliforme. E, filiforme. F, caténiforme. G, ramifié-capité. H, semifiliforme. I, acnide. J, monifiliforme. K, pseudofiliforme.*

PERISARC

Stolons and stems. The perisarc surrounds the stolonal system, the hydrocaulus and the hydrocladia of almost all hydroids, with the exception of some epizootic, parasitic or pelagic species, which are naked. Perisarcal structures are complex, being mainly composed of chitin and proteins; they are sometimes associated with calcareous elements (coenosteum). The perisarc serves for attachment, protection and support.

Generally present as distinct tubes running over the substrate, the stolons forming the hydrorhiza are sometimes fused or anastomosed in a complex and dense network covered with the common ectoderm of the colony. The perisarc covering the upper face of the stolons may even disappear, the hydrorhiza being then covered by naked coenosarc. The basal perisarc layer may produce spines that penetrate the coenosarc, reaching the surface (e.g., Hydractiniidae). The genera *Hydrocorella* and *Janaria* are similar to *Hydractinia*, but their skeleton is impregnated with calcium carbonate, as it is in the Milleporidae and Stylasteridae. In some erect flabellate species of Anthomedusan polyps, such as *Solanderia* and *Pseudosolanderia*, the perisarc forms a strong internal chitinous skeleton supporting the colonies. Pelagic hydroids (e.g., *Margelopsis*, *Pelagohydra*, *Climacocodon*) are usually deprived of perisarc, however the Porpitidae have a chitinous float or pneumatophore of perisarcal origin. The ectoderm sometimes gives rise to numerous digitations or villosities perforating the periderm and taking part in respiratory exchanges.

The chitinous perisarc of Anthomedusae polyps generally does not grow over the level of the hydranth sphincter and the peduncle of medusa buds (except in *Halitiara*, *Merona*, *Rhysia* and *Trichydra*), but these are covered by a mucoproteinic periderm.

Hydrothecae. In Leptomedusae polyps, the chitinous perisarc forms a solid theca around the hydranths (the hydrotheca), the reproductive organs (the gonotheca), and the protective polyps, or dactylozooids (the dactylotheca or nematotheca).

The hydrothecae usually have a chitinous diaphragm or an annular thickening at their base, isolating the inner space between the coenosarc and the perisarc from the outside water. The diaphragm is perforated, to allow the passage of coenosarc. In the Syntheciidae, the Sertulariidae, and the Plumulariidae the hydranth has a definite floor of perisarc with an asymmetrical or symmetrical hole or hydropore. The hydrothecae may be sessile or supported by a pedicel; sessile ones can be partly or wholly adnate to their support by their adcauline side, the abcauline one remaining free. The hydrothecal opening can be either unprotected or provided with either a single lid or an operculum, closing over the contracted hydranth. The operculum may be composed of several triangular flaps sharply or not sharply demarcated from hydrotheca. The hydrothecal

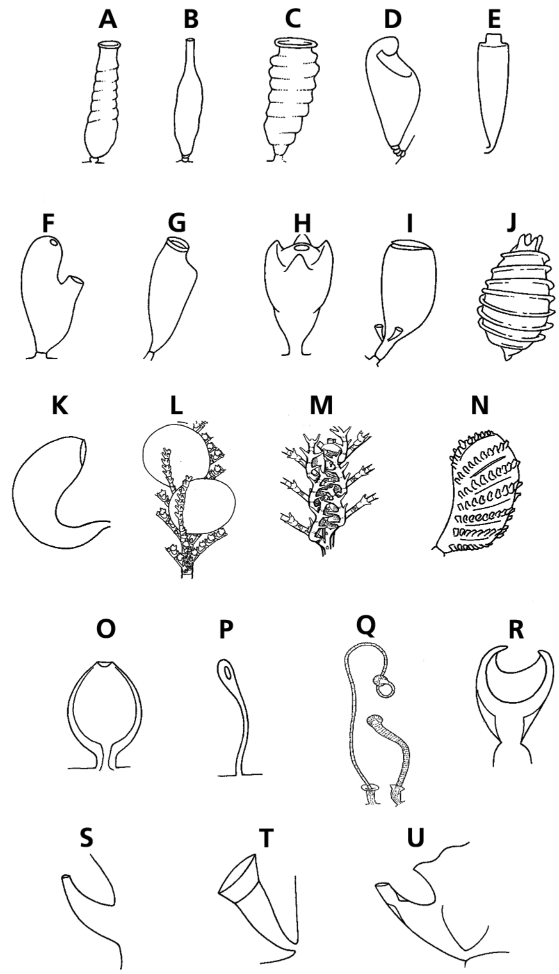


FIG. 9. Morphology of the hydroids. A-N, various forms of gonothecae: A, *Campanularia hincksi*; B, *Plumularia setacea*; C, *Clytia hemispherica*; D, *Laomedea calceolifera*; E, *Obelia* sp; F-G, *Halecium* sp; H, *Diphasia alata*; I, *Halopteris catharina*; J, *Symplectoscyphus tricuspidatus*; K, *Nemertesia* sp; L, *Macrorhynchia filamentosus*; M, *Cladocarpus valdiviae*; N, *Aglaophenia* sp. O-U, various forms of nematothecae: O, *Lovenella producta*; P, *Lafoeina tenuis*; Q, *Hydrodendron mirabilis*; R, *Halopteris catharina*; S, *Kirchenpaueria* sp; T, Plulmulariidae; U, *Aglaophenia* sp. (A-K, N-P, R-U after Cornelius, 1995; L, M & Q after Millard, 1975).

FIG. 9. *Morphologie des hydroïdes. A-N, différentes formes de gonothèques : A,* Campanularia hincksi *; B,* Plumularia setacea *; C,* Clytia hemispherica *; D,* Laomedea calceolifera *; E,* Obelia *sp ; F-G,* Halecium *sp ; H,* Diphasia alata *; I,* Halopteris catharina *; J,* Symplectoscyphus tricuspidatus ; *K,* Nemertesia *sp ; L,* Macrorhynchia filamentosus *; M,* Cladocarpus valdiviae *; N,* Aglaophenia *sp. O-U, différentes formes de nématothèques : O,* Lovenella producta *; P,* Lafoeina tenuis *; Q,* Hydrodendron mirabilis *; R,* Halopteris catharina *; S,* Kirchenpaueria *sp ; T,* Plulmulariidae *; U,* Aglaophenia *sp. (A-K, N-P, R-U d'après Cornelius, 1995 ; L, M & Q d'après Millard, 1975).*

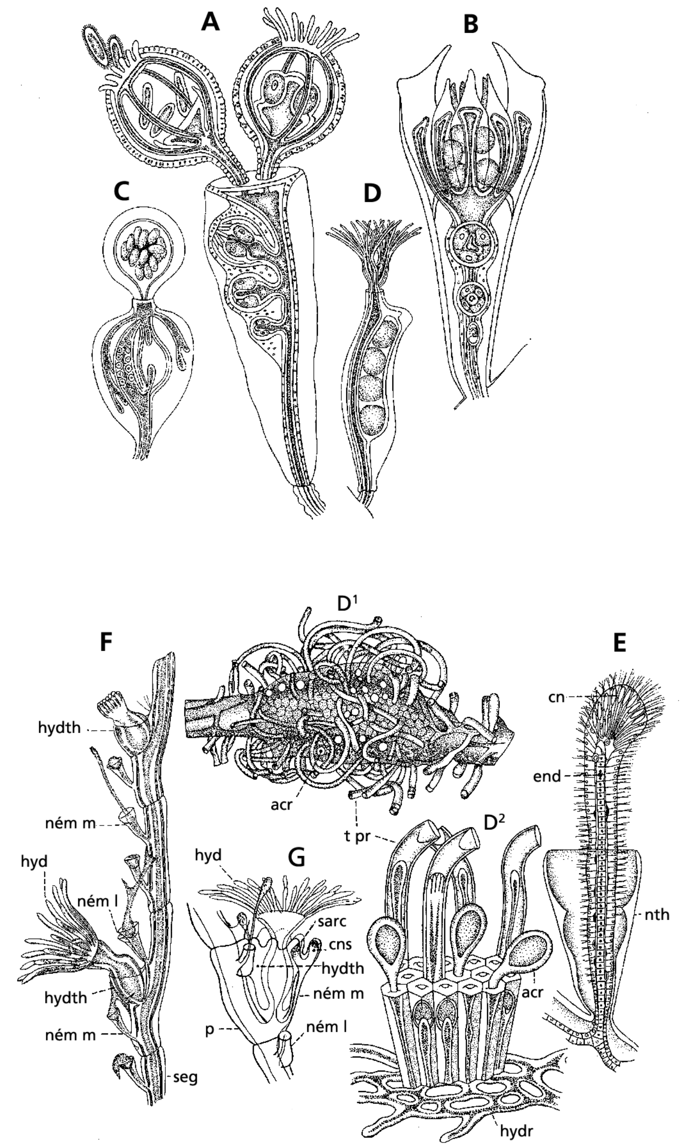


FIG. 10. Morphology of the hydroids, Leptomedusae. A-D, different types of gonothecae: A, meconodia of *Gonothyraea loveni*; B, marsupium of *Diphasia rosacea*; C, acrocysts of *Dynamena pumila*; D, gonangium with hydranths from *Halecium halecinum*. E-G, different types of protective organs: E, nematophore and nematotheca of a *Plumularia*; F, portion of a hydrocladium of *Nemertesia antennina* showing the lateral and median nematothecae; G, hydrocladium portion of an *Aglaophenia* sp. with details of the nematophores and nematothecae (all from Leloup, 1952). acr = acrocyst; cn = cnidocyst; cns = cnidostyle; D1 = coppinia of Lafoeidae; D2 = detail of a coppinia; end = endoderm; hyd = hydranth; hydr = hydrorhiza; hydth = hydrotheca; ném l = lateral nematotheca; ném m = median nematotheca; nth = nematotheca; p = perisarc; sarc = sarcostyle; seg = hydrocladium segment; t pr = tubes of the protective polyps.

***FIG. 10.** Morphologie des hydroïdes, Leptomedusae. A-D, différents types de gonothèques : A, méconodie de* Gonothyraea loveni ; *B, marsupium de* Diphasia rosacea ; *C, acrocyste de* Dynamena pumila ; *D, gonange avec hydranthe d'*Halecium halecinum. *E-G, différents types d'organes protectifs : E, nématophore et nématothèque d'une* Plumularia ; *F, portion d'hydroclade de* Nemertesia antennina *montrant les nématothèques latérales et médianes ; G, portion d'hydroclade d'*Aglaophenia *sp. montrant le détail des nématophores et nématothèques (d'après Leloup, 1952). acr = acrocyste ; cn = cnidocyste ; cns = cnidostyle ; D1 = coppinia de Lafoeidae ; D2 = détail d'une coppinia ; end = endoderme ; hyd = hydranthe ; hydr = hydrorhize ; hydth = hydrothèque ; ném l = nématothèque latérale ; ném m = nématothèque médiane ; nth = nématothèque ; p = périsarc ; sarc = sarcostyle ; seg = segment hydrocladial ; t pr = tubes des polypes protectifs.*

rim may be cusped or even. The shape of cusps is often species-diagnostic. The hydrothecae often present internal cusps and one or more intrathecal septa or ridges. Hydrothecae may have alternate or opposite arrangement on stem and branches; single or in pairs, sometimes they are said subalternate or subopposite when there is an intermediate arrangement. Hydrothecae often regenerate, the new hydrotheca developing within the older one, repetition of this process is common in some families (e.g., Haleciidae, some Lafoeidae, some Sertulariidae).

The presence of a hydrotheca is a useful feature to identify Antho- and Leptomedusae polyps, respectively known as athecate and thecate. Such identification, however, is not always easy. On the one hand,some Anthomedusae polyps are provided with a pseudohydrotheca, not homologous to perisarcal hydrothecae but similar in function (*Thamnostoma russelli*, *Bimeria vestita*, *Bougainvillia muscus*, *Leuckartiara octona*, *Clathrozoella drygalskii* etc.). On the other hand, many Leptomedusae polyps have very reduced thecae or even lack them (e.g., *Halecium, Melicertum octocostatum*, *Eutima gracilis*, *Eutima gegenbauri*, *Helgicirrha schulzei*, *Eugymnanthea*, etc.).

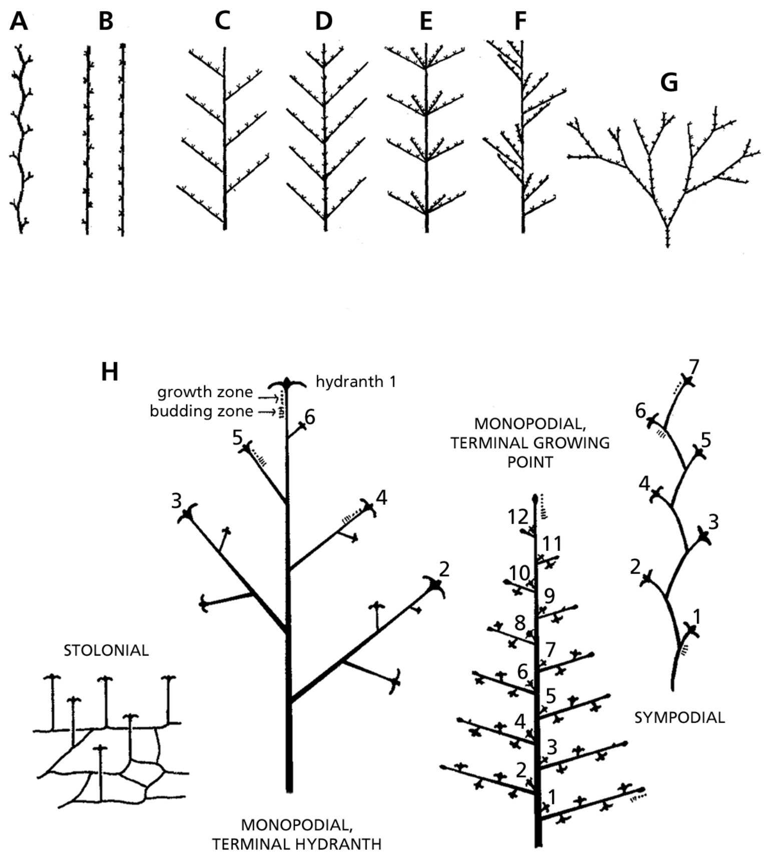


FIG. 11. Morphology of the hydroids. A-G, type of stem and branching: A, geniculate; B, straight; C, alternate; D, opposite; E, whorled; F, spiral; G, dichotomous. H, form of growth and colony formation (after Millard, 1975).

FIG. 11. *Morphologie des hydroïdes. A-G, type d'hydrocaule et de ramifications : A, géniculé ; B, droit ; C, alterne ; D, opposé ; E, verticillé ; F, spiral ; G, dichotome. H, forme de croissance et de formation des colonies (d'après Millard, 1975).*

In certain colonial forms (*Limnocnida*, *Craspedacusta*), the perisarc is reduced to the basal region, and is even lacking in some solitary species such as *Hydra* and *Protohydra*. In such cases, the hydranths are surrounded only by a mucoproteinic periderm.

Nematothecae. The nematothecae contain the protective nematophores, they may be sessile or pedicellate, one-chambered (monothalamic) or two-chambered (bithalamic), movable or immovable. They are either irregularly arranged on the colony or grouped in a very distinct manner around the hydrothecae, as in the Aglaopheniidae, the Halopterididae, the Kirchenpaueriidae, and the Plumulariidae. In these families, each hydrotheca has typically one basal (median inferior) nematotheca, and two lateral ones, one on each side. There may also be one or two nematothecae above the hydrotheca (superior nematothecae) and some on the athecate segments of the hydrocauli, as well as on the hydrocaulus (cauline nematothecae) and hydrorhiza.

Gonothecae. The gonothecae are the chitinous structures surrounding the blastostyles or the gonophores, they are typically closed on top, until the developing embryos are ready to be released, they are often operculate. In some Leptomedusae with fixed gonophores, the gonothecae have modified structures protecting the planulae until liberation, the "marsupium", formed by apical gonothecal expansions enveloping the planulae and forming an incubating chamber (e.g., some *Diphasia* and *Thuiaria*). The gonothecae may be simple or aggregated either into compound bodies "coppinia", "glomulus" or "scapus", or protected by special outgrowths formed by the hydrocladia or modified hydrocladia: phylactocarps, corbulae.

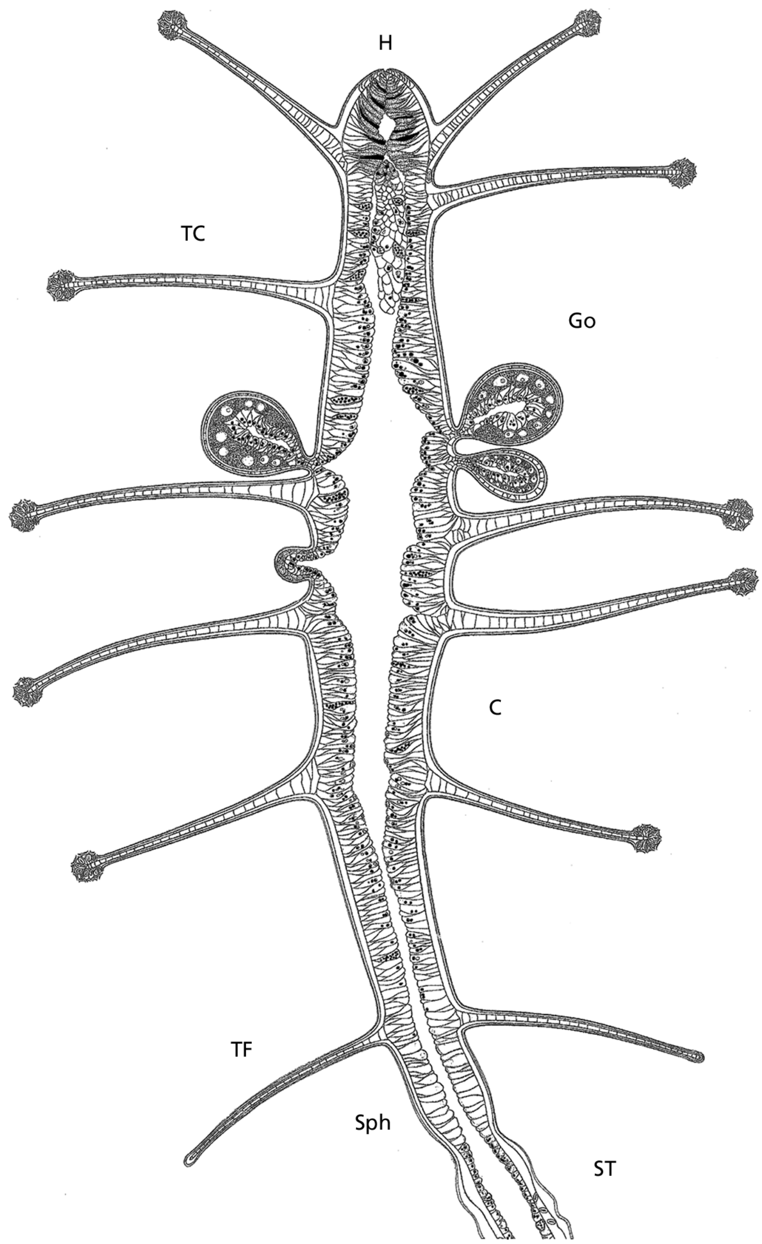


FIG. 12. Histology of the hydroids, schema of a longitudinal section of *Coryne filiformis*, Anthomedusae. C = gastric column; Go = gonophore; H = hypostome; Sph = sphincter; St = stolon; Tc = capitate tentacle; Tf = filiform tentacle.

FIG. 12. *Histologie des hydroïdes, schéma d'une section longitudinale de* Coryne filiformis, *Anthomedusae. C = colonne gastrique ; Go = gonophore ; H = hypostome ; Sph = sphincter ; St = stolon ; Tc = tentacule capité ; Tf = tentacule filiforme.*

POLYMORPHISM

Hydroid colonies are noted for their polymorphism. In addition to the nutritive polyps (hydranths or gastrozooids) they often include: special sexual polyps, the gonozooids, bearing medusae or medusoids in various stages of regression; protective polyps usually lacking mouth and largely provided with cnidocysts, the dactylozooids or machozooids (of several types: tentaculozooids, spiralozooids, nematophores or sarcostyles); protective individuals not provided with cnidocysts, but constituting chitinous spines, the acanthozooids.

HISTOLOGY OF POLYPS (FIGS 12-23)

The body wall of polyps is formed, as in all Cnidaria, by two clearly distinct epithelial layers (diploblastic): the ectoderm and the endoderm, separated by a supporting non-cellular layer, the mesoglea.

ECTODERM

The ectoderm is composed of vacuolated cells of different shapes (e.g., flattened, cubical or cylindrical) whose basal part, applied to the mesoglea, generally contains a bundle of longitudinal smooth muscle fibers: the epithelio-muscular cells. Muscle fibers are particularly developed in the region of the sphincter. The distal part of the ectodermal cells is sometimes either ciliated or flagellated, or may contain granulations playing a role in the formation of either the periderm or the perisarc (*Hydra*, *Pennaria*, *Clava*, etc.). These granulations, or inclusions, are well developed at the level of the adhesive basal part of solitary polyps (*Hydra*, *Acauloides*, etc.).

In certain genera of Corynoidea the ectoderm of the hypostomial apical region differentiates glandular cells containing mucous secretions, particularly involved

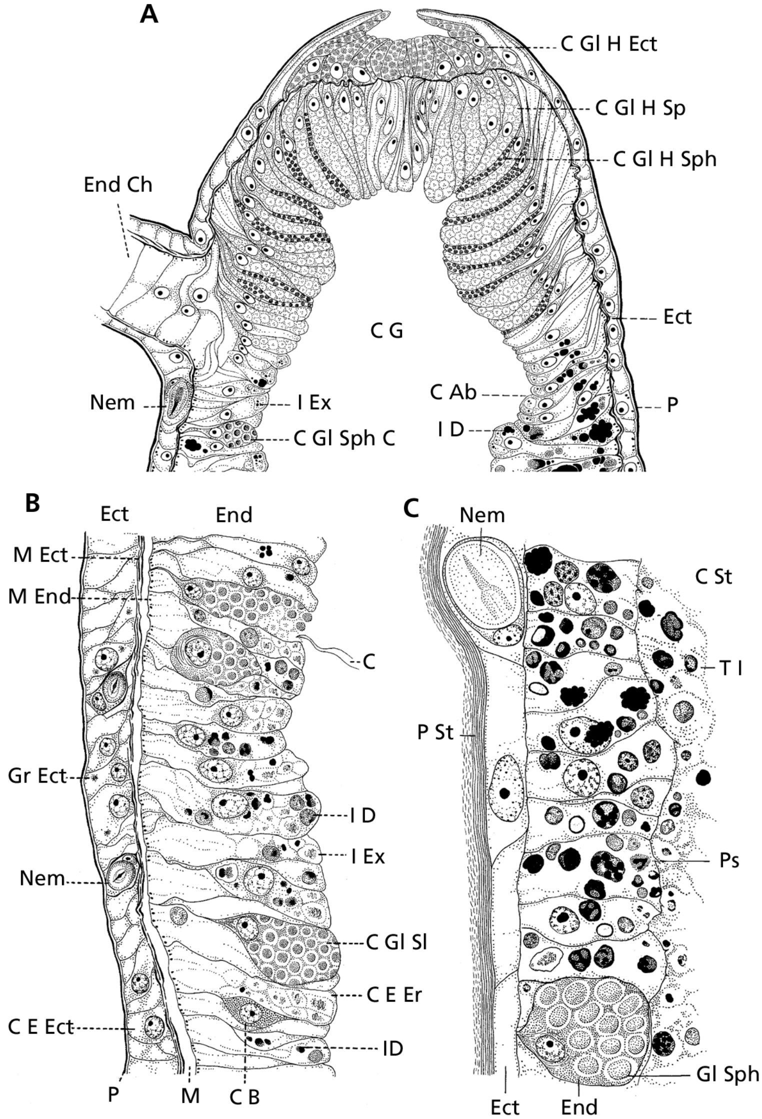


FIG. 13. Histology of the hydroids, illustration of longitudinal histological sections of the different parts of a hydranth of Anthomedusae. A, section of the hypostomial region, *Staurocladia portmanni*. B, section of a portion of the gastric column, *Cladocoryne floccosa*. C, section of a portion of the stolon, *Dipurena halterata* (Bouillon, original figures). C = cilia; C Ab = digestive cell; C B = basal cell; C E Ect = ectodermal epitheliomuscular cell; C E Er = absorbing epitheliomuscular endodermic cell; C G = gastric cavity; C Gl H Ect = ectodermal spherulous hypostomial gland cell; C Gl H Sp = endodermal spumous hypostomial gland cell; C Gl H Sph.= endodermal spherulous hypostomial gland cell; C Gl Sph C = endodermal stomacal spherulous gland cell; C St = cavity of the stolonal system; Ect = ectoderm; End = endoderm; End Ch = chordal tentacular endoderm; Gl Sph = spherulous gland cell; Gr Ect = ectodermal granulation; I D = digestive inclusion; I Ex = excretory inclusion; M = mesoglea; M Ect = ectodermal longitudinal muscle; M End = endodermal circular muscle; Nem = cnidoblast; P = periderm; Ps = pseudopodium; P St = stolonar perisarc; T I = ingested tissues.

FIG. 13. *Histologie des hydroïdes, illustrations de sections histologiques longitudinales de différentes parties d'un hydranthe d'Anthomedusae. A, section de la région hypostomiale,* Staurocladia portmanni. *B, section d'une portion de la colonne gastrique,* Cladocoryne floccosa. *C, section d'une portion du stolon,* Dipurena halterata *(Bouillon, figures originales). C = cil ; C Ab = cellule absorbante digestive ; C B = cellule basale ; C E Ect = cellule ectodermique épithéliomusculaire; C E Er = cellule épithéliomusculaire endodermique absorbante ; C G = cavité gastrique ; C Gl H Ect = cellule glandulaire sphéruleuse ectodermique de l'hypostome ; C Gl H Sp = cellule glandulaire spumeuse endodermique de l'hypostome ; C Gl H Sph = cellule glandulaire sphéruleuse endodermique de l'hypostome ; C Gl Sph C = cellule sphéruleuse stomacale endodermique ; C St = cavité du système stolonal ; Ect = ectoderme ; End = endoderme ; End Ch = endoderme tentaculaire chordal ; Gl Sph = cellule glandulaire sphéruleuse ; Gr Ect = granulation ectodermique ; I.D. = inclusion digestive ; I. Ex. = inclusion excrétrice ; M. = mésoglée ; M.Ect. = muscle ectodermique longitudinal ; M.End. = muscle endodermique circulaire ; Nem. = cnidoblaste ; P. = périderme ; Ps. = pseudopodes ; P.St. = périsarc stolonaire ; T.I. = tissu ingéré.*

in digestion. Those cells, called ectodermal hypostomial mucous gland cells, (present in: *Dipurena*, *Cladonema*, *Eleutheria*, *Staurocladia*) have not to be confused with normal epidermal cells thickenings. Some Sertulariidae and the Thyroscyphidae have a thin layer of ectoderm lining the interior of the hydrothecae: the mantle, or ectodermal supporting lamella or "haftlamella". The mantle is usually issued from the base of the hydranth and may completely wrap around withdrawn hydranths when forming a roofing plate. The mantle may present specialised regions of attachment to the hydranth and to the hydrotheca. In some genera, a medio-basal annular lamella, the annular ectodermal fold, may link, like a diaphragm, the mantle to the hydranth body; in other genera, the abcauline caecum region is attached to the mantle directly or by a cellular extension. In several genera, the distal part of the mantle may contain cnidocysts, often in large aggregations (= some kind of nematophores?). The ligula of *Sertularia ligulata* and *Salacia laxa*, for instance, is presumably a mantle differentiation.

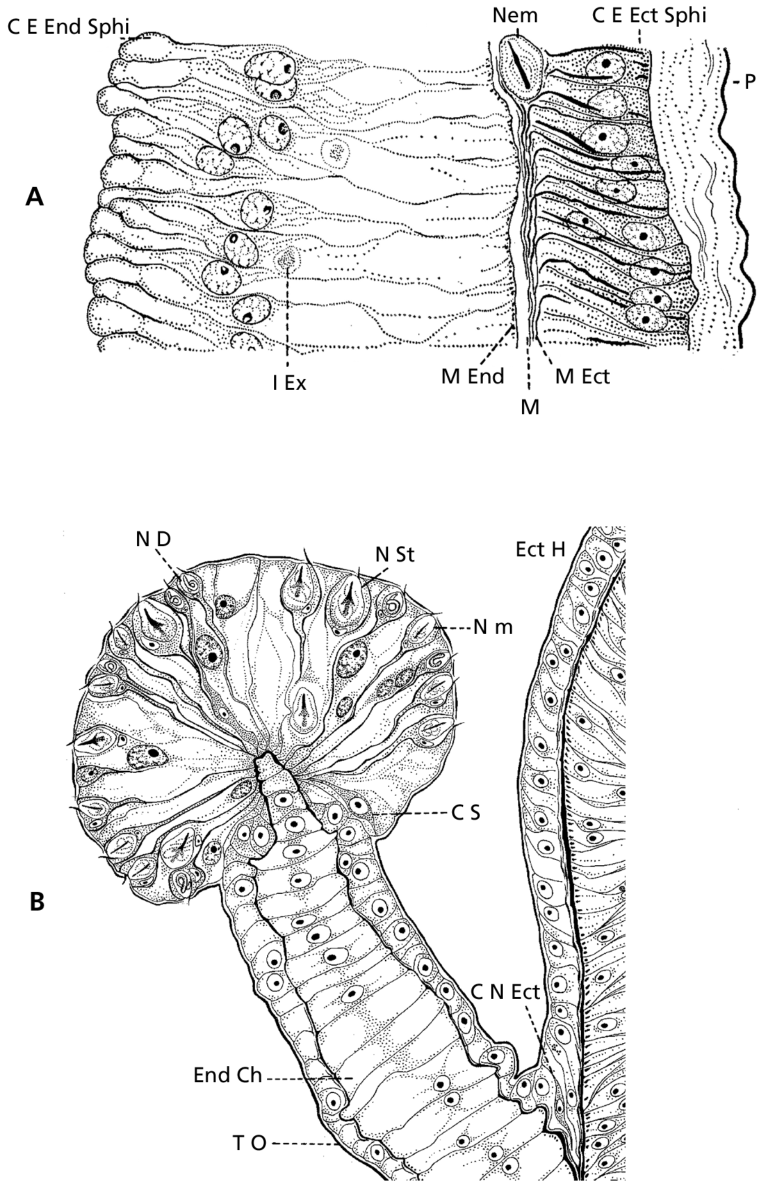


FIG. 14. Histology of the hydroids, illustration of longitudinal histological sections of the different parts of a hydranth of Anthomedusae. A, drawing of a portion of a hydranth of *Coryne muscoides* at the level of the sphincter. B, longitudinal section through a capitate tentacle of *Pennaria disticha* (A after Bouillon, 1968: p. 99, fig. 2; B Bouillon original). C E ECT Sphi. = ectodermal epitheliomuscular cell of the sphincter; C E End Sphi. = endodermal epitheliomuscular cell of the sphincter; C N Ect = ectodermal nerve cell; C S = ectodermal sensory cell; Ect H; = hypostomial ectoderm; End Ch = chordal tentacular endoderm; I Ex = excretory inclusion; M = mesoglea; M Ect = ectodermal longitudinal muscle; M End = endodermal circular muscle; N D = desmoneme; Nem = cnidoblast; N m = microbasic eurytele; N St; = stenotele; P = perisarc; T O = oral tentacle.

FIG. 14. *Histologie des hydroïdes, illustrations de sections histologiques longitudinales de différentes parties d'un hydranthe d'Anthomedusae. A, dessin d'une portion d'hydranthe de* Coryne muscoides *au niveau du sphincter. B, section longitudinale d'un tentacule capité de* Pennaria disticha *(A d'après Bouillon, 1968 : p. 99, fig. 2 ; B Bouillon original). C E ECT Sphi = cellule épithéliomusculaire ectodermique du sphincter ; C E End Sphi = cellule épithéliomusculaire endodermique du sphincter ; C N Ect = cellule nerveuse ectodermique ; C S = cellule sensorielle ectodermique ; Ect H ; = ectoderme hypostomial ; End Ch = endoderme tentaculaire chordal ; I Ex = inclusion excrétrice ; M = mésoglée ; M Ect = muscle ectodermique longitudinal ; M End = muscle endodermique circulaire ; N D = desmonème ; Nem = cnidoblaste ; N m = eurytèle microbasique ; N St ; = sténotele ; P = périsarc ; T O = tentacule oral.*

Interspersed between the ectoderm cells covering the hydranth, several categories of cells are observed:

Stinging cells. This section applies to all hydrozoan morphs and not only to polyps. Stinging cells, or cnidocytes, are diagnostic of the Cnidaria; they are usually in the ectoderm, at different stages of development, from very young cnidoblasts to cnidocytes containing functional cnidocysts. Most of the cytoplasm of a mature cnidocyte is occupied by the capsule or cnidocyst with its apical differentiation, the operculum. The wall of the capsule is continuous with the inward-invaginated cnidocyst tube. The cnidocyst tube can be either of uniform diameter or differentiated into a more or less dilated butt and a filament, each of these elements being either unarmed or armed with spines of variable size and shape. The capsule of stomocnide cnidocysts contains also a paralyzing and often venomous fluid, the capsular content, which is ejected through the filament tip when the cnidocyst discharges. Cnidocysts discharge occurs by eversion.

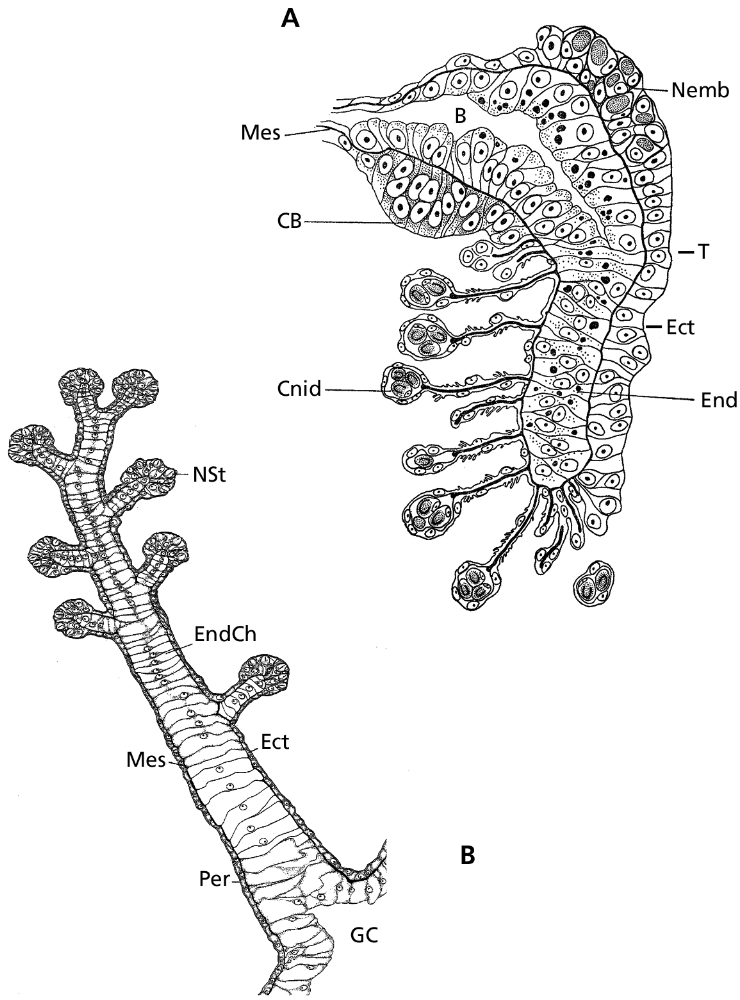


FIG. 15. Histology of the hydroids, illustration of longitudinal histological sections of the different parts of Anthomedusae. A, longitudinal section through a marginal tentacle of *Teissiera milleporoides* medusa showing the structure of the cnidophores. B, longitudinal section through a ramified-capitate tentacle of *Cladocoryne floccosa* (A after Bouillon, 1974; B Bouillon original). B = marginal bulb; CB = embryonic cells; Cnid = cnidophore; Ect = ectoderm; End = endoderm; End Ch = chordal tentacular endoderm; CG = gastric cavity; Mes = mesoglea ; Nemb = cnidoblast; Per = periderm; T = tentacle.

FIG. 15. *Histologie des hydroïdes, illustrations de sections histologiques longitudinales de différentes parties d'Anthomedusae. A, section longitudinale d'un tentacule marginal d'une méduse de* Teissiera milleporoides *montrant la structure des cnidophores. B, section longitudinale d'un tentacule ramifié-capité de* Cladocoryne floccosa *(A d'après Bouillon, 1974 ; B Bouillon original). B = bulbe marginal ; CB = cellule embryonnaire ; Cnid = cnidophore ; Ect = ectoderme ; End = endoderme ; End Ch = endoderme tentaculaire chordal ; GC = cavité gastrique ;Mes = mésoglée ; Nemb = cnidoblaste ; Per = périderme ; T = tentacule.*

A complex network of fibrils, forming a kind of basketwork, generally surrounds the capsule. The cnidocyst displaces the nucleus of the cnidocyte either toward the base of the cell, or laterally. In the Capitata, for example, the most basal region of the cnidocyts, or cnidopod, contains a bundle of fibrils, connecting the capsule to the mesoglea. The apical region of the cnidocyte bears an eccentric, birefringent, bristle-like expansion, the cnidocil, set in a tubular chimney; the structure of the cnidocil recalls that of a modified flagellum. The structure, function, and formation of the cnidocil complex remain to be determined.

Some nudibranchs, turbellarian flatworms, ctenophores, and priapulids may accumulate numerous ingested cnidocysts (cleptocnidae) in their own tissues or in specialized structures (cnidosacs) and apparently use them for defence.

The cnidome is the cnidocyst complement of each species. Cnidomes usually comprise from 1 to 4 cnidocyst types, all specimens of the same species typically have the same cnidome. It is often the case, however, that polyps and medusae of the same species have different cnidomes.

The list hereunder, modified after Mariscal (1974), describes the discharged stages of the most important cnidocysts, (see also Bouillon *et al.* 1986; 1988a; Östman 2000). The undischarged capsules may in some cases give also useful information and serve as a taxonomic character (see below, heteronemes, Bouillon *et al.* 1988) (Figs 19, 20).

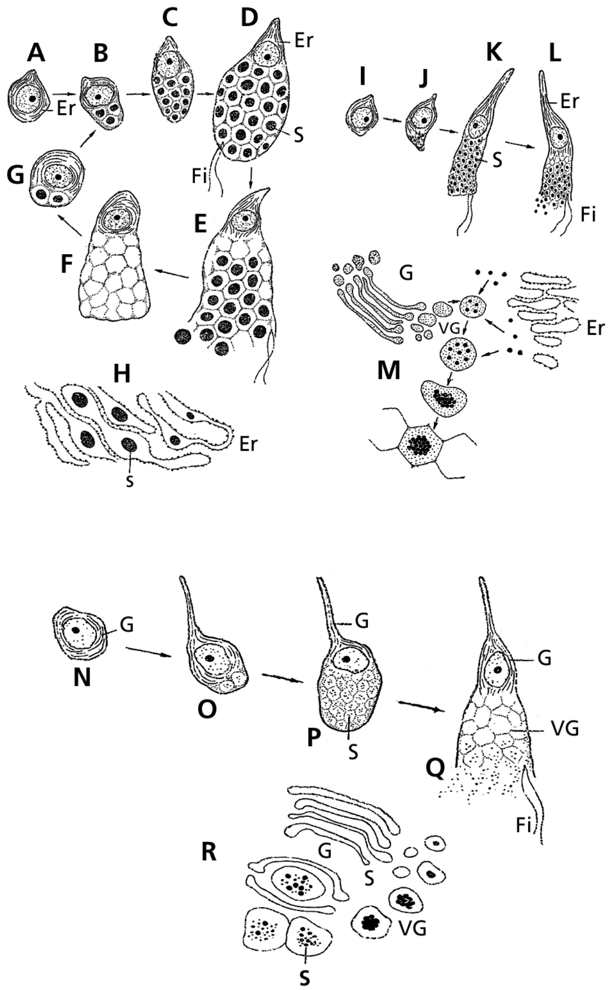


FIG. 16. Histology of the hydroids, diagrammatic figures illustrating the development and structure of the hypostomial and stomacal gland cells (the structure and development of the gland cells hereunder described are identical in the medusa stage). A-H, evolution of the glandular stomacal spherulous cells: A, embryonic cell; B-C, formation of the first secretions; D, mature glandular cell; E, glandular cell discharging its secretions; F, empty glandular cell; G, glandular cell starting a next cycle of secretion; H, detail of the formation of secretory granules inside the ergastoplasm or endoplasmic reticulum. I-M, development of the glandular spherulous hypostomial or oral cells: I, embryonic cell; J, formation of the first secretions; K, mature glandular cell; L, glandular cell discharging its secretions; M, detail of the formation of the secretion material in the endoplasmic reticulum and its concentration into vacuoles of Golgi system. N-R, development of the glandular spumous hypostomial cells: N, embryonic cell; O, formation of the first secretions; P, mature glandular cell; Q, glandular cell discharging its secretions; R, detail of the formation of the secretions inside the Golgi system (after Bouillon, 1995a: p. 121, fig. 46 A, B; p. 123, fig. 47). Er = endoplasmic reticulum; Fl = flagella; S = secretion; G = Golgi; VG = Golgi vacuole.

FIG. 16. *Histologie des hydroïdes, figures diagrammatiques illustrant le développement et la structure des cellules glandulaires hypostomiales et stomacales (la structure et le développement des cellules glandulaires décrites ci-dessous sont identiques pour le stade méduse). A-H, évolution des cellules glandulaires sphéruleuses stomacales : A, cellule embryonnaire ; B-C, formation des premières sécrétions ; D, cellule glandulaire mature ; E, cellule glandulaire déchargeant ses sécrétions ; F, cellule glandulaire vidée ; G, cellule glandulaire commençant un nouveau cycle de sécrétions ; H, détail de la formation d'un granule de sécrétions au sein de l'ergastoplasme ou reticulum endoplasmique. I-M, développement des celules glandulaires sphéruleuses hypostomiales ou orales : I, cellule embryonnaire ; J, formation des premières sécrétions ; K, cellule glandulaire mature ; L, cellule glandulaire déchargeant ses sécrétions ; M = détail de la formation du matériel de sécrétion dans le reticulum endoplasmique et sa concentration dans les vacuoles du système de Golgi. N-R, développement des cellules glandulaires spumeuses hypostomiales : N, cellule embryonnaire ; O, formation des premières sécrétions ; P, cellule glandulaire mature ; Q, cellule glandulaire déchargeant ses sécrétions ; R, détail de la formation des sécrétions dans le système de golgi (d'après Bouillon, 1995 : p. 121, fig. 46 A, B ; p. 123, fig. 47). Er = reticulum endoplasmique; Fl = flagelle ; S = sécrétion ; G = Golgi ; VG = vacuole golgienne.*

1 **ASTOMOCNIDAE**: thread closed at the tip
1.1 RHOPALONEMES: thread club-shaped and much greater in volume than the capsule
1.1.1 Anacrophores: thread without an apical projection*
1.1.2 Acrophores: thread with an apical projection*

1.2 SPIRONEMES: thread not club-shaped, generally forming a spiral coil distally
1.2.1 Haplonemes: thread without a well-defined shaft
1.2.1.1 Desmonemes: thread forming a corkscrew-like coil*
1.2.2 Heteronemes: thread with a well-defined shaft
1.2.2.1 Rhopaloides: shaft of unequal diameter
1.2.2.1.1 Euryteleloids: shaft dilated distally
1.2.2.1.1.1 Microbasic: shaft short, less than three times capsule length
1.2.2.1.1.1.1 Spiroteles: thread forms a spiral coil distally, 3 strong spines*
1.2.2.1.1.1.2 Aspiroteles: no thread beyond the shaft, 3 strong spines*

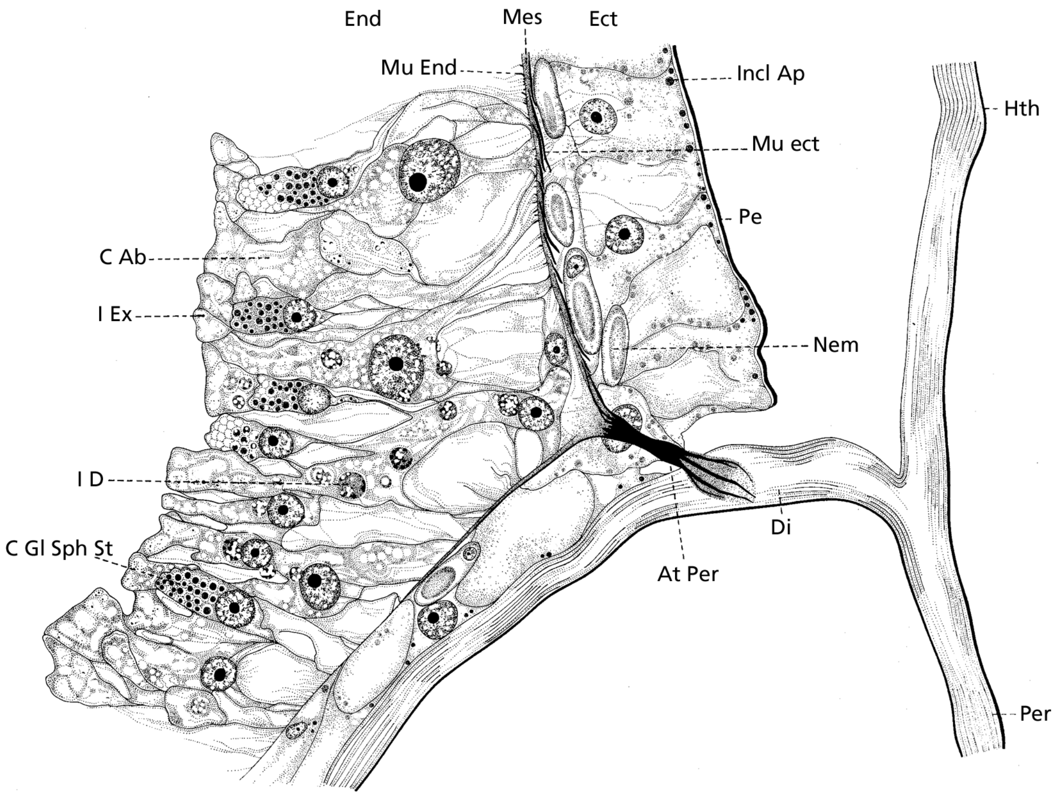


FIG. 17. Histology of the hydroids, illustration of a longitudinal histological section of the basal portion of a hydranth of *Laomedea flexuosa*, Leptomedusae, showing the structure of a desmocyte (after Bouillon & Lévi,1971). At Per = desmocyte; C Ab = digestive cell; C Gl Sph St = stomacal spherulous gland cell; Di = diaphragm; Ect = ectoderm; End = endoderm; Hth = hydrotheca; I D = digestive inclusion; I Ex = excretory inclusion; Incl Ap = apical inclusion; Mes = mesoglea; Mu Ect = ectodermal longitudinal muscle; Mu End. = endodermal circular muscle; Nem = cnidoblast; Pe = periderm; Per = perisarc.

FIG. 17. *Histologie des hydroïdes, illustration d'une section histologique longitudinale de la portion basale d'un hydranthe de* Laomedea flexuosa, *Leptomedusae, montrant la structure d'un desmocyte (d'après Bouillon & Lévi, 1971). At Per = desmocyte ; C Ab = cellule digestive ; C Gl Sph St = cellule glandulaire sphéruleuse stomacale ; Di = diaphragme ; Ect = ectoderme ; End = endoderme ; Hth = hydrothèque ; I D = inclusion digestive ; I Ex = inclusion excrétrice ; Incl Ap = inclusionapicale ; Mes = mésoglée ; Mu Ect = muscle ectodermique longitudinal ; Mu End = muscle endodermique circulaire ; Nem = cnidoblaste ; Pe = périderme ; Per = périsarc.*

2 **STOMOCNIDAE**: most thread open at the tip
2.1 HAPLONEMES: thread without a well-defined shaft
2.1.1. Isorhizas: thread with uniform diameter
2.1.1.1 Atrichous: thread without well-developed spines
2.1.1.2 Basitrichous: thread with well-developed spines only at base
2.1.1.3 Merotrichous: thread with well-developed spines on the intermediate portion only*
2.1.1.4 Apotrichous: thread with well-developed spines on the distal portion only *
2.1.1.5 Holotrichous: thread with well-developed spines along whole length
2.1.2. Anisorhizas: thread slightly dilated toward base*
2.1.2.1 Atrichous: thread without well-developed spines*
2.1.2.2 Homotrichous: thread spiny throughout, spines all of equal size*
2.1.2.3 Heterotrichous: thread spiny throughout, spines larger at base of thread*

2.2 HETERONEMES: thread with a well-defined shaft, visible in undischarged capsule
2.2.1 Rhabdoides: shaft cylindrical, of the same diameter throughout

2.2.1.1. Mastigophores: thread continues beyond the shaft
2.2.1.1.1. Microbasic: shaft short, in undischarged cnidocysts almost of same length than capsule, usually straight
2.2.1.1.1.1 Microbasic b-mastigophore: shaft tapers gradually into thread
2.2.1.1.1.2 Microbasic p-mastigophore: shaft tapers abruptly into thread, V-shaped notch prominent at base of unfired shaft
2.2.1.1.2 Macrobasic: shaft long, more than two and a half time capsule length, in undischarged cnidocysts shaft much longer than capsule length, horseshoe-shaped or wind up in several loops *
2.2.1.2 Amastigophores: no thread beyond the shaft **
2.2.1.2.1 Microbasic: shaft short, less than two and a half times capsule length**
2.2.1.2.2 Macrobasic: shaft long, more two and an half times capsule length, undischarged shaft much longer than capsule length**

2.2.2 Rhopaloides: shaft of unequal diameter
2.2.2.1 Mesoteles: shaft spindle-shaped, devoid of spines, no thread beyond the shaft
2.2.2.2 Euryteles: shaft dilated distally, thread continues beyond the shaft
2.2.2.2.1 Microbasic: shaft short, less than two and a half times capsule length, in undischarged cnidocysts almost of same length as capsule, usually straight
2.2.2.2.1.1 Homotrichous: spines of shaft all of same size*
2.2.2.2.1.2 Heterotrichous: spines of shaft of unequal size
2.2.2.2.1.3 Semiophoric: thread bent whip like, with large flat spine medially*
2.2.2.2.2 Macrobasic: shaft long, more than two and a half times capsule length, in undischarged cnidocysts shaft much longer than capsule length, horseshoe-shaped or wind up in several loops*
2.2.2.2.2.1 Telotrichous: spines on distal portion of shaft only*
2.2.2.2.2.2 Merotrichous: spines in the middle of shaft, found only on shaft area of uniform diameter proximal to terminal swelling*
2.2.2.2.2.3 Holotrichous: shaft spiny along whole length*

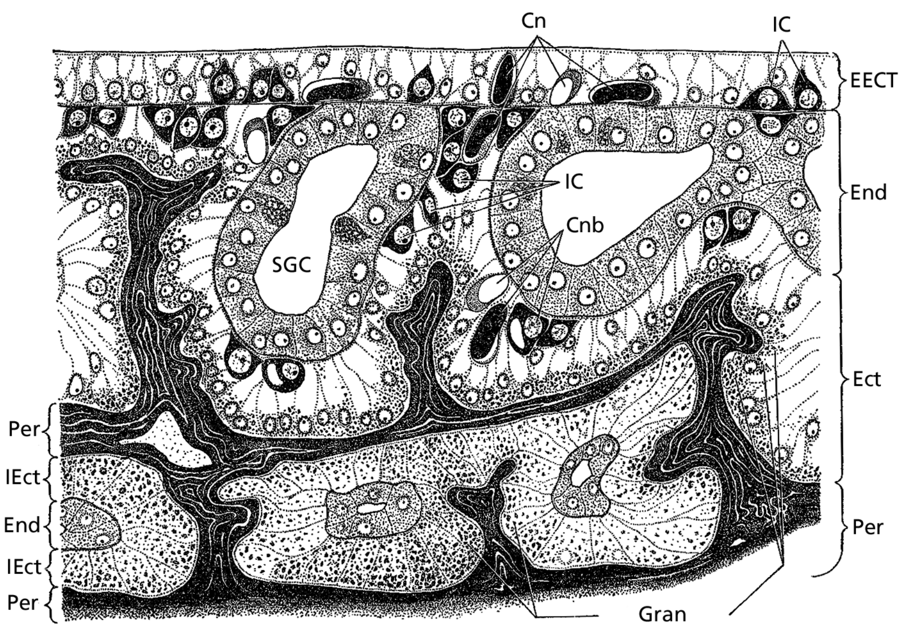


FIG. 18. Histology of the hydroids, illustration of a longitudinal histological section of the encrusting hydrorhiza of *Hydractinia echinata,* Anthomedusae (After Stokes 1974). Cn = cnidocyst; Cnb = cnidoblast; Ect = ectoderm; EECT = external ectoderm; End = Endoderm; Gran = granules; IC = interstitial cell; Iect = internal ectoderm; Per = perisarc; SGC = gastric cavity of the hydrorhiza.

FIG. 18. *Histologie des hydroïdes, illustration d'une section histologique longitudinale de l'hydrorhize encroûtante d'*Hydractinia echinata*, Anthomedusae (d'après Stokes 1974). Cn = cnidocyste ; Cnb = cnidoblaste ; Ect = ectoderme ; EECT = ectoderme externe ; End = Endoderme ; Gran = granule ; IC = cellule interstitielle ; Iect = ectoderme interne ; Per = périsarc ; SGC = cavité gastrique de l'hydrorhiza.*

2.2.2.3 Stenoteles: shaft dilated at base, proximal part longer than distal one, 3 strong spines between the two parts, distal portion armed by rows of lamellae or spines, thread continues beyond the shaft
2.2.2.4 Pseudostenoteles: shaft dilated at base, proximal part shorter than distal one, 2 to 4 strong spines at constriction between the two parts, smaller spines on distal part, sometimes also with a few large ones, thread continues beyond the shaft

2.2.3 Birhopaloides: discharged shaft with a distal and proximal dilatation either separated from each other or close together*
(Present only in Hydrozoa*; not present in Hydrozoa**)

Cnidocysts have different functions:
– adhesion to and entanglement of prey: acrophores, anacrophores, and desmonemes;
– penetration into prey: stenoteles, microbasic euryteles, microbasic mastigophores and isorhizae;
– adhesion of adults, larvae, and eggs to their substrate: desmonemes, isorhizae, euryteles, and mastigophores;
– defence: stenoteles, euryteles, mastigophores, and isorhizae.

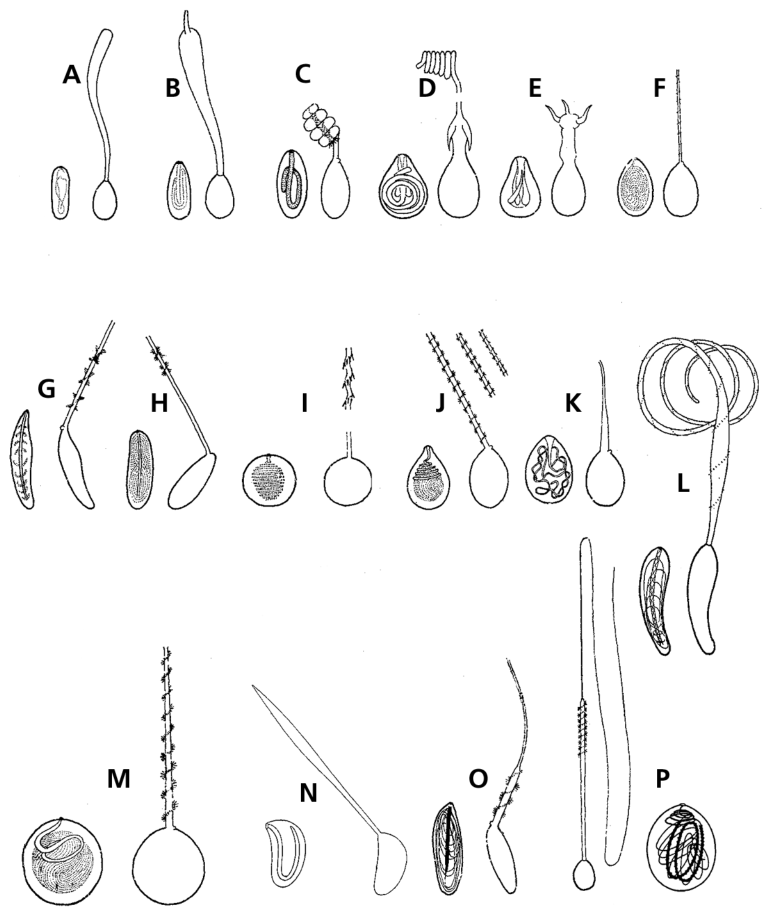


FIG. 19. Histology of the hydroids, different types of cnidocysts described in hydroids and medusae. A, anacrophore. B, acrophore. C, desmoneme. D, spirotele. E, aspirotele. F, atrichous isorhiza. G, basitrichous isorhiza. H, merotrichous isorhiza. I, apotrichous isorhiza. J, holotrichous isorhiza. K, atrichous anisorhiza. L, homotrichous anisorhiza. M, heterotrichous anisorhiza. N, macrobasic atrichous mesotele. O, microbasic mastigophore. P, macrobasic mastigophores (after Mariscal, 1974: p. 132, fig. 4; N after Bouillon *et al*., 1988).
FIG. 19. *Histologie des hydroïdes, différents types de cnidocystes décrits chez les hydroïdes et méduses. A, anacrophore. B, acrophore. C, desmonème. D, spirotèle. E, aspirotèle. F, isorhize atriche. G, isorhize basitriche. H, isorhize mérotriche. I, isorhize apotriche. J, isorhize holotriche. K, anisorhize atriche. L, anisorhize homotriche. M, anisorhize hétérotriche. N, mésotèle macrobasique atriche. O, mastigophore microbasique. P, mastigophore macrobasique (d'après Mariscal, 1974 : p. 132, fig. 4 ; N d'après Bouillon* et al.*, 1988).*

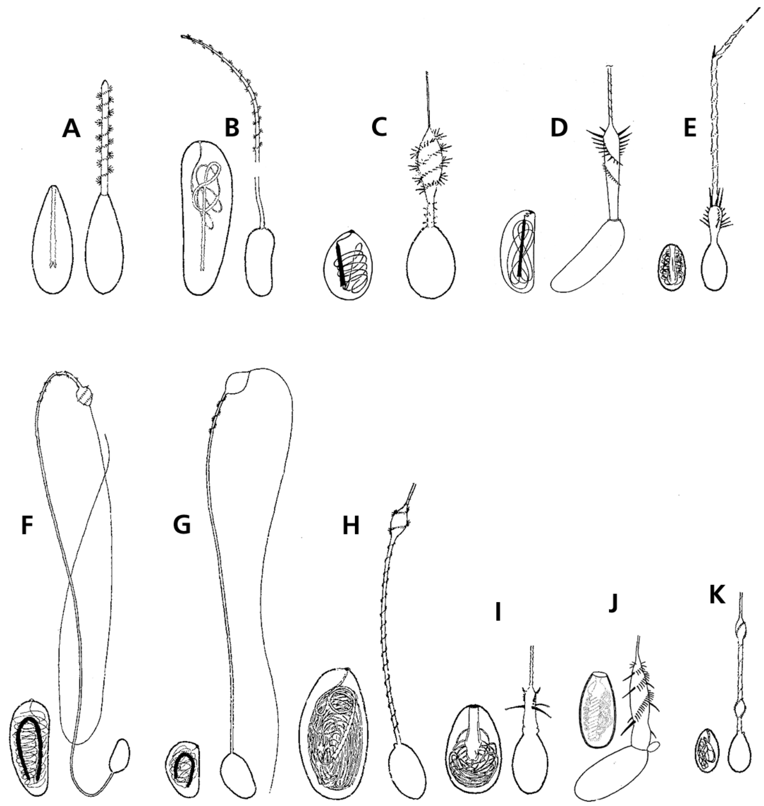


FIG. 20. Histology of the hydroids, different types of cnidocysts (end). A, microbasic amastigophores. B, macrobasic amastigophore. C, homotrichous microbasic eurytele. D, heterotrichous microbasic eurytele. E, semiophoric microbasic eurytele. F, telotrichous macrobasic eurytele. G, merotrichous macrobasic eurytele. H, holotrichous macrobasic eurytele. I, stenotele. J, pseudostenotele. K, birhopaloid (A-I, K after Mariscal 1974: p. 133, fig. 4 (Continued); J after Bouillon *et al*., 1986).

FIG. 20. *Histologie des hydroïdes, différents types de cnidocystes (fin). A, amastigophore microbasique. B, amastigophore macrobasique. C, eurytèle homotrichous microbasique. D, eurytèle microbasique hétérotriche. E, eurytèle sémiophorique microbasique. F, eurytèle télotriche macrobasique. G, eurytèle mérotriche macrobasique. H, eurytèle holotriche macrobasique. I, sténotèle. J, pseudosténotèle. K, birhopaloide (A-I, K d'après Mariscal 1974 : p. 133, fig. 4 (Continued) ; J d'après Bouillon* et al.*, 1986).*

Cnidocysts develop in specialised regions, and not at the place where they are finally utilised: the stolons in colonial forms, the median hydranth regions of certain colonial species without or with few stolons (*Craspedacusta*, *Limnocnida*, *Clava*, etc.) or of solitary ones (e.g., *Hydra*). In medusae, they differentiate either at the level of the nettle ring (Trachymedusae and some Limnomedusae) or, if this formation is missing, in the tentacular bulbs. Wrapped in the cnidocytes, they migrate from the cnidogenous regions toward the tentacles or other armed regions, through the ectoderm, the endoderm, the mesoglea or even the gastric cavity.

Interstitial cells. At the base of the ectodermal epithelio-muscular cells, and in between their interspaces, little cells of so-called embryonic character are found. These tiny cells have a basophilic cytoplasm, rich in ribonucleic acid (RNA); their dilated and vesicular nucleus contains a large, often double nucleolus.

As shown by TEM studies, the cytoplasm of these interstitial cells is rich in ribosomes, but is virtually devoid of endoplasmic reticulum. Their Golgi apparatus is little developed and they have few mitochondria. When a given species has interstitial cells, they are constantly found in all individuals. They are migratory, usually evenly dispersed in the tissues, although often grouped in small clusters. These peculiarities distinguish them from other cells with similar cytological characteristics, but which develop locally, sporadically and temporarily, by the dedifferentiation of normal epithelial tissues, for example at the level of the blastogenetic or sexual zones of many hydroids with no real interstitial cells (*Dipurena*, *Cladonema*, *Coryne*, *Sarsia*, etc.). The interstitial cells have been considered by many authors as totipotent, essential for budding, growth, regeneration, source of most of the different cell types, etc. Many experiments have nevertheless demonstrated that they have a more modest importance and that they mainly play role in the formation of new interstitial cells, cnidoblasts, nerve cells and sexual elements. When experimentally removed, and under certain conditions, the interstitial cells can be regenerated from the epithelial tissues.

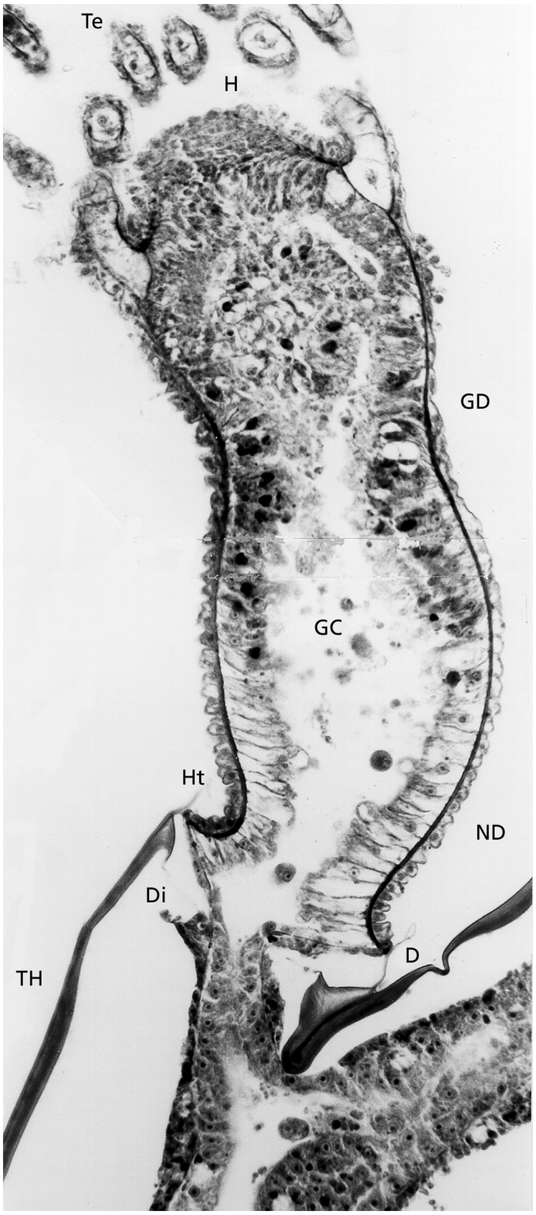


FIG. 21. Histology of the hydroids, photography of a longitudinal histological section of an expanded hydranth of *Halecium halecinum* (Leptomedusae) showing the two endodermic regions of the column characteristic of the Haleciidae (after Bouillon, original). D = desmocyte; Di = diaphragm; GC = gastric cavity; GD = digestive part of the column; H = hypostome; Ht = hydrotheca; ND = non digestive part of the column; Te = tentacle; Th = hydrocladium perisarc.

FIG. 21. *Histologie des hydroïdes, photographie d'une section histologique longitudinale d'un hydranthe en extension d'*Halecium halecinum *(Leptomedusae) montrant les deux régions endodermiques de la colonne gastrique, caractéristique des Haleciidae (d'après Bouillon, original). D = desmocyte ; Di = diaphragme ; GC = cavité gastrique ; GD = partie digestive de la colonne ; H = hypostome ; Ht = hydrothèque ; ND = partie non digestive de la colonne ; Te = tentacule ; Th = périsarc de l'hydroclade.*

Nerve cells. The nerve cells of hydroids are bipolar or multipolar neurons, located near the mesoglea at the base of both ectoderm and endoderm. They are interconnected to form ectodermal and endodermal nervous plexuses. Ectodermal nerve cells are of variable size, though generally rather small, with a very stainable oval nucleus, and a sparsely developed cytoplasm, interspersed with basophilic granules and containing fibrillar formations. Three types of neurons have been observed: neuro-sensory cells, neuro-secretory cells, and ganglionar cells; all with synaptic junctions.

Sensory cells. The ectodermal sensory cells generally have two or three basal roots spread on the mesoglea, and a cytoplasmic apical process ending in a sensory bristle. Their oval nucleus is interspersed with more or less regular chromatic blocks, and the cytoplasm is slightly basophilic. Such cells are dispersed throughout the hydranth ectoderm. They are particularly numerous on the tentacles, where they are interspersed among cnidocysts, often being elongated and with only one basal root.

Secretory cells. Certain hydranths possess specialised secretory cells, disseminated in the ectoderm, either exceptionally (e.g., *Clava*, *Cordylophora*) or permanently (many Leptomedusae hydroids); their function is poorly known.

In Leptomedusae hydroids, secretory cells with a granulous content have been considered as responsible for perisarc secretion. This hypothesis is not quite tenable, for several reasons: the granules of these cells present almost no staining or histochemical affinities with perisarc, and many forms with perisarc are deprived of such cells; furthermore, they are present in several species of Anthomedusae and Leptomedusae hydroids that do not secrete perisarc, and in many of their planula larvae. Those secretory cells have also been considered as being nutritive reserves, or to have an excretory function. In fact, there seems to be confusion between several types of cells not easily distinguishable with classical histological methods.

The ectoderm is relatively uniform throughout the polyp, except in specialized regions such as the cnidogenous centre, the sexual and blastogenic zone, or at the sphincter level.

ENDODERM

The endoderm of hydroids is also made of epithelio-muscular cells. These are very elongated, cylindrical, or club-shaped. Smooth and circular muscle fibrils characterise their basal region, spreading on the mesoglea. The contraction of endodermal circular fibers causes the extension of the polyps, which are contracted by the ectodermal longitudinal fibers. The free apical end of the endoderm cells is oriented toward the gastro-vascular cavity and bears many pseudopods, as well as two to five flagella. The structure of the endoderm layer is less uniform than that of the ectoderm and varies greatly in different hydranth regions.

In the hypostomial region of all hydranths, the pluristratified endoderm is typically constituted by a deep layer of absorbing epithelio-muscular cells lying on the mesoglea, and by a superficial layer of gland cells. These are of two types: spumous hypostomial gland cells, generally forming a button surrounding the mouth, alternating more distally almost regularly with hypostomial spherulous gland cells.

The endoderm of the gastric column is, on the contrary, almost entirely composed of absorbing endodermal cells among which a third type of gland cells can be recognised: the stomach glandular spherulous cells, easily distinguished from the hypostomial spherulous cells by the greater proportion of their secretions. The endoderm of the gastric column of Anthomedusan polyps is rather uniform in structure. In Leptomedusan polyps, the endoderm of the gastric column is, on the contrary, often differentiated into an aboral and an oral region, pending the families. In most Campanulinida (the Campanulinidae, the Eireneidae, the Lovenellidae, etc.) and in the Haleciidae, the oral part of the column is digestive and glandular; the aboral part is non-digestive and formed mostly by chordal cells. In others, like the Sertulariidae, the oral part is mainly glandular and the aboral region, including the abcauline caecum, is digestive. In some families, the endoderm of the gastric column is quite uniform (e.g., Campanulariidae, Lafoeidae).

When present, the hypostomial spherulous cells of the ectoderm, as well as the spumous cells of the endoderm, facilitate prey ingestion with their secretion. Food is then attacked by the enzymatic secretions of the hypostomial and gastric spherulous cells, rich in several enzymes allowing extracellular digestion. The absorbing cells of the gastric column participate actively to intracellular digestion; their vacuolated cytoplasm is generally cluttered up with all kinds of trophic inclusions originating from extracellular digestion and undergoing intracellular degradation. Digestive vacuoles bring trophic inclusions to the state of assimilated substances and then transform into excretory vacuoles (see also medusae).

In Anthomedusae colonial hydroids, the endoderm of the sphincter region is comparable to the endoderm forming the solid tentacle axis. These cells are highly vacuolated, turgescent, devoid of inclusions, and present a “chordal” appearance. This zone is also devoid of gland cells.

In Anthomedusae hydroids, the perisarc is continuous with the periderm at the level of sphincter and stolon intersection.

The stolon endoderm is composed of stubby absorbing epithelio-muscular cells among which spherulous gland cells of the same type than found in the column are dispersed. In this region, the absorbing cells are filled with trophic inclusions originating from the gastric cavity and brought to the stolon cavity by hydroplasmic movement due to ciliary and contraction activities taking place over the whole colony. Intense intracellular digestion occurs also in the stolon endoderm.

The endoderm of polyps also contains both nerve and sensory cells of the types described from the ectoderm layer.

Sometimes endoderm cells may contain symbionts, such as zoochlorellae (e.g., *Chlorohydra viridissima*) or zooxanthellae (e.g., *Aglaophenia tubiformis*, *Myrionema*). Finally, cnidoblasts migrating toward their functional location are often found interspersed among endoderm cells.

ENDODERMAL GLANDULAR CELLS

As seen above, three types of glandular cells are found in the endoderm of hydroids:

– hypostomial spumous or mucous gland cells: pear-like cells containing irregular vacuoles with weakly defined material. Mostly present in the oral region of the manubrium, they secrete mainly mucoproteins (mucus).

– hypostomial spherulous gland cells: elongated cells containing numerous, small, regular, vacuoles each occupied by a well defined droplet of secretion formed by various enzymes, namely: leucine amminopeptidases, proteinases of trypsic type, amylases and sometimes acid and alkaline phosphatases.

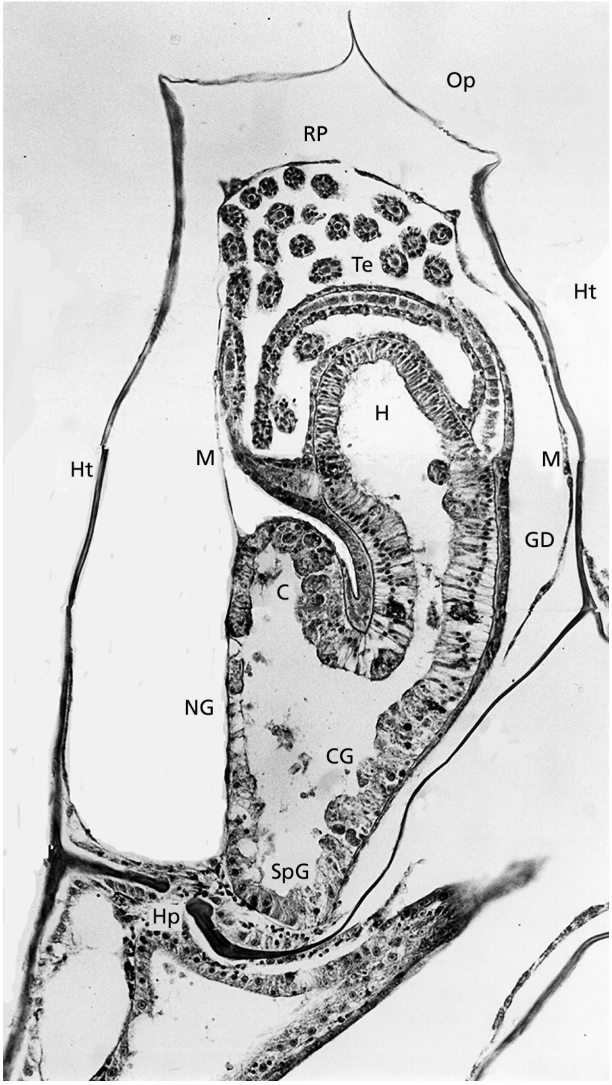


FIG. 22. Histology of the hydroids, photography of a longitudinal histological section of a contracted hydranth of *Sertularella polyzonias*, Leptomedusae, showing the abcauline gastric caecum, the ectodermal mantle and its roof (after Bouillon, original). C = abcauline gastric caecum; CG = gastric cavity; GD = glandular oral part of the column; H = hypostome; Hp = hydropore**;** Ht = hydrothecae; M = ectodermal mantel; NG = non glandular aboral part of the column; Op = operculum; RP = roof plate; SpG = sphincter glandular cells; Te = tentacle.

FIG. 22. *Histologie des hydroïdes, photographie d'une section histologique longitudinale d'un hydranthe contracté de* Sertularella polyzonias*, Leptomedusae, montrant le caecum gastrique abcaulinaire, le manteau ectodermique et la voûte terminale du manteau (d'après Bouillon, original). C = caecum gastrique abcaulinaire ; CG = cavité gastrique; GD = partie glandulaire orale de la colonne ; H = hypostome ; Hp =* hydropore *; Ht = hydrothèque ; M = manteau ectodermique ; NG = parte non glandulaire aborale de la colonne ; Op = opercule ; RP = voûte terminale du manteau ; SpG = cellule glandulaire du sphincter ; Te = tentacule.*

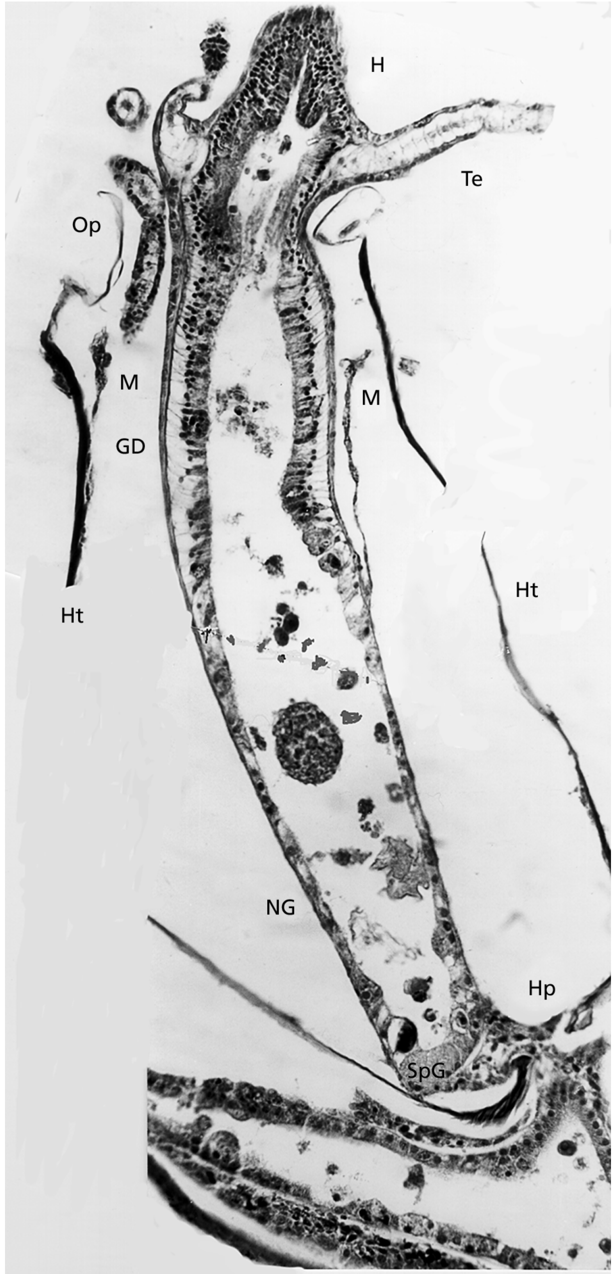


FIG. 23. Histology of the hydroids, photography of a longitudinal histological section of an expanded hydranth of a *Sertularella ellisi*, Leptomedusae, showing the ectodermal mantle, the absence of abcauline caecum and the sphincter glandular cells (after Bouillon, original). Hp = hydropore; other legends as fig. 22.

FIG. 23. *Histologie des hydroïdes, photographie d'une section histologique longitudinale d'un hydranthe en extension de* Sertularella ellisi*, Leptomedusae, montrant le manteau ectodermique, l'absence de caecum abcaulinaire et de cellules glandulaires du sphincter (d'après Bouillon, original). Hp = hydropore ; les autres légendes comme la fig. 22.*

– stomacal spherulous cells (or zymogenous gland cells): polymorphic cells found in the hydranth column and in the stolons. They contain about 70 large polyedric vacuoles each with a large spherical secretion of glycoproteic nature containing numerous enzymes, namely: leucine amino-peptidases, trypsin-like enzymes, esterases, and lipases.

MESOGLEA

The mesoglea of po1yps presents a peculiar aspect, and therefore Hyman (1940) preferred to define it as a “mesolamella”, thus indicating a possible distinction from the mesoglea of other Cnidaria. This mesoglea is generally a thin membrane devoid of cellular elements. TEM reveals a felting of thin feebly oriented fibers devoid of periodic structure and associated with rather uniform and dense granulations. The histological and histochemical tests applied to this mesoglean layer suggest an elastic and collagenic nature.

The hydroid mesoglea has several roles: it acts as skeleton, as way of migration for interstitial cells and cnidoblasts, as shifting layer for the two epithelia and, in freshwater polyps, as osmotic regulator.

MEDUSAE

MORPHOLOGY OF THE MEDUSAE (FIGS 24-27)

THE BELL

Hydrozoan medusae present essentially a tetramerous radial symmetry.

Their body, the swimming bell or umbrella, generally recalls the shape of a mushroom, a bell, a disk, a cone, a mitre etc.. The top of the umbrella is usually flattened, but some species may have a mesoglean thickening forming the apical projection or process, or may contain an apical canal (or umbilical canal) that is a vestige of the link between the gastric cavities of the hydroid and the medusa. The umbrella may also have exumbrellar cnidocyst patches, bands, or pouches (e.g., Zancleidae). Large hydromedusae can have a subumbrellar gelatinous projection (e.g., Aequorea). The umbrella of Hydroido- and Automedusae generally measures between 1 mm and 50 mm, but in numerous species the size may be greater, reaching 100 to 200 mm (*Aequorea*) and even exceptionally 400 mm of diameter (*Rhacostoma atlanticum*). The main part of the umbrella volume is occupied by a gelatinous mass, the mesoglea, the jelly of the jellyfish, which confers form and buoyancy. The convex, upper (aboral) umbrellar surface is called the exumbrella; the concave, lower (oral) surface is termed the subumbrella; the space enclosed by the umbrella is the subumbrellar cavity, delimited by the velum.

THE VELUM

The opening of the subumbrellar cavity is narrowed by a muscular horizontal marginal diaphragm, or velum, leaving only a central circular aperture, the velar opening. The velum plays an important role in medusan swimming; in certain medusae, it is strongly developed and even hangs downwards like a curtain (some Trachymedusae); in *Obelia* it is absent. Two nerve rings are situated at the base of the velum, separated by the velar mesoglea.

THE TENTACLES

The free rim of the umbrella usually bears marginal tentacles, sometimes also cirri of different kinds, usually associated with sensory cells and sense organs. In most medusae, the tentacles are peripheral, in the Laingiomedusae and the Narcomedusae they are inserted on the exumbrellar surface. Tentacles show a great diversity in form and number. They are said to be solid, when their endoderm is formed by a core of single vacuolated cells (chordal cells); or hollow, when containing an extension of the circular canal (tentacular cavity) or when the endoderm is composed of several peripheral rows of cells coming in juxtaposition, the cavity being lost or only partly retained at the tentacle base. Tentacle numbers may vary from zero to several hundreds (up to 640) according to species; their number does not necessarily equal the basic number of radial canals (4), or a multiple of it, but is usually not fixed, it may be even

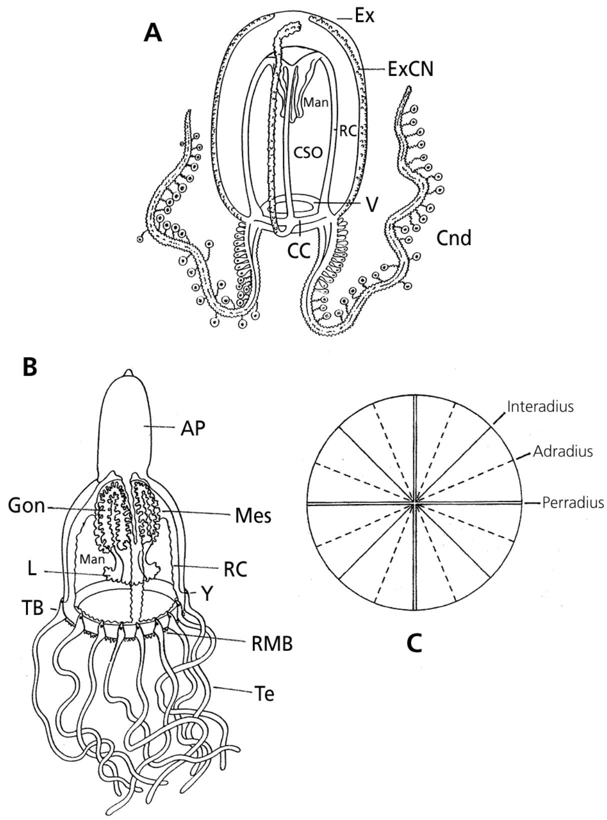


FIG. 24. Morphology of the medusae. A, medusae of Zanclea *spp* (Zancleidae, Anthomedusae) showing the cnidophores and the exumbrellar cnidocyst tracts. B, *Leuckartiara octona* (Pandeidae, Anthomedusae) showing the apical process, the mesenteries and the rudimentary marginal bulbs. C, diagram defining the radii of a hydromedusa with 4 radial canals (A-B after Mayer, 1910; C after Russell, 1953). AP = apical process; CC = circular canal; Cnd = cnidophore; CSO = subumbrellar cavity; Ex = exumbrella; ExCn = exumbrellar cnidocyst tract; Gon = gonad; L = lip; Man = manubrium; Mes = mesentery; RC = radial canal; RMB = rudimentary marginal bulb; RT = rudimentary tentacles; TB = tentacular bulbs; Te = marginal tentacle; V = velum; Y = ocelli.

FIG. 24. *Morphologie des méduses. A, méduse de* Zanclea spp *(Zancleidae, Anthomedusae) montrant les cnidophores et les tractus exombrellaires de cnidocystes. B,* Leuckartiara octona *(Pandeidae, Anthomedusae) montrant le processus apical, les mésentères et les bulbes rudimentaires marginaux. C, diagramme définissant les axes d'une hydroméduse avec 4 canaux radiares (A-B d'après Mayer, 1910 ; C d'après Russell, 1953). AP = processus apical ; CC = canal circulaire ; Cnd = cnidophore ; CSO = cavité sous-ombrellaire ; Ex = exombrelle ; ExCn = tractus exombrellaire de cnidocystes ; Gon = « gonade » ; L = lèvre ; Man = manubrium ; Mes = mesentère ; RC = canal radiaire ; RMB = bulbe rudimentaires marginaux ; RT = tentacule rudimentaire ; TB = bulbe tentaculaire ; Te = tentacule marginal ; V =velum ; Y = ocelle.*

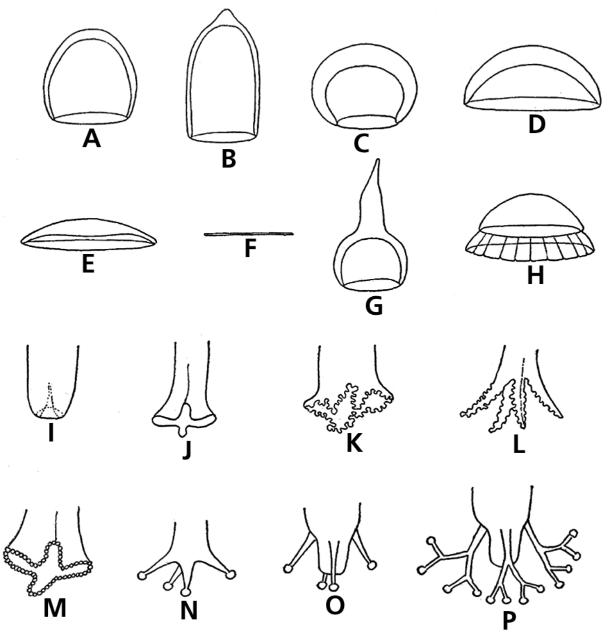


FIG. 25. Morphology of the medusae, detail of the umbrella, mouth and gonad structures. A-H, Diagrams of the umbrella shape of different medusae: A, *Sarsia* (Anthomedusae); B, *Aglantha* (Trachymedusae); C, *Bougainvillia* (Anthomedusae); D, *Phialella* (Leptomedusae); E, *Aequorea* (Leptomedusae); F, *Obelia* (Leptomedusae); G, *Amphinema* (Anthomedusae); H, Narcomedusae. I-P, Diagrams of the mouth form of different medusae: I, *Sarsia* (Anthomedusae); J, *Clytia* (*Phialidium*) (Leptomedusae); K, *Cosmetira* (Leptomedusae); L, *Eirene* (Leptomedusae); M, *Turritopsis* (Anthomedusae); N, *Hydractinia* (*Podocoryne*) (Anthomedusae); O, *Lizzia* (Anthomedusae); P, *Bougainvillia* (Anthomedusae).

FIG. 25. *Morphologie des méduses, détails de la structure ombrellaire, buccale et des « gonades ». A-H, Diagramme de la forme de l'exombrelle chez différentes méduses : A,* Sarsia *(Anthomedusae) ; B,* Aglantha *(Trachymedusae) ; C,* Bougainvillia *(Anthomedusae) ; D,* Phialella *(Leptomedusae) ; E,* Aequorea *(Leptomedusae) ; F,* Obelia *(Leptomedusae) ; G,* Amphinema *(Anthomedusae) ; H,* Narcomedusae. *I-P, Diagramme de forme de la bouche chez différentes méduses : I,* Sarsia *(Anthomedusae) ; J,* Clytia (Phialidium) *(Leptomedusae) ; K,* Cosmetira *(Leptomedusae) ; L,* Eirene *(Leptomedusae) ; M,* Turritopsis *(Anthomedusae) ; N,* Hydractinia (Podocoryne) *(Anthomedusae) ; O,* Lizzia *(Anthomedusae) ; P,* Bougainvillia *(Anthomedusae).*

or uneven and is generally increasing with growth. Tentacles are armed with cnidocysts, formed either at the level of tentacular bulbs, or in a specialised marginal cnidocyst ring, when it exists. In species with marginal bulbs, the development of a tentacle is always preceded by the formation of a tentacular bulb.

There are different tentacle types according to the mode of distribution of the cnidocysts (see polyps and glossary). Cnidocysts may be disposed either in a terminal button (capitate tentacles), in rings (moniliform tentacles), in spirals, or even irregularly along the tentacles (filiform tentacles). In some groups, tentacles bear specialized pedicellate and contractile stinging buttons, the cnidophores (e.g., Zancleidae). Tentacles are generally simple, but they can be bifurcated, one branch being armed with cnidocysts and the other one bearing adhesive organs (e.g., *Cladonema*, *Eleutheria*, and *Staurocladia*). When the tentacles are not in contact with the radial or circular canals, they may present a tentacular endodermal root expanding in the umbrellar mesoglea (e.g., *Blackfordia*, many Narcomedusae).

Medusan species usually have tentacles of one kind; in a few species, however, two kinds of marginal tentacles may be found (e.g., *Liriope*).

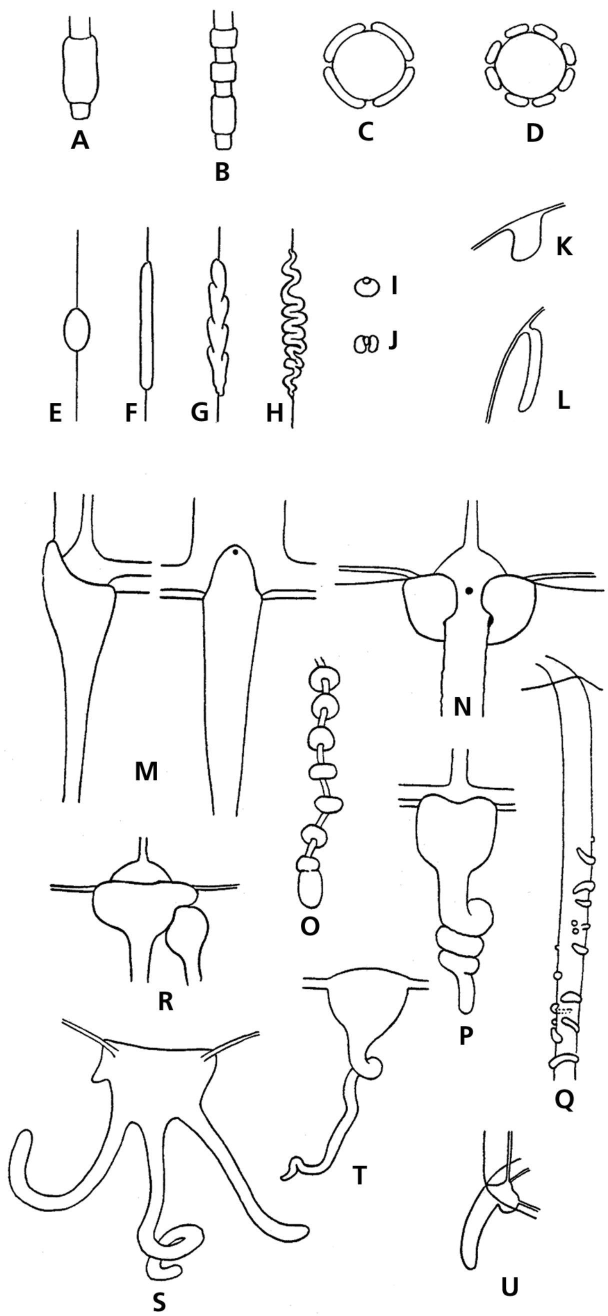


FIG. 26. Morphology of the medusae. A-L, Diagrams of the gonad forms of different medusae. A-B, lateral view of manubrium: A, *Sarsia*; B, *Dipurena*. C-D, cross-sections of the manubrium: C, *Bougainvillia muscus*; D, *B. principis*. E-H, types of gonads on radial canals: E, oval; F, linear; G, folded; H, sinuous. I-J, cross-sections of gonads on radial canal: I, *Clytia*; J, *Tiaropsis*. K-L, lateral view of gonads: K, *Craspedacusta*; L, *Aglantha* (after Russell, 1953). M-U = Diagrams of marginal tentacles of different medusae: M = *Leuckartiara octona* (Anthomedusae); N = *Sarsia tubulosa* (Anthomedusae); O = *Corymorpha nutans* (Anthomedusae); P = *Cosmetira pilosella* (Leptomedusae); Q = *Gossea corynetes* (Limnomedusae); R = *Hybocodon prolifer* (Anthomedusae); S = *Bougainvillia britannica* (Anthomedusae); T = *Clytia hemispherica* (Leptomedusae); U = *Proboscidactyla stellata* (Anthomedusae). (after Russell, 1953).

FIG. 26. *Morphologie des méduses. A-L, Diagramme de la forme des « gonades » chez différentes méduses. A-B, vue latérale du manubrium : A, Sarsia ; B,* Dipurena. *C-D, coupe transversale du manubrium : C,* Bougainvillia muscus *; D,* B. principis. *E-H, types de « gonades » sur les canaux radiaires : E, ovale ; F, lineaire ; G, plissée ; H, sinueuse. I-J, coupes transversales de « gonades » sur les canaux radiaires : I,* Clytia *; J,* Tiaropsis. *K-L, vues latérale de « gonades » : K,* Craspedacusta *; L,* Aglantha *(d'après Russell, 1953). M-U = Diagramme des tentacules marginaux chez différentes méduses : M =* Leuckartiara octona *(Anthomedusae) ; N =* Sarsia tubulosa *(Anthomedusae) ; O =* Corymorpha nutans *(Anthomedusae) ; P =* Cosmetira pilosella *(Leptomedusae) ; Q =* Gossea corynetes *(Limnomedusae) ; R =* Hybocodon prolifer *(Anthomedusae) ; S =* Bougainvillia britannica *(Anthomedusae) ; T =* Clytia hemispherica *(Leptomedusae) ; U =* Proboscidactyla stellata *(Anthomedusae) (d'après Russell, 1953).*

THE BULBS

Tentacle bases are usually swollen into an enlargement, the tentacular bulb; of various shape and size, the bulbs may be simple (bearing one tentacle) or compound (bearing two or more tentacles); sometimes they grow upwards, clasping the exumbrella with exumbrellar spurs; in some groups they may be absent (e.g., Calycopsidae, Limnomedusae, Trachymedusae). Not all marginal bulbs bear tentacles; some never do, they are called non-tentacular marginal bulbs, others will develop tentacles during growth (developing tentacular bulbs). Tentacular bulbs may carry ocelli, light-sensitive sense organs. In some species, tentacular bulbs have adaxial excretory pores, located or not at the apex of a papilla; sometimes the same structures can be found at the level of the circular canals. During development of medusae with more than four tentacles, the first tentacles to be formed are perradial, then interradial, adradial and finally subradial; but after the adradial tentacles are formed the mode of tentacle appearance is often irregular.

MARGINAL STRUCTURES

In addition to tentacles, the umbrellar margin may bear other structures: marginal warts or swellings; sense organs like ocelli, different types of statocysts (open, closed, ectodermal, ecto-endodermal), and cordyli; small tentacular-like structures, or cirri, usually of two types: spiral or flexile; and, finally, marginal tentaculae (see glossary).

THE MANUBRIUM

From the centre of the subumbrella hangs, like the clapper of a bell, a tubular or quadrangular projection of various length and form: the manubrium. The base of the manubrium may be attached either directly to the subumbrellar roof or to a cone-shaped thickening of the mesoglea projecting downwards in subumbrellar cavity, the gastric peduncle. The manubrium may present an apical chamber, or caecum, extending in the mesoglea, and/or perradial or interradial manubrial pouches increasing the gastric surface and often bearing the gonads. The manubrium contains the gastric cavity that extends proximally into the radial gastrovascular canals and opens distally, inside or outside the subumbrellar cavity, by the mouth. The manubrium wall may be attached to radial canals and subumbrella by mesenteries of various lengths.

THE MOUTH

The mouth margin may be simple and circular or may have lips or lobes. The latter can be short or long, simple, folded or crenulated to varying degrees, with or without a cnidocyst armature. The mouth margin may have simple or branched oral tentacles.

THE GASTROVASCULAR SYSTEM

The gastric cavity, the radial canals, the circular canal and the tentacular canals, when they exist, form the gastrovascular system which serves for the digestion and distribution of food and for the circulation of oxygen, waste, cnidoblasts or even of gametes. The radial canals connect, through the mesoglea, the gastric cavity to the circular canal which runs all along the marginal rim of the umbrella; they are generally four, but can be more numerous, sometimes more than one hundred (e.g., 250 in *Aequorea pensilis*), usually even in number. The radial canals may be simple or branched, sinuous, jagged, denticulate, with diverticula, etc.. They usually develop centrifugally from the base of manubrium; a few medusae have nevertheless radial canals arising from circular canal (i.e., *Melicertum*, *Orchistoma*). Most of the canals issued from the circular canal, however, never reach the manubrium, and form the so-called centripetal canals. The radii corresponding to the radial canals are named the perradii, intermediate between them lie the interradii and midway between the perradii and the interradii are the adradii. The circular canal is usually simple and narrow; occasionally it is not hollow and consists of a solid core of endodermal cells (Laingiomedusae, *Proboscidactyla*). In the Narcomedusae, the circular canal, when present, follows the exumbrellar lobes and the peronia, forming what is called the peripheral canal system and the peronial canals (see glossary).

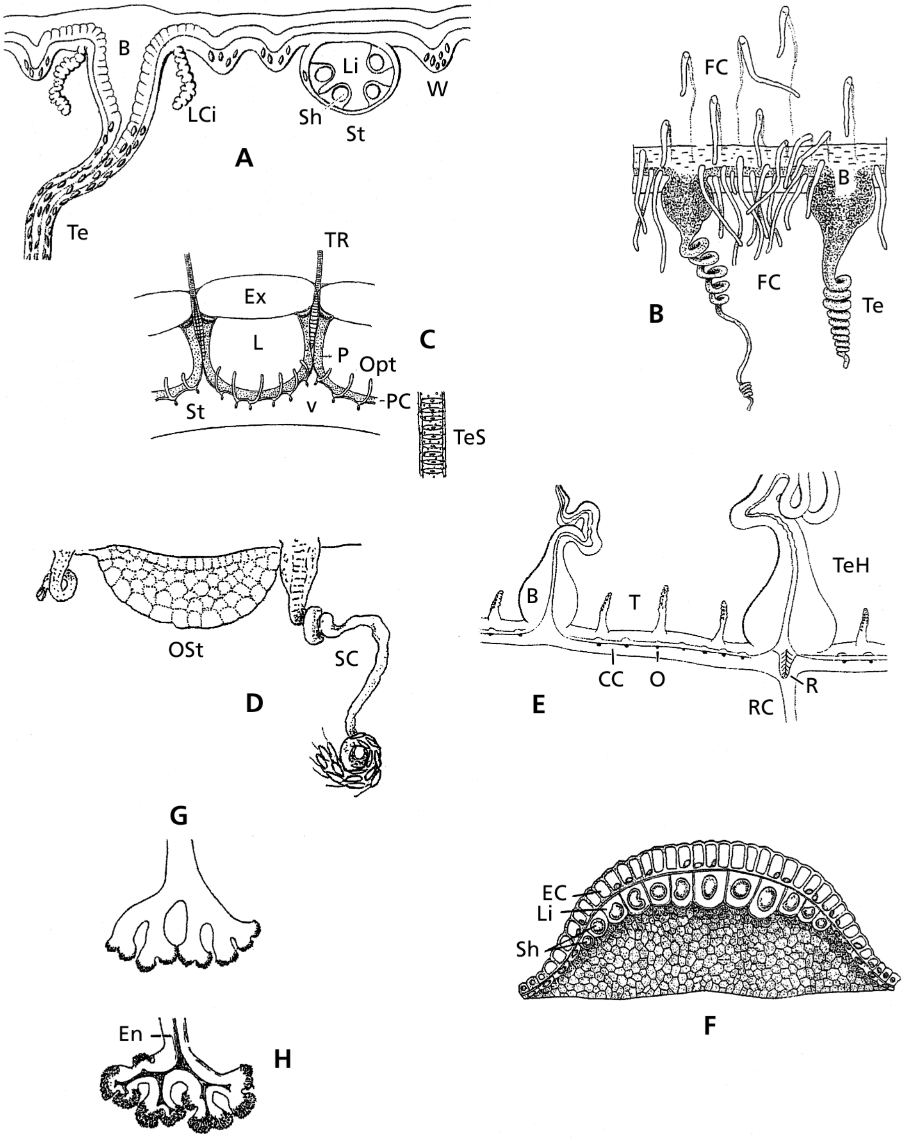


FIG. 27. Morphology of the medusae. A-F, Detail of marginal structures: A, part of the bell margin of *Eutima coerulea* (Leptomedusae) showing a closed statocyst, marginal warts and lateral cirri; B, portion of the umbrella margin of *Cosmetira pilosella* (Leptomedusae) showing the marginal flexile cirri; C, bell margin of the narcomedusae *Pegantha rubiginosa* showing the marginal lappets, the peronia, and the otoporpae; D, marginal open statocyst and marginal cirri of *Mitrocomella brownei*, Leptomedusae; E, part of the bell margin of *Orchistoma pileus* (Leptomedusae) showing the tentaculiform structures; F, detail of an open statocyst of *Mitrocoma* (Leptomedusae). G-H, detail of the lips of *Hydractinia* (*Podocoryne*) *areolata* (Anthomedusae): G, outer side; H, inner side showing the free gastric endoderm (A, C & E after Mayer, 1910; B & D after Russell, 1953; F after Hertwig & Hertwig, 1878; G-H after Kramp & Damas, 1925). B = marginal tentacular bulb; CC = circular canal; Ec = ectoderm; En = endoderm; Ex = exumbrella; FC = flexile marginal cirri; L = marginal lappet of Narcomedusae; LCi = lateral marginal cirri; Li = lithocyte; O = ocellus; Opt = otoporpae; Ost = open statocyst; P = peronia; PC = peripheral canal; R = endodermal tentacular root; RC = radial canal; SC = spiral marginal cirri; Sh = statolith; St = statocyst; T = tentaculiform structure of the Orchistomidae; Te = marginal tentacle; TeH= hollow marginal tentacle; TeS = solid marginal tentacle; TR = tentacular root; V = velum; W = marginal wart.

***FIG. 27.** Morphologie des méduses. A-F, Détail des structures marginales : A, partie du bord marginal exombrellaire de* Eutima coerulea *(Leptomedusae) montrant un statocyste clos, des protubérances ou verrues marginales et des cirres latéraux ; B, portion du bord exombrellaire de* Cosmetira pilosella *(Leptomedusae) montrant les cirres spiralés flexibles ; C, bord marginal exombrellaire de la Narcomedusae* Pegantha rubiginosa *montrant les lobes marginaux, les péronies et les otoporpes ; D, statocyste marginal ouvert et des cirres marginaux de* Mitrocomella brownei*, Leptomedusae ; E, partie du bord marginal exombrellaire d'*Orchistoma pileus *(Leptomedusae) montrant les structures tentaculiformes ; F, détail d'un statocyste ouvert de* Mitrocoma *(Leptomedusae). G-H, détail des lèvres buccales d'Hydractinia (*Podocoryne*)* areolata *(Anthomedusae) : G, côté externe ; H, côté interne montrant l'endoderme intérieur non couvert par de l'ectoderme (A, C & E d'après Mayer, 1910 ; B & D d'après Russell, 1953 ; F d'après Hertwig & Hertwig, 1878 ; G-H d'après Kramp & Damas, 1925). B = bulbe tentaculaire marginal ; CC = canal circulaire ; Ec = ectoderme ; En = endoderme ; Ex = exombrelle ; FC = cirre marginal spiralé flexible ; L = lobe marginal des Narcomedusae ; LCi = cirre marginal latéral ; Li = lithocyte ; O = ocelle ; Opt = otoporpe ; Ost = statocyste ouvert ; P = péronie ; PC = canal périphérique ; R = racine endodermique tentaculaire ; RC = canal radiare ; SC = cirre spiralé marginal ; Sh = statolithe ; St = statocyste ; T = structure tentaculiforme des Orchistomidae ; Te = tentacule marginal ; TeH= tentacule marginal creux ; TeS = tentacule marginal solide ; TR = racine tentaculaire ; V = velum ; W = protubérance ou verrue marginale.*

Crossing the mesoglea, a monostratified membrane, the "cathamnal" or endodermal lamella, interconnects the radial canals and, like these, connects the gastric cavity with the circular canal. It delimits two mesoglean layers, a thin, subumbrellar one (inner mesoglea), and a well developed, exumbrellar one (outer mesoglea).

THE GONADS

The sex cells may develop and ripen either on the manubrium, or on the radial canals, or on both. The position and form of the gonads are of great importance in medusan classification. When on the radial canals, gonads may or may not completely surround the canals, be oval, globular, linear, folded, sinuous, sac-like, etc. When on the manubrium, they may be either cylindrical, covering all its surface, or interradial, adradial, or perradial. Fertilisation is usually external, with free spawning of both males and females. In a few species, internal fertilisation may occur: males spawn freely in the water, the sperms reach the eggs while still in the female gonad and fertilise them there. The resulting planulae are then liberated through the velar opening (e.g., *Turritopsis*; *Eleutheria*).

Histology of the medusae (Figs 28-35)

EXUMBRELLA

In most hydromedusae, the marginal rim of the umbrella is smooth; in Narcomedusae, it is incised or lobed. The lobes are separated by grooves devoid of mesoglea and where subumbrellar and exumbrellar ectoderms are fused, forming the peronia. The exumbrellar ectoderm is essentially composed of a pavement-like monostratified epithelium made of flattened epithelio-muscular cells. Their muscle fibers are smooth, poorly developed, distant from each other and radially oriented. The exumbrellar ectoderm most often contains cnidocysts. It is sometimes lined by a thin periderm perforated, as in hydroids, by many villosities, well visible by TEM.

SUBUMBRELLA

The subumbrellar space is limited by a generally monostratified ectodermal epithelium. The cubic epithelio-muscular cells constituting this epithelium have a highly differentiated musculature, striated and circular. At the level of the radial canals, the subumbrellar epithelium of certain species (e.g., *Cladonema*, *Coryne*, *Sarsia*) is double, the outer cells possessing radial smooth fibers, whereas the innermost ones have circular striated fibers. The radial fibers are involved in the peristaltic movements of the radial canals, favouring the transfer of nutritive elements from the gastric cavity to the marginal canal, and can play a role in "introversion" (see glossary).

VELUM

The velar diaphragm is composed of two ectodermic epithelia, a subumbrellar and an exumbrellar one, separated by a generally well-developed layer of mesoglea. The subumbrellar internal ectoderm is composed of thick cells, presenting a well-developed musculature, striated and circular. The external ectoderm is composed of flattened epithelio-muscular cells, containing poorly differentiated radial smooth muscular fibers. The subumbrellar and velar striated circular fibers play a major role in swimming. When swimming starts, the striated muscle of the velum contracts, reducing the velar opening, then the subumbrellar striated muscles contract, forcing the water out of the subumbrellar cavity by the reduced velum opening, so that the medusa proceeds, the apical region forwards, by rhythmic jet propulsion. The elasticity of the compressed mesoglea provides the antagonistic force to restore the umbrella shape between contractions. The contraction of the radial smooth muscles of the velum, displacing the velar opening, determines the direction of swimming. When active swimming does not take place, the medusae slowly sink.

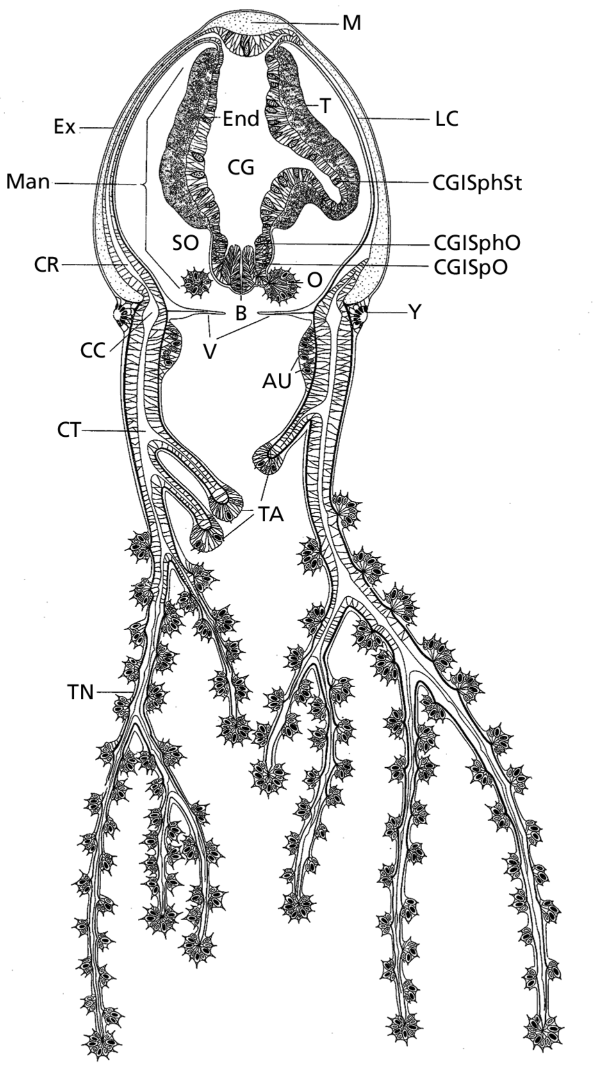


FIG. 28. Histology of the medusae, diagrammatic, optical, longitudinal section of a medusa of *Cladonema radiatum*, Anthomedusae. Perradial section (left side), interradial section (right side), (after Bouillon & Houvenhagel, 1970). AU = cnidocysts or nettle ring; B = mouth; CC = circular canal; CG = gastric cavity; CGlSpO = endodermal spumous oral gland cell; CglSphO = endodermal spherulous oral gland cell; CGlSphSt = endodermal stomacal spherulous gland cell; CR = radial canal; CT = tentacular canal; End = endoderm; Ex = exumbrella; LC = endodermal lamella or cathamnale lamella; M = mesoglea; Man = manubrium; O = oral tentacle; SO = subumbrella; T = male "gonad"; TA = adhesive tentacle; TN = stinging part of tentacle; V = velum;Y = ocelli.

FIG. 28. *Histologie des méduses, section longitudinale diagrammatique d'une méduse de* Cladonema radiatum*, Anthomedusae. Section perradiale (à gauche), section interradiale (à droite), (d'après Bouillon & Houvenhagel, 1970). AU = anneau marginal de cnidocystes ou anneau urticant ; B = bouche ; CC = canal circulaire ; CG = cavité gastrique ; CGlSpO = cellule glandulaire endodermique spumeuse orale ; CglSphO = cellule glandulaire endodermique sphéruleuse orale ; CGlSphSt = cellule glandulaire endodermique sphéruleuse stomacale ; CR = canal radiaire ; CT = canal tentaculaire ; End = endoderme ; Ex = exombrelle ; LC = lamelle endodermique ou lame cathamnale ; M = mésoglée ; Man = manubrium ; O = tentacule oral ; SO = sous-ombrelle ; T ="gonade" mâle ; TA = tentacule adhésif ; TN = partie urticante du tentacule ; V = velum ; Y = ocelle.*

TENTACLES

The tentacles are generally inserted on the umbrellar rim, but in the Narcomedusae, for instance, they are on the latero-dorsal exumbrellar face. The ectoderm of tentacles is formed by very flattened epithelio-muscular cells, and provided with longitudinal smooth muscular fibers, whose contraction leads to tentacle shortening. Solid tentacles are devoid of digestive or excretory inclusions, they present a «chordal» aspect, and they elongate by contraction of their smooth circular musculature. In hollow tentacles, the cells lining the cavity, although always very vacuolated, may contain digestive and excretory inclusions indicating that digestion may occur at their level. The tentacular bulbs and the annular marginal cnidocyst ring have a multistratified ectoderm very rich in cnidoblasts that, after development, will migrate to the body regions where they will become functional. The endoderm of the tentacular bulbs has active digestive activities, related to cnidogenesis; the annular cnidocyst ring is in direct contact with the circular canal, which also presents a high level of metabolic activity.

SENSE ORGANS

Ocelli. The eyes, or ocelli, are most developed in the Anthomedusae. They are also found in some Leptomedusae (e.g., Laodiceidae, Mitrocomidae, Tiaropsidae). From the outside, the ocelli appear as brown, red, or black spots on the tentacular bulbs or, in certain Leptomedusae, under the statocysts. Ocelli, according to the species, have a more or less complex structure. The eyes of *Eleutheria*, here considered as typical, are composed of a cupule constituted by intermixed ectodermal pigmented cells and by nerve cells, with a central crystalline formation. The whole is situated above the nettle ring, in the ectodermal layer from which it originates. In *Tiaropsis*, the pigment cells are endodermal.

Statocysts (lithocysts or otocysts). These organs of orientation and equilibrium are lacking in the Anthomedusae, but are present in the hydroids of *Euphysa*. They may be classified in two categories, those exclusively ectodermal, proper to Leptomedusae, and those of ecto-endodermal origin, found in Limnomedusae, Actinulidae, Trachymedusae, and Narcomedusae. The ectodermal statocysts of Leptomedusae develop in the velum, where they form open or closed pockets or vesicles, characterized by specialised cells, the lithocytes, containing a variable number of round

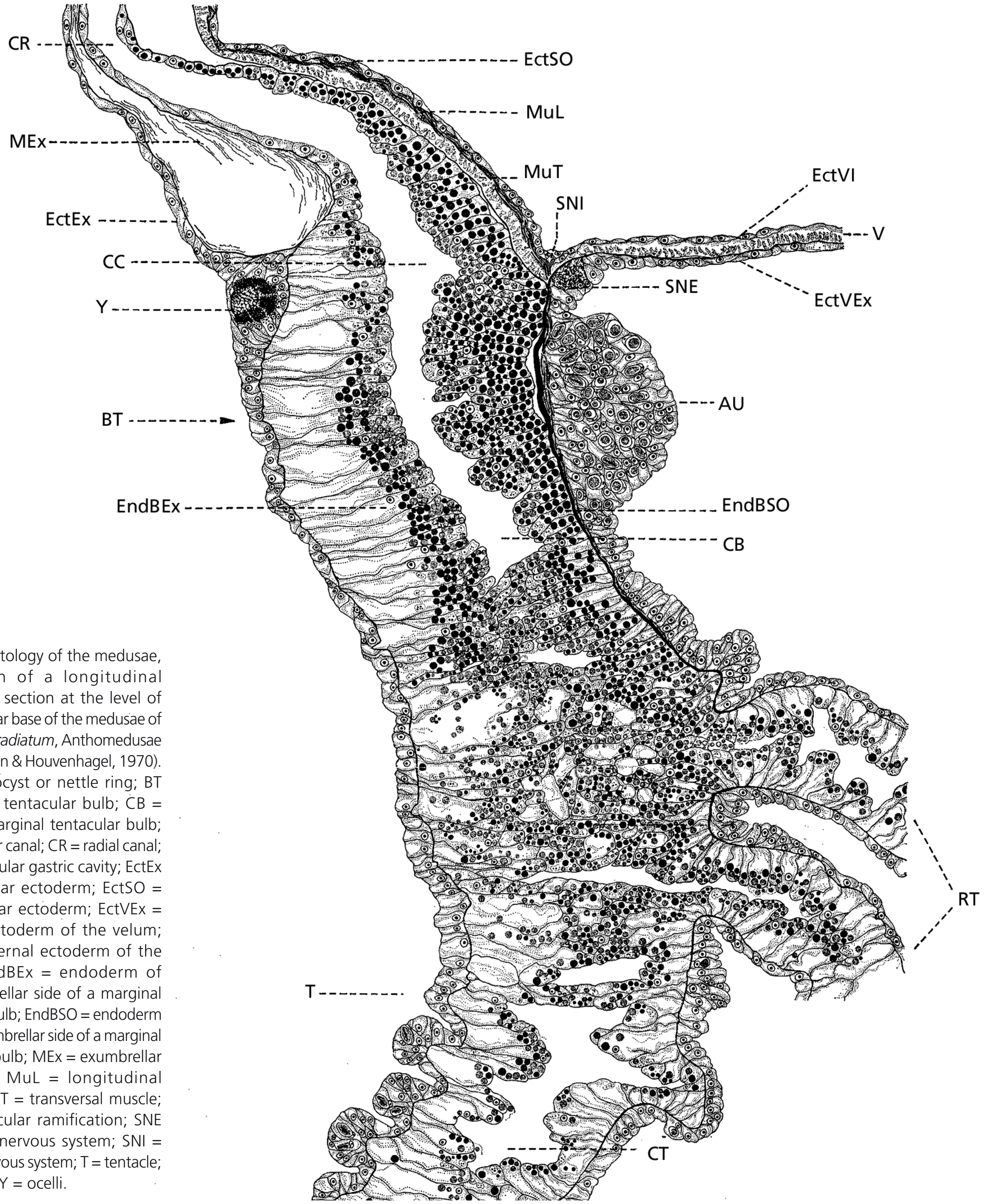


FIG. 29. Histology of the medusae, illustration of a longitudinal histological section at the level of the tentacular base of the medusae of *Cladonema radiatum*, Anthomedusae (after Bouillon & Houvenhagel, 1970). AU = cnidocyst or nettle ring; BT = marginal tentacular bulb; CB = cavity of marginal tentacular bulb; CC = circular canal; CR = radial canal; CT = tentacular gastric cavity; EctEx =exumbrellar ectoderm; EctSO = subumbrellar ectoderm; EctVEx = external ectoderm of the velum; EctVI = internal ectoderm of the velum; EndBEx = endoderm of the exumbrellar side of a marginal tentacular bulb; EndBSO = endoderm of the subumbrellar side of a marginal tentacular bulb; MEx = exumbrellar mesoglea; MuL = longitudinal muscle; MuT = transversal muscle; RT = tentacular ramification; SNE = external nervous system; SNI = internal nervous system; T = tentacle; V = velum; Y = ocelli.

FIG. 29. *Histologie des méduses, illustration d'une section histologique longitudinale au niveau de la base d'un tentacule de la méduse de* Cladonema radiatum, *Anthomedusae (d'après Bouillon & Houvenhagel, 1970). AU = anneau urticant ; BT = bulbe tentaculaire marginal ; CB = cavité du bulbe tentaculaire marginal ; CC = canal circulaire ; CR = canal radiaire ; CT = cavité tentaculaire gastrique ; EctEx = ectoderme exombrellaire ; EctSO = ectoderme sous-ombrellaire ; EctVEx = ectoderme externe du velum ; EctVI = ectoderme interne du velum ; EndBEx = endoderme du côté exombrellaire d'un bulbe tentaculaire marginal ; EndBSO = endoderme du côté sous-ombrelaire d'un bulbe tentaculaire marginal ; MEx = mésoglée exombrellaire ; MuL = muscle longitudinal ; MuT = muscle transversal ; RT = ramification tentaculaire ; SNE = système nerveux externe ; SNI = système nerveux interne ; T = tentacule ; V = velum ; Y = ocelle.*

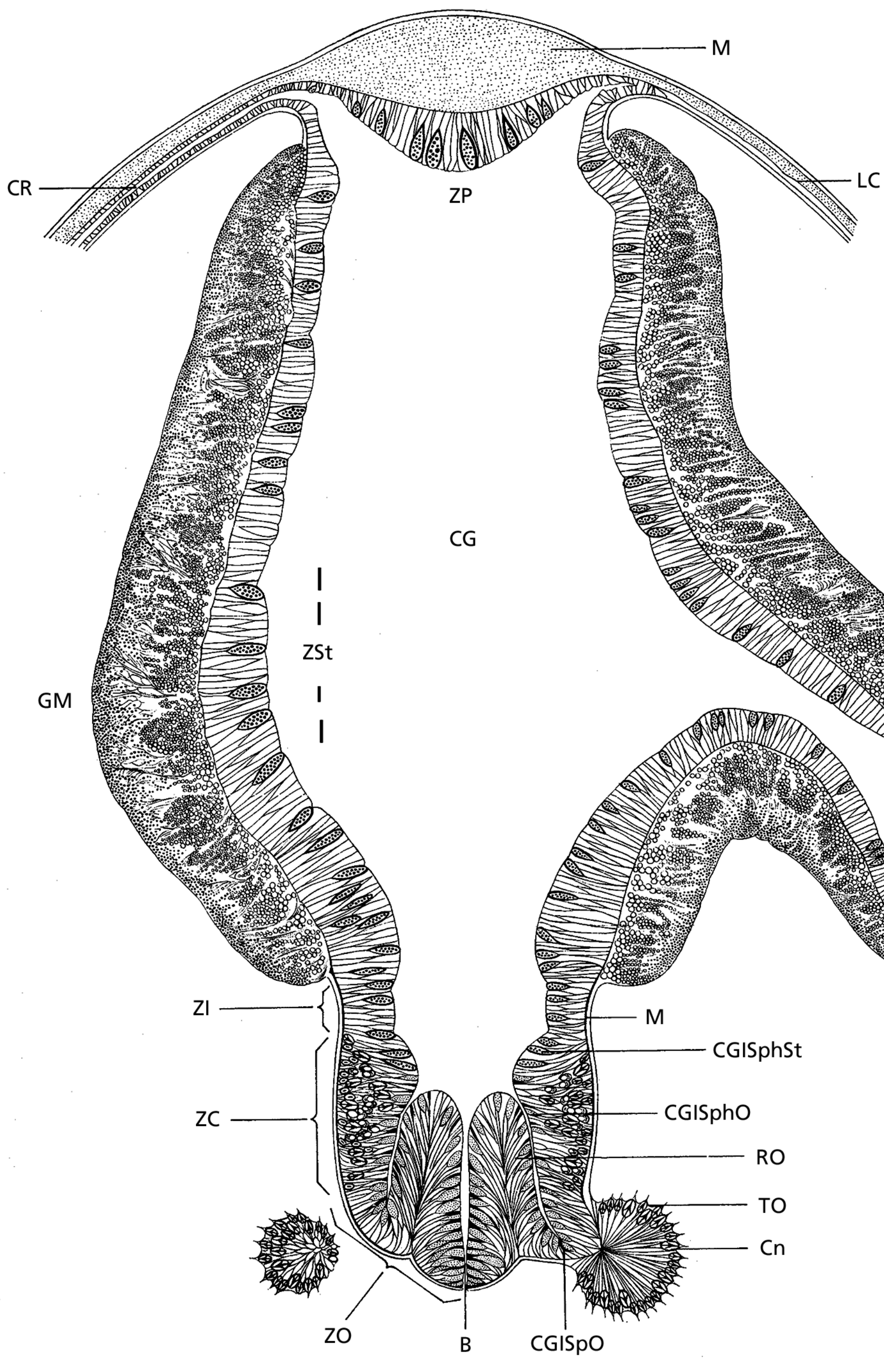


FIG. 30. Histology of the medusae, diagrammatic illustration of a histological section through the manubrium of a sexual mature male medusa of *Cladonema radiatum*, Anthomedusae (after Bouillon & Houvenhagel, 1970). B = mouth; CG = gastric cavity; CGlSpO = endodermal spumous oral gland cell; CglSphO = endodermal spherulous oral gland cell; CGlSphSt = endodermal stomacal spherulous gland cell; Cn = cnidocyst; CR = radial canal; GM = male "gonad"; LC = endodermal or cathamnal lamella; M = mesoglea; PLat = radial lateral manubrial pouch; RO = endodermal oral fold; TO = oral tentacle; ZC = cnidogenetic portion of the manubrium; ZI = intermediary zone of the manubrium; ZO = oral glandular zone of the manubrium; ZP = proximal digestive zone of the manubrium; ZSt = central or stomachal digestive portion of the manubrium.

FIG. 30. *Histologie des méduses, illustration diagrammatique d'une section histologique au travers du manubrium d'une méduse mâle sexuellement mature de* Cladonema radiatum, *Anthomedusae (d'après Bouillon & Houvenhagel, 1970). B = bouche ; CG = cavité gastrique ; CGlSpO = cellule glandulaire endodermique orale spumeuse ; CglSphO = cellule glandulaire endodermique orale sphéruleuse ; CGlSphSt = cellule glandulaire endodermique sphéruleuse stomacale ; Cn = cnidocyste ; CR = canal radiaire ; GM = "gonade " mâle ; LC = lamelle endodermique ou cathamnale ; M = mésoglée ; PLat = poche manubriale latérale radiaire ; RO = pli endodermique oral ; TO = tentacule oral ; ZC = portion cnidogène du manubrium ; ZI = zone intermediaire du manubrium ; ZO = zone orale glandulaire du manubrium ; ZP = zone proximale digestive du manubrium ; ZSt = portion centrale ou stomacale digestive du manubrium.*

concretions, called statoliths. The wall of the statocyst also bears sensory cells with long sensory bristles. According to the position of the medusa, the lithocytes press on the bristles, exciting the nerve cells.

The ecto-endodermal statocysts have a different structure. They are constituted by didermic clappers issued by the marginal circular canal in the fashion of a tentacle, and not by the velar ectoderm. The distal part of the clapper contains one or two endodermal cells provided with concretions (lithocytes). At the base of this club, ciliated sensory cells can be recognized. According to the inclination of the clapper, they strike the wall of the pocket or vesicle. Ecto-endodermal statocysts may be closed or open.

Cordyli. Ecto-endodermal sense organs in the form of clubs, devoid of statoliths, with or without cnidocysts. They are found implanted on the exumbrellar rim of the medusae of the families Hebellidae, Laodiceidae and Tiarannidae. Their function remains mysterious.

NERVOUS SYSTEM

In connection with the complexity and the concentration of the sensory organs, as well as the umbrellar and tentacular movements, the nerve cells of medusae are concentrated in a marginal-coordinating centre. This centre is typically formed by two nerve rings, situated at the base of the velum and separated by the velar mesoglean lamina. These nerve rings contain several types of nerve cells: giant bipolar cells, large multipolar cells and more tiny bi- tri- or multipolar nerve cells, as well as connective cells. Outside the two nervous rings, the medusae have also a subectodermal, tentacular, manubrial and subumbrellar nerve plexus. Moreover, certain elements of this plexus are concentrated at the level of radial canals, forming true radial nerves. This plexus communicates with the central marginal nervous rings, which are themselves interconnected.

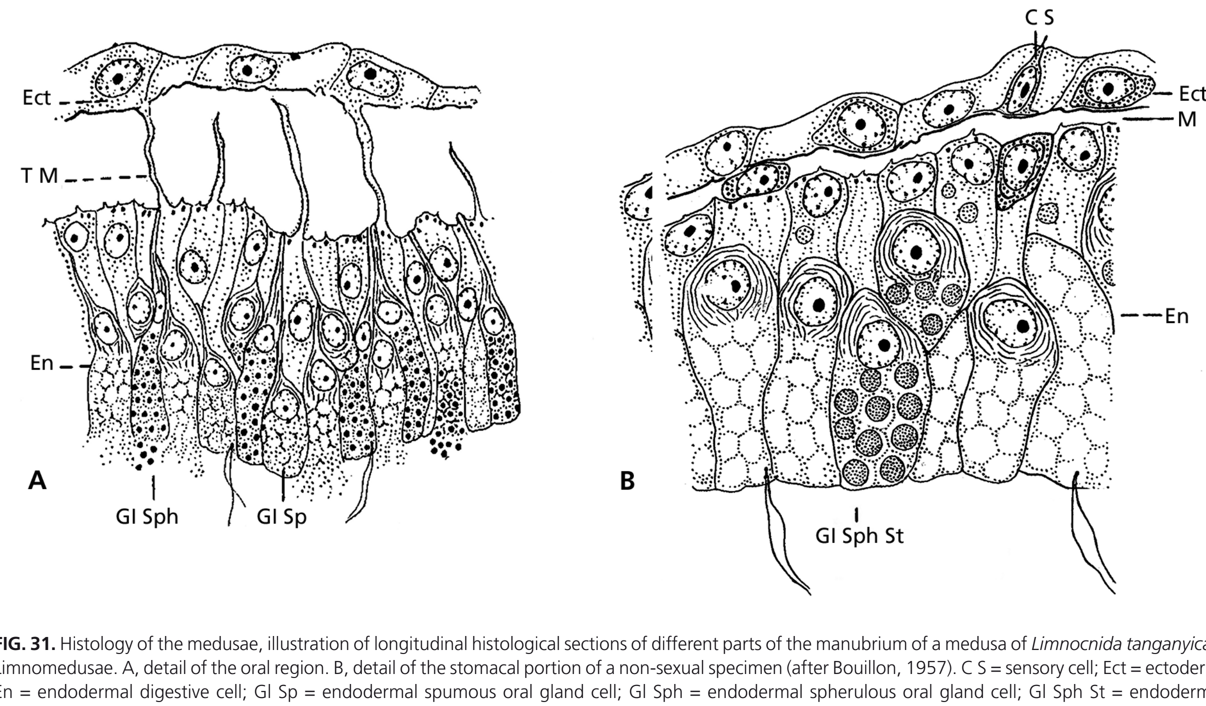


FIG. 31. Histology of the medusae, illustration of longitudinal histological sections of different parts of the manubrium of a medusa of *Limnocnida tanganyicae*, Limnomedusae. A, detail of the oral region. B, detail of the stomacal portion of a non-sexual specimen (after Bouillon, 1957). C S = sensory cell; Ect = ectoderm; En = endodermal digestive cell; Gl Sp = endodermal spumous oral gland cell; Gl Sph = endodermal spherulous oral gland cell; Gl Sph St = endodermal spherulous stomacal gland cell; M = mesoglea; T M = mesoglean bridges.

FIG. 31. *Histologie des méduses, illustrations de sections histologiques longitudinales de différentes parties du manubrium d'une méduse de* Limnocnida tanganyicae*, Limnomedusae. A, détail de la région orale. B, détail de la portion stomacale d'un spécimen immature (d'après Bouillon, 1957). C S = cellule sensorielle ; Ect = ectoderme ; En = cellule digestive endodermique ; Gl Sp = cellule glandulaire spumeuse orale endodermique ; Gl Sph = cellule glandulaire sphéruleuse orale endodermique ; Gl Sph St = cellule glandulaire sphéruleuse stomacale endodermique ; M = mésoglée ; T M = pont mésogléen.*

The medusae may present non-neural conduction linked with electric activities along non-nervous cell membranes.

GASTROVASCULAR SYSTEM

Manubrium. The size and shape of the manubrium of the hydromedusae is much varied, according to the species. In the Anthomedusae, certain Limnomedusae, and the Narcomedusae, its appearance also depends on the physiological state of the medusa: immature, sexual, or blastogenetic. The ectoderm of this didermic organ is generally composed of pavimentous epithelio-muscular cells, with ill-defined cell limits and with a cytoplasm containing smooth longitudinal muscle fibers. Among these epithelial cells, some sensory cells can be distinguished. In its most proximal region, the manubrial ectoderm is in continuity with the subumbrellar ectoderm.

The ectoderm of the middle part of the manubrium may show a number of specialised zones: a sexual zone, in mature species with gonads on the manubrium (i. e., Anthomedusae, *Limnocnida* and the Narcomedusae); a blastogenetic zone, in medusae budding out other medusae from the manubrium (some Anthomedusae and Limnomedusae); a cnidoblastic zone, when a cnidogenous manubrial centre exists, often linked to the presence of medusary buds (*i. e.*, *Limnocnida tanganyicae*, *Rathkea*).

Fundamentally, the manubrial endoderm presents three histologically well-defined regions: an oral region, a stomachal region, and a proximal region.

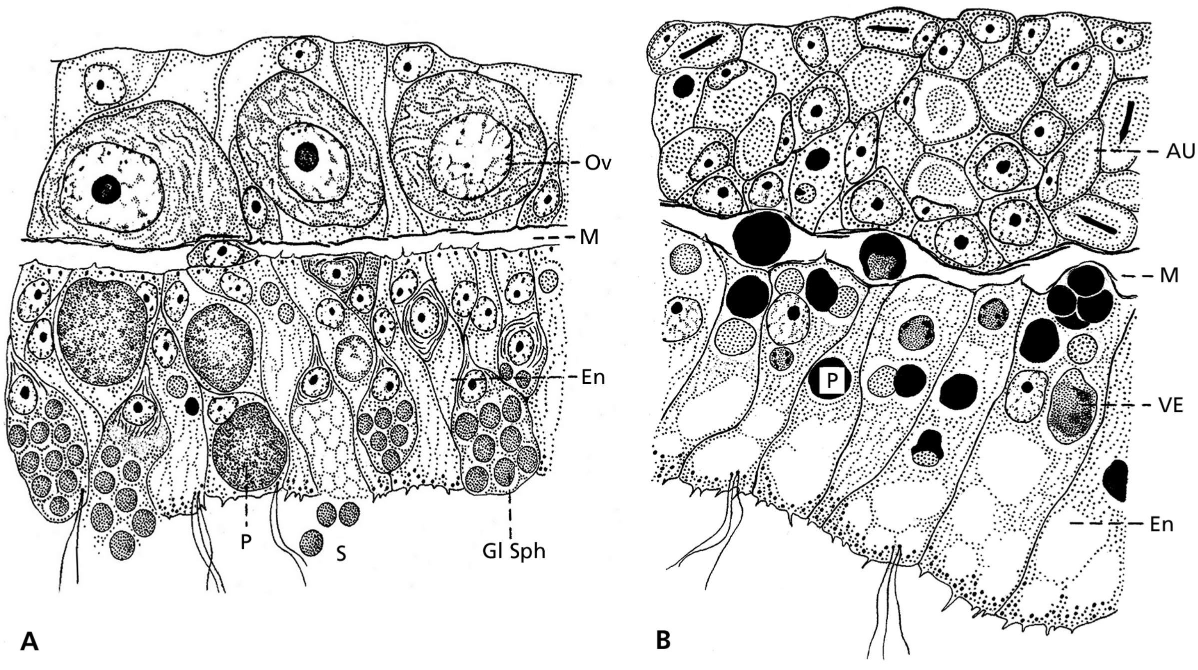


FIG. 32. Histology of the medusae, illustration of longitudinal histological sections of different parts of medusae of *Limnocnida tanganyicae*, Limnomedusae (end). A, detail of a portion of the manubrium of a sexual female specimen; B, detail of a portion of the cnidocyst or nettle ring (after Bouillon,1957). AU = cnidocyst or nettle ring; En = endoderm; Gl Sph = endodermal spherulous stomacal gland cell; M = mesoglea; Ov = ovule; P = digestive vacuole; S = glandular secretions; VE = excretory vacuoles.

FIG. 32. *Histologie des méduses, illustrations de sections histologiques longitudinales de différentes parties du manubrium d'une méduse de* Limnocnida tanganyicae*, Limnomedusae (fin). A, détail d'une portion de manubrium d'un spécimen sexué femelle ; B, détail d'une portion de l'anneau urticant (d'après Bouillon,1957). AU = anneau urticant ; En = endoderme ; Gl Sph = cellule glandulaire sphéruleuse stomacale endodermique ; M = mésoglée ; Ov = ovule ; P = vacuole digestive ; S = sécrétion glandulaire ; VE = vacuole excrétrice.*

– Oral region: its pluristratified endoderm is limited to the mouth opening and more or less to the proximal quarter of the manubrium. It is almost exclusively composed of glandular cells of the oral spumous and spherulous types, as well as of a few absorbing epithelio-muscular cells. These last cells are pushed against the mesoglea, the two types of glandular cells, which alternate almost regularly, occupying the whole of the superficial oral region. This structure is similar in all respects to the hypostomial zone of hydroids.

– Stomacal region: its endoderm is composed of a generally pluristratified, thickened epithelium of absorbing epithelio-muscular cells, among which many glandular cells are interspersed, of a different type from those found in the oral zone: the spherulous gastric gland cells. The absorbing cells are thick, cylindrical, or club-shaped. Their apical region is provided with many villosities, pseudopods, and two to five flagella. Their oval nucleus, little stainable, is generally pushed towards the cell base. The supra-nuclear cytoplasm is occupied by digestive and excretory vacuoles in variable number according to the stage of digestion. The structure of the endoderm of the stomacal zone largely depends on the physiological state of the manubrium, either sexual or blastogenetic.

– The proximal region: this is the most aboral and reduced region of the manubrium, represented solely by the opening of the radial canals and the ceiling of the manubrium, the endoderm of this region is mostly represented by short absorbent epithelio-muscular cells associated with a few spherulous stomacal gland cells.

The manubrial glandular cells. The manubrial endodermal glandular cells are identical to the glandular cells found in the endoderm of the polyps. In the medusae, they are called: oral endodermal spumous or mucous gland cells; oral endodermal spherulous gland cells; stomacal endodermal spherulous cells (or zymogenous gland cells).

Radial canals. These canals of variable appearance and number are continuous with the manubrial gastric cavity, reaching the circular canal. The endodermal epithelium supporting them is made of more or less elongated prismatic and flagellate cells. The epithelium adapted on the subumbrellar ectoderm differs from the epithelium of the face directed toward the exumbrella. The cells composing this epithelium contain rather numerous digestive inclusions and strong longitudinal smooth muscle fibers. The cells of the exumbrellar internal side are generally devoid of such inclusions and their muscle fibers are more slender. The radial canals are usually devoid of glandular cells. When the gonads are developing at the level of the radial canals, the adjacent endoderm becomes more developed and is the site of intense digestive activities. In some medusae, the radial canals open outside, near their junction with the marginal canal, through a kind of a pore which may or may not be situated at the top of a papilla (e.g., *Aequorea*). These structures, generally called excretory pores, are used for the elimination of undigested food, thereby being more similar to an anus (performing elimination) than to an excretory organ.

Other species (e.g., *Dipurena halterata*; some species of *Zanclea*) present enlargements at the level of the radial canals, with inflated cells, dilated by the accumulation of refringent inclusions. These enlargements seem to play an excretory role (accumulation of wastes).

Gastrodermal lamella. This monostratified endodermal lamina is constituted of elongated cells, very flattened, with ill-defined limits and provided with feebly developed circular smooth muscular fibers.

Circular canal. The circular canal is generally regular but weakly developed, except in Narcomedusae where it is most often lacking or modified, and in *Proboscidactyla* spp. and the Laingiomedusae where it is reduced to a solid endodermal string.

In its typical form, it is limited on the external side (marginal nettle ring or tentacular bulbs) by an epithelium of high flagellated epithelio-muscular cells containing many digestive and excretory inclusions. On the subumbrellar side, the endodermal epithelium is lower, almost cubical, flagellated, and poor in digestive inclusions.

At the base of these two types of epithelio-muscular cells, longitudinal muscular fibers are differentiated, running all along the canal. As well as the radial canals, the circular canal is also devoid of glandular elements, extracellular digestion being accomplished exclusively in the manubrial gastric cavity.

Digestion. The feeding behaviour of both hydromedusae and hydroids has not been studied much, and seems very varied (see Miglietta *et al.* 2000). Ingested prey is brought in intimate contact with the gland cells of the oral zone of the manubrium that envelop it in a film containing the mucous secretion of the spumous gland cells, making ingestion easier. The digestive enzymes of the oral spherulous gland cells begin, then, to break up the prey. Extracellular digestion proceeds in the gastric cavity by the action of the spherulous stomacal gland cells, reducing the prey to a heterogeneous fine magma of tissues and cellular elements. The smallest of these elements, by the combined action of the flagella, the peristaltic movements of the radial canal and the rhythmic contraction of the umbrella, is distributed throughout the gastrovascular system. The extracellularly digested material will finally be absorbed by phagocytosis and pinocytosis by the epithelio-muscular digestive cells. Intracellular digestion will reduce it to assimilable substances, the undigested matter being stored into excretory vacuoles that are then expelled into the gastric cavity. These excretion droplets, together with the matter not digested extracellularly, are ejected through the mouth and, when present, the excretory pores. A residual extracellular digestion occurs in the gastrovascular canal system devoid of glandular cells, whereas intracellular digestion is performed in specialised parts of the manubrial endoderm, of the circular canal, the tentacular bulbs and, to a less marked degree, of the radial canals, except in sexual forms with gonads on the radial canals (see above).

In hydromedusae, a definite correlation exists between the development of zones of cell proliferation (budding zones, gonads, cnidogenous zone, tentacular bulbs and marginal cnidocyst ring, etc.) and the increase of intracellular assimilation. Sometimes phagosomes may even migrate from the endoderm, through the meoglea, to active metabolic ectodermal locations.

MESOGLEA

All animals are made of cells attached to an extracellular matrix (ECM). In the Cnidaria, the ECM is very conspicuous and is known since a very long time, under the name of mesoglea. The greatest part of the body of hydromedusae, in fact, is made of a gelatinous mass, the mesoglea, containing fibrillar structures and a high percentage of water (in average about 96%). Mesoglea fibers are of various diameters and presumably comprise collagen and oxatalane (elastine) structures. The mesoglea is also found between the ectodermal and endodermal layers, in the form of a mesolamella. In the Hydrozoa, it is in principle acellular.

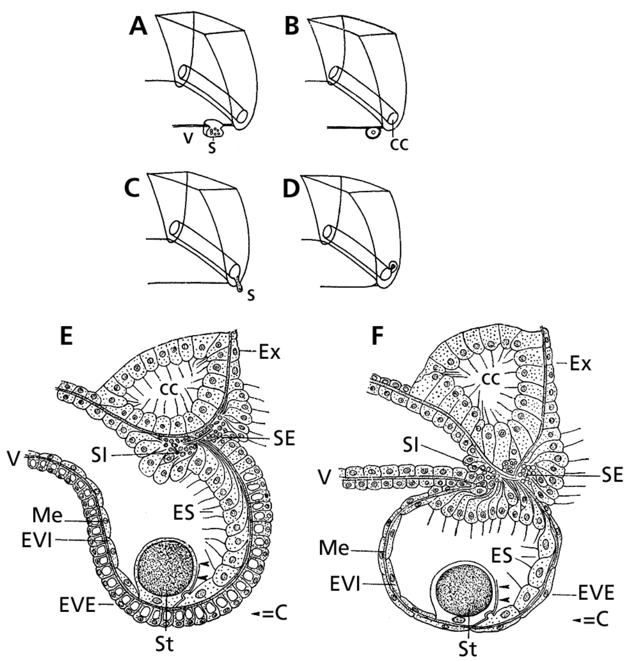


FIG. 33. Histology of the medusae, structure of sense organs: the statocysts. A-D, different types of statocysts: A, open ectodermal velar statocyst; B, closed ectodermal velar statocyst; C, free ecto-endodermal statocyst; D, enclosed ecto-endodermal statocyst. E, diagram of a radial section of an open ectodermal velar statocyst. F, diagram of a radial section of a closed ectodermal velar statocyst (A-D after Russell, 1953; E-F after Singla, 1975: p. 394, fig. 1; p. 395, fig. 2; p. 398, fig. 5; p. 402, fig. 9). C = kinocilium; CC = circular canal; Ex = exumbrella; ES = sensory epithelium; EVE = external epithelium of the statocyst vesicle; EVI = internal epithelium of the statocyst vesicle; Me = mesoglea; S = statocyst; SC = subumbrellar cavity; SE = exumbrellar or external nerve ring; SI = subumbrellar or internal nerve ring; St = concretion of the statolith; V = velum.

FIG. 33. *Histologie des méduses, structure des organes des sens : les statocystes. A-D, différents types de statocystes : A, statocyste ectodermique velaire ouvert ; B, statocyste ectodermique velaire fermé ; C, statocyste ecto-endodermique libre ; D, statocyste ecto-endodermique fermé. E, diagramme d'une section radiaire d'un statocyste ectodermique velaire ouvert. F, diagramme d'une section radiaire d'un statocyste ectodermique velaire fermé (A-D d'après Russell, 1953 ; E-F d'après Singla, 1975 : p. 394, fig. 1 ; p. 395, fig. 2 ; p. 398, fig. 5 ; p. 402, fig. 9). C = cnidocil ; CC = canal circulaire ; Ex = exombrelle ; ES = épithelium sensoriel ; EVE = épithelium externe de la vésicule statocystaire ; EVI = épithelium interne de la vésicule statocystaire ; Me = mésoglée ; S =* statocyste ; *SC = cavité sous-ombrellaire ; SE = anneau nerveux exombrellaire ou externe ; SI = anneau nerveux sous-ombrellaire ou interne ; St = concrétion du statolithe ; V = velum.*

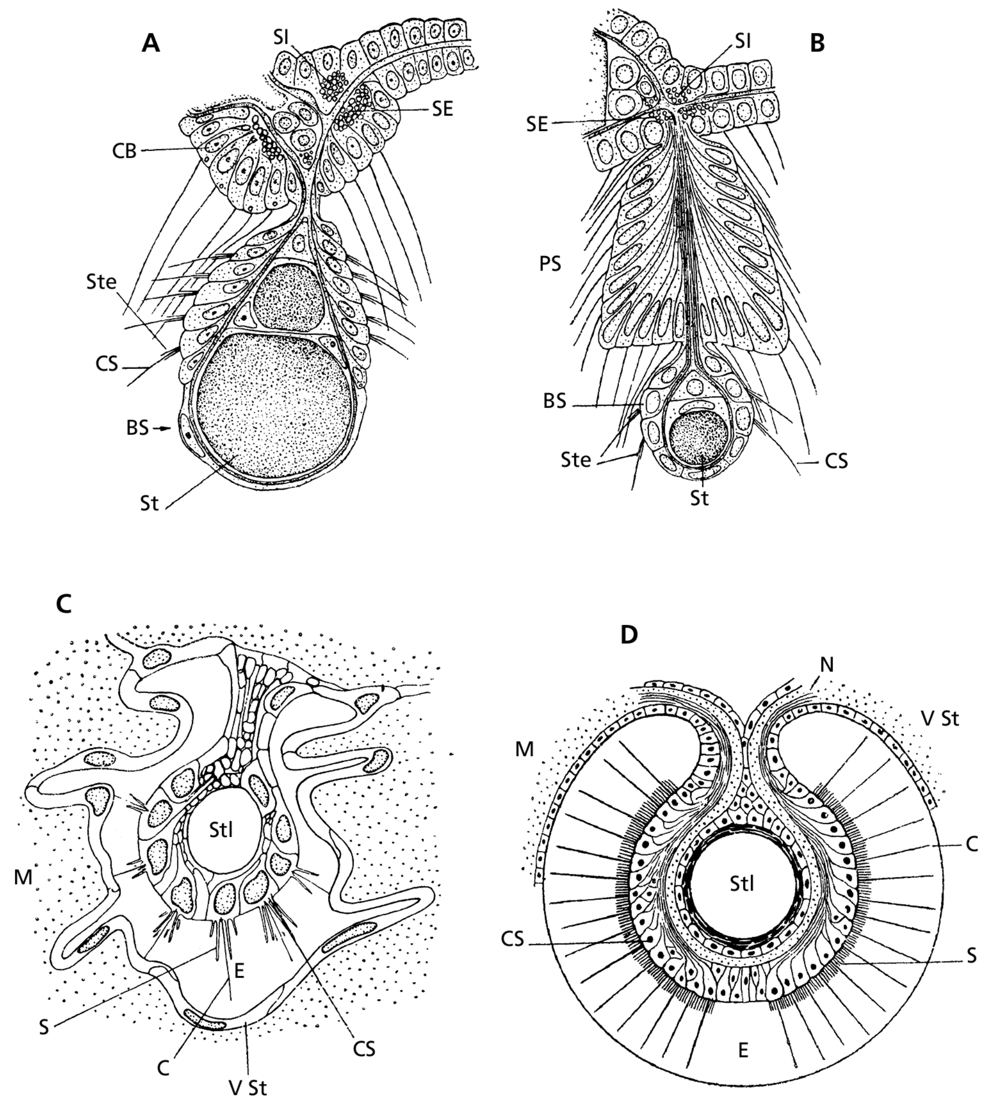


FIG. 34. Histology of the medusae, structure of sense organs: statocyst. A, diagram of a radial section of a free ecto-endodermal statocysts of *Aegina citrea*, Narcomedusae. B, diagram of a radial section of a free ecto-endodermal statocyst of *Solmissus marshalli*, Narcomedusae. C, diagram of a radial section of an enclosed ecto-endodermal statocyst of *Rhopalonema velatum*, Trachymedusae. D, diagram of an enclosed ecto-endodermal statocyst of *Geryonia proboscidalis*, Trachymedusae (A-B after Singla, 1975; C-D after Horridge, 1969). BS = sensory club; C = kinocilium; CB = basal cushion; CS = sensory epithelium; E = sea water; M = mesoglea; N = nerves; PS = sensorial papilla; S = stereocilia; SE = exumbrellar or external nerve ring; SI = subumbrellar or internal nerve ring; Ste = stereocilia; Stl = statolith; V St = enclosing vesicle of the statocyst.

FIG. 34. *Histologie des méduses, structure des organes des sens : les statocystes (fin). A, diagramme d'une section radiaire d'un statocyste ecto-endodermique libre d'*Aegina citrea*, Narcomedusae. B, diagramme d'une section radiaire d'un statocyste ecto-endodermique libre de* Solmissus marshalli*, Narcomedusae. C, diagramme d'une section radiaire d'un statocyste ecto-endodermique clos de* Rhopalonema velatum*, Trachymedusae. D, diagramme d'une section radiaire d'un statocyste ecto-endodermique clos de* Geryonia proboscidalis*, Trachymedusae (A-B d'après Singla, 1975 ; C-D d'après Horridge 1969). BS = battant sensoriel ; C = cnidocil ; CB = coussinet basal ; CS = épithelium sensoriel ; E = eau de mer ; M = mésoglée ; N = nerf ; PS = papille sensorielle ; S = stèréocils ; SE = anneau nerveux exombrellaire ou externe ; SI = anneau nerveux sous-ombrellaire ou interne ; Ste = steréocil ; Stl = statolithe ; V St = vésicule enveloppant le statocyste.*

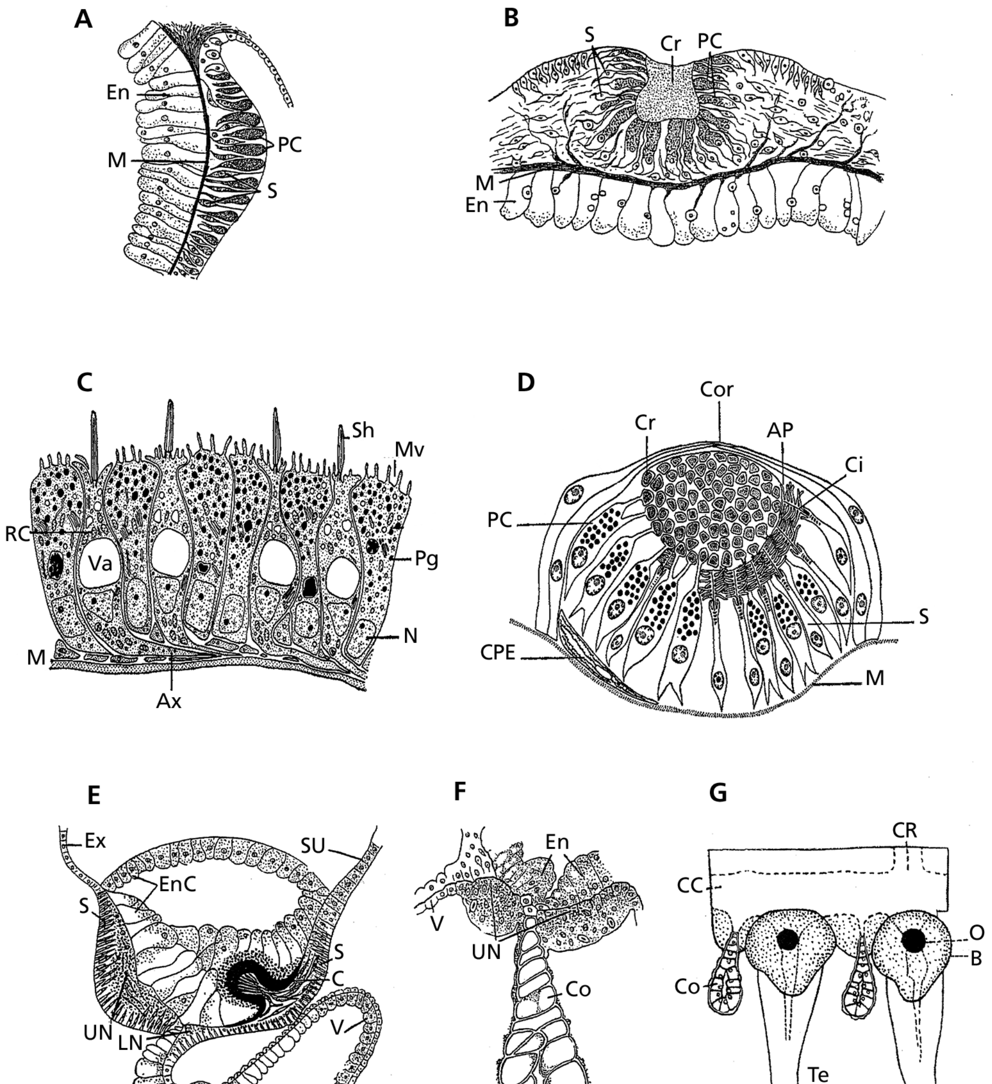


FIG. 35. Histology of the medusae, structure of sense organs: ocelli and cordyli. A, simple ocellus from *Neoturris* (Anthomedusae). B, complex ocellus from *Sarsia* (Anthomedusae). C, ultrathin section through a simple ocellus from *Leuckartiara octona* (Anthomedusae). D, ultrathin section through a complex ocellus of *Cladonema radiatum* (Anthomedusae). E, open statocyst with ecto-endodermal ocellus from *Tiaropsis* (Leptomedusae). F, cordylus from *Laodicea* (Leptomedusae). G, part of the bell margin of *Laodicea* showing the position of the cordyli (A-B & E after Linko, 1900; C after Singla, 1974: p. 417, fig. 3; D after Bouillon & Nielsen, 1974; F after Brooks, 1895; G after Kramp, 1919). AP = photoreceptor portion of the ocellus; Ax = axon; B = marginal bulb; C = pigment cup of the ocellus; CC = circular canal; Ci = cilia; Co = cordyli; Cor = cornea; CPE = embryonic pigmented cells; Cr = lens; CR = radial canal; En = endoderm; EnC = endoderm of the circular canal; Ex = exumbrella; LN= lower or internal nerve ring; M = mesoglea; Mv = microvilly; N = nucleus; O = ocellus; PC = pigmented cell; Pg = pigment; RC =photoreceptor cell; S = sensory cells; Sh = sensory cilia; St = statocyst; SU = subumbrella; Te = tentacle; UN = upper or external nerve ring; V = velum; Va = vacuole.

FIG. 35. *Histologie des méduses, structure des organes des sens : ocelles et cordyles. A, ocelle simple de* Neoturris *(Anthomedusae). B, ocelle complexe de* Sarsia *(Anthomedusae). C, ultracoupe d'un ocelle simple de* Leuckartiara octona *(Anthomedusae). D, ultracoupe d'un ocelle complexe de* Cladonema radiatum *(Anthomedusae). E, statocyste ectodermique ouvert associé à un ocelle ecto-endodermique de* Tiaropsis *(Leptomedusae). F, cordyle de* Laodicea *(Leptomedusae). G, partie du bord exombrellaire de* Laodicea *montrant la position des cordyles (A-B & E d'après Linko, 1900 ; C d'après Singla, 1974 : p. 417, fig. 3 ; D d'après Bouillon & Nielsen, 1974 ; F d'après Brooks, 1895 ; G d'après Kramp, 1919). AP = partie photoréceptrice de l'ocelle ; Ax = axone ; B = bulbe marginal ; C = cupule pigmentaire de l'ocelle ; CC = canal circulaire ; Ci = cil ; Co = cordyle ; Cor = cornée ; CPE = cellule pigmentée embryonnaire ; Cr = cristallin ; CR = canal radiaire ; En = endoderme ; EnC = endoderme du canal circulaire ; Ex = exombrelle ; LN= anneau nerveux interne ; M = mésoglée ; Mv = microvillosité ; N = noyau ; O = ocelle ; PC = cellule pigmentée ; Pg = pigment ; RC = cellule photoréceptrice ; S = cellule sensorielle ; Sh = cil sensoriel ; St = statocyste ; SU = sous-ombrelle ; Te = tentacule ; UN = anneau nerveux externe ; V = velum ; Va = vacuole.*

The mesoglea of the medusae plays a role in locomotion, being the antagonist of the striated muscles of the velum and subumbrella; it acts as a skeleton, conferring form and size; it may accumulate and stock metabolites (i.e., glycogen). Its high percentage of water content confers a relative buoyancy to the animal, this being modified by active ionic exchanges, light ions versus heavy ones or vice and versa, depending on its chosen trajectory; in freshwater medusae, the mesoglea regulates ionic balances.

GENERAL SIPHONOPHORAN STRUCTURE (FIGS 36-38)

Colonial, pelagic, swimming or floating Hydrozoa (except the deep-water, epibenthic, Rhodaliidae), forming highly polymorphic modular colonies of polypoid and medusoid zooids attached to a stem or stolon supported by a floating and swimming system.

Polypoid zooids of several sorts: pneumatophores, gastrozooids, dactylozooids, and bracts. All of them usually associated with the gonophores in repetitive groups, or cormidia, along the stolon. All polypoid structures without oral tentacles. The part of the stem below the floating system, bearing the cormidia, is the siphosome, usually representing most of animal's length. Floating system as pneumatophores and nectophores or swimming bells, together forming the nectosome. The complete and fully developed animal is referred to as the polygastric stage.

Histologically, the polypoid and medusoid zooids resemble the corresponding types of the other Hydroidomedusae.

POLYPOID STRUCTURES

THE PNEUMATOPHORE

The pneumatophore, or apical float, is present only in the Cystonectae and Physonectae. It is of larval ectodermal origin and consists of an external wall or pneumatocodon, and an inner ectodermal wall, or pneumatosaccus, lining the float cavity, typically lined by a chitinous layer. The pneumatosaccus differentiates the gas gland or pneumadenia, containing branched giant cells of unknown function. The pneumatophore may be of complex structure, its cavity may be divided in chambers by vertical septa. In most species, the cavity of the float communicates with the exterior by an apical pore.

THE GASTROZOOIDS

The gastrozooids, or feeding and digestive polyps, lack oral tentacles but have a long contractile basal trailing tentacle bearing lateral contractile branches or tentilla; they have usually a large basal thickening rich in cnidoblasts. The endoderm of the hypostomial region presents numerous folds rich in various gland cells. The gastrozooids are the only members of the colony capable of ingesting food, the extracellular digestion occurs in their cavity and their endodermal layer is the place of primary intracellular digestion. The feeding behaviour of the siphonophores has not been studied much (see Biggs 1977; Carré & Carré 1995). The polypoid origin of siphonophore gastrozooids is questionable: the presence of a basal tentacle suggests that they could also derive from a medusa with a reduced umbrella.

THE DACTYLOZOOIDS

The dactylozooids or palpons (= cystozooids or cystons) may bear small basal unbranched tentacles or palpacles. They have an accessory role in intracellular digestion and possess an apical pore involved in the elimination of small waste particles, the big ones being eliminated by the mouth of the gastrozooid; they seem to have also a sensory function. The dactylozooids are absent in the Calycophorae except *Stephanophyes*, and in the Cystonectae; in the Physonectae they are always several per cormidium.

THE BRACTS

The bracts are usually lamellar, they are bounded by an ectodermal layer, enveloping a thick mesoglea containing an endodermal blind canal (bracteal canal), they have a protective, floating and sensory function and may contain metabolic reserves. They are absent in Cystonectae, leaf-like with a simple bracteal canal in Physonects; in the Athorybiidae the bracts have a swimming function and replace the nectophores; in the Calycophorae they are more complexly organized and have a branched bracteal canal, except in the Hippopodiidae, where they are absent. Their medusoid or polypoid origin is still discussed.

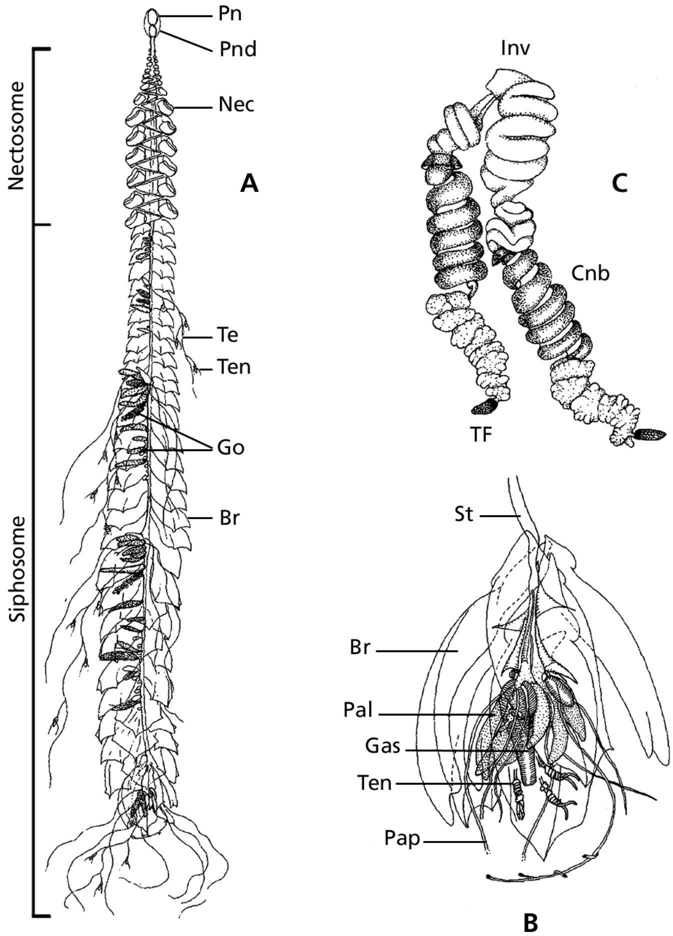


FIG. 36. Morphology of the Siphonophores. A-C, *Agalma elegans* (Physonectae): A, general structure of the polygastric stage; B, distal part of a siphosome; C, detail of a side branch of the tentacle or tentilla (all after Totton, 1965: p. 24, fig. 7 A, D). Br = bract; Cnb = cnidoband; Gas = gastrozooid; Go = gonophore; Inv = involucrum; Nec = nectophore; Pn = pneumatophore; Pal = palpon; Pap = palpacle; Pnd = pneumadenia; St = stolon; TF = terminal filament; Te = tentacle; Ten = tentillium.

FIG. 36. *Morphologie des Siphonophores. A-C,* Agalma elegans *(Physonectae) : A, structure générale d'un stade polygastrique ; B, partie distale d'un siphosome ; C, détail d'une branche d'un tentacule ou tentille (d'après Totton, 1965 : p. 24, fig. 7 A, D). Br = bractée ; Cnb = cnidobande ; Gas = gastérozoïde ; Go = gonophore ; Inv =* involucrum *; Nec = nectophore ; Pn = pneumatophore ; Pal = palpon ; Pap = palpacle ; Pnd = pneumadenia ; St = stolon ; TF = filament terminal ; Te = tentacule ; Ten = tentille.*

THE SIPHOSOMAL STEM

The siphosomal stem or stolon issues from the nectosome out of a more or less developed gutter-like furrow, the hydroecium, which gives a bilateral symmetry to the nectosome, protecting the siphosomal budding area and in which the stolon itself may sometimes withdraw. The stolon has the usual hydrozoan coenosarcal two-layered structure, separated by a thick mesoglea presenting radiating septa penetrating the ectoderm. In some Physonects, the stolon forms a large plate bearing the cormidia. The cormidia are borne on the surface of the stolon arbitrarily considered ventral, although they may sometimes appear to encircle the stolon, an optical illusion due to stolon twisting.

MEDUSOID STRUCTURES

They are of three sorts: nectophores or swimming bells and asexual or sexual medusoids.

THE NECTOPHORES

The nectophores or swimming bells correspond to reduced medusae, they possess an umbrella, a subumbrellar cavity or nectosac, a velum (ostium), an endodermal lamella, 4 unequal radial canals, a circular canal, 2 nerve rings, striated subumbrellar and velar muscle. The nectophores are deprived of manubrium, mouth, tentacles and elaborated visible sense organs. They are very muscular and hence have exceptionally good swimming power. A simple or branched extension of the original larval gastrovascular system, or somatocyst, sometimes containing oil droplets (= oleocysts), runs along the dorsal surface of the hydroecium. The point of convergence of the radial canals has often an eccentric position on the nectosac and is usually

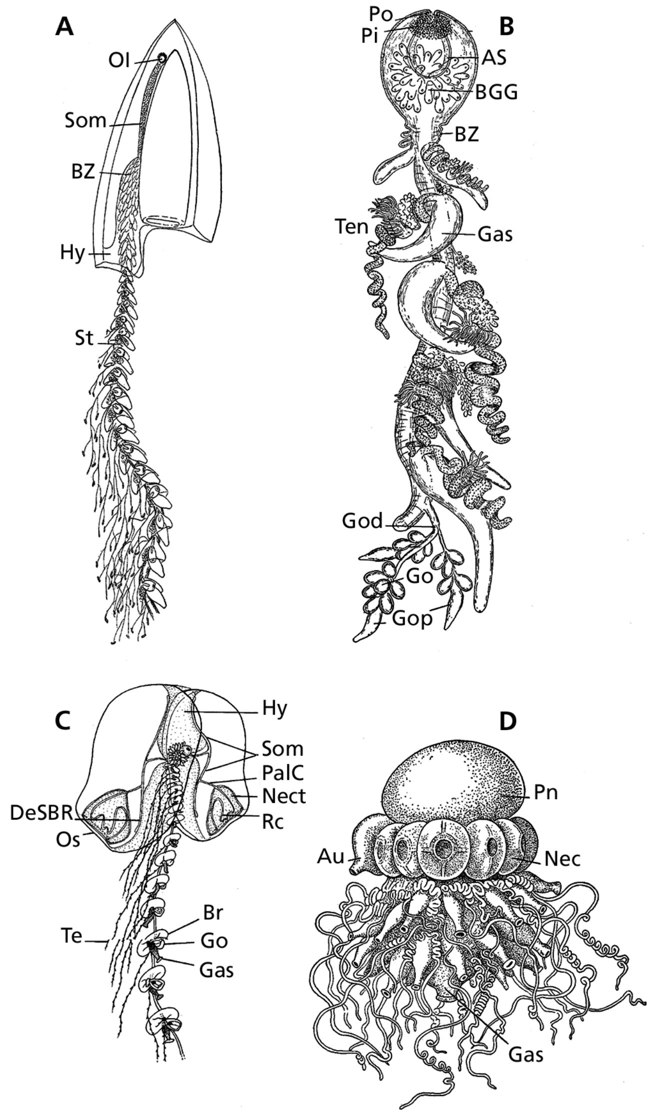


FIG. 37. Morphology of the Siphonophores, various morphological types. A, example of a monophyid calycophoran of the genus *Muggiaea*, Diphyidae. B, specimen of the genus *Rhizophysa*, Rhizophysidae, Cystonectae. C, whole polygastric phase of *Rosacea cymbiformis*, Prayinae, Calycophorae, with two opposite nectophores. D, specimen of the genus *Stephalia* with an aurophore, Rhodaliidae, Physonectae (A-B after Hyman, 1940; C after Totton, 1965; D after Haeckel, 1888). AS = air sac; Au = aurophore; BGG = branched gas gland; Br = bract; BZ = budding zone; DeSBR= descending branch**;** Gas = gastrozooid; Go = gonophore; God = gonodendron; Gop gonopalpon; Hy = hydroecium: Nec = nectophore; Nect = nectosac; Ol =oleocyte; Os = ostium; PalC = pallial canal; Pi = pigment; Pn = float or pneumatophore; Pnc = pneumatocodon; Po = pore; Rc = radial canal; Som = somatocyst; St = stolon; Te = tentacle; Ten = tentillium.

FIG. 37. *Morphologie des Siphonophores, différents types morphologiques. A, exemple d'un calycophore monophyide du genre* Muggiaea*, Diphyidae ; B, spécimen du genre* Rhizophysa*, Rhizophysidae, Cystonectae. C, stade polygastrique de* Rosacea cymbiformis*, Prayinae, Calycophorae, avec deux nectophores opposés. D, spécimen du genre* Stephalia *avec des aurophores, Rhodaliidae, Physonectae (A-B d'après Hyman, 1940 ; C d'après Totton, 1965 ; D d'après Haeckel, 1888). AS = sac aérifère ; Au = aurophore ; BGG = glande à gaz ramifié ; Br = bractée ; BZ = zone bourgeonnante ; DeSBR = branche descendante; Gas = gastérozoïde ; Go = gonophore ; God = gonodendron ; Gop gonopalpon ; Hy = hydroécie : Nec = nectophore ; Nect = nectosac ; Ol = oléocyte ; Os = ostium ; PalC = canal pallial ; Pi = pigment ; Pn = flotteur ou pneumatophore ; Pnc = pneumatocodon ; Po = pore ; Rc = canal radiaire ; Som = somatocyste ; St = stolon ; Te = tentacule ; Ten = tentille.*

connected to the somatocyst by the pedicular (palleal) canal. In most nectophores, the stomatocyst develops at the origin of the pedicular canal. Around the stem, the nectophores of physonects present apical-lateral processes or apical wings which are sometimes bordered by cross ridges or lateral wings, their aboral region presents a specialized area, or thrust block, separating the apical wings and abutting against the nectosomal stem.

Calycophorae usually have only one or two nectophores, an anterior and a posterior one; their nectophores have thin extensions, or basal lamellae, below the ostium of the nectosac, one or more of these lamellae comprise the mouth plate.

GONOZOOID - SEXUAL MEDUSOIDS

The gonozooids of siphonophores may be represented by a single gonophore or by clusters of gonophores attached on a branched stem or gonodendron (= blastostyle). There may be several groups of gonophores per gonozooid. The gonodendron is usually associated with a specialised palpon or gonopalpon. The gonophores are sexual medusoids, their budding occurs like in other Hydroidomedusae with the formation of a medusary nodule, and they have typical medusan characteristics; female ones, however, may be deeply modified. Siphonophores may be monoecious or dioecious. The germ cells develop on the manubrium of the sporosacs or of the eumedusoids, the latter being rarely liberated. The Physonectae female gonophores develop only one egg, but their cormidia may form a succession of several male or female new gonophores. Calycophorae gonophores contain several eggs (2 to 30), usually their cormidia become free as eudoxia, able to form successively several generations of new gonophores during their free life, with the alternation of male and females structures.

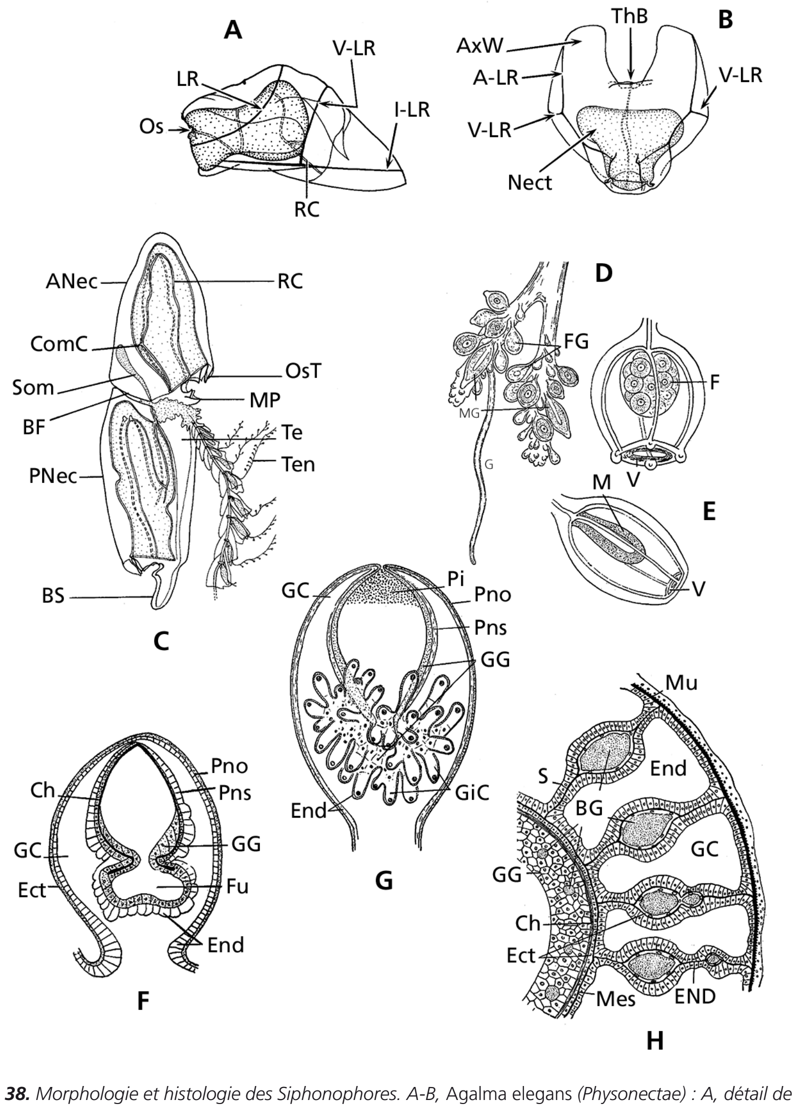


FIG. 38. Morphology and histology of the Siphonophores. A-B, *Agalma elegans* (Physonectae): A, detail of a lateral view of a nectophore; B, detail of an upper view of a nectophore. C, whole polygastric phase *Sulculeolaria quadrivalvis*, Diphyidae, Calycophoridae. D-E, gonophore and medusoid. F, vertical histological section of the pneumatophore of *Agalma*, Physonectae. G, vertical histological section of a float of *Rhizophysa*, Cystonectae, showing the branched gas gland. H, portion of a histological cross section of the complex of float of *Athorybia,* Athorybiidae, Physonectae, with septa and branched giant cells (A-B after Totton, 1965: p. 54, fig. 18 A, B; C after Carré, 1979; D-E, G-H after Hyman, 1940; F after Woltereck, 1905). A-LR = apico-lateral ridge; ANec= anterior nectophore; AxW = apical wings; BF = basal facet; BG = branches of the giant cells in the septa and gas gland; BS = basal lamella; Ch = chitinous lining; ComC = commisural canal; Ect = ectoderm; End = endoderm; Fu = funnel; F = female"gonad"; FG = female gonophore; G = gonopalpon; GC = gastrovascular cavity; GiC = giant cells of the gas gland; GG = gas gland; I-LR = infra-lateral ridge; LR = lateral ridge; M = male "gonad"; Mes = mesoglea; MG = male gonophore ; MP = mouth plate; Mu = muscle; Nect = nectosac; Ost = ostium; OsT = ostial teeth; Pi = pigment; PNec = posterior nectophore; Pno = pneumatocodon (exumbrella); Pns = pnematosaccus (subumbrella); RC = radial canal; S = septa; Som = somatocyst; V-LR = vertical lateral ridge; Te = tentacle; Ten = tentillum; ThB = thrust block; V = velum.

FIG. 38. *Morphologie et histologie des Siphonophores. A-B,* Agalma elegans *(Physonectae) : A, détail de la vue latérale d'un nectophore ; B, détail de la vue dorsale d'un nectophore. C, stade polygastrique de* Sulculeolaria quadrivalvis*, Diphyidae, Calycophoridae. D-E, détail d'un gonophore et de medusoïdes. F, section verticale histologique d'un pneumatophore d'*Agalma*, Physonectae. G, section verticale histologique d'un flotteur de* Rhizophysa*, Cystonectae montrant la glande à gaz ramifiée. H, portion d'une section histologique transversale du complexe de flottaison d'*Athorybia *Athorybiidae, Physonectae, montrant les septa et les cellules géantes ramifiées (A-B d'après Totton, 1965 : p. 54, fig. 18 A, B ; C d'après Carré, 1979 ; D-E, G-H d'après Hyman, 1940 ; F d'après Woltereck, 1905). A-LR = crête apico-latérale ; ANec = nectophore antérieur ; AxW = lobe ou aile apical ; BF = facette basale ; BG = branches des cellules géantes dans les septa et la glande à gaz ; BS = lamelle basale ; Ch = couche chitineuse ; ComC = canal commisural ; Ect = ectoderme ; End = endoderme ; Fu = entonnoir ; F = "gonade" femelle ; FG = gonophore femelle ; G = gonopalpon; GC = cavité gastrovasculaire ; GiC = cellule géante de la glande à gaz ; GG = glande à gaz ; I-LR = crête infra-latérale ; LR = crête latérale ; M = « gonade » mâle ; Mes = mésoglée ; MG = gonophore mâle ; MP = plaque buccale ; Mu = muscle ; Nect = nectosac ; Os = ostium ; OsT = dent ostiale ; Pi = pigment ; PNec = nectophore postérieur ; Pno = pneumatocodon (exombrelle) ; Pns = pnematosaccus (sous-ombrelle) ; RC = canal radiaire ; S = septa ; Som = somatocyste ; V-LR = crête verticale latérale ; Te = tentacule ; Ten = tentille ; ThB = échancrure entre les deux lobes supérieurs du nectophore ; V = velum.*

ASEXUAL MEDUSOIDS

Sterile or asexual medusoids may be associated with the sexual gonophores namely in the Cystonectae and in a few Calycophorae. They may have a propulsive and floating function.

The survival of isolated zooids seems impossible, but the cormidia of most Calycophorae represent real colonial units, breaking loose before the maturation of the gonophores and leading an independent existence, being then termed eudoxia.

CNIDOME

The Siphonophorae have a global cnidome of nine cnidocyst types depending on the suborders: acrophores, anacrophores, desmonemes, stenoteles, homotrichous anisorhizae, atrichous isorhizae, microbasic mastigophores and birhopaloids, 4 of them being exclusive to the group but not common to all species: acrophores, anacrophores (doubtfully recorded from *Tiaricodon coeruleus* by Wenqiao and Xu 1990), homotrichous isorhizae and birhopaloids. The Cystonectae seems to possess only isorhizae and stenoteles; the Physonectae have a general cnidome formed by acrophores, desmonemes, homotrichous anisorhizae, atrichous isorhizae, microbasic mastigophores and stenoteles; in the Calycophorae anacrophores, desmonemes, stenoteles, homotrichous anisorhizae, microbasic mastigophores have been described, the birhopaloids being exclusively found in *Apolemia uvaria* and *Tottonia contorta*. The singlet microtubules of the cnidocyst cilium are very numerous, varying from 300 to 400, whereas in the other Hydrozoa the number varies between 8 and 22.

REMARKS. – The Siphonophorae can be considered as colonies of cormidia, formed by polypoid structures that are so specialised to be assimilated to the organs of an individual (the colony). They are sometimes considered as an enlarged larval nurse carrier or paedophore not becoming sexually mature but budding off sexual medusoids that may be released along with other stem constituents (Totton 1965). The cnidome suggests affinity with the Anthomedusae since desmonemes, typical of this subclass, are present in some groups; also, stenoteles are typical of Anthomedusae but are shared also with some Automedusae. There is no alternation of benthic and pelagic life stages, the colonies remaining pelagic and exploiting a single environment for all their cycle. Each gonophore has a limited number of eggs (1 in the Physonects, 2 to 30 in the Calycophorans, see above), but a cormidium can form successive gonophores increasing so the number of eggs, and the modular colonies, furthermore, are formed by numerous cormidia. Compared to most Antho- and Leptomedusae, whose benthic colonies are long-lived, can undergo a resting phase and produce higher numbers of eggs or medusae, the Siphonophorae have a much lower reproductive rate.

DEVELOPMENT

LIFE CYLES (FIGS 39-43; FIG. 192)

Not all the Hydrozoa present the classical life cycle usually described in text books, i. e.: fertilised eggs, planula, larval hydroid, adult medusae, eggs and sperms, fertilised eggs and so on. This cycle is characteristic, as far it is known, for most Hydroidomedusae with the exception of the Siphonophorae, where the planula gives rise to specialized larvae (i. e., calyconula and siphonula) developing directly into the sipohonophoran adult polygastric stage. The above-described Hydroidomedusae cycle may present several modifications. The most important one is the suppression of the medusa stage, a feature of almost half of the species. Even when medusae are not liberated, however, most gonophores retain a medusan architecture. Other life-cycle modifications include, for instance: the presence of an embryonic encysted stage (e.g., *Hydra*, *Margelopsis, Paracoryne*) which is presumably more common than currently believed; the transformation of the planula into a single planktonic polyp that buds a single medusa that, during its formation, completely resorbs the hydroid (i. e., *Eirene hexanemalis*); the existence of two different cycle patterns, depending on the season, a typical one and another one in which the planula settles and directly produces a gonotheca liberating medusae without forming hydranths (i. e., *Laodicea indica*), or forming a single hydranth, with an attached gonotheca (i. e., *Clytia viridicans*) etc.. The study of Hydroidomedusae life cycles is one of the most promising fields in Hydrozoa biology and may give important indications for the understanding of their evolution.

In the Actinulidae and the Automedusae, development is direct, the embryo giving rise directly to a medusa without the presence of a true larval hydroid stage; in the Narcomedusae the embryonic stages may be external parasites of other animals.

The Polypodiozoa are represented by a single species, *Polypodium hydriforme*, 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.

SEXUAL REPRODUCTION (FIGS 44-52)

SEX DETERMINATION

Species can be either monoecious or dioecious. Simultaneous hermaphrodites occur rarely (e.g., *Eleutheria*, certain *Hydra* and *Tubularia*, *Eudendrium motzkossowskae*, some Aglaopheniidae and Halopterididae). In *Plumularia setacea,* both monoecious and dioecious colonies are recorded. The mechanism of sex determination is not well known in the Hydrozoa. In several cases (e.g., *Hydra*, *Clytia*), sex determination appears ruled by environmental conditions, mainly by temperature. In *Hydra,* multiple genes are thought to influence sex with the degree of manifestation of either sex being dose-dependent.

GAMETES AND FERTILISATION

The gametes of the Hydrozoa are generally of ectodermal origin, but they may also be formed in the endoderm (e.g., Actinulidae, *Nannocoryne*, *Pegantha clara*, *Polypodium*, *Protohydra* and *Solmaris flavescens*).

In most medusan forms, ripe eggs are shed immediately into the external medium. Nevertheless, there are forms in which the eggs remain either fixed on the gonads, or in the subumbrellar space (e.g., *Corymorpha*, *Hybocodon*), where they are fertilised and develop into planulae. In the species with reduced medusae, the eggs remain most often inside the gonophore, where fertilisation occurs and development proceeds to a very advanced stage, from planulae to even young hydranths (e.g., *Cordylophora*, *Halecium*, *Clava*, etc.). Brood chambers can be present both in the medusa stage (*Eleutheria*) and in the hydroid stage (the marsupium of some sertulariids). Other species produce a mucous mass, the acrocyst, where development is completed (e.g., *Calycella syringa*, *Dynamena pumila*, *Opercularella lacerata*, *Thuiaria arctica*, etc.). *Gonothyraea* species have "meconidia", reduced sexual stages disengaged from the gonothecae as cryptomedusoids but remaining attached to the blastostyle by a slender peduncle. The embryos develop inside these reduced medusae till they are liberated as planulae.

Male spawning normally occurs in the water and no copulation is known in the Hydrozoa. The existence of sperm attractants, produced by the eggs, was first demonstrated in the Hydrozoa (Miller 1972). Fertilisation can be internal (when the sperms reach the eggs while these are still on the female) or external (when sperms and eggs are shed in the water and meet there).

CLEAVAGE

The segmentation of the egg is subequal, total, often radial or almost radial. The blastomeres may nevertheless displace themselves, and the embryo then takes an indefinite form, without affecting the following stages. Segmentation leads to a morula.

GASTRULATION

Gastrulation, starting from the morula stage, takes place along different patterns, the most important ones being:

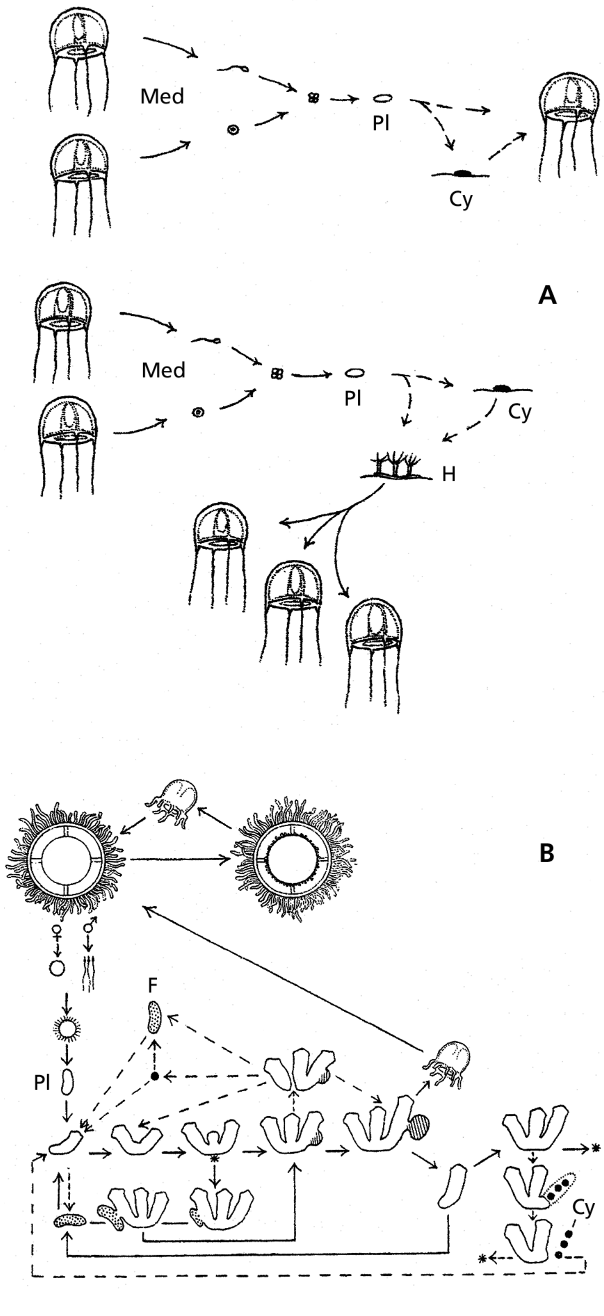


FIG. 39. Development, type of life cycles. A, typical hydroidomedusae life cycle patterns. B, schema of the life cycle of *Limnocnida tanganyicae*, Limnomedusae, the dashed lines show the parts of the cycle that happens in bad ecological conditions. Stippled areas indicate frustules (normal resistant and dispersive stages); large dots indicate resistant cysts; hatched areas show medusa budding (A after Boero, Bouillon & Piraino, 1992; B after Bouillon, 1957). Cy = cyst; F = frustule; H = hydroid; Med = medusae; Pl = planula

FIG. 39. *Développement, type de cycles vitaux. A, modèle du cycle vital des hydroidomedusae. B, schéma du cycle de* Limnocnida tanganyicae, *Limnomedusae, les traits pointillés indiquent les parties du cycle qui se déclenchent dans de mauvaises conditions écologiques. Les surfaces pointillées indiquent la formation de frustules (stades normaux de résistance et de dispersion) ; les gros points noirs indiquent la formation de cystes ; les surfaces hachurées montrent le bourgeonnement médusaire (A d'après Boero, Bouillon & Piraino, 1992 ; B d'après Bouillon, 1957). Cy = cyste ; F = frustule ; H = hydroïde ; Med = méduse ; Pl = planula.*

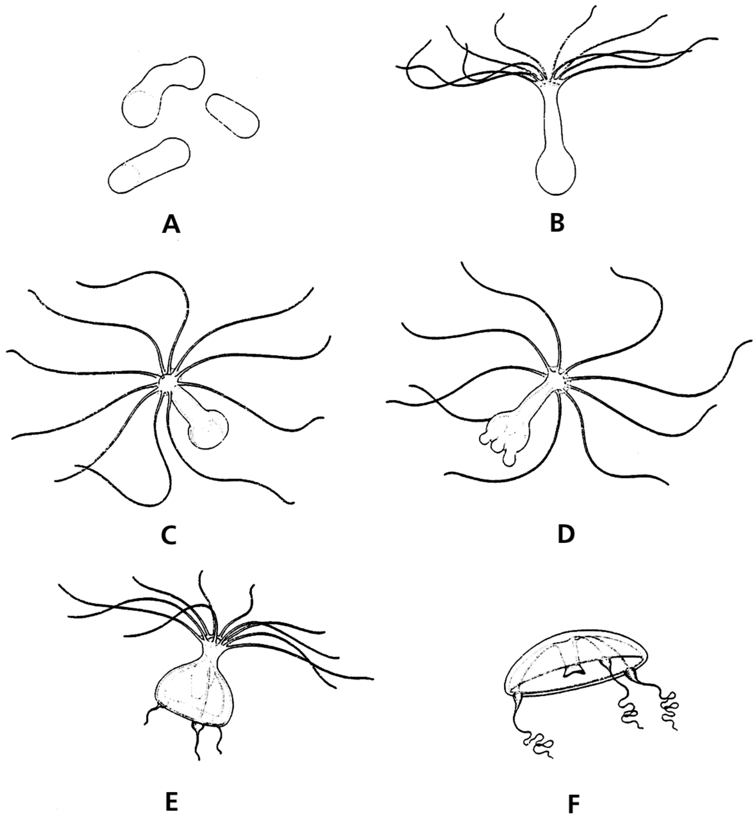


FIG. 40. Development, type of life cycles. Life cycle of *Eirene hexanemalis*, Leptomedusae. The planula develops in a pelagic solitary hydranth which transforms itself in a single medusa. A-F, different stages of the transformation of the hydranth in medusa (after Bouillon, 1983).

FIG. 40. *Développement, type de cycles vitaux. Cycle vital d'*Eirene hexanemalis, *Leptomedusae. La planula se développe en un hydranthe pélagique solitaire qui se transforme lui même ultérieurement entièrement en une simple méduse. A-F, différents stades de la transformation d'un hydranthe en méduse (d'après Bouillon, 1983).*

– the morula gives rise, by division and "delamination", to a cell-filled stage, or stereoblastula, devoid of blastocoelic cavity and which, by active arrangement of the cells, develops into a didermic embryo (i. e., most of the Anthomedusae and Leptomedusae with fixed sporosacs, some Tubulariidae and Acauloidae, some Trachymedusae);
– the morula gives rise to a hollow embryo, the coeloblastula (i. e., most of the Anthomedusae and Leptomedusae with free medusae, the Limnomedusae, the Narcomedusae and some Trachymedusae), which may gastrulate by different ways:

(a) unipolar, or polar, migration: the endoderm is formed by migration of cells issued only from the vegetative pole (i. e., *Rathkea*, *Aequorea*, *Obelia*, etc.).

(b) multipolar migration: the endoderm is formed by cell migration from the entire blastoderm surface (i. e., some *Sarsia*, *Solmundella*);

(c) simple coeloblastic delamination: the cells of the coeloblastula undergo paratangential mitoses, the outer ones differentiate into ectoderm, the inner ones giving the endoderm (i. e., *Geryonia*, *Liriope*);

(d) syncytial delamination: in eggs with high yolk content the total cleavage of the blastomeres does not occur, and only the nuclei with their surrounding cytoplasm divide synchronously, forming a syncytium (i.e. *Aglaophenia*, some *Eudendrium*, *Distichopora*);

(e) mixed multipolar and epibolic gastrulation (*Hydra*).

Gastrulation processes often present intermediate stages between those defined above, or occur by mixed patterns (i. e., delamination and multipolar migration, epiboly and multipolar migration etc.).

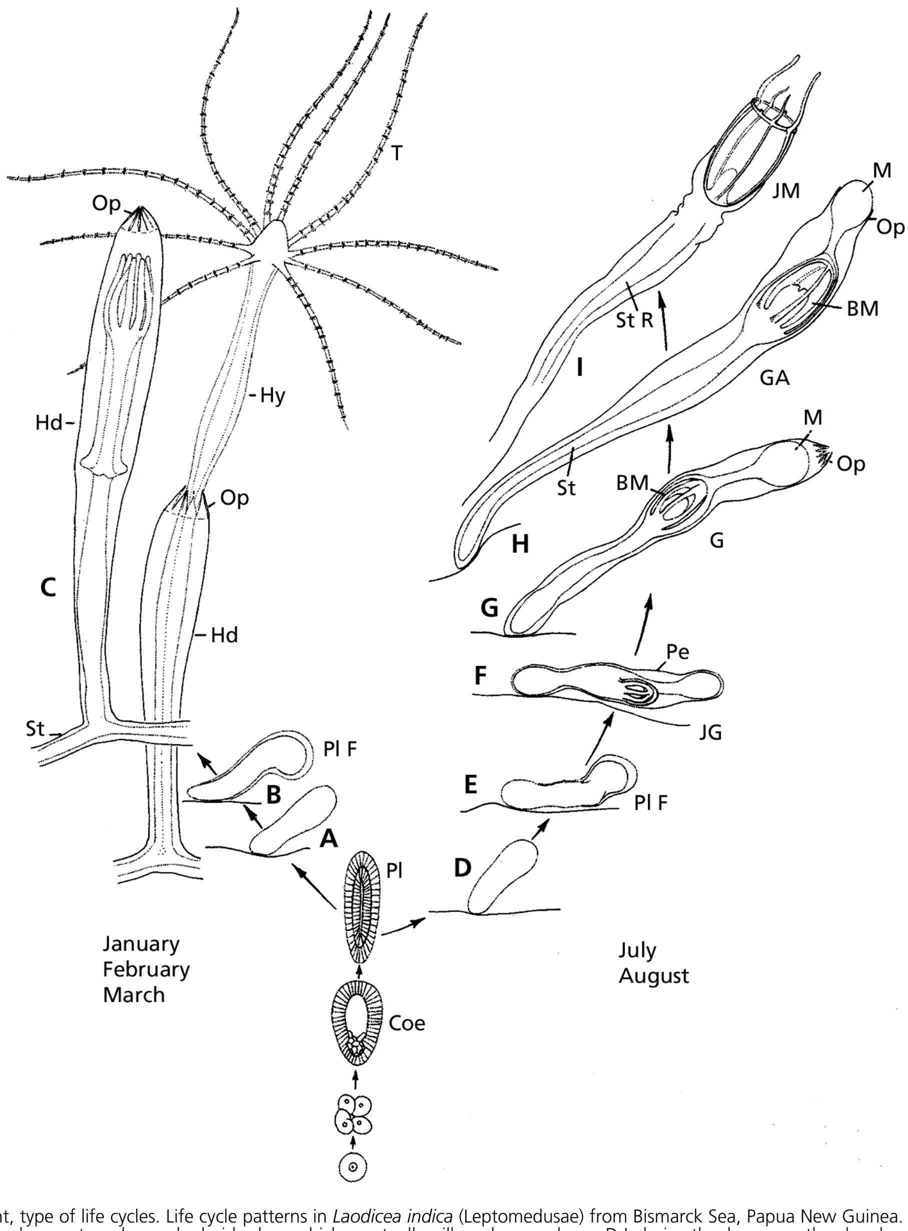


FIG. 41. Development, type of life cycles. Life cycle patterns in *Laodicea indica* (Leptomedusae) from Bismarck Sea, Papua New Guinea. A-C, during the wet season the planula development produces a hydroid colony which eventually will produce medusae. D-I, during the dry season the planula produces a gonotheca which will degenerate after producing a single medusa (after Bouillon *et al*., 1991: p. 153, fig. 1). BM = medusa bud; Coe = gastrulating coeloblastula; G = gonophore; GA = adult gonophore; Hd = hydrotheca; Hy = hydranth; JG = young gonophore; JM = young medusa ready to be liberated; M = terminal fig.; Op = operculum; Pe = perisarc; Pl = planula; Pl F = settling planula; St = stolon; St R degenerating stolon; T = tentacle.

FIG. 41. *Développement, type de cycles vitaux. Modèle de cycle chez* Laodicea indica *(Leptomedusae) dans la mer de Bismarck, Papua New Guinea. A-C, durant la saison des pluies le dévelopement de la planula produit une colonie d'hydroïdes qui peut éventuellement produire des méduses. D-I, durant la saison sèche chaque planula produit une gonothèque qui dégénère après avoir produit une seule méduse (d'après Bouillon et al., 1991 : p. 153, fig. 1). BM = bourgeon médusaire ; Coe = coeloblastule gastrulant ; G = gonophore ; GA = gonophore adulte ; Hd = hydrothèque ; Hy = hydranthe ; JG = jeune gonophore ; JM = jeune méduse prête à se libérer ; M = fig. au terminal ; Op = opercule ; Pe = périsarc ; Pl = planula ; Pl F planula se fixant ; St = Stolon ; St R= stolon en dégénérescence ; T = tentacule.*

PLANULA

All these types of gastrulation lead to the formation of a diblastic embryo: the planula. This embryo presents already a complex structure, much differentiated but also very different from one group to another.

In the Hydroidomedusae, with the exception of the Siphonophorae (see below), the ectoderm of planulae is constituted of generally flagellated ectoblastic cells (and not ciliated as reported by almost all authors!) among which several cellular types can be recognized: glandular cells of the spumous type which may or may not be accompanied by glandular cells of the spherulous type, granulous cells, nerve cells, sensory cells, and cnidoblasts and interstitial cells. These two latter cell types, however, originate most often in the endoblast, where they differentiate, to migrate in the ectoblast only at a later stage of development. In the planula body, endoblastic cells present several stages of evolution into normal epithelio-muscular cells. Fully-developed planulae lead a free life of variable duration, from a few hours to several days, then attach by the anterior pole, generally enlarged, and glandular, to an appropriate support, collapse, and give rise to a primary polyp. The anterior region of the embryo is transformed into the fixation sole. The median zone, by evagination, becomes the primary stolon, whereas the posterior region constitutes the primordia of the first hydranth. The embryonic neural and glandular cells, which function in cementing the anterior end to the substrate, are destroyed during the transformation of the planula into a polyp. Sometimes, several polyps bud off from a single planula (e.g., *Oceania armata*, *Mitrocoma annae*).

In certain hydroids, the planula does not immediately leave the gonophore, but continues its development in it, either partially, producing an intermediate stage, the actinula (i.e. *Tubularia*, *Myriothela),* or completely, a normal polyp leaving the gonophore (certain gonophores of *Cordylophora*). Some hydroids have zooxanthellate planulae (e.g., *Halecium*) that can survive for months before metamorphosing into a polyp. Planula

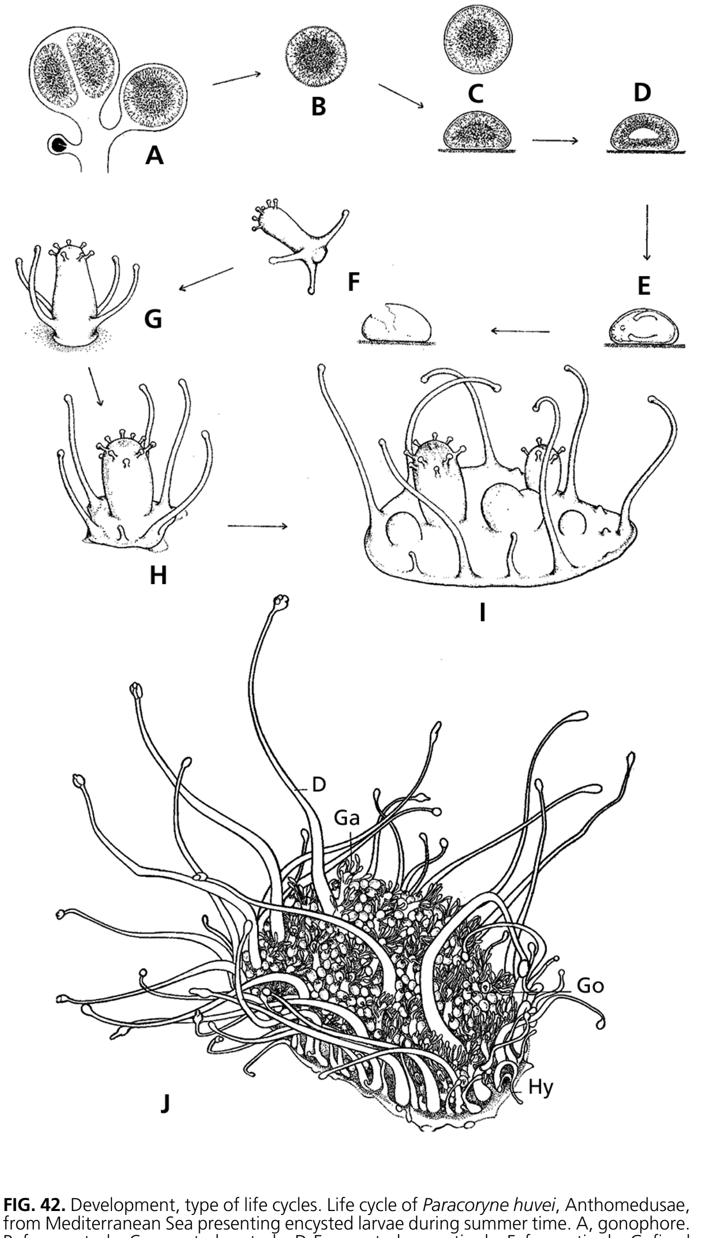


FIG. 42. Development, type of life cycles. Life cycle of *Paracoryne huvei*, Anthomedusae, from Mediterranean Sea presenting encysted larvae during summer time. A, gonophore. B, free gastrula. C, encysted gastrula. D-E, encysted pre-actinula. F, free actinula. G, fixed actinula. H, beginning of the differentiation of a young colony. I, developing colony. J, adult colony (after Bouillon, 1975). D = dactylozooid; Ga = gastrozooid; Go = gonozooid; Hy = hydrorhiza.

FIG. 42. *Développement, type de cycles vitaux. Cycle vital de* Paracoryne huvei*, Anthomedusae, de la Mediterranée présentant une larve encystée durant la période estivale. A, gonophore. B, gastrula libre. C, gastrula encystée. D-E, pré-actinule encystée. F, actinule libre. G, actinule fixée. H, début de la différentiation d'une jeune colonie. I, colonie en développement. J, colonie adulte (d'après Bouillon, 1975). D = dactylozoïde; Ga = gastérozoïde; Go = gonozoïde; Hy = hydrorhize.*

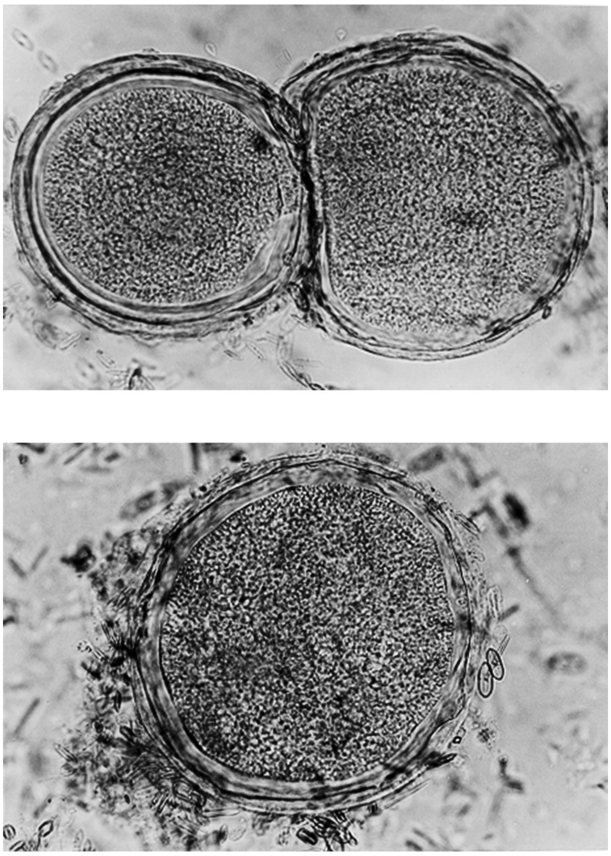


FIG. 43. Development, type of life cycles. Life cycle of *Paracoryne huvei*, Anthomedusae (see fig. 42). Photographs of living encysted gastrula (after Bouillon, 1975).

FIG. 43. *Développement, type de cycles vitaux. Cycle vital de* Paracoryne huvei*, Anthomedusae (voir fig. 42). Photographies de gastrulas vivantes encystées (d'après Bouillon, 1975).*

encystment is probably very common in the development of hydroids with fixed gonophores, since many species reproduce sexually at the end of the favourable season and then disappear. Sexual reproduction, in these cases, is not followed by an increase in population size but, instead, by the disappearance of all active stages. It is then reasonable to assume that planula encystment occurs.

In the Siphonophorae, the planulae remain pelagic and are without the cellular differentiation typical of the other Hydroidomedusae planulae. They have a short lifetime, usually much less than 24 hours, metamorphosing rapidly into specialised pelagic larvae, the siphonula (usually with a primary or larval aboral bract and a primary oral gastrozooid) in the Physonects, and the calyconula (with a unique latero-aboral, usually deciduous, larval nectophore and an oral primary gastrozooid) in the Calycophorans. Both larval types develop into the adult sexual form or polygastric stage.

The Automedusae do not present a hydroid stage (hypogenetic) and possess either direct or parasitic development (certain Narcomedusae). They develop into young medusae either directly or through intermediate tentaculate, post-embryonic stages inappropriately called "actinulae" that, in fact, are not polyps but larval medusae. Their planulae have a simple embryonic didermic cellular organisation lacking the specialised neural and glandular cells characterising most Hydroidomedusae.

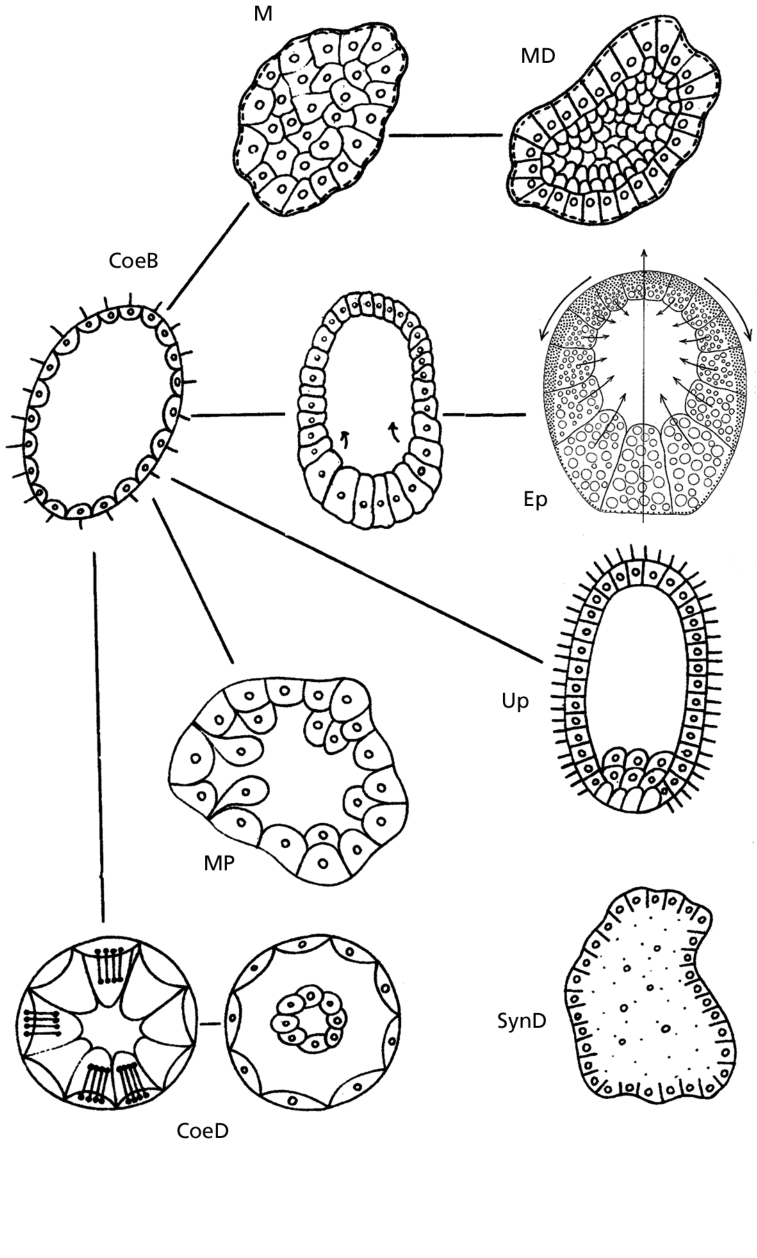


FIG. 44. Development, sexual reproduction of the Hydroidomedusae: Some of the various possible types of gastrulation (redrawn from various sources). CoeB = coeloblastula; CoeD = gastrulation by coeloblastic delamination; Ep = mixed multipolar and epibolic gastrulation; M = morula; MD = gastrulation by morula delamination or cellular arrangement; MP = multipolar gastrulation; SynD = gastrulation by syncitial delamination; UP = gastrulation by unipolar migration.

FIG. 44. *Développement, reproduction sexuelle chez les Hydroidomedusae : Quelques uns des types de gastrulation possibles (repris de différentes sources). CoeB = coeloblastula ; CoeD = gastrulation par délamination coeloblastique ; Ep = gastrulation mixe multipolaire et épibolique ; M = morula ; MD = gastrulation par délamination morulaire ou arrangement cellulaire ; MP = gastrulation multipolaire ; SynD = gastrulation par délamination syncitiale ; UP = gastrulation par migration unipolaire.*

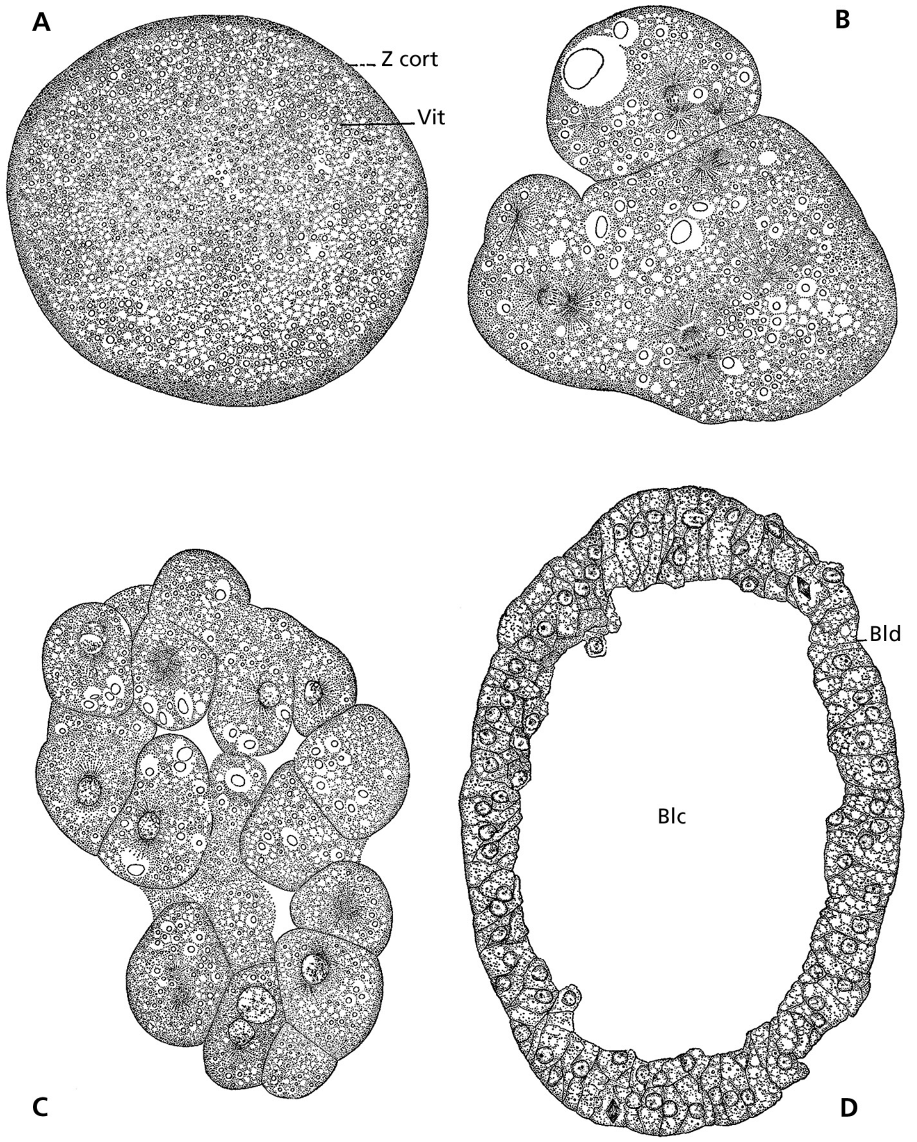


FIG. 45. Development, sexual reproduction of the Hydroidomedusae: Histological sections through the early developmental stages of *Coryne* (*Sarsia*) *eximia*, Anthomedusae. A, oocyte. B, first cleavages. C, morula. D, coeloblastula (after Bodo & Bouillon, 1968). Blc = blastocoelic cavity; Bld = blastoderm; Vit = vitellus; Z cort = cortical area.

FIG. 45. *Développement, reproduction sexuelle chez les Hydroidomedusae : Sections histologiques de stades de développement de* Coryne *(*Sarsia*)* eximia*, Anthomedusae. A, oocyte. B, premières divisions. C, morula. D, coeloblastula (d'après Bodo & Bouillon, 1968). Blc = cavité blastocoeliène ; Bld = blastoderme ; Vit = vitellus; Z cort = zone corticale.*

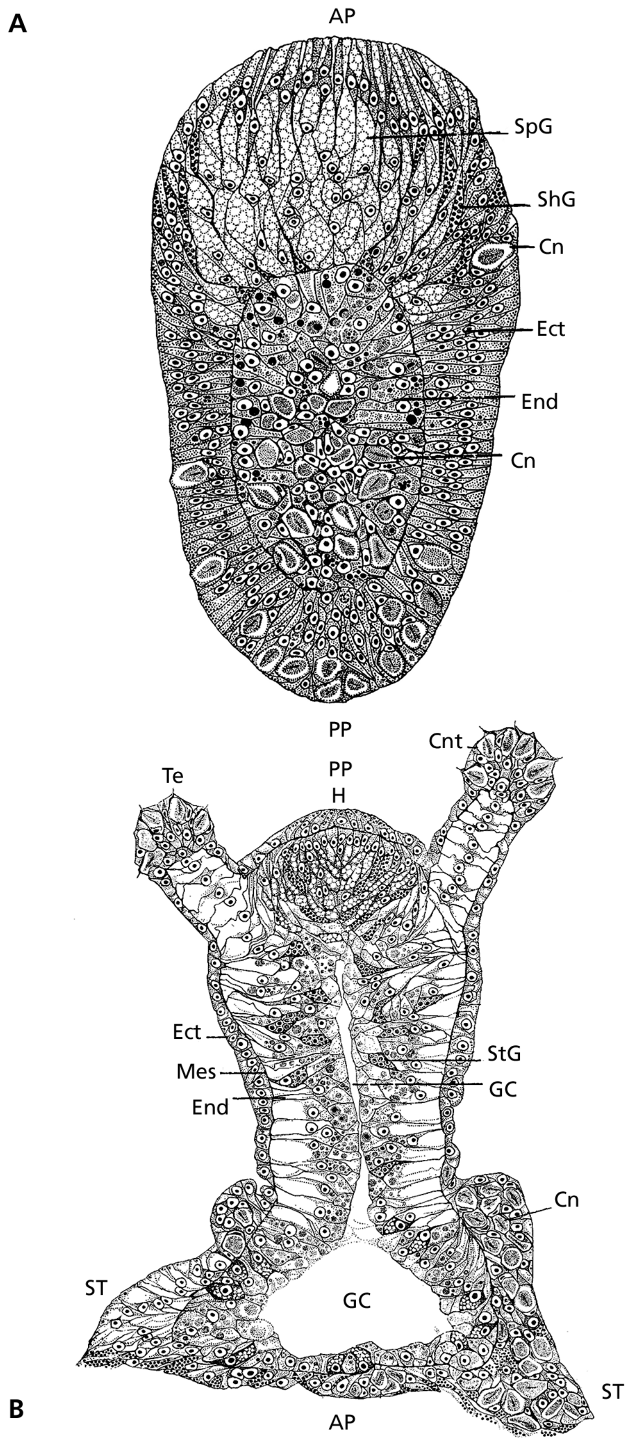


FIG. 46. Development, sexual reproduction of the Hydroidomedusae: Histological longitudinal section of the final stages of the development of *Coryne (Sarsia) eximia*, Anthomedusae. A, planula. B, young polyp issued from the planula (after Bodo & Bouillon, 1968). AP = anterior pole; Cn = cnidoblast; Cnt = cnidocyst; Ect = ectoblast; End = endoblast; GC = gastric cavity; H = hypostome; Mes = mesoglea; PP = posterior pole; ShG = spheroulous embryonic gland cell; Spg = spumous embryonic gland cell; ST = stolon; StG = stomacal spheroulous gland cell of the hydranth; Te = tentacle.

FIG. 46. *Développement, reproduction sexuelle chez les Hydroidomedusae : Sections histologiques longitudinales des stades terminaux du développement de* Coryne (Sarsia) eximia*, Anthomedusae. A, planula. B, jeune polype issu de la planula (d'après Bodo & Bouillon, 1968). AP = pôle antérieur; Cn = cnidoblaste ; Cnt = cnidocyste ; Ect = ectoblaste ; End = endoblaste ; GC = cavité gastrique ; H = hypostome ; Mes = mésoglée ; PP = pôle postérieur ; ShG = cellule glandulaire sphéruleuse embryonnaire ; Spg = cellule glandulaire spumeuse embryonnaire ; ST = stolon ; StG = cellule glandulaire sphéruleuse stomacale de l'hydranthe ; Te = tentacule.*

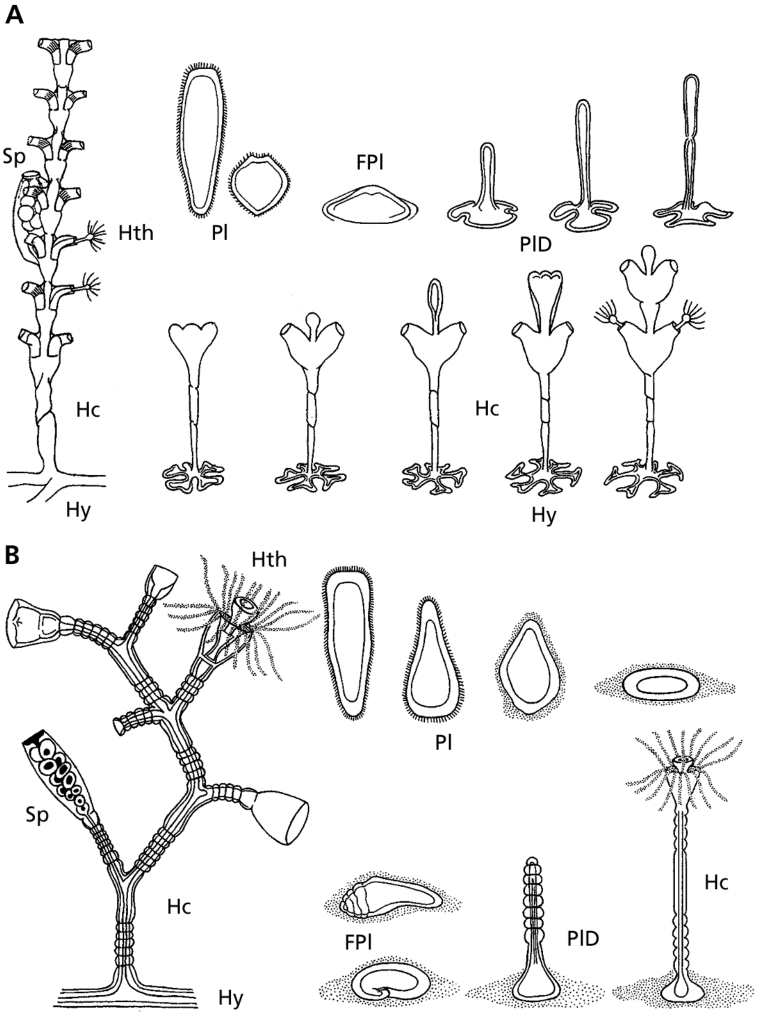


FIG. 47. Development, sexual reproduction of the Hydroidomedusae: Different stages of the differentiation of the planula into a hydroid colony. A, *Dynamena pumila*. B, *Laomedea flexuosa*, both Leptomedusae (redrawn from Tardent, 1978). Hc = hydrocaulus; FPl = fixed planula; Hth = hydranth; Hy = hydrorhiza; Pl = planula; PlD = developing planula; Sp = sporosac.

FIG. 47. *Développement, reproduction sexuelle chez les Hydroidomedusae : Différents stades de la différentiation de la planula en une colonie d'hydroïdes. A,* Dynamena pumila. *B,* Laomedea flexuosa*, deux Leptomedusae (d'après Tardent, 1978). Hc = hydrocaule ; FPl = planula fixée ; Hth = hydranthe ; Hy = hydrorhize ; Pl = planula ; PlD = planula se développant ; Sp = sporosac.*

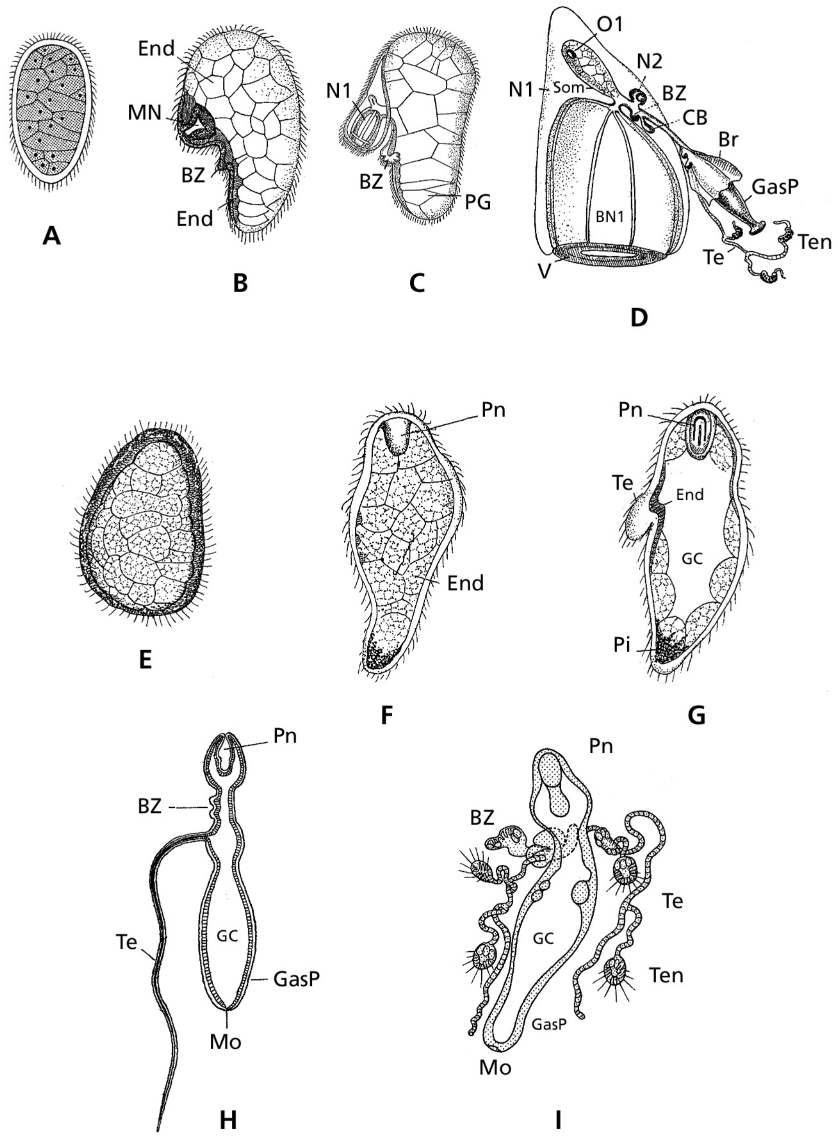


FIG. 48. Development, sexual reproduction of the Hydroidomedusae: Siphonophores. A-D, developmental stages of a calycophorid. E-I, developmental stages of a physophorid (A after Metschnikoff, 1874; B-G redrawn from Dawydoff, 1928; H after Delage & Hérouard, 1901; I after Woltereck, 1905). BN1= umbrella of the primary nectophore Br = bract; BZ = primary budding zone; CB = cormidial bud; End = primary endoblast; GasP = primary gastrozooid; GC = gastric cavity; MN = medusary nodule of the primary bell or nectophore; MO = mouth; N1= primary deciduous nectophore; N2 = bud of the secondary or permanent nectophore; Ol = oleocyte; PG = outline of the future gastrozooid; Pi = pigmented area; Pn = pneumatophore; Som = somatocyst; Te = fishing tentacle; Ten = tentilla; V = velum.

FIG. 48. *Développement, reproduction sexuelle chez les Hydroidomedusae : Siphonophores. A-D, stades développementaux d'un calycophorid. E-I, stades développementaux d'un physophorid (A d'après Metschnikoff, 1874 ; B-G d'après Dawydoff, 1928 ; H d'après Delage & Hérouard, 1901 ; I d'après Woltereck, 1905). BN1= ombrelle du nectophore primaire ; Br = bractée ; BZ = zone bourgeonnante primaire ; CB = bourgeon cormidial ; End = endoblaste primaire ; GasP = gastérozoïde primaire ; GC = cavité gastrique ; MN = nodule médusaire de l'ombrelle primaire ou nectophore ; MO = bouche ; N1= premier nectophore, caduc ; N2 = bourgeon du second nectophore ou nectophore permanent ; Ol = oléocyte ; PG = ébauche du futur gastérozoïde ; Pi = surface pigmentée area ; Pn = pneumatophore ; Som = somatocyste ; Te = tentacule pêcheur ; Ten = tentille ; V = velum.*

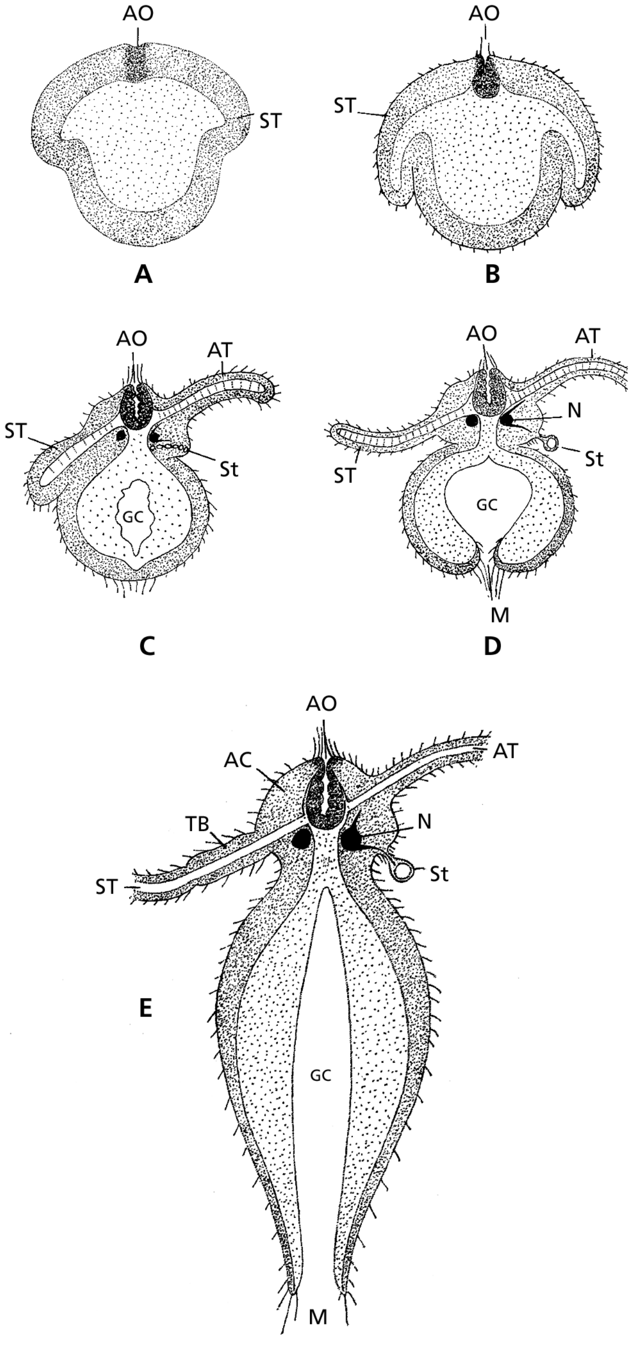


FIG. 49. Development, sexual reproduction. Actinulidae: Longitudinal section of different stages of the development of *Halammohydra schulzei*, Halammohydridae. A-B, postgastrulation stage. C, young halhydrula. D, halhydrula. E, adult *Halammohydra* (after Swedmark & Teissier, 1966). AC = aboral cone; AO = adhesive organ; AT = tentacle of the aboral girdle; GC = gastric cavity; M = mouth; N = nerve ring; St = statocyst; ST = tentacle of the subaboral girdle; TB = tentacular bulb.

FIG. 49. *Développement, reproduction sexuée. Actinulidae : Section longitudinale de différents stades de développement d'*Halammohydra schulzei*, Halammohydridae. A-B, stade postgastrulation. C, jeune halhydrule. D, halhydrule. E,* Halammohydra *adulte (d'après Swedmark & Teissier, 1966). AC = cône aboral ; AO = organe adhésif ; AT = tentacule de la ceinture aborale ; GC = cavité gastrique ; M = bouche ; N = anneau nerveux ; St = statocyste ; ST = tentacule de la ceinture subaborale ; TB = bulbe tentaculaire.*

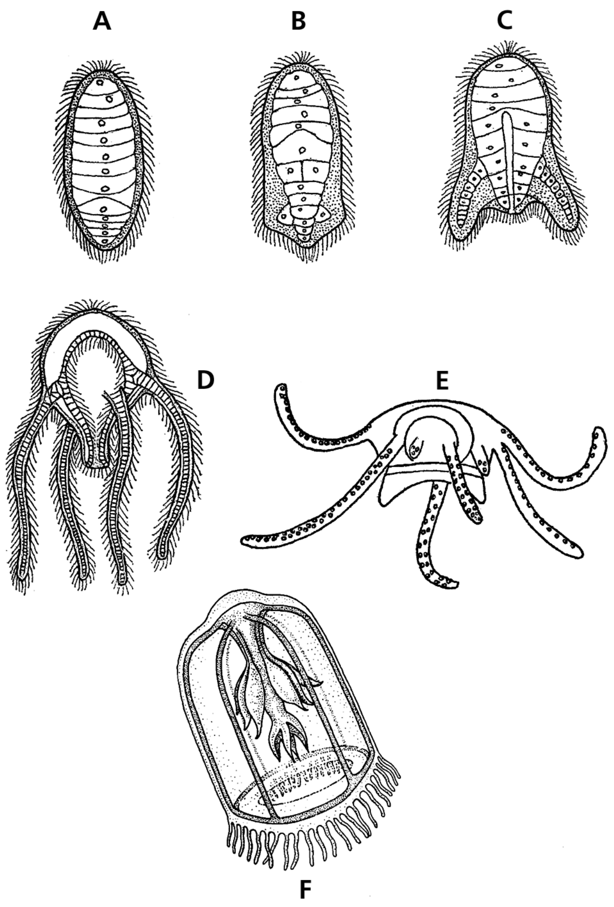


FIG. 50. Development, sexual direct reproduction of Automedusae. A-F, development of *Aglaura hemistoma*, Trachymedusae. A, planula. B, planula with tentacle buds and mouth cone. C, older planula sprouting of the tentacles, developing the gastric cavity and mouth. D, young medusae with tentacles and manubrium. E, juvenile medusae developing subumbrellar cavity. F, adult *Aglaura* (A-E after Metschnikoff, 1886; F after Bayer & Owre, 1968).

FIG. 50. *Développement, reproduction sexuelle directe des Automedusae. A-F, développement d'*Aglaura hemistoma*, Trachymedusae. A, planula. B, planula avec des ébauches de bourgeons tentaculaires et de cône buccal. C, planula plus âgée montrant les ébauches tentaculaires, le développement de la cavité gastrique et de la bouche. D, jeune méduse avec tentacules et manubrium. E, méduse juvénile développant la cavité sous-ombrellaire. F,* Aglaura *adulte (A-E d'après Metschnikoff, 1886 ; F d'après Bayer & Owre, 1968).*

ASEXUAL REPRODUCTION (FIGS 53-57)

In the Hydrozoa, several types of asexual reproduction occur, being one of the main characteristics of the group. The Trachymedusae and the Actinulidae, however, do not present asexual reproduction. The main patterns of asexual reproduction are:

FISSION

Certain hydranths and a few hydromedusae may also reproduce by longitudinal or transversal fission (i. e., *Protohydra*, *Hydra,* the medusae of *Cladonema* and *Clytia*).

PODOCYSTS OR PROPAGULES

Under adverse ecological conditions, some hydroid colonies isolate fragments of hydrocauli, hydrocladia or stolon, enveloped by perisarc, ensuring the propagation and direct dissemination of the species but that may act as resting stages or cysts.

BUDDING OF PLANULA-LIKE BODIES, OR FRUSTULES, OF DIFFERENT TYPES

This is more common in hydroids, but can occur exceptionally also in some medusae (i. e., *Eucheilota paradoxica*).

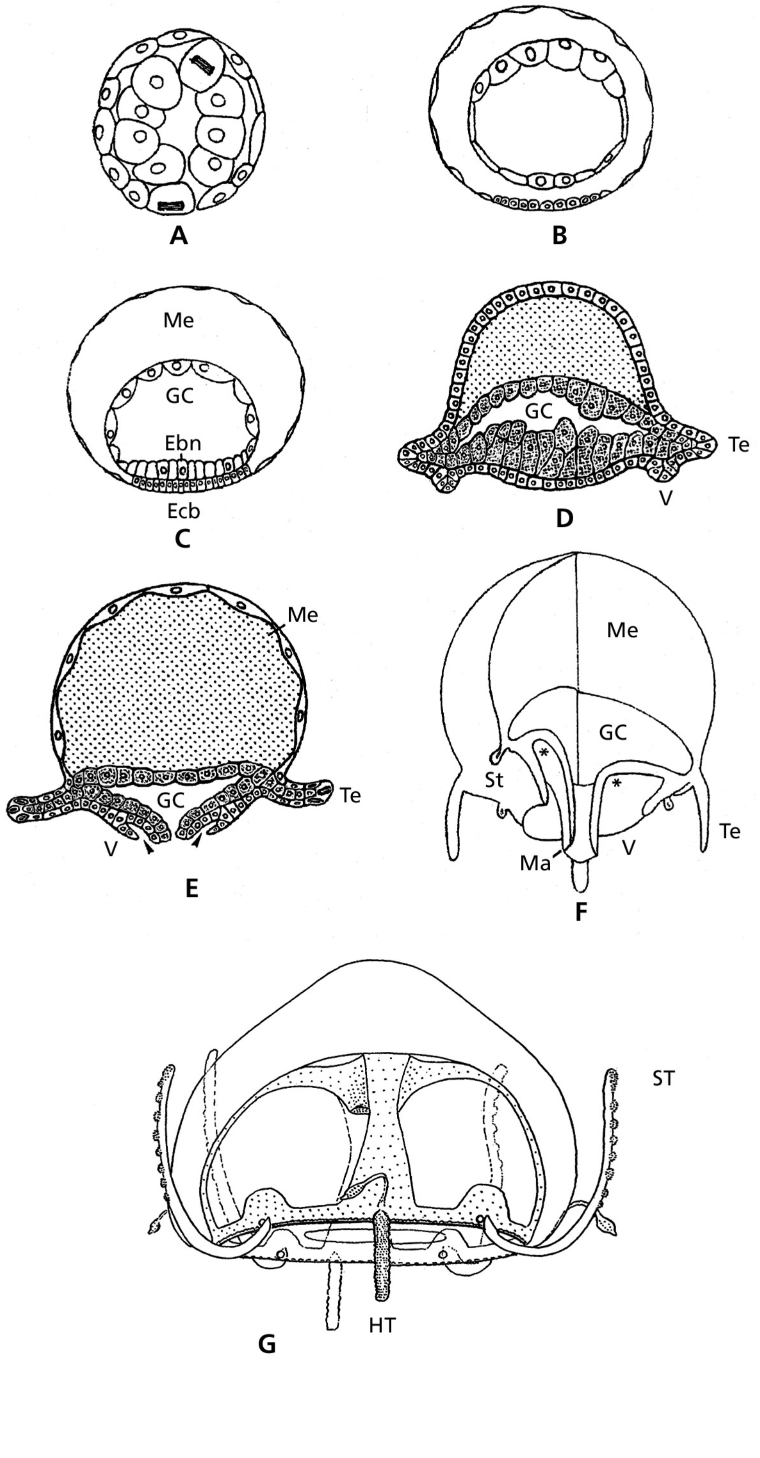


FIG. 51. Development, sexual direct reproduction of Automedusae. A-G, development of *Liriope tetraphilla*, Trachymedusae. A-B, planula. C, planula developing the gastric cavity and the oral ectodermal thickening. D, oral thickening forming the tentacles and the velum. E, differentiation of the velum, the manubrium and the subumbrellar cavity, increasing development of the mesoglea. F, fully developed juvenile medusae, an interradial section (left side), a perradial section (right side). G, young specimen of *Liriope* (A-C, E after Metschnikoff, 1886; D after Maas, 1905; F redrawn from Delage & Herouard, 1901; G after Russell, 1953). Arrows and asterisk = subumbrellar cavity; Ecb = ectoblastic thickening; Enb = endoblastic thickening; GC = gastric cavity; HT = secondary hollow perradial marginal tentacle; Ma = manubrium; Me = Mesoglea; St = statocyst; ST = solid interradial marginal tentacle; Te = marginal tentacle of young medusae; V = velum.

FIG. 51. Développement, reproduction sexuelle directe des Automedusae. A-G, développement de Liriope tetraphilla, *Trachymedusae. A-B, planula. C, planula développant la cavité gastrique et l'épaississement ectodermique oral. D, épaississement oral différenciant les tentacules et le velum. E, différentiation du velum, du manubrium et de la cavité sous-ombrellaire, accroissement du volume mésogléen. F, méduse juvenile développée, section interradiaire (à gauche), section perradiale (à droite). G, jeune spécimen de* Liriope *(A-C, E d'après Metschnikoff, 1886; D d'après Maas, 1905; F d'après Delage & Herouard, 1901; G d'après Russell, 1953). Flèches et astérisques = cavité sous-ombrellaire ; Ecb = épaississement ectoblastique; Enb = épaississement endoblastique; GC = cavité gastrique; HT = tentacule marginal perradial secondaire creux; Ma = manubrium; Me = mésogléе; St = statocyste; ST = tentacule marginal interradiaire solide ou plein; Te = tentacule marginal d'une jeune méduse; V = velum.*

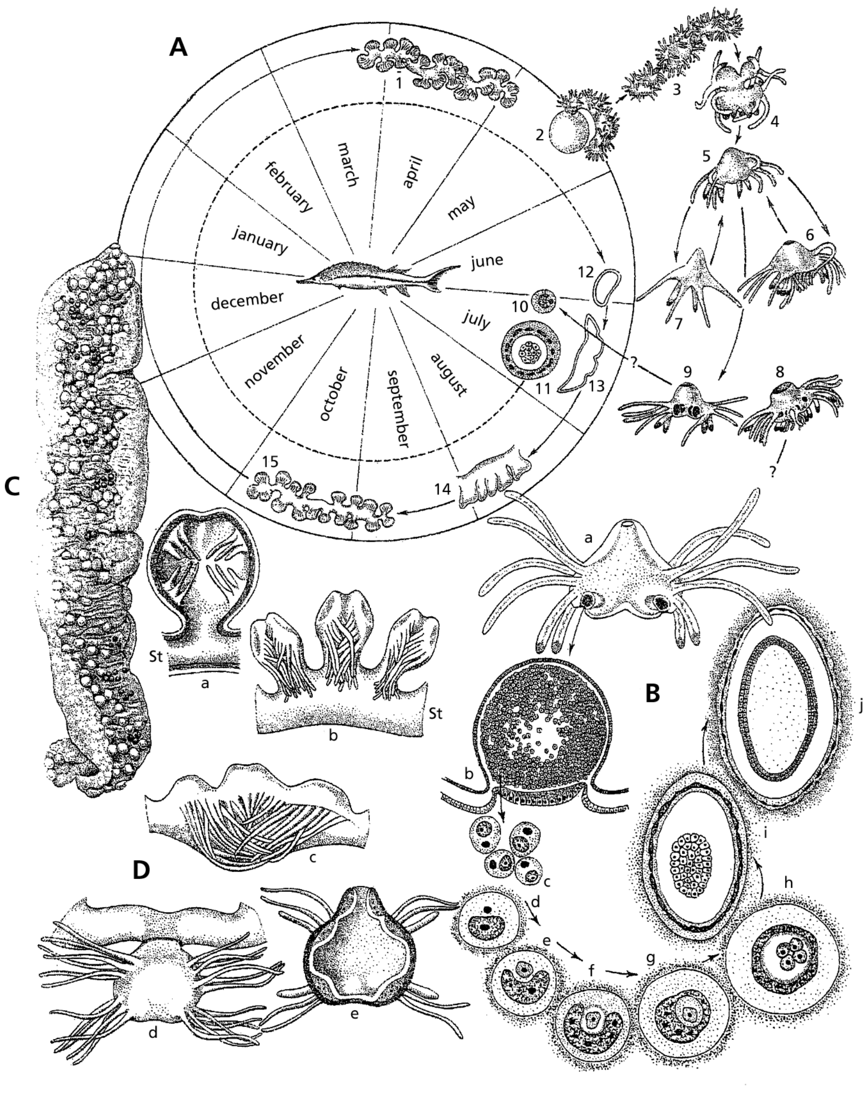
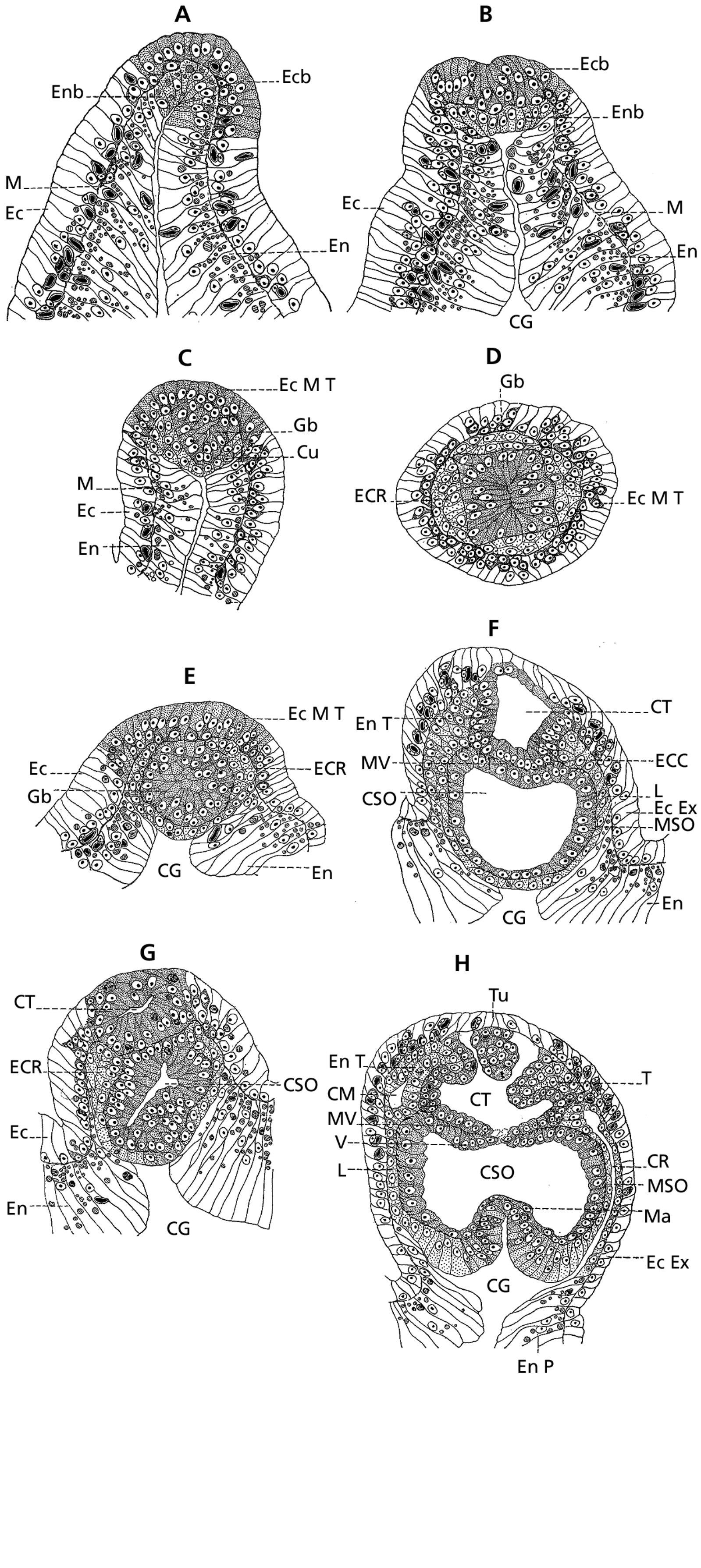


FIG. 52. Development, sexual and asexual reproduction of the Polypodiozoa, life cycle of *Polypodium hydriforme* internal parasite of Acipenserid fishes. A, General cycle: 1, reversed stolon prolifer; 2, stolon prolifer leaving an infected Acipenserid egg, the tentacles are external; 3, stolon prolifer in the water; 4, fragment of a stolon; 5, polyp with 12 tentacles; 6, polyp with 24 tentacles; 7, polyp with 6 tentacles; 8, female polyp; 9, male polyp; 10, binucleate cell parasite of an Acipenserid oocyte; 11, morula encapsulated in the trophamion; 12, planula; 13, budding planula; 14, stolon prolifer without tentacles; 15, stolon prolifer reversed with internal tentacles. B, Diagram of the formation of the trophamion: a, sexual medusa; b, gonad with binucleated cells; c, binucleated cells; d-g, binucleated cells parasite of a fish oocyte; h, segmentation of the embryo; i, morula developed stage inside the trophamion; j, planula stage inside the trophamion. C, ovary of an *Acipenser*: the large eggs are parasitised, the small ones are not. D, a-c, reversed buds with internal tentacles on a stolon prolifer (St); d, stolon prolifer with external tentacles; e, medusae liberated from an infected fish egg (Redrawn from Bouillon, 1987).

FIG. 52. *Développement, reproduction sexuelle et asexuelle des Polypodiozoa, cycle vital de* Polypodium hydriforme *parasite interne des poissons Acipenserides. A, cycle général : 1, stolon prolifère aux feuillets inversés ; 2, stolon prolifère quittant l'œuf d'un Acipenserides infecté, les tentacules sont devenus externes ; 3, stolon prolifère dans l'eau ; 4, fragment d'un stolon ; 5, polype avec 12 tentacules ; 6, polype avec 24 tentacules ; 7, polype avec 6 tentacules ; 8, polype femelle ; 9, polype mâle ; 10, cellule binuclée parasite d'un oocyte d'Acipenserides ; 11, morula encapsulée dans le trophamion ; 12, planula ; 13, planula bourgeonnante ; 14, stolon prolifère sans tentacules ; 15, stolon prolifère à feuillet inversé et tentacules internes. B, diagramme de la formation du trophamion : a, méduse sexuée libre ; b, gonade avec des cellules binuclées ; c, cellule binuclée ; d-g, cellules binuclées parasite d'oocyte de poisson ; h, segmentation de l'embryon ; i, morula se développant dans le trophamion ; j, planula à l'intérieur du trophamion. C, ovaire d'un* Acipenser : *les œufs volumineux sont parasités, les petits œufs non. D, a-c, bourgeons de stolons prolifère inversés avec des tentacules internes (St) ; d, stolon prolifère retouné avec des tentacules externes ; e, méduse liberée d'un œuf de poisson infecté (d'après Bouillon, 1987).*



FIGS 53-54. Development, asexual reproduction: Organogenesis of the medusa budding in Hydroidomedusa (Limnocnida). A, dedifferentiation of the ectoderm and endoderm in ectoblast and endoblast at the beginning of the budding processes. B, ectoblastic proliferation and formation of the endoblastic plate. C, origin of the medusary nodule and the endodermal cup. D-E, growth of the medusary nodule, formation of the ectodermal tentacular plate and origin of the radial canal from the endodermal cup. F-G, appearance of the subumbrellar cavity within the medusary nodule, formation of the tentacular cavity within the ectodermal tentacular mass and of the radial canals. H, almost fully grown medusae, showing the subumbrellar cavity, the manubrium, the radial canals, the circular canal, the gastric cavity, the velum, and the tentacles (from Bouillon, 1957). A-C, E-H, longitudinal sections; D, transversal section. CG = gastric cavity of the budding hydroid or medusae; CM = marginal or circular canal; CR = radial canal; CSO = subumbrellar cavity; CT = tentacular cavity; Cu = endoblastic cup; Ec = ectoderm; Ecb = ectoblast; ECC = outline of the circular or marginal canal; Ec M T = tentacular ectoblastic mass or plate; ECR= outline of the radial canals; Ec Ex = exumbrellar ectoderm; En = endoderm; Enb = endoblast; En P = parental endoderm; En T = tentacular endoderm; Gb = glockenkern or medusary nodule; L = endodermal or cathamnal lamella; M = mesoglea; Ma = manubrium; MSO = subumbrellar muscles; MV = velar muscles; T = tentacular bud; Tu = tunic; V = velum.

***FIG. 53-54.** Développement, reproduction asexuelle : Organogénèse du bourgeonnement médusaire chez les Hydroidomedusae (Limnocnida). A, dédifférentiation de l'ectoderme et de l'endoderme en ectoblaste et en endoblaste au début des processus bourgeonnants. B, prolifération ectoblastique et formation de la plaque endoblastique. C, origine du nodule médusaire et de la cupule endodermique. D-E, croissance du nodule médusaire, formation de la plaque ectodermique tentaculaire et origine des canaux radiaires à partir de la cupule endodermique. F-G, apparition de la cavité sous-ombrellaire au sein du nodule médusaire, formation de la cavité tentaculaire dans la masse ectodermique tentaculaire et formation des canaux radiaires. H, méduse presque constituée, montrant la cavité sous-ombrellaire, le manubrium, les canaux radiares, le canal circulaire, la cavité gastrique, le velum et les tentacules (d'après Bouillon, 1957). A-C, E-H, sections longitudinales ; D, section transversale. CG = cavité gastrique de hydroïde ou de la méduse bourgeonnante ; CM = canal marginal ou circulaire ; CR = canal radiaire ; CSO = cavité sous-ombrellaire ; CT = cavité tentaculaire ; Cu = cupule endoblastique ; Ec = ectoderme ; Ecb = ectoblaste ; ECC = ébauche du canal circulaire ou marginal ; Ec M T = masse ectoblastique tentaculaire ; ECR = ébauche du canal radiaire ; Ec Ex = ectoderme exombrellaire ; En = endoderme ; Enb = endoblaste ; En P =* endoderme parental; *En T = endoderme tentaculaire ; Gb = glockenkern ou nodule médusaire ; L = lamelle endodermique ou cathamnale ; M = mésoglée ; Ma = manubrium ; MSO = muscle sous-ombrellaire ; MV = muscle velaire ; T = bourgeon tentaculaire ; Tu = tunique ; V = velum.*

RESTING STAGES OR CYSTS

Encysted embryos (from zygote to later stages) and planulae, can withstand adverse conditions by encystment. Cysts are presumably much more common than supposed, presently they are mainly known from solitary forms like *Climacocodon*, *Corymorpha*, *Fukaurahydra*, *Gonionemus*, *Hataia*, *Margelopsis*, *Moerisia* etc. and in freshwater species as *Craspedacusta*, *Limnocnida*, *Hydra* etc... They are less common in colonial forms (present in *Paracoryne*) where the fragments of perisarc-covered hydrocaulus or stolons play the same role. Cysts may survive sometimes several years (e.g., *Craspedacusta*, 40 years).

POLYP BUDDING, LEADING EITHER TO COLONY FORMATION, OR TO A POPULATION INCREASE IN SOLITARY FORMS

Exceptionally, some medusae produce polypoid structures (i. e., *Bougainvillia platygaster, Proboscidactyla ornata, Teissiera medusifera, Zanclea medusopolypata*).

MEDUSA BUDDING, GIVING RISE TO THE FREE SEXUAL PHASE, THE MEDUSA, OR TO SESSILE, REDUCED GONOPHORES

Some medusae multiply by budding, which may take place at various levels: on the manubrium (i. e., *Dipurena gemmifera*, *Limnocnida tanganyicae*, *Cunina fowleri* and *C. frugifera*), on the radial canals (i. e., *Eucheilota paradoxica*, *Proboscidactyla ornata*, *Kantiella enigmatica*), on the tentacular bulbs (i. e., *Coryne prolifera*, *Hybocodon prolifer*, *Niobia dendrotentaculata*), on the exumbrellar rim (i. e., *Eleutheria dichotoma*) or on the subumbrellar rim (i. e., *Eleutheria claparedei*). In the medusae of *Clytia mccradyi* and *Eirene elliceana,* the gonads produce blastostyles giving rise to medusary buds.

In the Hydroidomedusae, the medusary buds derive either from polyps or from medusae, developing in remarkably similar ways, which can be summarized as follows. Medusa buds initially appear as didermic evaginations of the blastogenetic region. The apical ectoderm of this blastogenetic hernia rapidly thickens, becomes multistratified and proliferates into a massive ectoblastic button, the medusary nodule, or entocodon. The medusary nodule is one of the most characteristic and important features in the medusary or gonophoral budding of Hydroidomedusae. It seems endowed

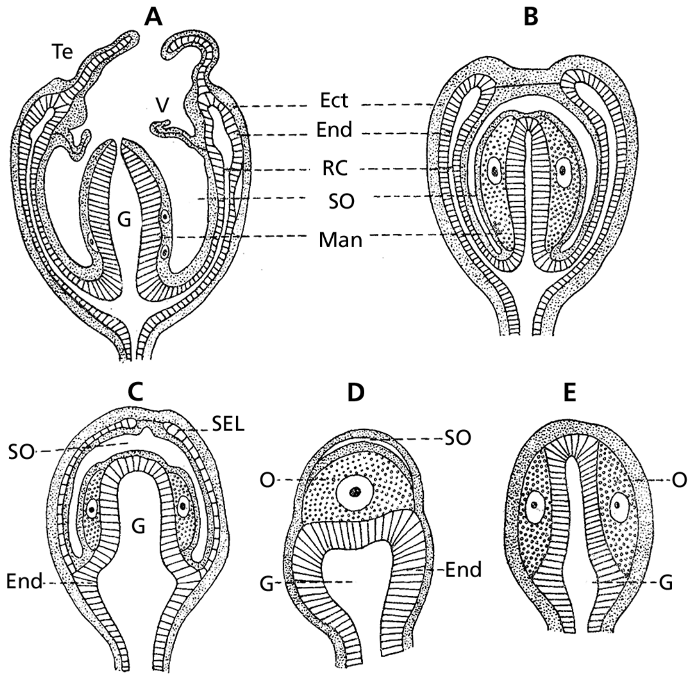


FIG. 55. Development, asexual reproduction: regressive evolution of the medusa. A, fully developed medusa. B, eumedusoid. C, cryptomedusoid. D, heteromedusoid. E, styloid (after Kühn, 1913). Ect = ectoderm; End = endoderm; G = gastric cavity; Man = manubrium; O = ovocyte; RC = radial canal; SEL = subumbrellar endodermic lamella; SO = subumbrellar cavity; Te = tentacle; V = velum.

FIG. 55. *Développement, reproduction asexuelle : évolution régressive de la méduse. A, méduse normale. B, eumédusoïde. C, cryptomédusoïde. D, hétéromédusoïde. E, styloïde (d'après Kühn, 1913). Ect = ectoderme ; End = endoderme ; G = cavité gastrique ; Man = manubrium ; O = ovocyte ; RC canal radiaire ; SEL = lamelle sous-ombrellaire endodermique ; SO = cavité sous-ombrellaire ; Te = tentacule ; V = velum.*

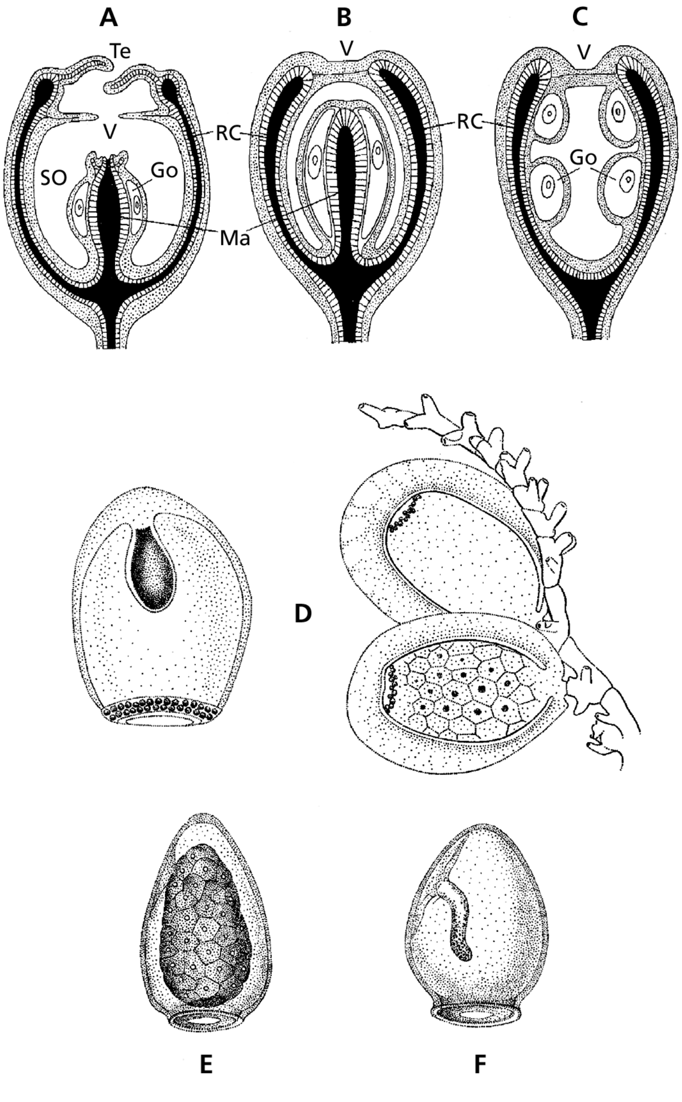


FIG. 56. Development, asexual reproduction: eumedusoids and swimming sporosacs. A, eumedusoid of *Hydractinia carnea* (Anthomedusae) having usually a short life-time. B, more regressed an ephemeral eumedusoid of *Pennaria* (Anthomedusae) with gonads on manubrium. C, ephemeral regressed eumedusoid of *Orthopyxis integra* (Leptomedusae) with gonads on radial canals and without manubrium. D, gonophores and free swimming sporosac of *Macrorhynchia* (*Lytocarpus*) *philippinus* (Leptomedusae), the gonads are on an eccentric manubrium. E, free swimming female sporosac of *Amphisbetia operculata* (Leptomedusae) before spawning. F, idem E but after spawning, note also in the two figures the eccentric position of the manubrium (A-C after Kühn, 1914; D after Gravier, 1970; E-F after Teissier, 1922). Go = ''gonad''; Ma = manubrium; RC = radial canal; SO = subumbrellar cavity; Te = tentacle; V = velum.

***FIG. 56.** Développement, reproduction asexuelle : eumedusoïdes et sporosacs nageant libres. A, eumedusoïde d'*Hydractinia carnea *(*Anthomedusae*) ayant usuellement qu'une courte vie libre. B, eumedusoïde plus régressé et éphémère de *Pennaria *(*Anthomedusae*) avec des gonades sur le manubrium. C, eumedusoïde éphémère, très regressé d'*Orthopyxis integra *(*Leptomedusae*) avec des gonades sur les canaux radiaires et sans manubrium. D, gonophore et sporosac nageant libre de *Macrorhynchia *(*Lytocarpus*) *philippinus *(Leptomedusae), les gonades sont excentriques et sur le manubrium. E, sporosac nageant libre femelle d'*Amphisbetia operculata *(Leptomedusae) avant la ponte. F, idem E mais après la ponte, notez aussi dans ces deux figures la position excentrique du manubrium (A-C d'après Kühn, 1914 ; D d'après Gravier, 1970 ; E-F d'après Teissier, 1922). Go = ''gonade'' ; Ma = manubrium ; RC = canal radiaire ; SO = cavité sous-ombrellaire ; Te = tentacule ; V = velum.*

with an inducing power, as organizer of the budding processes. The medusary nodule is located between the apical ectoderm of the medusa bud, from which it is separated, and the endoblast of the gastric cavity of the supporting colony. This is pushed back and takes the appearance of a cup surrounding the base of the nodule. The latter, solid at first, soon becomes hollow, this cavity later becoming the subumbrellar space, while the endoblastic cup, in the meantime, produces four distal didermic masses, the outlines of the radial canals.

These outlines, disposed as a cross and still contiguous, later separate from each other as the bud grows, but remain connected by a monostratified endodermal lamina, the gastrodermal lamella. While the outlines of the radial canals differentiate, the apical ectoderm produces a new ectoblastic mass that soon becomes hollow by the formation of the tentacular cavity. At this stage the first tentacles also appear, developed from the digitiform outgrowths of the endoderm of the radial canals, lined with ectoderm originating from the tentacular cavity. Simultaneously, the circular canal is formed by the confluence of the digital ends of the radial canals. Thereafter, the endoblastic cavity of the bud produces a median diverticulum pushing on the ectoderm of the subumbrellar space, forming the spadix, or future manubrium.

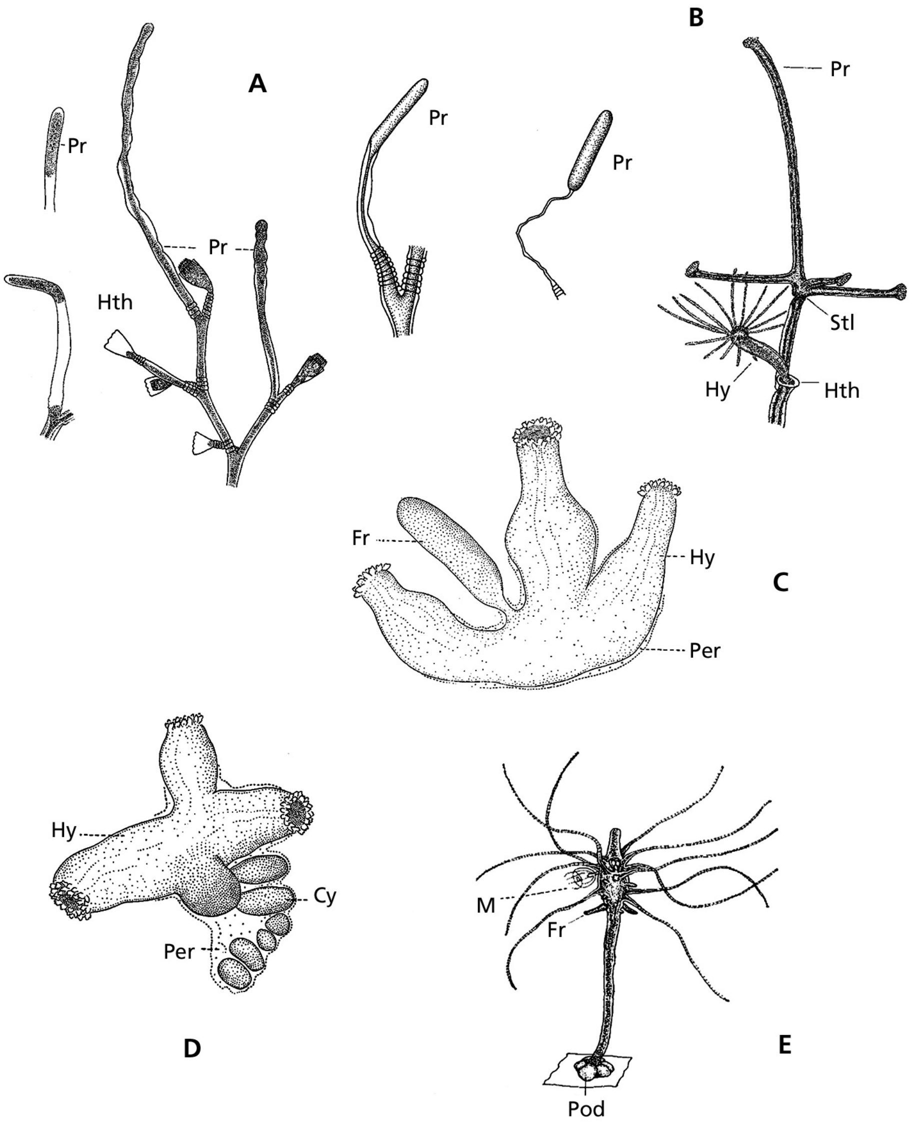


FIG. 57. Development, asexual reproduction: cysts, frustules, propagules, podocysts. A, different types of propagules observed in the genus *Obelia*, Leptomedusae. B, propagule of *Halecium pusillum*, Leptomedusae. C, frustule formation in the polyps of *Limnocnida tanganyicae*, Limnomedusae. D, cyst formation in *Limnocnida tanganyicae*, Limnomedusae. E, podocysts of *Moerisia horii*, Anthomedusae (A after Billard, 1904; B after Werner, 1984; C-D after Bouillon, 1957; E after Uchida & Nagao, 1959). Cy = cyst; Fr = frustule; Hth =hydrotheca; Hy = hydranth; M = medusa; Per = periderm; Pr = propagules; Stl = stolon.

FIG. 57. *Développement, reproduction asexuelle : cystes, frustules, propagules, podocystes. A, différent types de propagules observées dans le genre* Obelia, *Leptomedusae. B, propagule d'*Halecium pusillum, *Leptomedusae. C, formation de frustules chez les polypes de* Limnocnida tanganyicae, *Limnomedusae. D, formation de cystes chez* Limnocnida tanganyicae, *Limnomedusae. E, podocystes de* Moerisia horii, *Anthomedusae (A d'après Billard, 1904 ; B d'après Werner, 1984 ; C-D d'après Bouillon, 1957 ; E d'après Uchida & Nagao, 1959). Cy = cyste ; Fr = frustule ; Hth = hydrothèque ; Hy = hydranthe ; M = méduse ; Per = périderme ; Pr = propagules; Stl = stolon.*

The velum is formed, opposite to the manubrium, by the superimposition of the ectoderm of the subumbrellar cavity and that of the tentacular cavity. The perforation of the velum connects the subumbrellar cavity with the exterior. The organs of the young medusa are therefore differentiated and the medusa is ready to be liberated.

In certain Hydroidomedusae belonging to the families Bougainvilliidae (i. e., *Lizzia blondina*, *Bougainvillia niobe*), Hydractiniidae (*Hydractinia minima*), and Rathkeidae (*Rathkea octopunctata*), the medusary budding takes place by peculiar and remarkable processes, being exclusively ectodermic.

In the Automedusae, medusa budding occurs 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.

In many Hydroidomedusae, the medusae develop only incompletely and remain attached to the polyp colony as fixed gonophores. Several stages of medusa reduction have been recognised and several types of fixed gonophores may be distinguished.

Eumedusoids. Medusae almost complete, with radial canals, a subumbrellar space, sometimes with a manubrium, but generally without tentacles, sense organs, and velum; some have a free pelagic life. In the eumedusoids, "gonads" are on the manubrium when Anthomedusae (i. e., *Pennaria*, *Hydractinia*, *Tubularia*), on radial canals when Leptomedusae (i. e., *Eugymnanthea*, *Orthopyxis*).

Cryptomedusoids. More regressed stages, not presenting radial canals any more, but exclusively an endodermal lamina homologous to the gastrodermal lamella: the umbrella endoderm; still provided with a reduced subumbrellar space, or without any space which is then represented only by an ectodermal layer, the internal ectoderm (e.g., *Cladocoryne floccosa*, *Clava squamata*, *Coryne muscoides*).

Heteromedusoids. Highly atrophied fixed gonophores, devoid of umbrellar endoderm, but still possessing an internal ectoderm (e.g., *Sertularia argentea*, *Laomedea flexuosa*, *Kirchenpaueria echinulata*).

Styloids type I. The most regressed gonophores without internal ectoderm, or umbrellar endoderm, a simple evagination of the two constituting layers, the genital elements accumulating between both layers around a central or lateral axis, the spadix (e.g., *Dicoryne*, *Eudendrium*, *Bimeria*, *Cordylophora*).

Styloids type II. The regression is sometimes even more complete, with no trace left of gonophores, the gonads developing either in the ectoderm (e.g., *Hydra*, *Gymnogonos*, *Hydrodendron*) or in the endoderm (Actinulidae). A given species is not characterised by a single type of gonophores, the gonophores of one sex being often different from those of the other. In many cases, a gonophoral sexual dimorphism is thus observed.

Swimming gonophores. Sometimes strongly reduced medusa stages (cryptomedusoids and perhaps heteromedusoids) may become secondarily free gamete carriers again. They have gonads on the manubrium (spadix) both in the Lepto- and the Anthomedusae. Swimming gonophores, termed swimming sporosacs, have been reported for *Dicoryne conybearei* in form of flagellated gamete-carriers, deprived of any medusan structure. Several Leptomedusan species (of the genera *Amphisbetia*, *Anthohebella*, *Dentitheca*, *Macrorhynchia*, *Monotheca*, *Nemalecium*, *Sertularia*) have pelagic stages with medusan architecture, often without radial canals and circular canal, without tentacles and sense organs. The sexual elements are always on the "manubrium" in these Leptomedusae, the "manubrium" being in eccentric position. They cannot be confused with eumedusoids, the first step of medusa reduction, that have most of the original non reproductive structures of the medusa: radial canals, circular canal, velum, sense organs, with maturation of the sexual cells according the classes (gonads on manubrium in Anthomedusae and 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 (*Aglaopheniidae*, Sertulariidae, Haleciidae).

DIAGNOSTIC CHARACTERS

Species descriptions must provide information about the state of diagnostic characters. Insufficient description is the main cause of taxonomic confusion and it is often the case that new species are based on slight variations of probably irrelevant characters. The following is a list of the diagnostic characters of both hydroids and medusae and of their possible states. A description should report on the state of all the diagnostic characters present in the material under description. The character state "absent" is not mentioned, since it is useless to state that a given character is not present. This, however, is to be mentioned when an important character (e.g., the presence of ocelli), present in phylogenetically near species, can be either present or absent. Stating the absence of ocelli, in this case, means that they have been searched for (since they are usually present in a given genus), but that they were not present in the described specimen. Character states are often split into further sub-states.

DIAGNOSTIC CHARACTERS AND CHARACTER STATES TO DESCRIBE MEDUSAE

UMBRELLA
Flat
Hemispherical
Lens-shaped
Saucer-shaped
Dome-shaped
Conical
Globular
Maximum diameter
Maximum height
Colour
Mesoglea:
- Thin
- Thick
- Stiff
- Soft

Marginal portion thinner than apical portion
Marginal portion as thick as apical portion
With apical process = apical projection
With apical or umbilical canal

EXUMBRELLAR CNIDOCYST POUCHES OR CLUSTERS
Size
Shape
Position on exumbrella
Number and types of cnidocysts

MANUBRIUM
Shape:
- Cruciform
- Cylindrical
- Quadratic
- Vasiform

Colour
Length versus subumbrellar cavity height
Presence of gastric peduncle
Length of peduncle in relation to subumbrellar cavity height
Manubrial pouches:
- Position
- Shape
- Size in relation to subumbrellar cavity height

MOUTH
Shape:
- Circular
- Quadrangular
- Cruciform

Lips:
- Number of lips
- Simple
- Crenulated
- Folded
- Oral cnidocyst clusters

Mouth arms:
- Unarmed
- Armed with cnidocyst clusters

Oral tentacles:
- Simple
- Branched

Position of oral tentacles:
- Arising from mouth rim
- Arising above mouth rim

MESENTERIES
Length in relation to subumbrellar cavity

RADIAL CANALS
Number
Simple
With diverticula
Bifurcated
Branched
Jagged
Swollen at some zones
With gonads (see gonads)
Incomplete:
- Centripetal
- Centrifugal

RING CANAL
Tubular
Filled by endodermal core

"GONADS"
Number
Colour
Position:
- On radial canals:
  - Near manubrium
  - Near umbrellar margin
  - In the middle of radial canal
  - Along the whole radial canal
- On manubrium:
  - Proximal
  - Distal
  - Median
  - Completely surrounding manubrium
  - In one mass
  - In several masses
- In longitudinal bands:
  - Interradial
  - Perradial
  - Adradial

SHAPE
Oval
Linear
Sinuous
Folded
Pendulous
Pouch-like
Split by a median groove
Egg size and number

VELUM
Straight
Pendulous
Wide
Narrow

MARGINAL CNIDOCYST RING
Broad
Narrow

MARGINAL TENTACLES
Number
Length
Simple
Branched
Capitate
Filiform
Moniliform
Position:
- On margin,
- Above margin

With cnidophores
Hollow
Solid
Secondary tentacles different in structure and length from primary ones
With endodermal roots inserted in the mesoglea
With marginal bulbs

MARGINAL BULBS
Without tentacles:
- Developing tentacular marginal bulbs
- Permanent rudimentary bulbs

With tentacles
Number
Colour
Shape
Position on exumbrellar margin:
- Perradial
- Interradial
- Adradial

With exumbrellar abaxial spurs
Simple
Compound:
- Number of tentacles per bulb

MARGINAL SWELLINGS OR WARTS
Number
Position

CIRRI
Position:
- On margin
- Above margin

Associated with marginal bulbs
Non Associated with marginal bulbs
Type:
Flexile
Spiral
Tentaculae

"Excretory pores"
Position:
On bulbs
On exumbrellar margin
On papillae

Statocysts
Number
Type:
Ectodermic
Ecto-endodermic
Open
Closed
Position
Number of statoliths

Cordyli
Position
With nematocysts

Ocelli
Position:
Abaxial
Adaxial
Location:
On bulbs
On margin
On exumbrellar pouches
Colour
Ectodermal
Ecto-endodermal (associated with statocyst)
With lens
Round
Oblong
Elongate

Cnidome
State all nematocyst types and their position on the medusan body

Medusa buds
Position:
On marginal bulbs
On manubrium
On margin
On radial canals
On exumbrella
On gonads
In gonothecae borne on radial canals

Specific characters exclusive for the narcomedusae
Position of manubrial pouches:
Interradial
Perradial
Number of primary tentacles (above peronia)
Secondary marginal tentacles (on marginal lappets = exumbrellar lobes)
Peripheral and peronial canals (peripheral canal system)
Number of marginal lappets
Number of peronia
Number of otoporpae

Specific characters exclusive for the actinulidae
Body shape:
Oval
Worm-like
Oral cone
Adhesive aboral organ
Nerve ring
Tentacular bulbs
Statocysts:
Aboral
Marginal
Number
Brood pouches
Gonads:
Gonochoristic

DIAGNOSTIC CHARACTERS AND CHARACTER STATES TO DESCRIBE POLYPS

Solitary
Type of fixation:
By anchoring filaments
By mucus secretion

Colonial
Pelagic
Floating
Fixed
Stolonal
Erect
With coenosteum (calcareous)

Hydrorhiza
Simple
Reticular
Rhizocaulomic
Encrusting
Covered by perisarc
Covered by coenosarc

With spines (acanthozooids):
- Smooth
- Serrate

Hydrocaulus
Monosiphonic
Polysiphonic
Simple
Divided in internodes
Internodes with apophysis
Annulated
Unbranched
Branched:
- Arborescent
- Bushy
- Cymose
- Flabellate
- Flexuose
- Pinnate (alternate or opposite)
- Plumose
- Racemose
- Spiral
- Straight (biseriate or uniseriate)
- Whorled
- Verticillate

Hydrocladia
Alternate
Annulated
Branched
Opposite
Pinnate
Plumose
Spiral
Unbranched
Verticillate

Hydranth (gastrozooid in polymorphic species)
Size range (can change much due to contraction and feeding)
Naked
Protected:
- Hydrotheca (see character states below)
- Pseudohydrotheca (see character states below)

With abcauline caecum
With mantle = ectodermal lamella
Mantle with cnidocyst armature or ligula
With annular ectodermal fold

Hypostome
- Conical
- Simple
- With a glandular preoral chamber or button
- Peduncled with a buccal cavity (sometimes termed: trumpet-shaped)

Oral tentacles
- Number
- Length
- Amphicoronate
- Unicoronate
- Asymmetrically arranged (one, two, etc.)
- With intertentacular web (umbrellula)

Aboral tentacles
- Length
- Scattered:

Number
- In whorls:

Number of whorls
Number of tentacles per whorl

Tentacle type
- Hollow
- Solid
- Capitate
- Capitate ramified
- Cateniform
- Filiform
- Moniliform
- Pseudofiliform
- Semifiliform
- Semimoniliform
- Transformed into nematodactyls
- Transformed into sense organs (acnide)

Cnidocyst pouches on column

Gonophores (either fixed or medusa buds)
- Above aboral tentacles
- Among aboral tentacles
- Below aboral tentacles
- Single
- In clusters

Pseudohydrotheca
Covering hydranth base
Covering hydranth and tentacle bases

Hydrotheca
On hydrorhiza:
- Reptant (i. e., creeping)
- Sessile
- Pedicellate

On stem, and/or branches, and/or hydrocladia:
- Pedicellate
- Adnate
- Sunk
- Sessile
- On apophysis (or hydrophore)
- Alternate
- Opposite
- In longitudinal rows (state number)
- Irregularly arranged

FORM
- Tubular
- Campanulate
- Cup-like
- Dish-like
- Armed with nematothecae (see nematothecae character states)
- Operculate (see operculum character states)
- Asymmetrical
- With horizontal stripes
- With longitudinal stripes
- Perisarc of irregular thickness

OPERCULUM
- Pleated (folded)
- Segmented (discrete opercular flaps):
  - With crease line at base
- Number of flaps:
  - One:
    - Abcauline
    - Adcauline
  - Two
  - Three
  - Four
  - Many
- Pyramidal
- In form of a gabled roof

Everted rim

HYDROTHECAL CUSPS (OFTEN CALLED TEETH)
- Number
- Straight
- Obliquous
- Flat
- Folding inwards (this leads to the formation of longitudinal lines on the theca)

Shape:
- Triangular
- Castellate
- Bicuspidate
- Rounded

INTERNAL TEETH BELOW MARGIN
- Number

Intrathecal septum
Perisarcal diaphragm
Annular perisarcal thickening
Desmocytes
Spherule

DACTYLOZOOIDS
Position:
- On hydrorhiza
- On stem (mainly nematophores)
- On hydranth (the so-called cnidophore of *Eudendrium*)
- Solid (Tentaculozooids)
- Hollow
- With tentacles

Nematocyst arrangement:
- Capitate
- Filiform
- Semimoniliform

Contraction:
- Spiral (spiral zooids)
- Linear

NEMATOPHORES
- Sessile
- Pedicellate

Naked sarcophores
With nematothecae:
- One-chambered (monothalamic)
- Two-chambered (bithalamic)

Position of nematothecae:
- Hydrothecal
- Lateral
- Mesial (inferior median)
- Superior
- Cauline
- Gonothecal

GONOZOOID
Size
Position of gonophores:
- Scattered
- In whorls
- In clusters
- Isolated

Tentacles:
- Number
- Arrangement
- Type (see above for character states)
- Mouth present

GONOPHORES
Simple
In clusters
On blastostyles
Aggregated
Position:
- On hydranth
- On hydrocaulus and/hydrocladia
- On hydrorhiza
- Sessile
- Pedicellate

Giving rise to:
- Free medusae
- Eumedusoids
- Fixed sporosacs

Swimming gonophores:
- With gastrovascular system

Without gastrovascular system
With central "manubrium" (spadix)
With eccentric "manubrium" (spadix)

With nematothecae
Without nematothecae

DIAGNOSTIC CHARACTERS AND CHARACTER STATES TO DESCRIBE SIPHONOPHORES

For detailed description of Siphonophoran characters and character states see section B3.

NECTOSOME
See section B3

PNEUMATOPHORE
See section B3

NECTOPHORES
Number
Position:
Anterior
Posterior
Lateral bridges
Apical wings
Ascending branches
Basal facet
Basal lamella
Commissural canals
Commissures
Descending branches
Hydroecium
Lateral wings
Mouth plate
Ostial teeth
Pallial canal
Somatocyst

SIPHOSOMES
GASTROZOOID
Tentilla

PALPONS
Palpacles

BRACTS
See section B3

GONODENDRON
Gonopalpon
Gonophores:
Eumedusoids
sporosacs

EUDOXID
Central canal
Neck shield
Phyllocyst
Spur canals

CNIDOME
State all nematocyst types and their position

SIMPLIFIED KEY FOR IDENTIFICATION OF HYDROZOA SUB-CLASSES

FOR HYDROIDS

1. Polyp generation planktonic, in the form of polymorphic colonies with a float and central gastrozooid . . . . Anthomedusae Porpitidae
– Polyp generation usually sedentary; exceptionally planktonic but different from above 2

2. Hydranth generally with a definite hydrotheca and gonothecae of definite shape . . . . . Leptomedusae
– Hydranth with no definite hydrothecae, or gonothecae 3

3. Hydranth solitary or colonial, usually rather conspicuous; sometimes with a coenosteum; mostly with desmonemes. . . . . Anthomedusae
– Hydranth small, sessile; generally solitary or forming small reptant or bipolar colonies; never with desmonemes . . . . Limnomedusae

KEY FOR IDENTIFICATION OF PELAGIC HYDROZOA

Usually with sense organs, ocelli or statocysts, individuals as free swimming medusae, never colonial = hydromedusae.

Pelagic and floating, modular, highly polymorphic colonies formed by the association of medusoid and polypoid zooids, medusoids never developing into complete medusae, no visible sense organs = siphonophores.

HYDROMEDUSAE

The term hydromedusae is used here in the sense of “the medusae of the Hydrozoa” and comprises both Hydroidomedusa and Automedusa, without having a formal taxonomic rank. The key is just an identification tool, and is not intended to reflect phylogeny.

WITHOUT STATOCYSTS, GONADS ON MANUBRIUM

— “gonads” on manubrium, occasionally extending for a short distance along basal region of radial canals; marginal tentacles solid or hollow; usually with tentacular bulbs; umbrella generally entire; with radial and circular canals; sense organs, when present, ocelli; umbrella typically bell-shaped; with hydroid stage: Anthomedusae.

— “gonads” exclusively on manubrium; tentacles solid, above exumbrellar margin; with or without tentacular bulbs; umbrella lobed, divided by peronial grooves or similar structures; with radial canals, circular canal as a solid core of endodermal cells; umbrella roughly hemispherical; hydroid stage unknown: Laingiidae.

WITH GONADS ON RADIAL CANALS AND, USUALLY, ECTODERMAL STATOCYSTS

— “gonads” on radial canals, exceptionally contiguous with base of manubrium; marginal tentacles usually hollow; with tentacular bulbs; umbrella entire; with radial and circular canals; sense organs, when present, statocysts formed exclusively by the velar ectoderm, open or closed, sometimes cordyli, rarely ocelli; umbrella usually flattened; with hydroid stage: Leptomedusae.

STATOCYSTS ECTO-ENDODERMAL, WITH ENDODERMAL AXIS

— "gonads" on radial canals; marginal tentacles solid (a mixture of solid and hollow tentacles in Geryoniidae); without tentacular bulbs; exumbrella entire; with an exumbrellar marginal cnidocyst ring; with radial and circular canals; statocysts as free marginal clubs, usually free, rarely enclosed by exumbrellar ectoderm; umbrella tall to hemispherical; without hydroid stage: Trachymedusae.

— "gonads" on manubrium (often on manubrial pouches); primary tentacles solid, above exumbrellar margin, sometimes secondary, marginal tentacles; without tentacular bulbs; umbrella lobed, divided by peronial grooves; usually without radial canals; circular canal, when present, jagged, in form of peripheral system; statocysts usually as free marginal clubs; umbrella typically flatter than an hemisphere, with a central lens-shaped mass of mesoglea; without true hydroid stage: Narcomedusae.

— "gonads" on radial canals, exceptionally on manubrium; marginal tentacles hollow; without tentacular bulbs; umbrella entire; with radial and circular canals; with statocysts enclosed into the mesoglea near ring canal or in the velum; with hydroid stage: Limnomedusae.

— "gonads" on manubrium, between ectoderm and endoderm; tentacles solid, with or without tentacular bulbs; umbrella entire or very reduced; without radial and circular canals; statocysts aboral or marginal; manubrium elongated, terminating in a simple mouth-opening; without hydroid stage: Actinulidae.

SIPHONOPHORES

Pelagic, free swimming or floating Hydrozoa (except the deep-water, epibenthic Rhodaliidae), forming highly polymorphic modular colonies of polypoid and medusoid zooids attached to a stem or stolon supported by a floating and swimming system or nectosome.

OUTLINE CLASSIFICATION

Class AUTOMEDUSA Lameere, 1920

Subclass Actinulidae Swedmark & Teissier, 1959
- Family Halammohydridae Remane, 1927
- Family Otohydridae Swedmark & Teissier, 1958

Subclass Narcomedusae Haeckel, 1879
- Family Aeginidae Gegenbaur, 1857
- Family Cuninidae Bigelow, 1913
- Family Solmarisidae Haeckel, 1879

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

Class HYDROIDOMEDUSA Claus, 1877

Subclass Anthomedusae Haeckel, 1879
- Order Filifera Kühn, 1913
- Suborder Margelina Haeckel, 1879
  - Family Australomedusidae Russell, 1971
  - Family Balellidae Stechow, 1922
  - Family Bougainvilliidae 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 Rhysiidae Brinckmann, 1965
  - Family Stylasteridae Gray,1847
  - Family Trichydridae Hincks, 1868

Suborder Pandeida Haeckel, 1879
- Family Bythotiaridae Maas, 1905. (= Calycopsidae)
- Family Eudendriidae Agassiz,1862
- Family Niobiidae Petersen, 1979
- Family Pandeidae Haeckel, 1879
- Family Proboscidactylidae Hand & Hendrickson, 1950
- Family Protiaridae, Haeckel 1879
- Family Russelliidae Kramp, 1957
- Order Capitata Kühn, 1913

Suborder Moerisiida Poche, 1914
- Family Boeromedusidae Bouillon, 1995
- Family Halimedusidae Arai & Brinckmann-Voss, 1980
- Family Hydridae Linneaus,1758
- Family Moerisiidae Poche, 1914
- Family Polyorchidae Agassiz, 1862
- Family Protohydridae Allman, 1888

Suborder Sphaerocorynida Petersen, 1990
- Family Hydrocorynidae Rees, 1957
- Family Sphaerocorynidae Prévot, 1959
- Family Zancleopsidae Bouillon, 1978

Suborder Tubulariida, Fleming, 1828
- Family Acaulidae Fraser, 1924
- Family Boreohydridae Westblad, 1947
- Family Candelabridae de Blainville, 1830
- Family Cladonematidae Gegenbaur, 1857
- Family Corymorphidae Allman, 1872
- Family Corynidae Johnston, 1836
- Family Euphysidae Haeckel, 1879
- Family Margelopsidae Uchida, 1927
- Family Paracorynidae Picard,1957
- Family Pennariidae McCrady, 1859
- Family Solanderiidae Marshall, 1892
- Family Tricyclusidae Kramp, 1949
- Family Tubulariidae Fleming, 1828

Suborder Zancleida Russell, 1953
- Family Asyncorynidae Kramp, 1949
- Family Cladocorynidae Allman, 1872
- Family Porpitidae Goldfuss, 1818
- Family Milleporidae Fleming, 1828
- Family Pseudosolanderiidae Bouillon & Gravier-Bonnet, fam. nov.
- Family Rosalindidae Bouillon, 1985a
- 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 L. Agassiz, 1862
Family Barcinidae Gili, Bouillon, Pagès, Palanques & Puig, 1999
Family Blackfordiidae Bouillon, 1984
Family Campanulinidae Hincks, 1868
Family Cirrholoveniidae Bouillon, 1984
Family Clathrozoellidae Peña Cantero, Vervoort & Watson, 2003
Family Clathrozoidae Hirohito, 1967
Family Dipleurosomatidae Russell, 1953
Family Eirenidae Haeckel, 1879
Family Haleciidae Hincks, 1868
Family Halopterididae Millard, 1962
Family Hebellidae Fraser, 1912
Family Kirchenpaueriidae Stechow, 1921
Family Lafœidae A. Agassiz, 1865
Family Laodiceidae Agassiz, 1862
Family Lineolariidae Allman, 1864
Family Lovenellidae Russell, 1953
Family Malagazziidae Bouillon, 1984
Family Melicertidae Agassiz, 1862
Family Mitrocomidae Haeckel, 1879 (part); Torrey, 1909
Family Octocannoidae Bouillon, Seghers & Boero, 1991
Family Orchistomatidae Bouillon, 1984
Family Phialellidae Russell, 1953
Family Plumulariidae Agassiz, 1862 (Hincks, 1868)
Family Sertulariidae Lamouroux, 1812
Family Sugiuridae Bouillon, 1984
Family Syntheciidae Marktanner-Turneretscher, 1890
Family Teclaiidae Bouillon, Pagès, Gili, Palanques, Puig & Heussner, 1999
Family Thyroscyphidae Stechow, 1920
Family Tiarannidae Russell, 1940
Family Tiaropsidae Boero, Bouillon & Danovaro, 1987
Order Proboscoida Broch, 1910
Family Bonneviellidae Broch, 1909
Family Campanulariidae Johnston, 1836
Family Phialuciidae Bouillon, 1984

Subclass Limnomedusae Kramp, 1938
Family Armorhydridae Swedmark & Teissier, 1958
Family Microhydrulidae Bouillon & Deroux, 1967
Family Olindiidae Haeckel, 1879

Subclass Siphonophorae Eschscholtz, 1829
Order Cystonectae Haeckel, 1887

Family Physaliidae Linnaeus, 1758
Family Rhizophysidae Brandt, 1835
Order Physonectae Haeckel, 1888
Family Agalmidae Brandt, 1835
Family Apolemiidae Huxley, 1859
Family Athorybiidae Huxley, 1859
Family Erennidae Pugh, *in press*
Family Forskaliidae Haeckel,1888
Family Physophoridae Eschscholtz, 1829
Family Pyrostephidae Moser,1925
Family Rhodaliidae Haeckel, 1888
Order Calycophoridae Leuckart, 1854
Family Abylidae Agassiz, 1862
Family Clausophyidae Totton, 1965
Family Diphyidae Quoy & Gaimard, 1827
Family Hippopodiidae Kölliker, 1853
Family Prayidae Kölliker, 1853
Family Sphaeronectidae Huxley, 1859

Class POLYPODIOZOA Raikova, 1988

Family Polypodiidae Poche, 1914

DIAGNOSES AND KEYS OF THE FAMILIES AND GENERA

The diagnoses have been built according to standard works on the various taxa, often using exactly the same phrasing. Unless explicitly specified, the main sources for diagnoses are: Bouillon, 1985; Bouillon & Boero, 2000, Calder, 1988, 1991, 1997; Cornelius, 1995; Hirohito, 1988, 1995, Kramp, 1959, 1968; Millard, 1975; Naumov, 1960, Pugh, 1999; Schuchert, 1996, 1997.

Class AUTOMEDUSA (see page 15 for diagnosis)

Subclass ACTINULIDAE

Free living, solitary, minute (up to 1.5-2 mm) members of the interstitial fauna of marine sand, resembling "actinuloid" larvae (e.g., *Solmundella* larvae); umbrella present or reduced; manubrium, or gastric tube, elongated, terminating into a simple mouth-opening; without canal system; with or without a cone-shaped aboral adhesive organ formed by incurved ectoderm; with one or two amphicoronate rings of solid tentacles, either aboral or marginal; with or without brood chamber (= remains of subumbrellar cavity); sexual cells in the endoderm of the manubrium wall; free ecto-endodermal statocysts similar to those of the Trachy- and Narcomedusae, inserted between adjacent tentacles; body covered by flagella; direct development and no classical planula-like stage, embryonic development giving rise to halhydrula larvae; no asexual reproduction; cnidome containing stenoteles, microbasic euryteles, microbasic mastigophores, and three types of cnidocysts peculiar to the Actinulidae: atrichous anisorhizae, spirotele and aspirotele spironemes.

Distinctive Automedusa features: statocyst structure, embryonic development, formation of the brood chamber (subumbrellar cavity) by means of a circular invagination around the manubrium (Fig. 49).

With conical aboral adhesive organ; a nerve ring; two aboral amphicoronate rings of tentacles; gonochoric; without brood pouch (i.e., subumbrellar cavity) = Halammohydridae.
— No aboral adhesive organ; no nerve ring; one marginal ring of tentacles of two kinds, adhesive and armed ones; with or without a brood pouch (i. e., subumbrellar cavity); hermaphroditic, viviparous = Otohydridae.

Family HALAMMOHYDRIDAE Remane, 1927

Body as a long gastric tube (manubrium) with a terminal mouth, with a small aboral cone, separated from manubrium by a neck, bearing an adhesive organ; aboral nerve ring; one aboral whorl of amphicoronate solid tentacles, alternating with ecto-endodermic statocysts; gonochoric; without brood pouch.

Recent references: Thiel (1988); Bouillon & Boero (2000).

Genus ***HALAMMOHYDRA*** Remane, 1927

Figs 49, 58A, B
See family characters

Halammohydra adherens Swedmark & Teissier, 1958a
Halammohydra andamanensis Rao, 1978
Halammohydra chauhani Rao, 1975
Halammohydra coronata Clausen, 1967
Halammohydra intermedia Clausen, 1967
Halammohydra intermedium Rao, 1993 [invalid name]
Halammohydra octopodides Remane, 1927
Halammohydra sagarensis Rao & Misra, 1980
Halammohydra schulzei Remane, 1927
Halammohydra vermiformis Swedmark & Teissier, 1957

Family OTOHYDRIDAE Swedmark & Teissier, 1958

Umbrella ovoid, containing the manubrium; one ring of marginal tentacles of two kinds: adhesive and armed ones; with or without a brood pouch (= subumbrellar cavity); hermaphroditic, viviparous.

Genus ***OTOHYDRA*** Swedmark & Teissier, 1958

Fig. 58C, D
See family characters

Otohydra tremulans Lacassagne, 1973
Otohydra vagans Swedmark & Teissier, 1958b

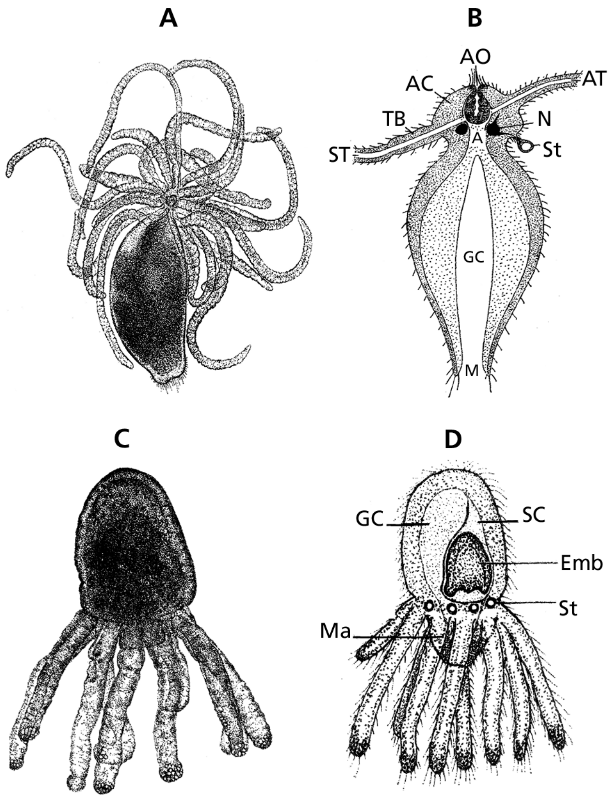


FIG. 58. Actinulidae. A-B, Halammohydridae (*Halamomohydra schulzei*): A, general view; B, structural organization. C-D, Otohydridae (*Otohydra vagans*): C, general view; D, structural organization (A-B after Swedmark & Teissier, 1966; C-D after Swedmark & Teissier, 1958 a & b). AC = aboral cone; AO = adhesive organ; AT = tentacle of the aboral girdle; Emb = embryo; GC = gastric cavity; M = mouth; Ma = manubrium; N = nerve ring; SC = subumbrellar cavity; St = statocyst; ST = tentacle of the subaboral girdle; TB = tentacular bulb.

FIG. 58. *Actinulidae. A-B, Halammohydridae (*Halamomohydra schulzei*) : A, vue générale ; B, organisation interne. C-D, Otohydridae (*Otohydra vagans*) : C, vue générale ; D, organisation interne (A-B d'après Swedmark & Teissier, 1966 ; C-D d'après Swedmark & Teissier, 1958 a & b). AC = cône aboral ; AO = organe adhésif ; AT = tentacule de la ceinture aborale ; Emb = embryon ; GC = cavité gastrique ; M = bouche ; Ma = manubrium ; N = anneau nerveux ; SC = cavité sous-omnbrellaire ; St = statocyste ; ST = tentacule de la ceinture subaborale ; TB = bulbe tentaculaire.*

Subclass NARCOMEDUSAE (Figs 59-64)

Umbrella usually flattened, with a central, lens-shaped mass of mesoglea and much thinner rim. Umbrellar margin lobed, divided by peronial grooves. Tentacles solid, inserted on exumbrella, just above peronial grooves, without tentacular bulbs, with endodermal core in contact with manubrial endoderm, passing through umbrellar mesoglea as a "root"; sometimes small secondary tentacles on margin. Manubrium broad and short, with entire circular periphery, or with perradial or interradial peripheral pouches. Generally no radial canals; circular canal absent or looped into the marginal flaps to form a "peripheral canal system". "Gonads" on manubrium and/or on manubrial pouches. Medusae with direct development or with tentacled larvae parasitizing other medusae, polychaetes, or fishes; primary larvae giving rise, by successive budding, to numerous juvenile medusae or to secondary larvae that transform later on into juvenile medusae. They may also develop more complicated structures (stolo-prolifers) that give rise to numerous medusae, representing perhaps the first step to colony formation and modular life (Fig. 25: H). Medusa buds do not develop through a medusary nodule. Longitudinal axis of both larvae and adults perpendicular to longitudinal planula axis (these axes coincide in other medusae). Marginal sense organs as free ecto-endodermal statocysts (only one species with closed ecto-endodermal statocysts). With or without otoporpae. Cnidome: atrichous and apotrichous isorhizae (see Carré *et al.* 1989).
Recent references: Bouillon (1987); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. without manubrial pouches .... *Solmarisidae*
– with manubrial pouches 2

2. pouches perradial .... *Cuninidae*
– pouches interradial .... *Aeginidae*

Family AEGINIDAE Gegenbaur, 1857

Manubrial pouches interradial, divided in two parts, bearing the "gonads"; with or without peripheral canal system; exumbrellar, perradial, primary tentacles between marginal lobes; with or without secondary tentacles on umbrellar margin. Primary tentacles originating above manubrial pouches. With or without otoporpae.
Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. 2 tentacles .... *Solmundella*
– 4 or more tentacles 2

2. 8 (or more) primary tentacles; with or without secondary tentacles 3
– 4-6 primary tentacles, without secondary tentacles 4

3. no secondary tentacles; 8 manubrial pouches (7-9), with peripheral canal; with otoporpae .... *Otoporpa*
– secondary tentacles; 16 manubrial pouches; peripheral canal absent or degenerated; without otoporpa .... *Aeginura*

4. 4 tentacles, 8 peronia and 16 manubrial pouches .... *Aeginopsis*
– 4 to 6 tentacles, 4-6 peronia and 8-12 manubrial pouchess .... *Aegina*

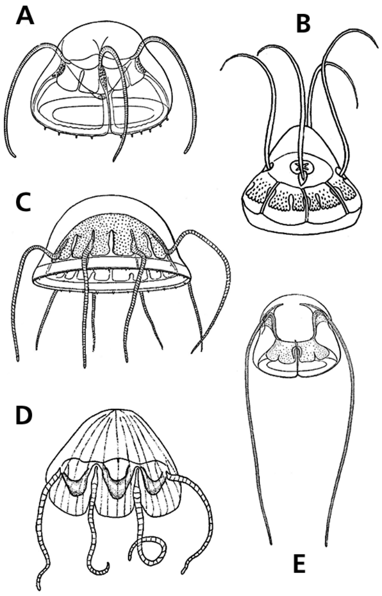


FIG. 59. Narcomedusae, Aeginidae. A, *Aegina citrea*. B, *Aeginopsis laurentii*. C, *Aeginura grimaldii*. D, *Otoporpae polystriata*. E, *Solmundella bitentaculata* (A-C, E after Mayer, 1910; D after Xu & Zhang, 1978).

***FIG. 59.** Narcomedusae. Aeginidae. A,* Aegina citrea. *B,* Aeginopsis laurentii. *C,* Aeginura grimaldii. *D,* Otoporpae polystriata. *E,* Solmundella bitentaculata *(A-C, E d'après Mayer, 1910 ; D d'après Xu & Zhang, 1978).*

Genus ***AEGINA*** Eschscholtz, 1829

Figs 34A, 59A

Typically 8 (but occasionally 10 to 12) primary manubrial pouches; with peripheral canal system; usually with 4 (sometimes 5 or 6) primary tentacles; no secondary tentacles; no otoporpae.

Aegina citrea Eschscholtz, 1829

Genus ***AEGINOPSIS*** Brandt, 1838

Fig. 59B

16 manubrial pouches; peripheral canal system absent; 4 primary tentacles and 8 peronia; no secondary tentacles; no otoporpae.

Aeginopsis laurentii Brandt, 1838

Genus ***AEGINURA*** Haeckel, 1879

Fig. 59C

16 manubrial pouches; peripheral canal system absent or reduced; 8 primary tentacles and peronia; with secondary marginal tentacles; no otoporpae.

Aeginura beebei Bigelow, 1940
Aeginura grimaldii Maas, 1904

Genus ***OTOPORPA*** Xu & Zhang, 1978

Fig. 59D

Eight manubrial pouches; peripheral canal present; with 8 primary tentacles and 8 peronia; without secondary tentacles; with otoporpae.

Otoporpa polystriata Xu & Chang, 1978

Genus ***SOLMUNDELLA*** Haeckel, 1879

Figs 59E, 63A

Eight manubrial pouches; without peripheral canal system; 4 peronia, 2 long tentacles; no secondary tentacles; no otoporpae.

Solmundella bitentaculata (Quoy & Gaimard, 1833)

Aeginidae *incertae sedis*:

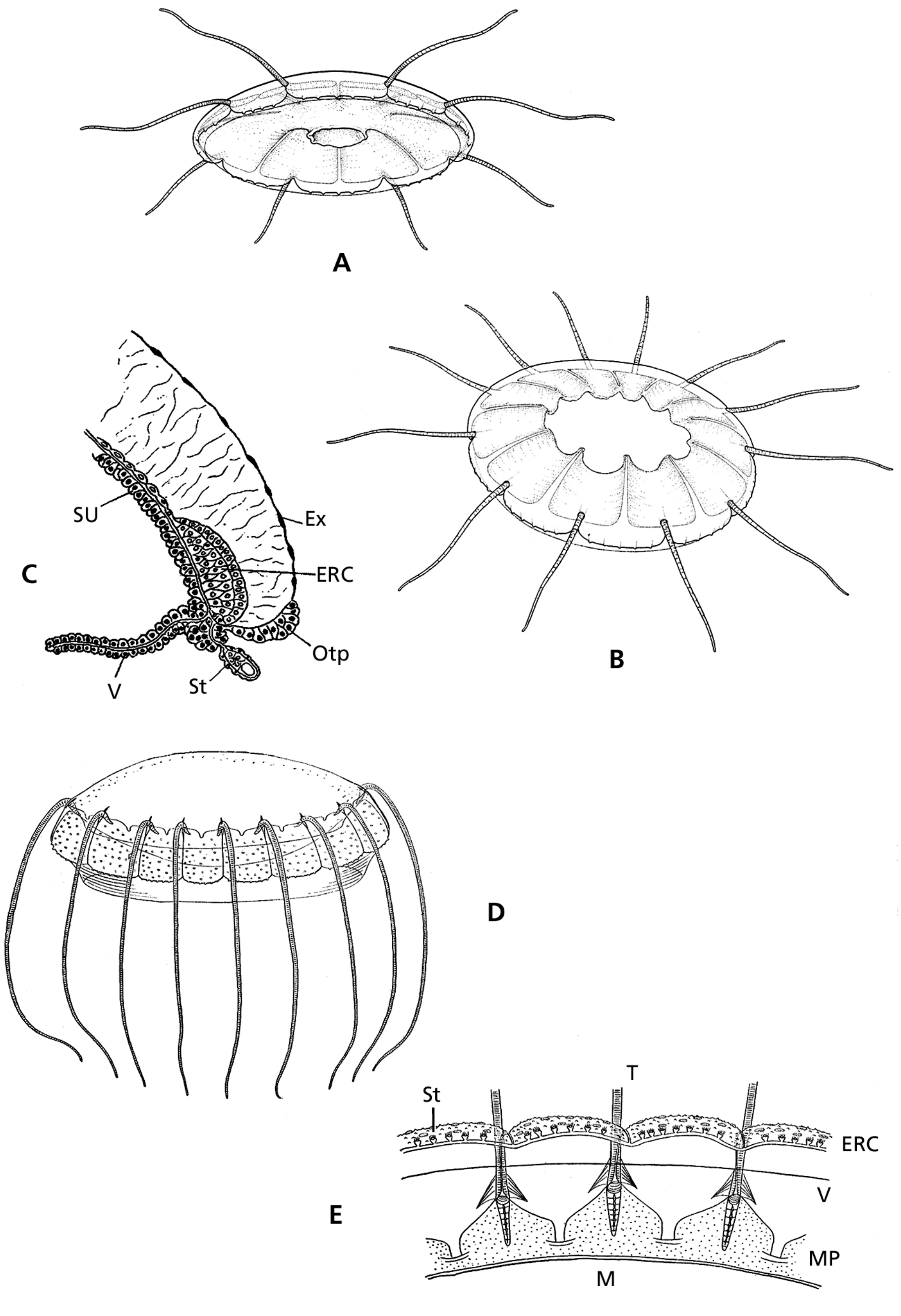


FIG. 60. Narcomedusae, Cuninidae. A-B, *Cunina octonaria*: A, side view; B, aboral view. C, *Cunina proboscidea*, radial section through a statocyst and an otoporpae (side view). D-E, *Solmissus albescens* (detail of umbrella margin) (A-B after Bouillon, 1987; C-E after Mayer, 1910). ERC = solid core replacing the ring canal; Ex = exumbrella; M = mouth; MP = manubrial pouches; Otp = otoporpae; St = statocyst; SU = sub-umbrella; T = tentacle; V = velum.

***FIG. 60.** Narcomedusae, Cuninidae. A-B,* Cunina octonaria *: A, vue latérale ; B, vue aborale. C,* Cunina proboscidea*, section radiaire d'un statocyste et d'un otoporpae (vue latérale). D-E,* Solmissus albescens *(détail du bord ombrellaire) (A-B d'après Bouillon, 1987 ; C-E d'après Mayer, 1910). ERC = axe endodermique solide remplaçant le canal circulaire ; Ex = exombrelle ; M = bouche ; MP = poches manubriales ; Otp = otoporpae ; St = statocyste ; SU = sous-ombrelle ; T = tentacule ; V = velum.*

Genus ***AEGINODISCUS*** Haeckel, 1879

16 peronial strands, 8 tentacles and 32 (16 clefts) peripheral stomach pouches. Briefly described by Haeckel, 1879, without figures, genus of doubtful status.

Aeginodiscus actinodiscus Haeckel, 1879 [doubtful status]

Genus ***TETRAOTOPORPA*** Zamponi & Suarez Morales, 1991

Aeginidae with 4 tentacles, 4 manubrial pouches; 4 peronia and 4 otoporpae. Genus of doubtful status.

Tetraotoporpa siankaanensis Zamponi & Suarez Morales, 1991 [doubtful status]

Family CUNINIDAE Bigelow, 1913

Manubrial pouches perradial and undivided, bearing the "gonads"; exumbrellar, perradial primary tentacles between marginal lobes, inserted on to the centre of each manubrial pouch; pouches not extending beyond point of tentacle origin; with or without secondary marginal tentacles; with or without peripheral canal system; with or without otoporpae.

Recent references: Pagès et al. (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. with secondary tentacles . . . . *Sigiweddelia*
– without secondary tentacles. 2

2. without otoporpae. . . . . *Solmissus*
– with otoporpae . . . . *Cunina*

Genus ***CUNINA*** Eschscholtz, 1829

Figs 60A-B, 63A, 64

Cuninidae with otoporpae, with or without peripheral canal system.
Recent reference: Gili, Bouillon, Pagès, Palanques, Puig, Heussner (1998).

Cunina becki Bouillon, 1985b
Cunina duplicata Maas, 1893
Cunina fowleri (Browne, 1906)
Cunina frugifera Kramp, 1948
Cunina globosa Eschscholtz, 1829
Cunina mucilaginosa (Chamisso & Eysenhardt, 1821) [doubtful status]
Cunina octonaria McCrady, 1859
Cunina oligotis Haeckel, 1879 [doubtful status]
Cunina peregrina Bigelow, 1909
Cunina polygonia (Haeckel, 1879) [doubtful status]
Cunina proboscidea E. & L. Metschnikoff, 1871
Cunina simplex Gili *et al.*, 1998
Cunina tenella (Bigelow, 1909)
Cunina vitrea Gegenbaur, 1857 [only juveniles known; perhaps *C. proboscidea*]

Genus ***SIGIWEDDELIA*** Bouillon, Pagès & Gili, 2001

Fig. 61A-D

Cuninidae without otoporpae; with secondary tentacles on umbrella margin; with enclosed sensory clubs, with peripheral canal.

Sigiweddelia benthopelagica Bouillon, Pagès & Gili, 2001

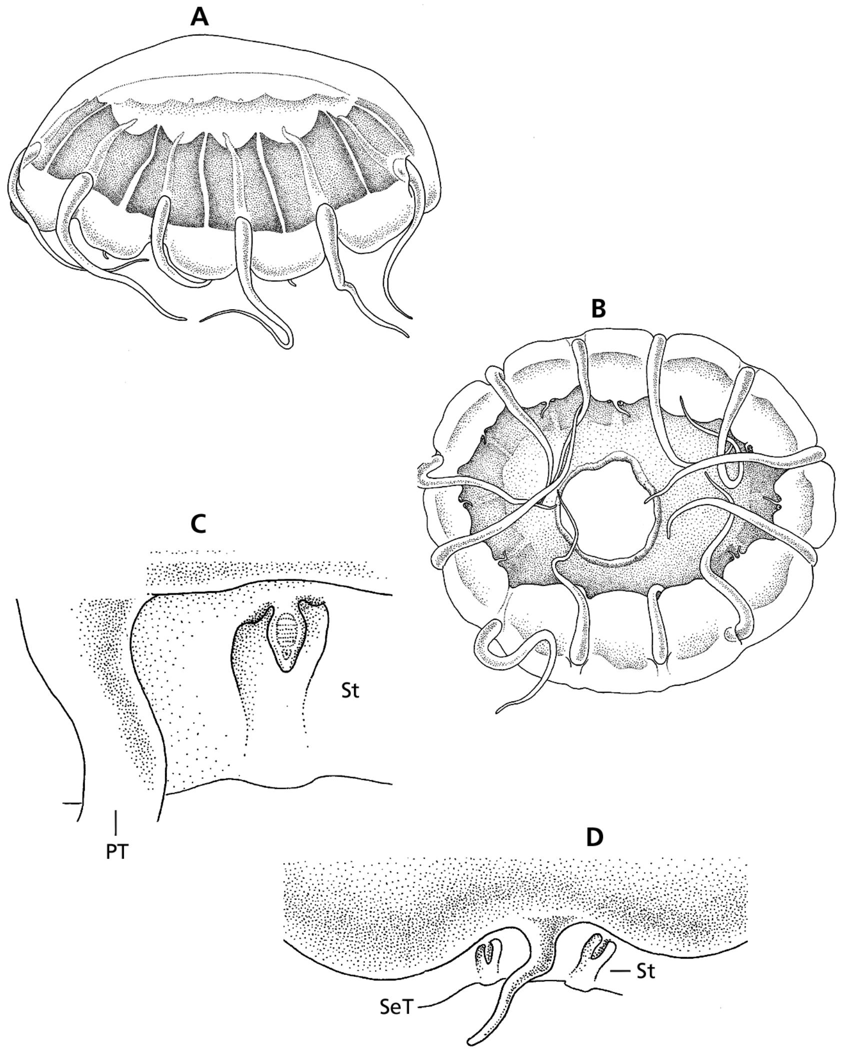


FIG. 61. Narcomedusae, Cuninidae. A-D, *Sigiweddelia bathypelagica*. A, side view. B, oral view. C, primary tentacle and statocyst. D, secondary tentacle and statocyst (all after Bouillon *et al*., 2001: p. 840, figs 1 A, B, fig. 2; p. 841, fig. 3). PT = primary tentacle; St = statocyst; SeT = secondary tentacle.

FIG. 61. *Narcomedusae, Cuninidae. A-D,* Sigiweddelia bathypelagica. *A, vue latérale. B, vue orale. C, tentacule primaire et statocyste. D, tentacule secondaire et statocyste (d'après Bouillon* et al.*, 2001 : p. 840, fig. 1 A, B, fig. 2; p. 841, fig. 3). PT = tentacule primaire ; St = statocyste ; SeT = tentacule secondaire.*

Genus ***SOLMISSUS*** Haeckel, 1879

Figs 34B, 60D-E

Cuninidae without otoporpae, without peripheral canal system.

Recent reference: Gili *et al.* (1998).

Solmissus albescens (Gegenbaur, 1857)
Solmissus atlantica Zamponi, 1983 [doubtful position, perhaps referable to Aeginidae]
Solmissus bleekii Haeckel, 1879 [doubtful status]
Solmissus faberi Haeckel, 1879
Solmissus incisa (Fewkes, 1886)
Solmissus marshalli Agassiz & Mayer, 1902
Solmissus sp. Ganapati & Nagabhushanam, 1958

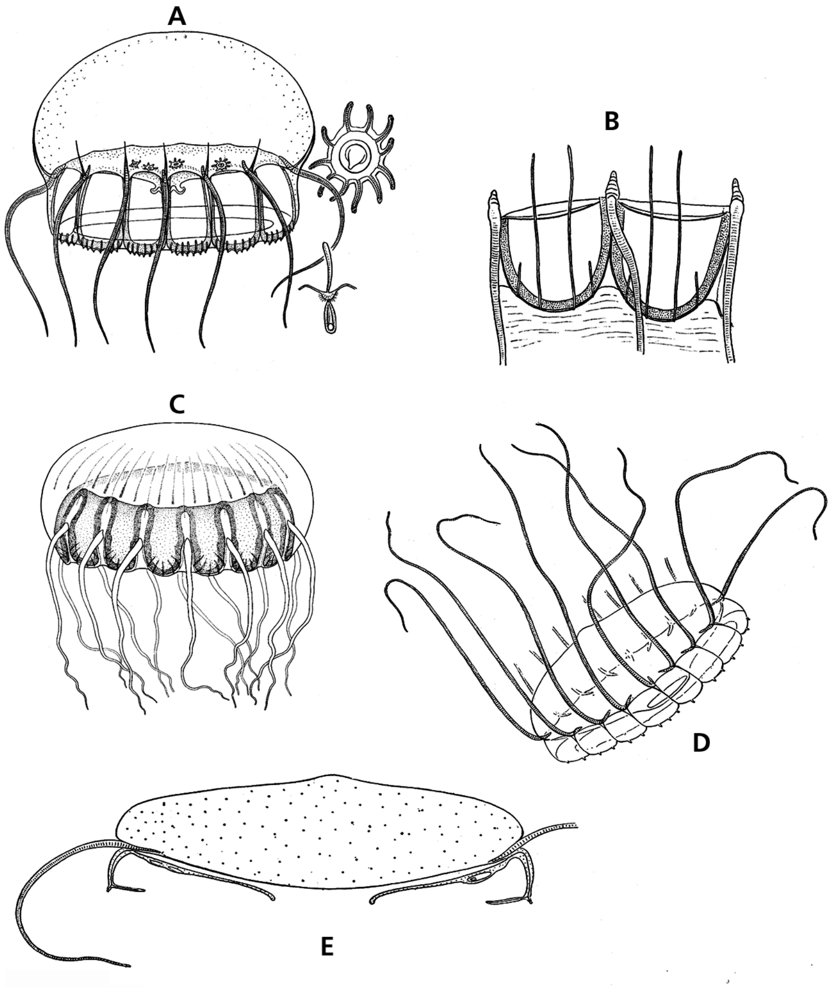


FIG. 62. Narcomedusae, Solmarisidae. A-B, *Pegantha rubiginosa*: A, adult medusa with juveniles of first sexual generation inside manubrium, at right late stage of embryonic generation and statocyst; B, portion of umbrella margin showing peronia and otoporpae. C, *Pegantha triloba*. D-E, *Solmaris flavescens*: D, general view; E, diagrammatic section of a medusa (A-B, D-E after Mayer, 1910; C after Pagès *et al*., 1992).

FIG. 62. *Narcomedusae, Solmarisidae. A-B,* Pegantha rubiginosa *: A, méduse adulte avec des juvéniles de première génération sexuées dans le manubrium, à droite stade embryonnaire tardif et statocyste ; B, portion du bord ombrellaire montrant les péronies et les otoporpes. C,* Pegantha triloba*. D-E, Solmaris flavescens : D, vue générale ; E, section diagrammatique d'une méduse (A-B, D-E d'après Mayer, 1910 ; C d'après Pagès et al., 1992).*

Cuninidae *incertae sedis:*

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 appearing twice as numerous as tentacles; peripheral canal?; otoporpae? Doubtful genus.

Cunissa duplicata Maas, 1893
Cunissa polyphera Haeckel, 1879 [doubtful status]
Cunissa polyporpa Haeckel, 1879 [doubtful status]

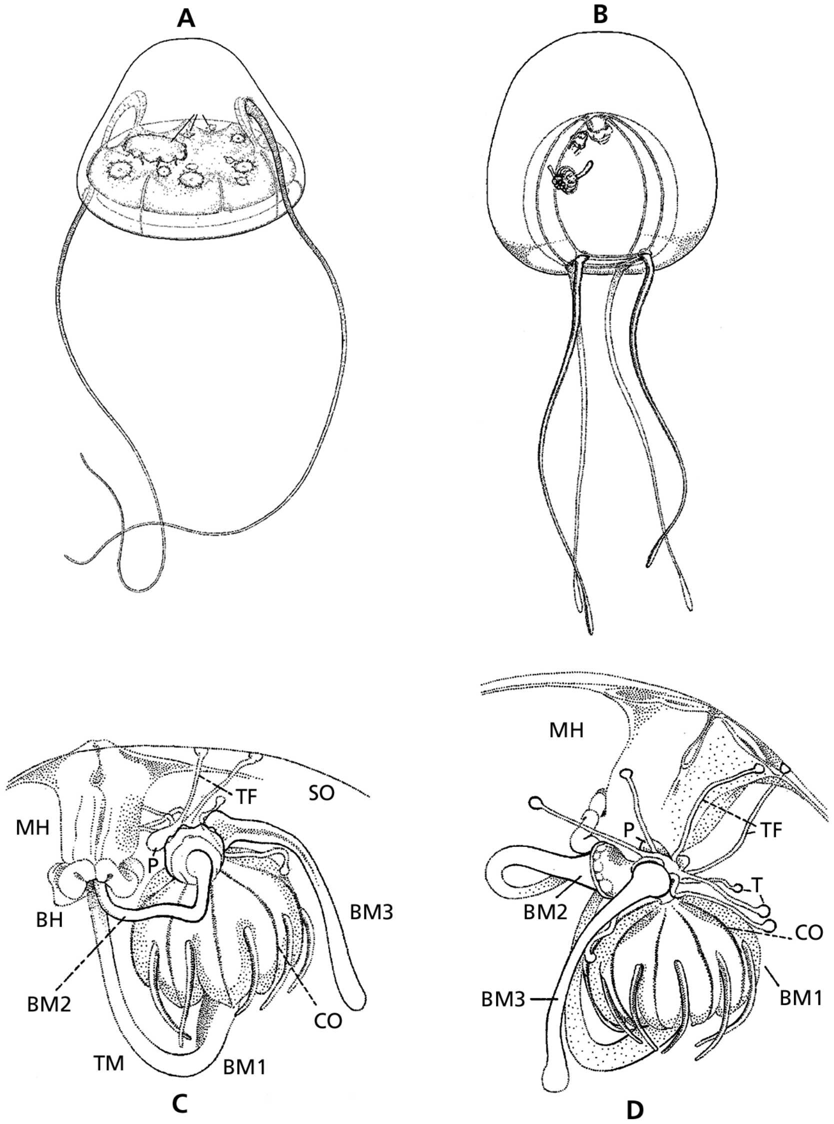


FIG. 63. Narcomedusae, stages of parasitic reproduction. A, *Solmundella bitentaculata* parasitized by *Cunina peregrina* at different stages of reproduction. B, *Pseudotiara tropica*, Anthomedusae, parasitized by polypoid stages of *Pegantha triloba*. C-D, details of the parasitic stages of B (all after Bouillon, 1987). BH = mouth of the host; BM1, BM2 & BM3 = successive stages of medusa buds formed by the primary larval parasitic stage; CO = median crests of umbrellar lobes of *Pegantha triloba* medusa buds; MH = manubrium of the host; P = primary larval stage of the parasite; SO = subumbrellar ectoderm of the host; TF = tentacles of the primary larval stage stage serving for fixation; TM = manubrial tube of the young medusae parasites penetrating the manubrium of the host trough the mouth.

FIG. 63. *Narcomedusae, stades de reproduction parasitaire. A,* Solmundella bitentaculata *parasitée par* Cunina peregrina *à différent stades de reproduction. B,* Pseudotiara tropica*, Anthomedusae, parasitée des stades larvaires primaires de* Pegantha triloba*. C-D, détails des stades parasitaires de B (d'après Bouillon, 1987). BH = bouche de l'hôte ; BM1, BM2 & BM3 = stades successifs de bourgeons médusaires formés par le stade larvaire primaire ; CO = crête médiane des lobes ombrellaires des bourgeons médusaires de Pegantha triloba ; MH = manubrium de l'hôte ; P = stade larvaire primaire du parasite ; SO = ectoderme sous-ombrellaire de l'hôte ; TF = tentacules des larves primaires servant à la fixation de la larve ; TM = tube manubrial des jeunes méduses parasites penetrant le manubrium de l'hôte par leur bouche.*

Family SOLMARISIDAE Haeckel, 1879

Narcomedusae without manubrial pouches; with or without peripheral canal system; "gonads" on manubrial wall or on manubrial wall diverticula; with numerous tentacles leaving exumbrella at the level of manubrium attachment to subumbrella. With or without otoporpae.

Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. peripheral canal system; otoporpae . . . . . . *Pegantha*
– no peripheral canal system; no otoporpae . . . . . . *Solmaris*

Genus ***Pegantha*** Haeckel, 1879

Figs 27C, 62A-C, 63B-D

Solmarisidae with "gonads" forming diverticula on margin of oral manubrium wall; with peripheral canal system; with otoporpae.

Pegantha aureola (Haeckel, 1879) [doubtful status]
Pegantha cyanostylis (Eschscholtz, 1829) [doubtful status]
Pegantha dodecagona (Péron & Lesueur, 1810a) [doubtful status]
Pegantha forskalii (Haeckel, 1879) [doubtful status]
Pegantha godeffroyi (Haeckel, 1879) [doubtful status]
Pegantha laevis Bigelow, 1909
Pegantha lunulata (Haeckel, 1879) [syn. *P. clara* Bigelow, 1909]
Pegantha magnifica Haeckel, 1879
Pegantha martagon Haeckel, 1879
Pegantha mollicina (Forskål, 1775) [doubtful status]
Pegantha pantheon Haeckel, 1879 [probably a syn. of *P. triloba*]
Pegantha punctata (Quoy & Gaimard, 1824) [doubtful status]
Pegantha quadriloba Haeckel, 1879 [probably a syn. of *P. triloba*]
Pegantha rubiginosa (Kölliker, 1853a)
Pegantha sieboldi (Haeckel, 1879) [probably a syn. of *P. triloba*]
Pegantha triloba Haeckel, 1879 [syn. *P. biloba* Haeckel, 1879 and *P. dactyletra* Maas, 1893]
Pegantha weberi (Haeckel, 1879) [doubtful status]
Pegantha zonaria (Haeckel, 1879) [doubtful status]
Pegantha zonorchis (Haeckel, 1879) [doubtful status]

Genus ***SOLMARIS*** Haeckel, 1879

Fig. 62D-E

Solmarisidae without peripheral canal system; without otoporpae, with simple annular "gonads".

Recent references: Bouillon *et al.* (1991); Arai *et al.* (2000).

Solmaris corona (Keferstein & Ehlers, 1861) [syn. *S. multilobata* Maas, 1893]
Solmaris flavescens (Kölliker, 1853b)
Solmaris lenticula Haeckel, 1879
Solmaris leucostyla (Will, 1844)
Solmaris quadrata Bouillon, Boero & Seghers, 1991
Solmaris rhodoloma (Brandt, 1838)
Solmaris solmaris (Gegenbaur, 1857)
Solmaris vanhoeffeni Neppi & Stiasny, 1911 [juvenile specimens]

Subclass TRACHYMEDUSAE

Umbrella hemispherical or deep bell-shaped, margin entire with a thickened peripheral cnidocyst ring, with radial canals and circular canal, with or without centripetal canals, velum often with heavy musculature. "Gonads" usually on radial canals. Marginal tentacles solid or alternatively solid and hollow, without true tentacular bulbs, with endodermal cores continuing in the mesoglea of the umbrella as short "roots". Manubrium with or without gastric peduncle. Free marginal sensory clubs, exceptionally enclosed in the mesoglea or in the velum. No polyp stage; a differentiated planula

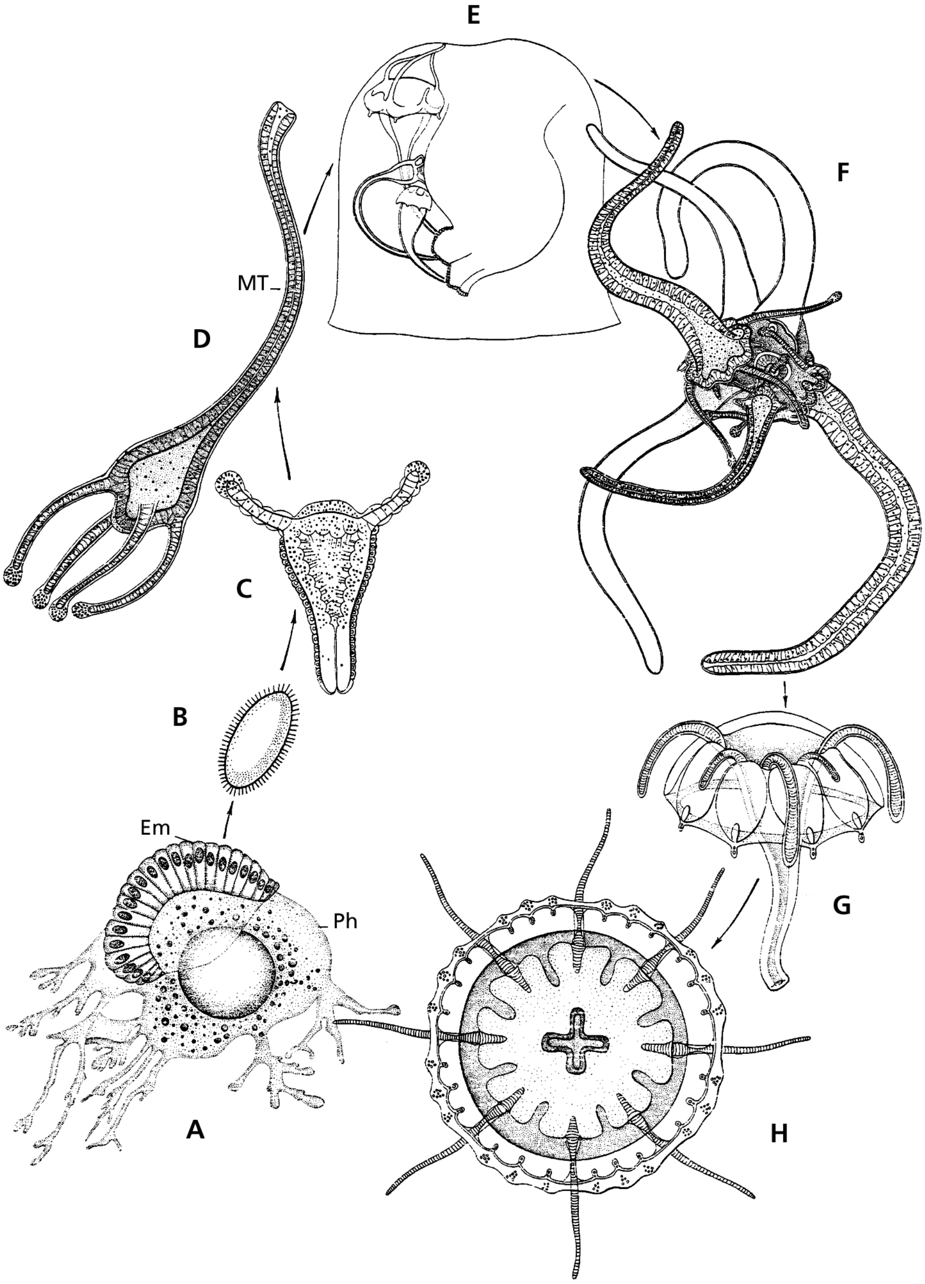


FIG. 64. Narcomedusae, stages of parasitic reproduction (concluded). Development of *Cunina octonaria* parasitizing *Turritopsis nutricula*, Anthomedusae. A, Young embryo (Em), blastula, in its phorocyte (Ph) developing in the gastro-vascular pouches of the *Cunina* mother. B, free planula stage. C, bitentaculate primary larva issued from the planula. D, primary larva with four tentacles and manubrial tube, ready to parasite its future host. E, primary larva fixed by the tentacles on the subumbrellar ectoderm of the *Turritopsis* host. F, primary larva budding off secondary larvae from their aboral end. G, young *Cunina* issued from a parasitic larva. H, adult medusae of *Cunina octonaria* (from Bouillon, 1987).

FIG. 64. *Narcomedusae, stades de reproduction parasitaire (fin). Développement de* Cunina octonaria *parasitant* Turritopsis nutricula*, Anthomedusae. A, jeune embryon (Em) au stade blastula, dans son phorocyte (Ph) se développant dans les poches gastro-vasculaires de la* Cunina octonaria *maternelle. B, stade planula libre. C, larve primaire bitentaculée issue de la planula. D, larve primaire pourvue de quatre tentacules et d'un tube manubrial, prête à parasiter son futur hôte. E, larve primaire fixée par ses tentacules à l'ectoderme sous-ombrellaire de la* Turritopsis *hôte. F, larve primaire bourgeonnant des larves secondaires au niveau de son extrémité aborale. G, jeune Cunina issue d'une larve parasite secondaire. H, méduse adulte de* Cunina octonaria *(copié de Bouillon, 1987).*

is lacking in a number of Trachymedusae, the gastrula developing immediately into young medusae; in others, the planula is retained and gives rise to a post-embryonic tentacled larva before transforming into medusae. No adult or larval asexual budding. Cnidome: generally stenoteles associated with microbasic euryteles or/and atrichous isorhizae.
Recent reference: Bouillon & Boero (2000).

KEY TO MEDUSAE

1. numerous tentacles, mostly terminal adhesive disk, arranged in groups; manubrium broad, with eight radial lobes . . . . Ptychogastriidae
– tentacles without adhesive disk 2

2. centripetal canals . . . . Geryoniidae
– no centripetal canals 3

3. 4 radial canals . . . . Petasidae
– 8, rarely more radial canals 4

4. broad, circular manubrium and broad radial canals . . . . Halicreatidae
– manubrium and radial canals narrow . . . . Rhopalonematidae

Family GERYONIIDAE Eschscholtz, 1829

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

Remarks: The Geryoniidae forms a well-defined and rather original family inside the Trachymedusae.
Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. 6 radial canals, six "gonads", mouth with six lips . . . . *Geryonia*
– usually 4 radial canals and "gonads" (sometimes more), mouth with 4 lips . . . . *Liriope*

Genus ***GERYONIA*** Péron & Lesueur, 1810

Figs 34D, 65A-C

Geryoniidae with six lips; 6 radial canals and 6 "gonads".

Geryonia proboscidalis (Forskål, 1775)

Genus ***LIRIOPE*** Lesson, 1843

Figs 51, 65D-I

Synonyms: *Heptaradiata* Zamponi & Genzano 1988, *Octoradiata* Zamponi & Genzano 1988, *Pentaradiata* Zamponi & Genzano 1988.
Geryoniidae always with 4 lips; usually 4 radial canals and 4 "gonads".
Remarks: aberrant specimens with more than 4 radial canals and "gonads", but invariably with 4 oral lips.
Liriope tetraphylla (Chamisso & Eysenhardt, 1821)

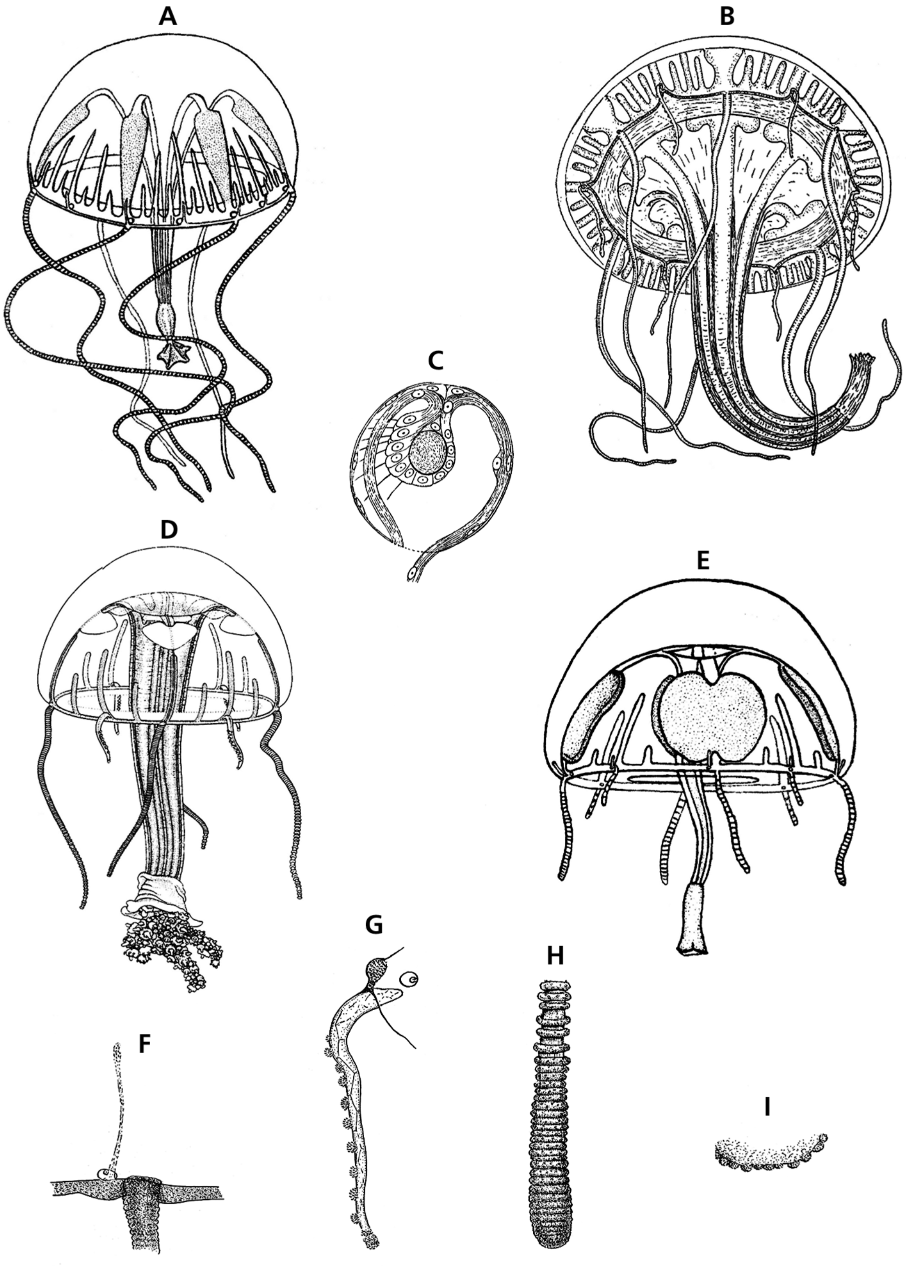


FIG. 65. Trachymedusae, Geryoniidae. A-C, *Geryonia proboscidalis*: A-B, general view. C, statocyst. D-I, *Liriope tetraphylla*: D, adult medusa parasitised by *Cunina octonaria*; E, general view of adult medusa; F, base of a solid interradial marginal tentacle with a centripetal canal and statocyst; G, lateral view of a solid marginal tentacle showing a statocyst and the marginal cnidocyst ring of the umbrella; H, terminal portion of a hollow perradial tentacle; I, portion of margin of mouth-lip (A after Trégouboff, 1957: pl. 71, fig 7; B after Hyman, 1940; C after Hertwig O. & R., 1878; D after Bouillon, 1987; E after Trégouboff, 1957: pl. 71, fig. 5; F-I after Russell, 1953).

FIG. 65. *Trachymedusae, Geryoniidae. A-C,* Geryonia proboscidalis *: A-B, vues générales ; C, statocyste. D-I,* Liriope tretraphylla *: D, méduse adulte parasitée par* Cunina octonaria *; E, vue générale d'une méduse adulte ; F, vue de la base d'un tentacule interradiare solide, d'un canal centripète et d'un statocyste ; G, vue latérale d'un tentacule marginal solide montrant un statocyste et l'anneau cnidocytaire marginal exombrellaire ; H, portion terminale d'un tentacule creux perradiaire ; I, portion du bord marginal d'une lèvre buccale (A d'après Trégouboff, 1957 : pl. 71, fig. 7 ; B d'après Hyman, 1940 ; C d'après Hertwig O. & R., 1878 ; D d'après Bouillon, 1987 ; E d'après Trégouboff, 1957 : pl. 71, fig. 5 ; F-I d'après Russell, 1953).*

Family HALICREATIDAE Fewkes, 1886

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 a single series; each marginal tentacle with flexible proximal portion and stiff spine-like distal portion; with free ecto-endodermal statocysts.

Recent references: Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. about 16 or more radial canals . . . . *Halitrephes*
– 4 or 8 radial canals 2

2. 4 radial canals . . . . *Varitentaculata*
– 8 radial canals 3

3. tentacles arranged in 16 groups . . . . *Botrynema*
– tentacles in a continuous row 4

4. perradial gelatinous papillae on exumbrella . . . . *Halicreas*
– no exumbrellar papillae . . . . *Haliscera*

Genus ***BOTRYNEMA*** Browne, 1908

Fig. 66A

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

Fig. 66B-C

With 8 radial canals; with continuous tentacle row; perradial gelatinous papillae on exumbrella.

Halicreas minimum Fewkes, 1882

Genus ***Haliscera*** Vanhöffen, 1902

Fig. 66D-E

With 8 radial canals; with a continuous row of marginal tentacles; without exumbrellar papillae.

Haliscera alba Vanhöffen, 1902
Haliscera bigelowi Kramp, 1947a
Haliscera conica Vanhöffen, 1902
Haliscera racovitzae (Maas, 1906)

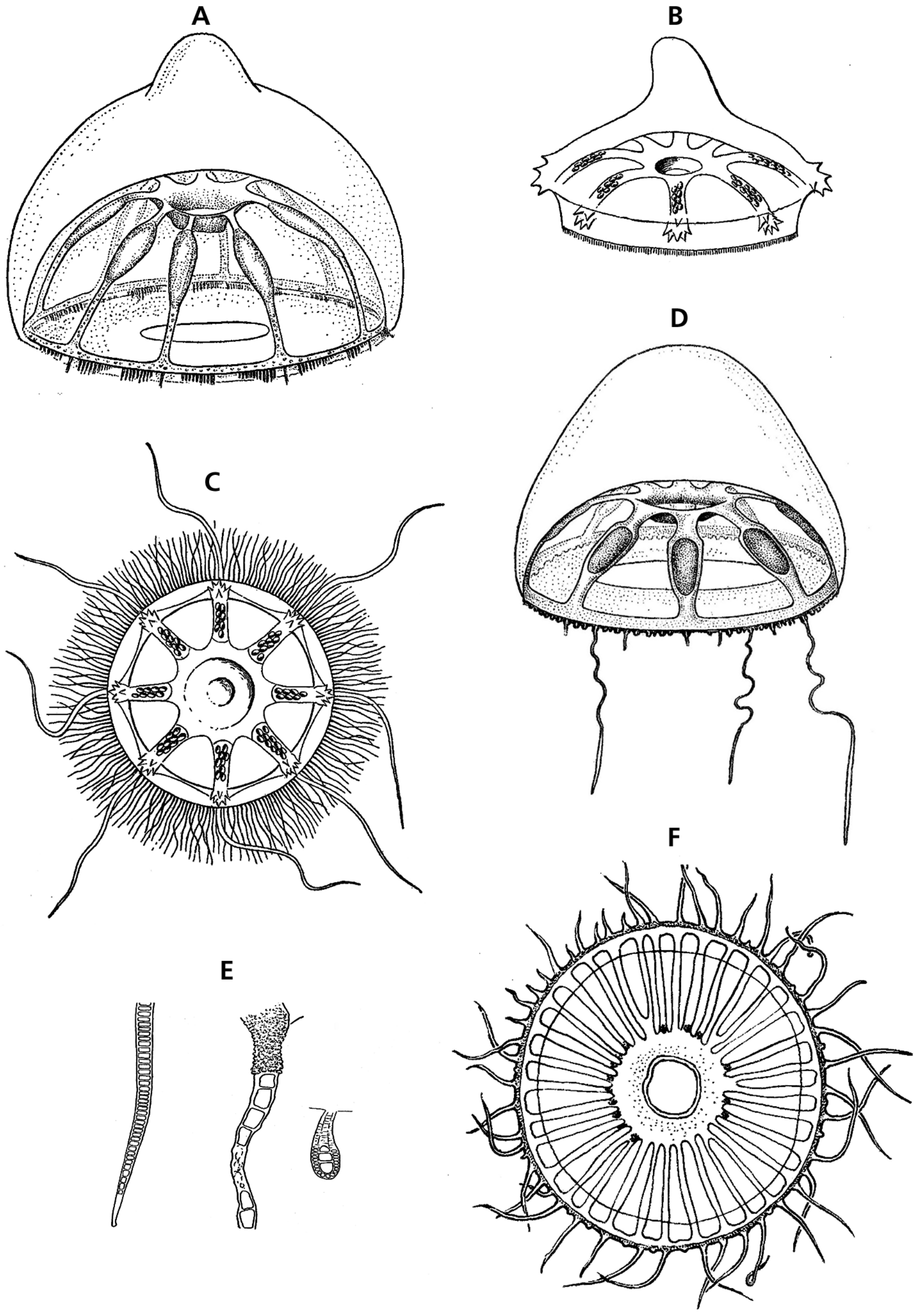


FIG. 66. Trachymedusae, Halicreatidae. A, *Botrynema brucei*. B-C, *Halicreas minimum*: B, lateral general view; C, dorsal general view. D-E, *Haliscera bigelowi*: D, lateral general view; E, stiff distal end of a marginal tentacle (left), flexile proximal portion of marginal tentacle (middle), statocyst (right). F, *Halitrephes maasi* (A after Kramp,1968; B-C after after Mayer,1910; D & F after Kramp, 1959b; E after Russell, 1953).

FIG. 66. *Trachymedusae, Halicreatidae. A,* Botrynema brucei. *B-C,* Halicreas minimum *: B, vue générale latérale ; C, vue générale dorsale. D-E,* Haliscera bigelowi *: D, vue générale latérale ; E, portion distale rigide d'un tentacule marginal (à gauche), portion proximale flexible d'un tentacule marginal (au milieu), statocyste (à droite). F,* Halitrephes maasi *(A d'après Kramp, 1968 ; B-C d'après Mayer, 1910 ; D & F d'après Kramp, 1959b ; E d'après Russell, 1953).*

Genus ***Halitrephes*** Bigelow, 1909

Fig. 66F

With 16 or more radial canals; with a continuous row of tentacles; without papillae on exumbrella.

Halitrephes maasi Bigelow, 1909

Genus ***Varitentaculata*** He Zhen-Wu, 1980

Fig. 67A

Halicreatidae with only 4 radial canals.

Varitentaculata yantaiensis He Zhen-Wu, 1980

Family PETASIDAE Haeckel, 1879

Trachymedusae with 4 radial canals; no peduncle and centripetal canals; manubrium well developed; 4 sac-like "gonads" on radial canals; marginal tentacles not in clusters, solid, with a terminal club-shaped knob of cnidocysts; free statocysts.

Recent references: Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. tentacles asymmetrically arranged . . . . *Petasiella*
– tentacles regularly arranged . . . . *Petasus*

Genus ***PETASIELLA*** Uchida, 1947

Fig. 67B-C

Petasidae with marginal tentacles arising asymmetrically, at unequal intervals.
Petasiella asymmetrica Uchida, 1947a

Genus ***PETASUS*** Haeckel, 1879

Fig. 67D

Petasidae with regularly arranged marginal tentacles.
Petasus atavus Haeckel, 1879
Petasus digonimus (Haeckel, 1879) [doubtful status]
Petasus tiaropsis (Haeckel, 1879) [doubtful status]

Family PTYCHOGASTRIIDAE Mayer, 1910

Trachymedusae with either simple manubrium without mesenteries, or with eight-lobed manubrium, with 8 mesenteries; 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.

Recent references: Gili *et al.* (1999); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

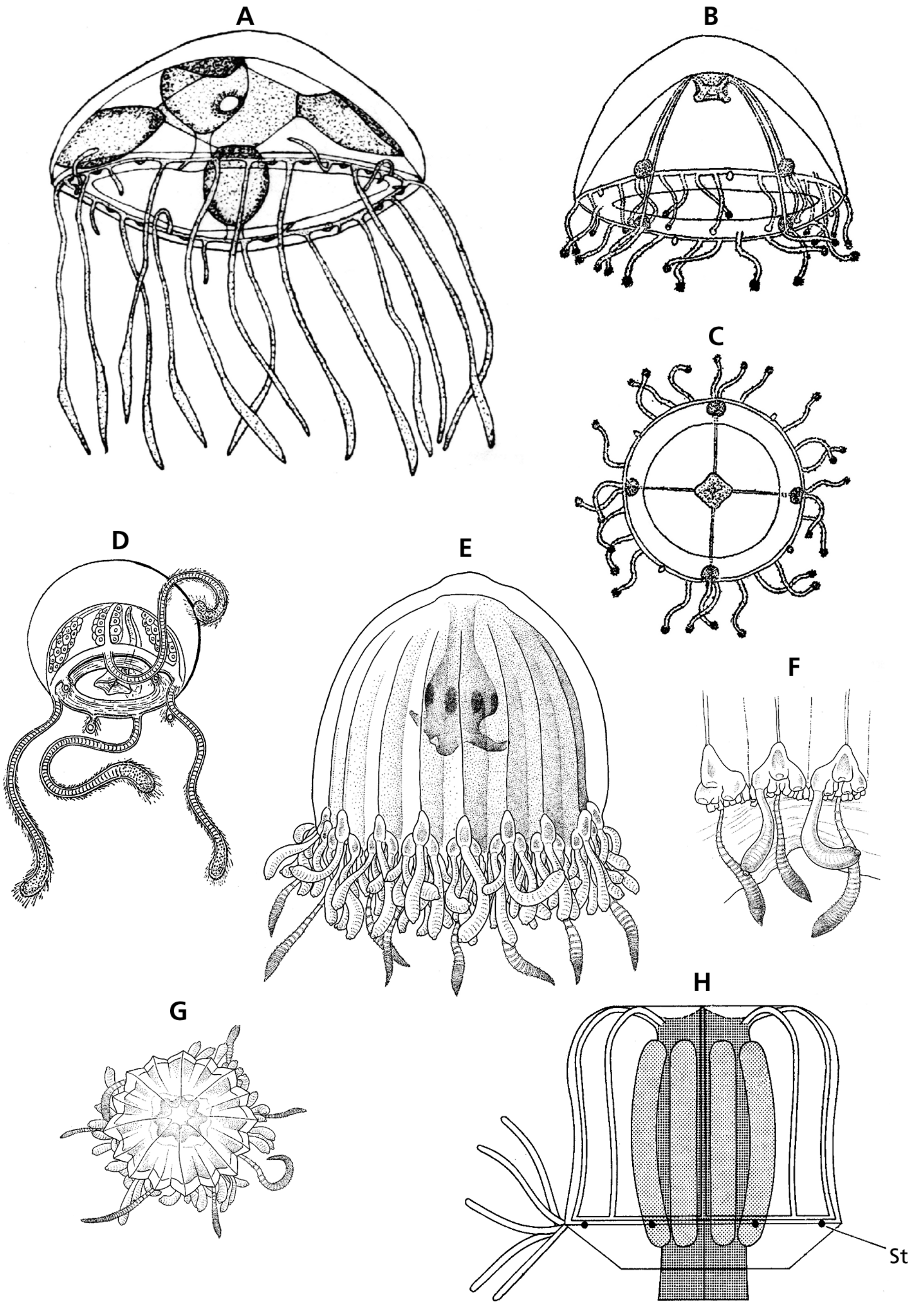


FIG. 67. Trachymedusae. A, Halicreatidae (concluded). *Varitentaculata yantaiensis*. B-D, Petasidae. B-C, *Petasiella assymmetrica*: B, lateral view; C, dorsal view; D, *Petasus atavus*. E-G, Ptychogastriidae, *Ptychogastria asteroides*: E, lateral general view; F, detail of the marginal border; G, upper view of the umbrella of a juvenile specimen. H, *Tesserogastria musculosa* slightly schematic lateral view (A after He, 1980; B-C after Kramp, 1968; D after Mayer, 1910; E-G after Gili *et al*., 1999; H after Hesthagen, 1971). St = statocyst.

FIG. 67. *Trachymedusae. A, Halicreatidae (fin).* Varitentaculata yantaiensis. *B-D, Petasidae. B-C,* Petasiella assymetrica *: B, vue latérale ; C, vue dorsale ; D,* Petasus atavus. *E-G, Ptychogastriidae,* Ptychogastria asteroides *: E, vue générale latérale ; F, détail du bord ombrellaire ; G, vue dorsale de l'ombrelle d'une jeune méduse. H,* Tesserogastria musculosa *vue latérale légèrement schématisée (A d'après He, 1980 ; B-C d'après Kramp, 1968 ; D d'après Mayer, 1910 ; E-G d'après Gili et al., 1999 ; H d'après Hesthagen, 1971). St = statocyste.*

KEY TO MEDUSAE

1. tentacles into more or less defined clusters, some with adhesive organs . . . . *Ptychogastria*
– tentacles not in clusters, with no adhesive organs . . . . *Tesserogastria*

Genus ***PTYCHOGASTRIA*** Allman, 1878

Fig. 67E-G

Ptychogastriidae with marginal tentacles in clusters, some with adhesive disks; manubrium with lateral lobes; with 8 mesenterial partitions; "gonads" on the sides of the manubrial lobes or on radial canals adjacent to manubrial lobes.
Recent reference: Panteleeva *et al.* (1999).

Ptychogastria antarctica (Haeckel, 1879) [doubtful status]
Ptychogastria asteroides (Haeckel, 1879)
Ptychogastria polaris Allman, 1878

Genus ***TESSEROGASTRIA*** Beyer, 1959

Fig. 67H

Ptychogastriidae with a great number of solid tentacles inserted at varying distances from the velum, not in clusters, without adhesive pads; manubrium simple, without peduncle, mesenteries, or pouches; 8 "gonads" attached along manubrium.

Tesserogastria musculosa Beyer, 1959

Family RHOPALONEMATIDAE Russell, 1953

Trachymedusae with a narrow manubrium; with or without peduncle; no centripetal canals; usually 8, rarely more, narrow radial canals; mouth with distinct lips; marginal tentacles evenly distributed, sometimes of two kinds, each marginal tentacle of uniform structure throughout or with proximal portion differing from distal one; "gonads" either on radial canals, or forming a continuous ring around base of manubrium and extending outwards along radial canals; ecto-endodermal statocysts either free, or rarely enclosed by an exumbrellar outgrowth.
Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. "gonads" in a continuous band around manubrium extending outwards on radial canals . . . . *Homoeonema*
– "gonads" isolated, on radial canals, sometimes adjacent to manubrium 2

2. no gastric peduncle 3
– gastric peduncle 10

3. 4 "gonads" only, pendulous; 4 large and 24 small marginal tentacles . . . . *Tetrorchis*
– 8 (rarely more) "gonads" 4

4. two kinds of marginal tentacles; enclosed statocysts. . . . . *Rhopalonema*
– all tentacles of one kind; free club-shaped statocysts 5

5. "gonads" adjacent to manubrium (sometimes also 8 "gonads" free from manubrium); very numerous tentacles. . . . . *Arctapodema*
– "gonads" separated from manubrium 6

6. exumbrella with numerous meridional furrows 7
– exumbrella smooth 8

7. “gonads” sausage-shaped, pendulous . . . . *Crossota*
– “gonads” not pendulous, tubular, attached longitudinally to radial canals . . . . *Vampyrocrossota*

8. “gonads” globular, distal, contiguous to circular canal; with 8 tentacles . . . . *Sminthea*
– “Gonads” linear, with 32 or more marginal tentacles 9

9. 32 tentacles all of one kind developed in succession . . . . *Colobonema*
– 48 or more tentacles of equal size . . . . *Pantachogon*

10. umbrella with centripetal canals . . . . *Voragonema*
– no centripetal canals 11

11. gastric peduncle short conical (in young specimens almost invisible); “gonads” attached on subumbrellar portions of radial canals 2
– gastric peduncle long, slender 13

12. only 2 pendulous “gonads” . . . . *Persa*
– 8 “gonads” . . . . *Amphogona*

13. “gonads” linear, wavy, along the radial canals for most of their length 14
– “gonads” sausage shaped, definitively pendulous 15

14. “gonads” along peduncle part of radial canals only . . . . *Ransonia*
– “gonads” along most of radial canals . . . . *Benthocodon*

15. “gonads” attached to peduncle . . . . *Aglaura*
– “gonads” attached to subumbrellar portions of radial canals . . . . *Aglantha*

Genus ***AGLANTHA*** Haeckel, 1879

Figs 25B, 26L, 68A

Rhopalonematidae with a long and slender gastric peduncle; 8 pendulous sausage-shaped “gonads” on subumbrellar portions of the 8 radial canals; tentacles numerous; marginal statocysts free, club-shaped.

Aglantha digitale (O.F. Müller, 1776)
Aglantha elata (Haeckel, 1879)
Aglantha ignea Vanhöffen, 1902 [doubtful status]
Aglantha intermedia Bigelow, 1909

Genus ***AGLAURA*** Péron & Lesueur, 1810

Figs 50, 68B

Rhopalonematidae with slender gastric peduncle; 8 sausage-shaped “gonads” attached on peduncle, not on subumbrella; tentacles numerous, statocysts free, club-shaped.

Aglaura hemistoma Péron & Lesueur, 1810b

Genus ***AMPHOGONA*** Browne, 1905

Fig. 68C

Rhopalonematidae with short, conical gastric peduncle, exumbrella smooth; ellipsoidal or sac-shaped, pendulous “gonads” on the 8 radial canals, usually of unequal size; tentacles not densely crowded; statocysts free, club-shaped.

Amphogona apicata Kramp, 1957
Amphogona apsteini (Vanhöffen, 1902)
Amphogona pusilla Hartlaub, 1909b

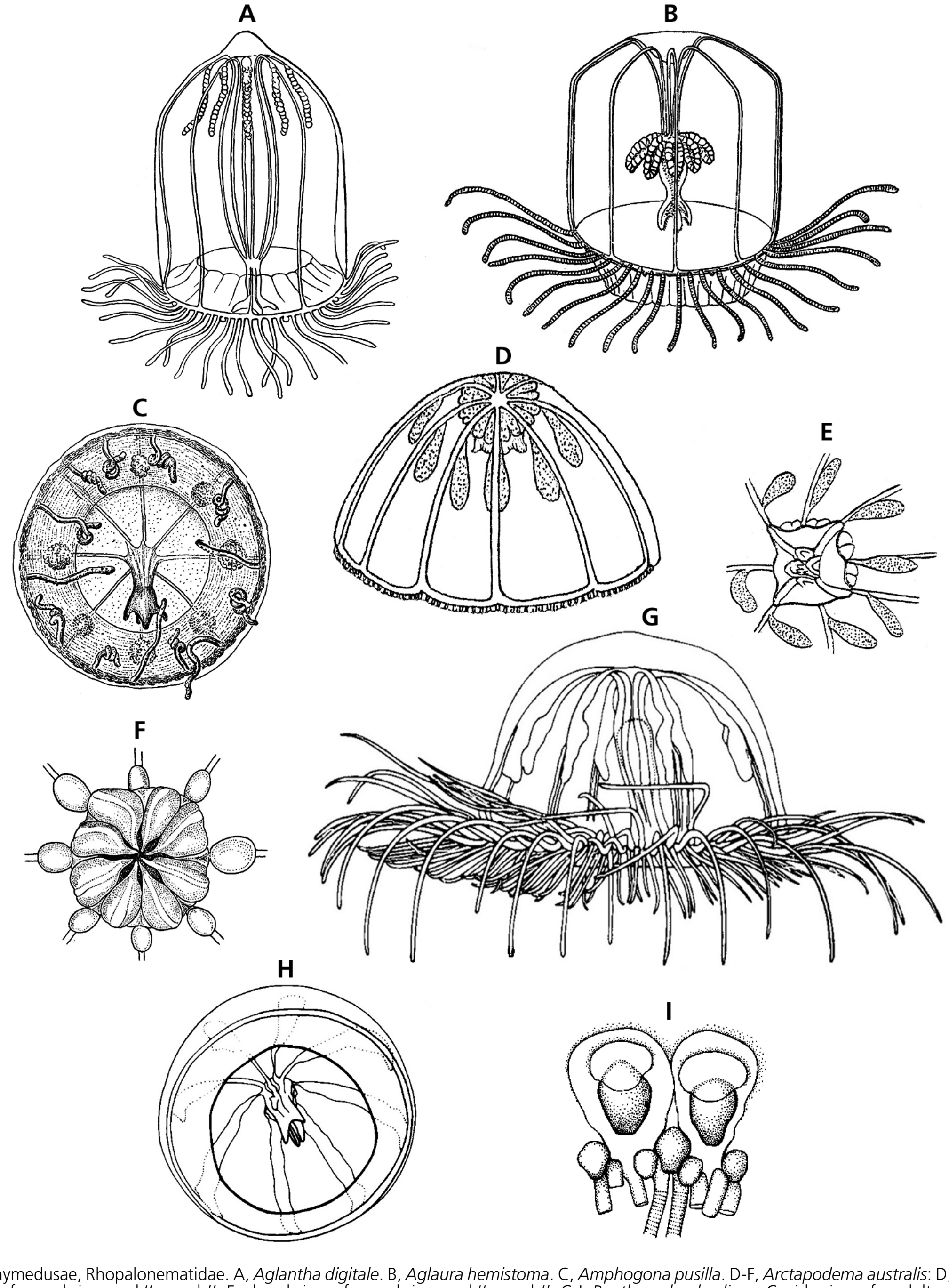


FIG. 68. Trachymedusae, Rhopalonematidae. A, *Aglantha digitale*. B, *Aglaura hemistoma*. C, *Amphogona pusilla*. D-F, *Arctapodema australis*: D, lateral general view; E, view of manubrium and ''gonads''; F, aboral view of manubrium and ''gonads''. G-I, *Benthocodon hyalinus*: G, side view of a adult medusa; H, velar view of a adult medusa; I, side view of umbrella margin showing several ranks of tentacles (A-B after Broch, 1929; C after Kramp, 1959b; D-E after Vanhoeffen, 1912; F after Kramp, 1968; G-I after Larson & Harbison, 1990: p. 22, fig. 2 A, B; p. 23, fig. 4).

FIG. 68. *Trachymedusae, Rhopalonematidae. A,* Aglantha digitale. *B,* Aglaura hemistoma. *C,* Amphogona pusilla. *D-F,* Arctapodema australis *: D, vue générale latérale ; E, vue du manubrium et des « gonades » ; F, vue aborale du manubrium et des « gonades ». G-I,* Benthocodon hyalinus *: G, vue latérale d'une méduse adulte ; H, vue velaire d'une méduse adulte ; I, vue latérale du bord exombrellaire montrant plusieurs rangées de tentacules (A-B d'après Broch, 1929 ; C d'après Kramp, 1959b ; D-E d'après Vanhoeffen, 1912 ; F d'après Kramp, 1968 ; G-I d'après Larson & Harbison, 1990 : p. 22, figs 2 A, B ; p. 23, fig. 4).*

Genus *ARCTAPODEMA* Dall, 1907

Fig. 68D-F

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

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

Genus *BENTHOCODON* Larson and Harbison, 1990

Fig. 68G-I

Rhopalonematidae without exumbrellar furrows; without centripetal canals; with 8 radial canals; "gonads" linear to wavy, pendulous only distally; gastric peduncle well developed; tentacles numerous, superimposed in several rows; marginal sense organs not observed.

Benthocodon hyalinus Larson & Harbison, 1990

Genus *COLOBONEMA* Vanhöffen, 1902

Fig. 69A-B

Rhopalonematidae without gastric peduncle; apical outlines of subumbrellar muscular fields forming a star-shaped figure; "gonads" elongate along 8 radial canals; tentacles of different size, developing in succession; statocysts free, club-shaped.

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

Genus *CROSSOTA* Vanhöffen, 1902

Fig. 69C-E

Rhopalonematidae without peduncle; numerous meridional exumbrellar furrows; 8 or more radial canals; pendulous sausage-shaped "gonads" on radial canals; numerous densely crowded tentacles; free club-shaped statocysts.
Recent references: Thuesen (1993, 2003).

Crossota alba Bigelow, 1913
Crossota brunnea Vanhöffen, 1902
Crossota millsae Thuesen, 2003
Crossota norvegica Vanhöffen, 1902
Crossota rufobrunnea (Kramp, 1913)

Genus *HOMOEONEMA* Browne, 1903

Fig. 69F-I

Rhopalonematidae without gastric peduncle; "gonads" forming a continuous band around base of manubrium and extending outwards along proximal half of 8 radial canals; tentacles numerous; statocysts vesicular.
Recent reference: Gili *et al.* (1998).

Homoeonema platygonon Browne, 1903

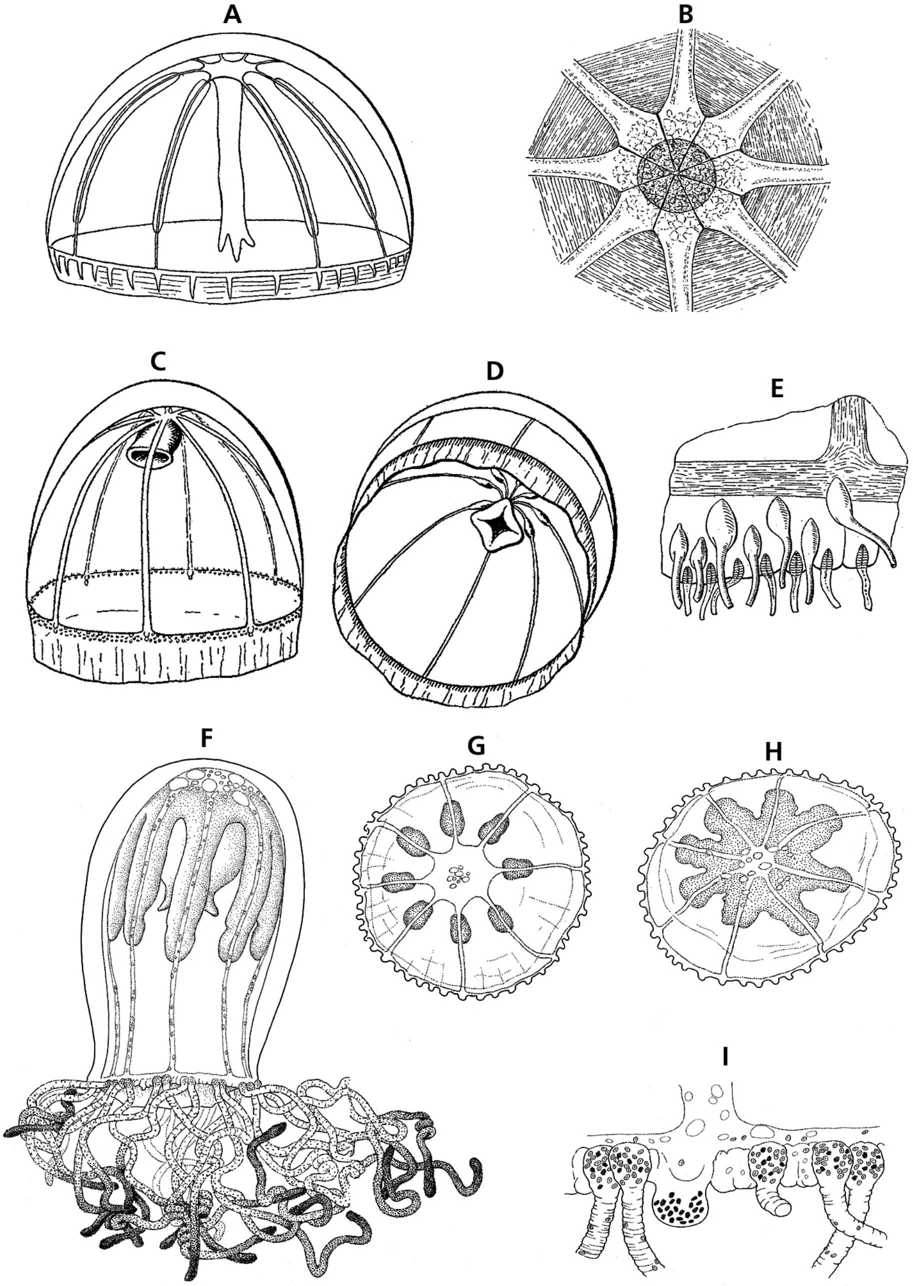


FIG. 69. Trachymedusae, Rhopalonematidae. A, *Colobonema typicum*. B, *Colobonema sericeum*, apical view of the summit of the umbrella showing the manubrium, the radial canals and the subumbrellar muscle fields. C-E, *Crossota brunnea*: C, lateral general view; D, velar view; E, portion of exumbrella showing insertions of tentacles at various levels above umbrellla margin. F-I, *Homoeonema platygonon*: F, adult medusa; G, aboral view of a juvenile specimen; H, aboral view of a mature specimen; I, detail of umbrella margin (A, C-E after Mayer, 1910; B after Russell, 1953; F-I after Gili *et al*., 1998).

FIG. 69. *Trachymedusae, Rhopalonematidae. A, Colobonema typicum. B, Colobonema sericeum, vue apicale du sommet de l'ombrelle montrant le manubrium, les canaux radiaires et les champs musculaires sous-ombrellaire. C-E, Crossota brunnea : C, vue générale latérale ; D, vue velaire ; E, portion de l'exombrelle montrant l'insertion de tentacules à divers niveaux au dessus du bord marginal exombrellaire. F-I, Homoeonema platygonon : F, méduse adulte ; G, vue aborale d'un spécimen juvénile ; H, vue aborale d'un spécimen mature ; I, détail du bord de l'exombrelle (A, C-E d'après Mayer, 1910 ; B d'après Russell, 1953 ; F-I d'après Gili et al., 1998).*

Genus ***PANTACHOGON*** Maas, 1893

Fig. 70A-D

Rhopalonematidae without gastric peduncle; apical outlines of subumbrellar muscular fields forming an entire circle; “gonads” on the 8 radial canals; 48 or more tentacles; statocysts free, club-shaped.

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

Genus ***PERSA*** McCrady, 1859

Fig. 70E-F

Rhopalonematidae with short gastric peduncle; only 2 oval or sausage-shaped “gonads”, pendulous, near middle point of subumbrellar portions of two opposite radial canals; 8 radial canals; tentacles numerous, long, capitate; statocysts free, club-shaped.

Persa incolorata McCrady, 1859

Genus ***RANSONIA*** Kramp, 1947

Fig. 71A-C

Rhopalonematidae with high conical umbrella (similar to *Aglantha*); gastric peduncle long and narrow; 8 radial canals; “gonads” linear, discontinuous, along peduncular portions of radial canals, not on subumbrella; tentacles numerous; marginal sense organs not observed.

Ransonia krampi (Ranson, 1932)

Genus ***RHOPALONEMA*** Gegenbaur, 1857

Figs 34C, 71D-E

Rhopalonematidae without gastric peduncle; “gonads” along radial canals; marginal tentacles solid, of two kinds: large, club-shaped, perradial, with swollen end; inter-and adradial short, stiff, cirrus-like, with swollen end; statocysts enclosed.

Rhopalonema funerarium Vanhöffen, 1902
Rhopalonema velatum Gegenbaur, 1857

Genus ***SMINTHEA*** Gegenbaur, 1857

Fig. 71F-H

Rhopalonematidae without gastric peduncle; “gonads” globular, on very distal parts of the 8 radial canals; only 8 perradial tentacles; statocysts enclosed.

Sminthea arctica Hartlaub, 1909a [doubtful status]
Sminthea eurygaster Gegenbaur, 1857

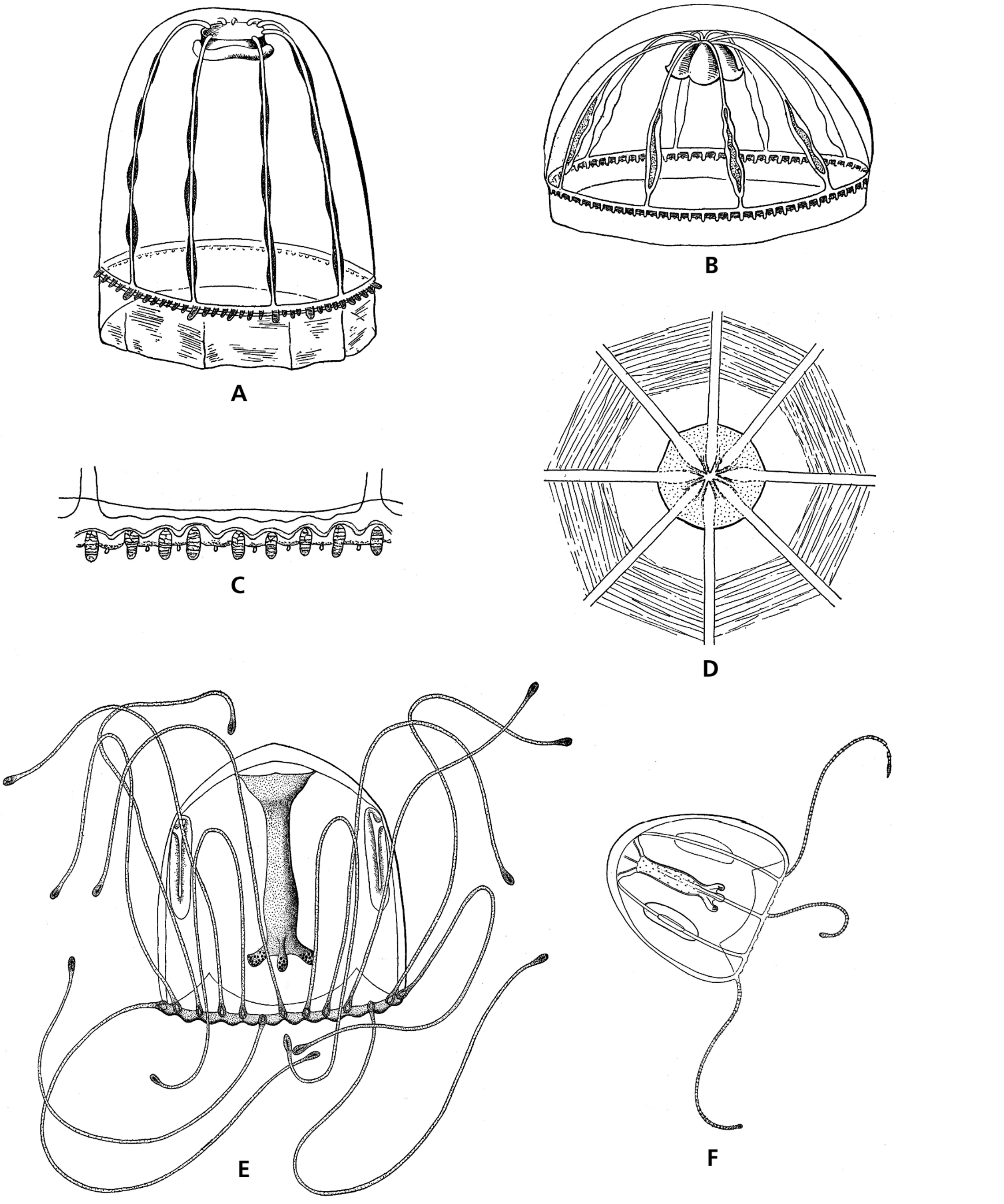


FIG. 70. Trachymedusae, Rhopalonematidae. A-D, *Pantachogon haeckeli*: A-B, general view of different specimens; C, detail of umbrella margin; D, apical view showing the summit of the umbrella. E-F, *Persa incolorata*: E, adult medusa; F, juvenile medusa (A-B, E-F after Mayer, 1910; C-D after Russell, 1953).

***FIG. 70.** Trachymedusae, Rhopalonematidae. A-D,* Pantachogon haeckeli *: A-B, vue générale de différents spécimens ; C, détail du bord exombrellaire ; D, vue apicale montrant le sommet de l'ombrelle. E-F,* Persa incolorata *: E, méduse adulte ; F, méduse juvénile (A-B, E-F d'après Mayer, 1910 ; C-D d'après Russell, 1953).*

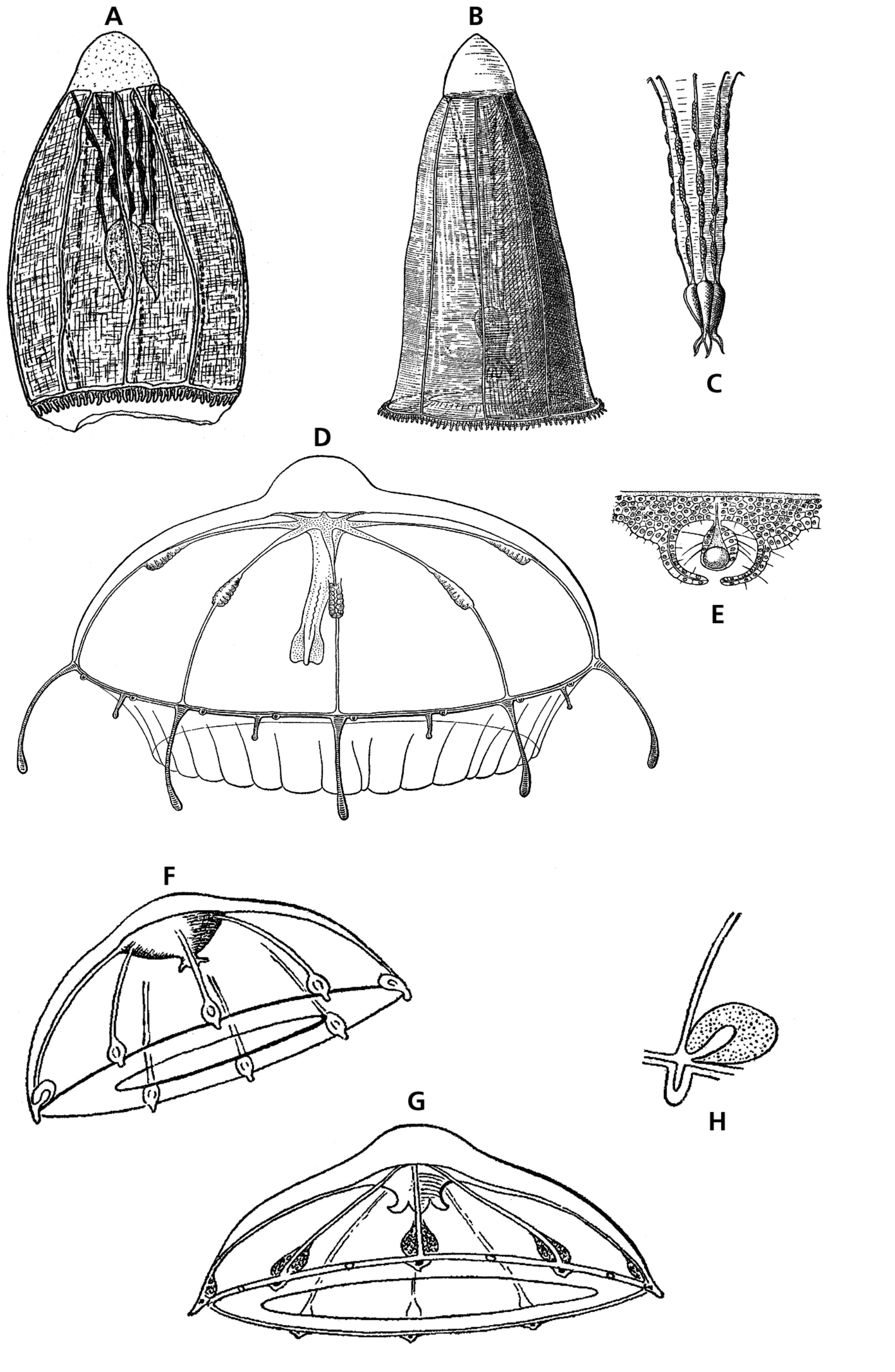


FIG. 71. Trachymedusae, Rhopalonematidae. A-C, *Ransonia krampi*: A-B, general lateral view of two different specimens; C, detail of manubrium. D-E, *Rhopalonema velatum*: D, general view; E, statocyst. F-H, *Sminthea eurygaster*: F-G, two different lateral views; H, enlarged view of ''gonads'' (A after Gili, 1986; B-C after Kramp, 1959b; D, F-H after Mayer, 1910; E after Hertwig O. & R., 1878).

FIG. 71. *Trachymedusae, Rhopalonematidae. A-C,* Ransonia krampi *: A-B, vue générale latérale de deux spécimens différents ; C, détail du manubrium. D-E,* Rhopalonema velatum *: D, vue générale ; E, statocyste. F-H,* Sminthea eurygaster *: F-G, vues latérales de deux spécimens différents ; H, vue agrandie des ''gonades'' (A d'après Gili, 1986 ; B-C d'après Kramp, 1959b ; D, F-H d'après Mayer, 1910 ; E d'après Hertwig O. & R., 1878).*

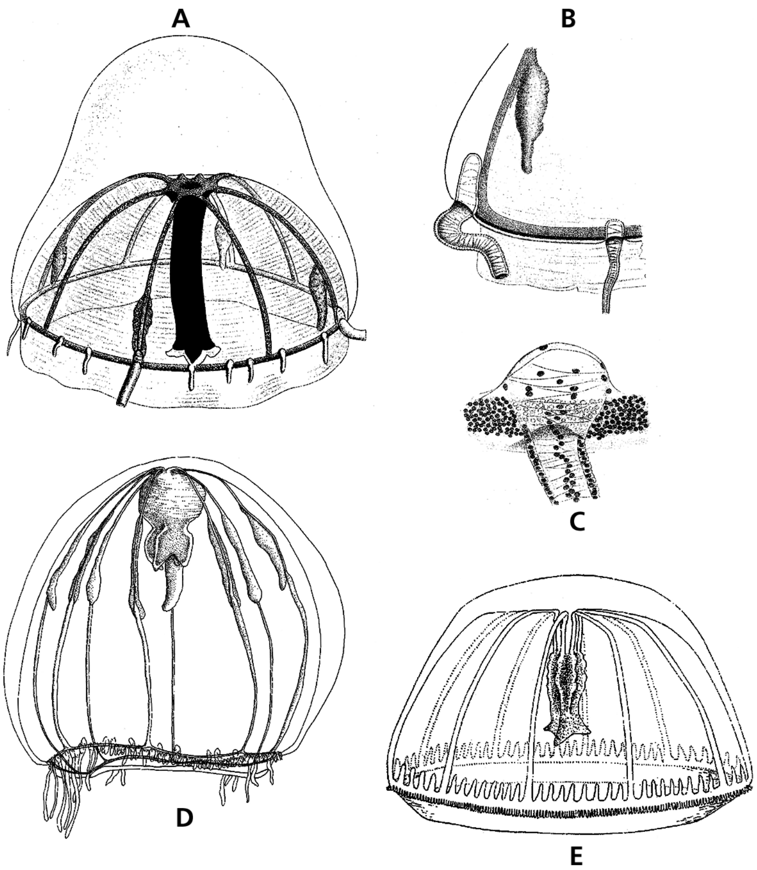


FIG. 72. Trachymedusae, Rhopalonematidae. A-C, *Tetrorchis erythrogaster*: A, general view; B, side view of a portion of the umbrella showing the position of the ''gonad'' and the endodermic tentacular root of a perradial tentacle; C, base of a small tentacle with rounded endodermic tentacular root. D, *Vampyrocrossota childressi*. E, *Voragonema profundicola* (A-C after Bigelow, 1909; D after Thuesen, 1993; E after Naumov, 1971).

FIG. 72. *Trachymedusae, Rhopalonematidae. A-C,* Tetrorchis erythrogaster : *A, vue générale ; B, vue latérale d'une portion de l'ombrelle montrant la position des « gonades » et des racines endodermiques des tentacules perradiaires ; C, base des petits tentacules présentant des racines tentaculaires arrondies. D,* Vampyrocrossota childressi. *E,* Voragonema profundicola *(A-C d'après Bigelow, 1909 ; D d'après Thuesen, 1993 ; E d'après Naumov, 1971).*

Genus ***TETRORCHIS*** Bigelow, 1909

Fig. 72A-C

Rhopalonematidae without gastric peduncle; only 4 sausage-shaped, pendulous, "gonads" attached near the middle points of 4 of the 8 radial canals; 4 large perradial and several small marginal tentacles; no marginal sense organs.

Tetrorchis erythrogaster Bigelow, 1909

Genus ***VAMPYROCROSSOTA*** Thuesen, 1993

Fig. 72D

Rhopalonematidae without gastric peduncle; with exumbrellar furrows; 8 radial canals; "gonads" attached longitudinally to radial canals; tentacles of one kind; no marginal sense organs.

Vampyrocrossota childressi Thuesen, 1993

Genus ***VORAGONEMA*** Naumov, 1971

Figs 72E, 73A-D

Rhopalonematidae with gastric peduncle; 8 radial canals, numerous centripetal canals; up to 500-2000 marginal tentacles superimposed in several rows; statocysts free, club-shaped.

Voragonema laciniata Bouillon, Pagès & Gili, 2000
Voragonema pedunculata (Bigelow, 1913) [as *Crossota*]
Voragonema profundicola Naumov, 1971

Rhopalonematidae *incertae sedis*:

Genus ***STAURAGLAURA*** Haeckel, 1879

Rhopalonematidae with a well-developed manubrial peduncle; 4 peduncled gonads, on every other of the 8 radial canals, 4 radial canals without gonads.
Stauraglaura tetragonima Haeckel, 1879 [probably a synonym of *Aglaura hemistoma*]

Class HYDROIDOMEDUSA (see page 15 for diagnosis)

Taxonomic problems caused by the inconsistent evolution of the hydroids and medusae of the Hydroidomedusa.

The construction of a single classification for hydroids and medusae is a long and difficult process. At first, difficulties were because polyps and medusae were studied by different people, producing different classifications. At the beginning of the last century, however, a meticulous work started, aimed at the building of a single classification comprising both stages. The approaches, however, remained biased by the "preference" of the proposing author. The first "single classification", for instance, was proposed by Naumov (1960) and was based on the hydroid stage, with little attention to the medusae, these being simply "dragged" into the polyp classification. It is evident, for instance, that species that medusan specialists refer to different families have hydroids referable to a single genus, and vice-versa. The most amazing case is that of *Obelia*, the traditional hydrozoan in all zoology textbooks. Its hydroids are evidently Campanulariid, similar to those of *Clytia*. The medusae of *Obelia*, however, are so different from all other hydrozoan medusae that, if their hydroids were unknown,

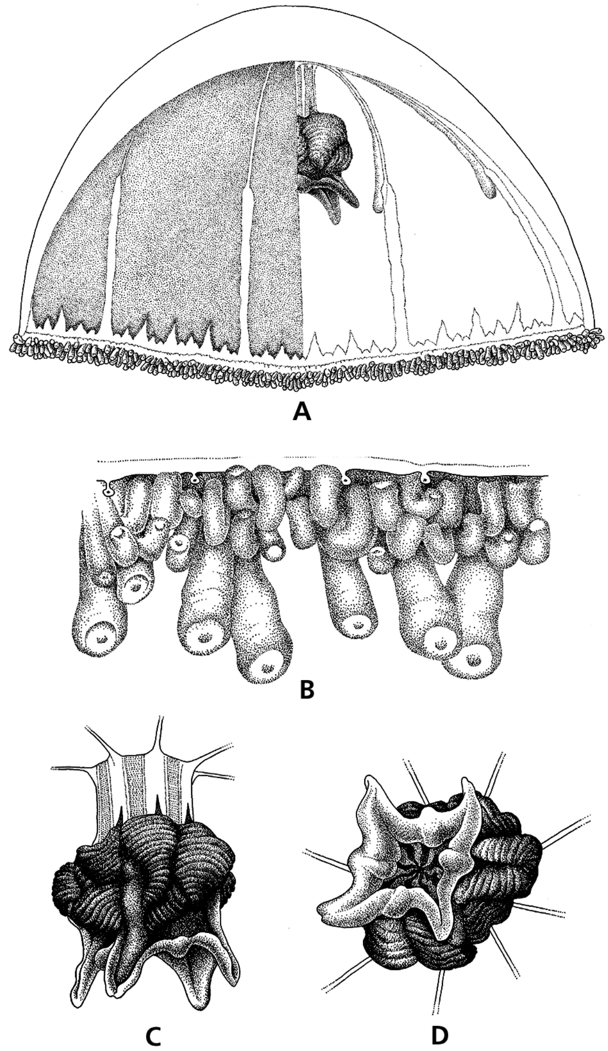


FIG. 73. Trachymedusae, Rhopalonematidae (concluded). A-D, *Voragonema laciniata*. A, lateral view of the medusa, the left half shows the dark subumbrella which has been deleted in he right half to illustrate the peduncle, the manubrium and the gonads. B, detail of the bell margin showing the proximal part of autotomized marginal tentacles superimposed in several rows and the statocysts. C, lateral view of the peduncle and the manubrium with the gastric pouches. D, oral view of the manubrium showing the oral lips and gastric pouches (all after Bouillon *et al*., 2001: p. 841, fig. 4; p. 842, figs A, B, C).

FIG. 73. *Trachymedusae, Rhopalonematidae (fin). A-D,* Voragonema laciniata. *A, vue latérale d'une méduse, la moitié gauche montre l'opacité de la sous-ombrelle qui a été enlevée dans la moitié droite afin d'illustrer le pédoncule manubrial, le manubrium et les « gonades ». B, détail du bord exombrellaire montrant les parties proximales autotomisées des tentacules marginaux disposées en plusieurs rangées ainsi que les statocystes. C, vue latérale du pédoncule et du manubrium avec ses poches gastriques. D, vue orale du manubrium montrant les lèvres orales et les poches gastriques (d'après Bouillon et al., 2001 : p. 841, fig. 4 ; p. 842, fig. A, B, C).*

they might be ascribed to a separate class. The problem is so hard to solve that Hennig proposed to test his phylogenetic approach to classification by building two cladograms with it, one for the medusae and one for the hydroids. If cladistics were a sound method of classification, he argued, then the two cladograms must result identical under all respects. Unfortunately for cladistics, and for all hydrozoan students, this apparently easy test is proving very difficult. Moreover, chances are good that the performance of cladistics might prove poor in this case.
In this monograph, we tried to build keys for every taxonomic group besides the species within genera. Keys are tools to help identify specimens. In many cases, however, a specimen cannot be reliably identified if not linked to its life cycle, and keys become impracticable, or one has to go back to one-stage oriented identification.
Even concise diagnoses are sometimes impossible for both stages. The Margelina, for instance, are a quite compact suborder of the Filifera, if the medusa stage is considered, but their hydroids are far less differentiated than the medusae, making a concise diagnosis impossible. The Filifera suborders Margelina and Pandeida are nevertheless considered here as valid in spite of the difficulties in reconciling hydroid features with medusan ones.

For the above-mentioned reasons, keys are useful only for identification but not for classification. These problems will be hopefully resolved with molecular tools. Generic diagnoses are refinements of family diagnoses and do not repeat the diagnostic characters of the family.

Subclass ANTHOMEDUSAE

Hydroid: typically athecate, without a rigid perisarcal theca covering the hydranth body, a gelatinous or membranous pseudohydrotheca may sometimes cover the base of the hydranth, adhering closely to the ectoderm.
Medusa: 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 for 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; cnidome normally including desmonemes.
The Anthomedusae are divided into two orders: the Filifera (with cnidome including desmonemes and euryteles) and the Capitata (with cnidome including stenoteles). The name Filifera refers to the filiform tentacles of the hydroid stage, whereas the name Capitata refers to the mostly capitate tentacles of hydroids.

Order FILIFERA Kühn, 1913

Hydroid: hydranth with filiform tentacles (except in the dactylozooids of the Ptilocodiidae).
Medusa: “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 circular, surmounted by oral manubrial tentacles; marginal tentacles solid or hollow; cnidome including usually desmonemes and microbasic euryteles, never stenoteles; planulae with only one type of ectodermal glandular cells: spumous cells. Based on their medusae characters the Filifera may be divided in two suborders the Margelina and the Pandeida.

GENERAL KEY TO HYDROID STAGES OF THE FILIFERAN FAMILIES

1. hydranth with peduncled hypostome. . . . . Eudendriidae
– hydranth with conical or rounded hypostome 2

2. colonies with hydrorhiza forming a massive calcareous coenosteum . . . . Stylasteridae
– colonies without massive calcareous coenosteum. 3

3. dactylozooids present. 4
– dactylozooids absent 9

4. hydranth with tentacles. 5
– hydranths without tentacles . . . . Ptilocodiidae

5. hydranth with two tentacles . . . . Proboscidactylidae
– hydranth with more than two tentacles 6

6. dactylozooids naked. . . . . Hydractiniidae
– dactylozooids covered entirely or partially by perisarc forming nematothecae (except for *Balella mirabilis* where the perisarc may be absent or very low). 7

7. hydranths with pseudohydrothecae. . . . . Clathrozoellidae
– hydranths without pseudohydrothecae. 8

8. with two distinct and widely separated whorls of filiform tentacles, one oral under hypostome and one at aboral base; gonophores as free medusae . . . . Balellidae
– with one oral whorl of tentacles; gonophores styloid, gonads inside hydranth walls . . . . Rhysiidae

9. tentacles in distal (oral) whorls only 11
– tentacles in several whorls over the body or scattered over the entire body 10

10. hydranth with tentacles scattered all over the body (exceptionally with dactylozooids and nematothecae = *Merona*), colonies erect or stolonal . . . . Clavidae
– hydranths with up to five irregular whorls of filiform tentacles; hydrorhiza forming a plate giving rise to unbranched colonies living in the prebranchial cavity of ascidians . . . . Bythotiaridae

11. colonies generally erect; polyps usually with a pseudohydrotheca covering partially or totally the body and tentacles; hypostome surrounded by one or more whorls of distal tentacles . . . . . . Bougainvilliidae
– colonies stolonal. 12

12. hydranth usually with base surrounded by a collar-like tube of perisarc or with a thin basal mucous-like perisarc structure. 13
– hydranth with completely free base or with the body covered with a pseudohydrotheca 16

13. hydranth slender and extensible; with conspicuous cylindrical perisarc tube, into which the hydranth can partially retract 14
– hydranth columnar, not retractable in the reduced basal perisarcal cup. 15

14. oral tentacles 10 or more alternating with large cnidocysts; cnidome where known containing, among other cnidocysts, merotrichous isorhizas . . . . Protiaridae
– oral tentacles with one whorl of 6 amphicoronate filiform tentacles, no large cnidocysts; cnidome without merotrichous isorhizas. . . . . Trichydridae

15. hydranth with one more or less regular whorl of oral tentacles or with two closely alternating oral whorls; surrounding a conical hypostome; perisarcal collar where present chitinous, small, cup-shaped or vase-like, reproduction by medusa buds or fixed sporosacs arising from stolons . . . . Cytaeididae
– hydranth with a single distal whorl of threadlike tentacles surrounding a rounded hypostome; with hydranth base surrounded by a gelatinous, mucous perisarcal structure; reproduction by medusa buds arising from hydrorhiza or more rarely from the base of hydranth . . . . Rathkeidae

16. hydranth with naked base, with long proboscis-like hypostome; with a single whorl of filiform tentacles located near the middle of the body; medusa buds borne just below tentacles . . . . . Australomedusidae
– hydranth with a naked base or with body surrounded by a developed mucous pseudohydrotheca; hypostome conical; hydranth normally bearing one oral whorl of filiform tentacles, seldom accompanied by two or more aboral whorls or exceptionally by scattered tentacles; secondarily with no tentacles in forms linked with parasitic mode of life; reproduction by medusa buds usually issued from hydrorhiza sometimes from hydrocaulus . . . . Pandeidae

Suborder MARGELINA

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 (see key above).
Recent references: for medusae see Bouillon (1999); Bouillon and Barnett (1999); Bouillon & Boero (2000).

Key to Margelina medusae

1. with oral tentacles. 2
– without oral tentacles 3

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

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

4. lips simple, without cnidocyst clusters 5
– mouth armed with cnidocyst clusters 6

5. tentacles in groups, 4-8 simple radial canals . . . . Australomedusidae
– 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
– 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
– without didermic exumbrellar centripetal canals or refringent spot rows, without marginal cnidocyst ring 8

8. marginal tentacles solitary . . . . Hydractiniidae
– marginal tentacles in 8 groups. . . . . Rathkeidae

Family AUSTRALOMEDUSIDAE Russell, 1971

Hydroid: colony stolonal, hydranth naked, with a single row of filiform oral tentacles near the middle of the body. Only known in *Australomedusa*.
Medusa: mouth lips simple; 4 or exceptionally 8 simple radial canals; 4 groups of perradial tentacles, 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.
Recent reference: Harris (1990); Bouillon & Boero (2000).

Key to medusae

1. 8 radial canals . . . . *Octorathkea*
– 4 radial canals. 2

2. only 4 groups of perradial tentacles. . . . . *Platystoma*
– more than 4 groups of marginal tentacles 3

3. 4 groups of perradial tentacles and 4 interradial rudimentary bulbs. . . . . *Australomedusa*
– 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, 1970

Fig. 74A-B

Hydroid: colony small, stolonal; hydranth naked, sessile, with a single ring of filiform tentacles near the middle of column; medusa buds just below tentacles.

Medusa: manubrium cylindrical, with 4 simple lips; 4 radial canals, 4 groups of perradial tentacles and 4 rudimentary bulbs; "gonads" mainly on manubrium (female) or on manubrium and on proximal part of radial canals (male); with ocelli.

Recent references: Harris (1990); Russell (1971); Jankowski (2001)

Australomedusa baylii Russell, 1970a

Genus ***OCTORATHKEA*** Uchida, 1927

Fig. 74C

Hydroid: unknown.

Medusa: manubrium cruciform, with 4 simple lips; 8 radial canals; 8 groups of marginal tentacles; mature "gonads" unknown.

Octorathkea onoi Uchida, 1927a

Genus ***ZHANGIELLA*** nom. nov.

Nom. nov. pro *Platystoma* Zhang, 1982, non *Platystoma* Meigen, 1803 [Diptera], nec *Platystoma* Agassiz, 1829 [Pisces], and several others (Fig. 74D-G)

Hydroid: unknown.

Medusa: manubrium cruciform, with 4 simple lips; 4 radial canals; 4 groups of marginal tentacles; "gonads" only on manubrium; with ocelli.

Zhangiella bitentaculata Xu, Huang & Chen, 1991
Zhangiella dongshanensis Xu & Huang, 1994
Zhangiella nambaiense Zhang, 1982

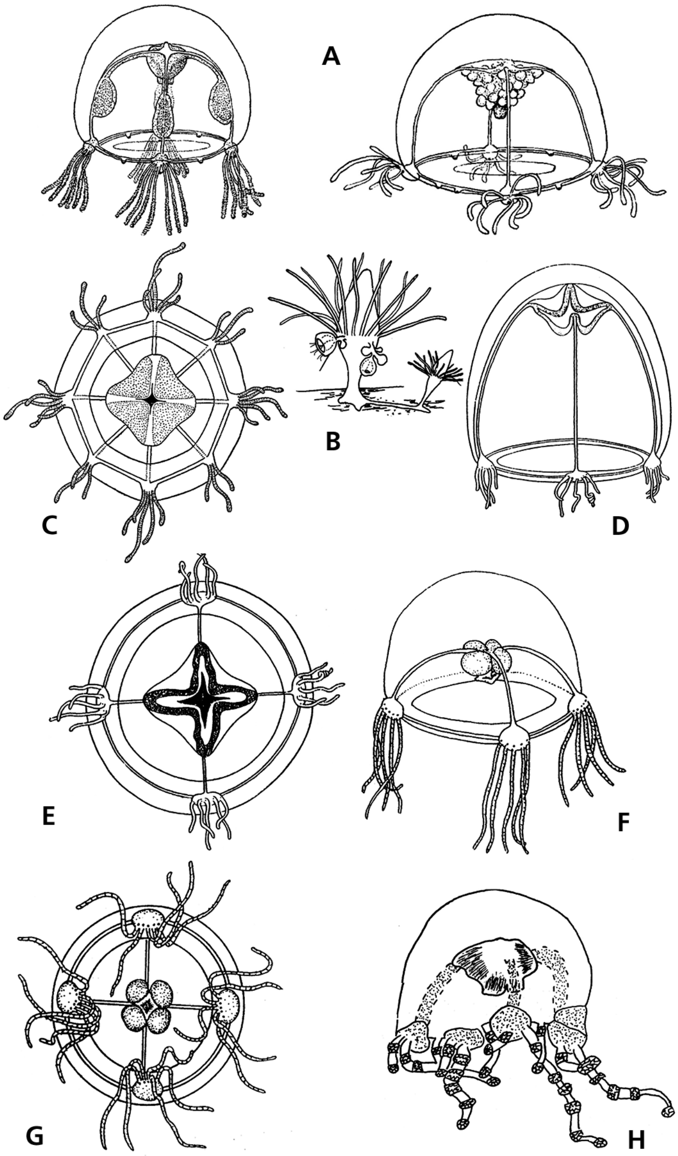


FIG. 74. Anthomedusae, Australomedusidae. A-B, *Australomedusa baylii*: A, medusa: male (left), female (right); B, polyp. C, *Octorathkea onoi*: medusa. D-E, *Zhangiella nanhainense*: D, medusa lateral view; E, medusa oral view. F-G, *Zhangiella dongshanensis*: F, medusa lateral view; G, medusa facing mouth view. H, *Octobulbacea montehermosensis* medusa (A left: after Russell, 1970a; A right: after Russell, 1971; B after Harris, 1990: p. 224, fig. 11.1 a; C after Uchida, 1927a; D-E after Zhang Jinbiao, 1982; F-G after Xu Zhenzu & Huang Jiaqui, 1994; H after Zamponi, 1983).

FIG. 74. *Anthomedusae, Australomedusidae. A-B,* Australomedusa baylii : *A, méduses : spécimen mâle (à gauche), spécimen femelle (à droite) ; B, polype. C,* Octorathkea onoi : *méduse. D-E,* Platystoma nanhainense : *D, méduse vue latérale ; E, méduse vue orale. F-G,* Platystoma dongshanensis : *F, méduse vue latérale ; G, méduse vue orale. H,* Octobulbacea montehermosensis, *méduse (A à gauche : d'après Russell, 1970a ; A à droite : d'après Russell, 1971 ; B d'après Harris, 1990 : p. 224, fig. 11.1 a ; C d'après Uchida, 1927a ; D-E d'après Zhang Jinbiao, 1982 ; F-G d'après Xu Zhenzu & Huang Jiaqui, 1994 ; H d'après Zamponi, 1983).*

Australomedusidae *incertae sedis*:

Genus ***OCTOBULBACEA*** Zamponi, 1983

Fig. 74H

Hydroid: unknown.
Medusa: 8 marginal bulbs; 24 moniliform tentacles, 2 per each marginal bulb and 8 adradial tentacles, without marginal bulbs; "gonads" interradial.

Octobulbacea montchermosensis Zamponi, 1983 [not referable to Margelopsidae as supposed by Zamponi (see Petersen 1990)]

Family BOUGAINVILLIIDAE Lütken, 1850

Hydroid: colony stolonal or erect, branched or unbranched, monosiphonic or polysiphonic; perisarc firm, terminating either at base of hydranths or forming a pseudohydrotheca; hydranths with one or more definite whorls of filiform distal tentacles, more or less close-set beneath conical hypostome; gonophores as free medusae or fixed sporosacs developing mostly on hydrocauli, hydrocladia, occasionally on hydrorhiza and rarely from modified hydranths.
Medusa: usually bell-shaped; manubrium short; mouth simple, circular, with simple or dichotomously branched oral tentacles, inserted distinctly above mouth rim and armed with cnidocyst clusters; 4 radial canals and circular canal; marginal tentacles solid, either solitary or in clusters, borne on 4, 8, or 16 tentacular bulbs; "gonads" on manubrium, either forming a continuous ring or on adradial, interradial or perradial axes; adaxial ocelli absent or present.
Remarks: the Bougainvilliidae comprise genera with well-known free medusae and an assemblage of hydroid-based genera with fixed gonophores bearing one or more whorls of filiform tentacles beneath hypostome. As the reduction of free medusae to fixed gonophores may have occurred several times independently during the evolution of the Bougainvilliidae, it is impossible to refer paedomorphic species to any presently known medusa genus. Many of the hydroids of those genera have an almost similar morphology and few reliable diagnostic characters; they have been lumped and separated several times according to different criteria. Furthermore, most bougainvilliid hydroids are not distinguishable from the presently known Pandeidae hydroids and, paradoxically, no hydroid species with fixed sporosacs has been described in this family (see Pandeidae)! It is thus not to exclude that some of the Bougainvilliidae genera with fixed sporosacs could in fact belong to Pandeidae, or even to the Clavidae. Rees (1938) re-erected the genus *Rhizorhagium* Sars, 1874 for all the unbranched colonial bougainvilliid polyps with pseudohydrotheca not enveloping the tentacles, with one whorl of tentacles and with fixed sporosacs. Millard (1975), followed by Bouillon (1985a), mistakenly included *Parawrightia* as synonym of *Rhizorhagium*. Calder (1988a) proposed a division of the Bougainvilliidae into four sub-families, the Pachycordylinae, Rhizorhagiinae, Bimeriinae, Bougainvilliinae according to one or more of the following hydroid characters: presence of pseudohydrotheca, form of the hypostome (nipple-shaped, dome-shaped), number of tentacle whorls, position of gonophores. Since the systematic value of some of these characters is questionable even at the generic level, this separation in sub-families is not adopted here. The pseudohydrothecae can cover the hydranth body and a variable proportion of the tentacles as in the genera *Bimeria*, *Koellikerina* and *Thamnostoma* or extend only around hydranth as in the other Bougainvilliidae genera. Calder's distinction between subfamilies based on the shape of the hypostome, dome-shaped in the Pachycordylinae, nipple-shaped in the Rhizorhagiinae, is nor convincing. The hypostome shape is, in fact, very variable, depending upon the degree of expansion or contraction of the concerned specimen; it is also linked to state of feeding, fixation etc. and several members of the Rhizorhagiinae do not have nipple-shaped hypostome and have so to be redistributed into other doubtful resurrected genera like *Gravelya* and *Aselomaris,* not conforming to Calder's definition of the subfamily. It seems preferable to refrain from splitting the Bougainvilliidae with fixed sporosacs into too many genera

and we follow here with some slight modifications Rees' suggestion (see key below), pending a more natural classification. This seems not very realistic, if not impossible, without the help of molecular tools. The bougainvilliids with fixed sporosacs and a single whorl of tentacles could even be grouped into two genera, *Bimeria* with pseudohydrotheca covering part or all of the tentacles and *Garveia* with pseudohydrotheca extending only on hydranth body; the main difference between *Rhizorhagium* and *Garveia* is tenuous, unbranched colonies in *Rhizorhagium* or branched in *Garveia*.

Recent references: Wedler & Larson (1986); Calder (1988a); Pagès *et al.* (1992); Migotto (1996); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bavestrello *et al.* (2000); Bouillon & Boero (2000); Schuchert (2001a).

Key to hydroids

1. pseudohydrotheca absent 2
– pseudohydrotheca present 4

2. 2-4 alternating close whorls of tentacles beneath hypostome 3
– with two whorls of tentacles; fresh-water . . . . . *Velkovrhia*

3. sporosacs on gonozooids beneath a whorl of 4 to 5 tentacles. . . . . *Millardiana*
– sporosacs or eumedusoids on stem . . . . . *Pachycordyle*

4. pseudohydrotheca covering tentacle bases 5
– pseudohydrotheca not covering tentacle bases 6

5. fixed sporosacs . . . . . *Bimeria*
– free medusae. . . . . *Koellikerina* or *Thamnostoma*

6. gonophores developing into free medusae 7
– gonophores not developing into free medusae 8

7. - hydranth with one whorl of tentacles . . . . . *Bougainvillia* or *Nemopsis*

7a. - hydranth with two or more whorls of tentacles . . . . . *Silhouetta*

8. gonophores on blastostyles and producing swimming sporosacs . . . . . *Dicoryne*
– gonophores not on blastostyles and producing fixed sporosacs 9

9. hydranth with one whorl of tentacles 10
– hydranth with tentacles in several alternating whorls . . . . . *Parawrightia*

10. colonies unbranched. . . . . *Rhizorhagium*
– colonies with branching stems. . . . . *Garveia*

Key to medusae

1. oral tentacles simple, unbranched. 2
– oral tentacles dichotomously branched. 4

2. 4 radial canals . . . . . *Nubiella*
– 8 radial canals. 3

3. 8 equal groups of marginal tentacles. . . . . *Lizzella*
– marginal tentacles solitary or in 8 unequal groups. . . . . *Lizzia*

4. solitary marginal tentacles. . . . . *Thamnostoma*
– marginal tentacles in 4 or 8 groups 5

5. marginal tentacles in 4 perradial groups 7
– marginal tentacles in 8 groups, 4 perradial, 4 interradial 6

6. marginal groups of tentacles cleft. . . . . *Chiarella*
– marginal groups of tentacles uncleft . . . . *Koellikerina*

7. in each group a median pair of club-shaped tentacles . . . . *Nemopsis*
– marginal tentacles all alike . . . . *Bougainvillia*

Genus ***BIMERIA*** Wright, 1859

Fig. 75D-L

Synonym: *Calyptospadix* Clarke, 1882.
Hydroid: colony stolonal or with erect branching hydrocauli; stem with firm perisarc enveloping hydranth, extending as a pseudohydrothecal sheath over proximal portion of tentacles; hydranths ovoid to vasiform, hypostome dome-shaped, sometimes with a preoral cavity (i.e., *Bimeria rigida*), with one or two close oral whorls of tentacles; gonophores as fixed sporosacs, completely invested in perisarc on hydrorhiza and branches.
Recent references: Calder (1988a); Calder *et al.* (2003).

Bimeria australis Blackburn, 1937
Bimeria cerulea (Clarke, 1882)
Bimeria currumbinensis Pennycuik, 1959
Bimeria fluminalis Annandale, 1915
Bimeria humilis Allman, 1877
Bimeria rigida Warren, 1919
Bimeria robusta Torrey, 1902
Bimeria tunicata Fraser, 1943
Bimeria vestita Wright, 1859

Genus ***BOUGAINVILLIA*** Lesson, 1830

Figs 25C, P, 26C, S, 75M-N, 76A-H

Hydroid: colony usually erect, branched or unbranched, more rarely stolonal; perisarc terminating at base of hydranth or extending upwards as a pseudohydrotheca; hydranth fusiform to clavate, hypostome dome-shaped, with one distal whorl of tentacles, never enveloped by the pseudohydrotheca. Gonophores as free medusae, arising singly or in clusters from hydrocaulus, hydrocladia or hydrorhiza.
Medusa: 4 perradial clusters of identical solid marginal tentacles; 4 perradial oral tentacles dichotomously branching in normally developed medusae; "gonads" on manubrium, adradial, interradial or, rarely, perradial; with or without ocelli.
Recent references: Calder (1988a, 1993); Bouillon (1995b); Schuchert (1996); Schuchert (2001a).

Bougainvillia aberrans Calder, 1993
Bougainvillia alderi (Hodge, 1863)
Bougainvillia aurantiaca Bouillon, 1980
Bougainvillia bitentaculata Uchida, 1925
Bougainvillia bougainvillea (Brandt, 1835)
Bougainvillia britannica (Forbes, 1841) [syn. *Bougainvillia flavida* Hartlaub, 1897]
Bougainvillia carolinensis (McCrady, 1859)
Bougainvillia charcoti Le Danois, 1913 [doubtful status]
Bougainvillia crassa Fraser, 1938a
Bougainvillia dimorpha Schuchert, 1996
Bougainvillia frondosa Mayer, 1900a
Bougainvillia fulva Agassiz & Mayer, 1899
Bougainvillia glorietta Torrey, 1902
Bougainvillia inaequalis Fraser, 1944
Bougainvillia involuta Uchida, 1947a
Bougainvillia longicirra Stechow, 1914
Bougainvillia macloviana (Lesson, 1830)
Bougainvillia maniculata Haeckel, 1864
Bougainvillia meinertiae Jaderholm, 1923a
Bougainvillia multicilia (Haeckel, 1879)
Bougainvillia multitentaculata Foerster, 1923
Bougainvillia muscoides (Sars, 1846) [syn. *Bougainvillia nigritella* Forbes and *Bougainvillia nordgaardi* (Browne, 1903)]
Bougainvillia muscus (Allman, 1863)
Bougainvillia niobe Mayer, 1894
Bougainvillia paraplatygaster Xu, Huang & Chen, 1991
Bougainvillia platygaster (Haeckel, 1879)
Bougainvillia principis (Steenstrup, 1850)
Bougainvillia prolifera (Lendenfeld, 1885a) [doubtful status]
Bougainvillia pyramidata (Forbes & Goodsir, 1851)
Bougainvillia robusta (Fraser, 1938a)

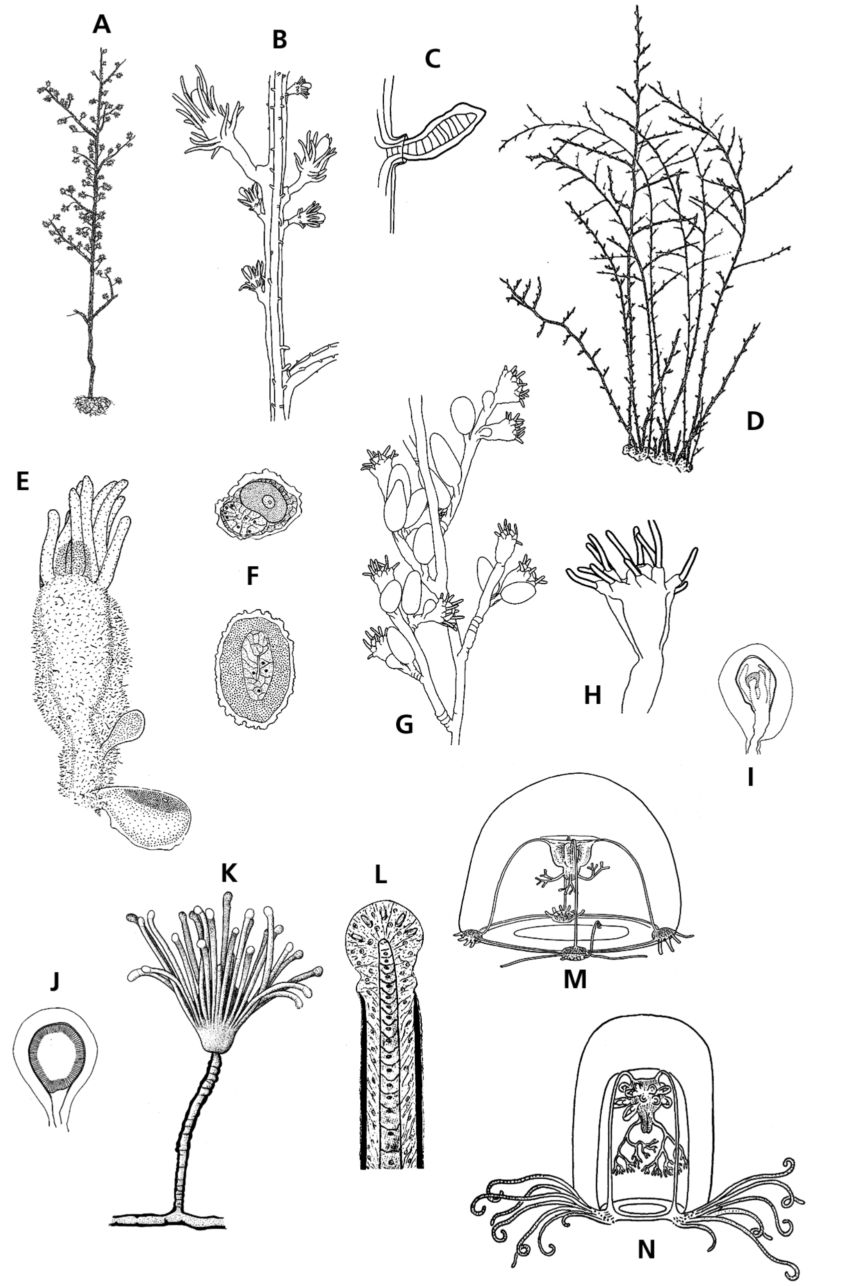


FIG. 75. Anthomedusae, Balellidae. A-C, *Balella mirabilis*: A, stem; B, part of stem with hydranths and dactylozooids; C, detail of a dactylozooid. Bougainvillidae. D-L, *Bimeria*. D-F, *Bimeria fluminalis*: D, general view of a colony; E, hydranth with two young female gonophores; F, female gonophore (above), male gonophore both enveloped in perisarc (below); G-J, *Bimeria vestita*: G, part of stem with hydranths and male gonophores, H, hydranth showing perisarcal sheats around tentacles base; I-J, female gonophores enveloped in a perisarcal coat; K-L, *Bimeria rigida*: K, hydranth; L, detail of the end of a tentacle showing the length of the perisarcal cover. M-N, *Bougainvillia*: M, *Bougainvillia muscus* adult medusa; N, *Bougainvillia niobe* adult medusa showing manubrial medusa budding (A-C, G-J after Hirohito, 1995; E-F & K after Millard, 1975; L after Warren, 1919; M after Russell, 1953; N after Kramp, 1959b).

FIG. 75. *Anthomedusae, Balellidae. A-C,* Balella mirabilis : *A, portion de colonie ; B, branche avec des hydranthes et des dactylozoïdes ; C, détail d'un dactylozoïde. Bougainvillidae. D-L,* Bimeria. *D-F,* Bimeria fluminalis : *D, vue générale d'une colonie ; E, hydranthe avec deux jeunes gonophores femelles ; F, gonophore femelle (au-dessus), un gonophore mâle (au-dessous), tous deux enveloppés de périsarc ; G-J,* Bimeria vestita *: G, partie d'une colonie avec des hydranthes et des gonophores mâles ; H, hydranthe montrant l'enveloppe de périsarc entourant la base des tentacules ; I-J, gonophores femelles enveloppés de périsarc ; K-L,* Bimeria rigida : *K, hydranthe ; L, détail de l'extrémité d'un tentacule montrant l'étendue de la gaine de périsarc. M-N,* Bougainvillia : *M,* Bougainvillia muscus : *méduse adulte ; N,* Bougainvillia niobe : *méduse adulte montrant le bourgeonnement médusaire manubrial (A-C, G-J d'après Hirohito, 1995 ; E-F & K d'après Millard, 1975 ; L d'après Warren, 1919 ; M d'après Russell, 1953 ; N d'après Kramp, 1959b).*

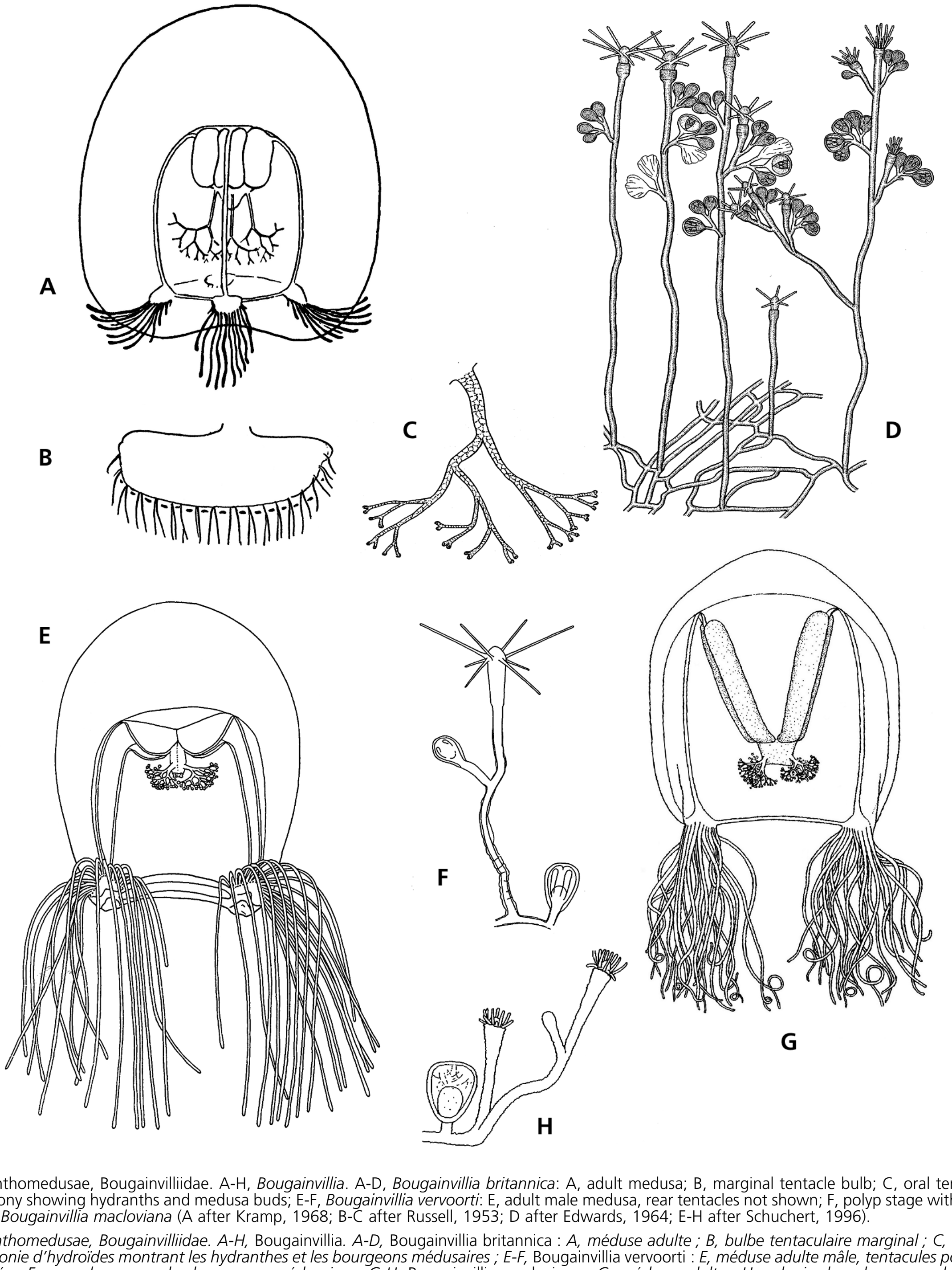


FIG. 76. Anthomedusae, Bougainvilliidae. A-H, *Bougainvillia*. A-D, *Bougainvillia britannica*: A, adult medusa; B, marginal tentacle bulb; C, oral tentacle; D, hydroid colony showing hydranths and medusa buds; E-F, *Bougainvillia vervoorti*: E, adult male medusa, rear tentacles not shown; F, polyp stage with medusa buds; G-H, *Bougainvillia macloviana* (A after Kramp, 1968; B-C after Russell, 1953; D after Edwards, 1964; E-H after Schuchert, 1996).

FIG. 76. *Anthomedusae, Bougainvilliidae. A-H,* Bougainvillia. *A-D,* Bougainvillia britannica : *A, méduse adulte ; B, bulbe tentaculaire marginal ; C, tentacule oral ; D, colonie d'hydroïdes montrant les hydranthes et les bourgeons médusaires ; E-F,* Bougainvillia vervoorti : *E, méduse adulte mâle, tentacules postérieurs non dessinés ; F, un polype avec des bourgeons médusaires ; G-H,* Bougainvillia macloviana : *G, méduse adulte ; H, colonie de polypes avec bourgeons médusaires (A d'après Kramp, 1968 ; B-C d'après Russell, 1953 ; D d'après Edwards, 1964 ; E-H d'après Schuchert, 1996).*

Bougainvillia rugosa Clarke, 1882
Bougainvillia simplex (Forbes & Goodsir, 1851) [doubtful status]
Bougainvillia superciliaris (Agassiz, 1849)
Bougainvillia trinema (von Lendenfeld, 1885a) [doubtful status]
Bougainvillia vervoorti Bouillon, 1995b

Genus ***CHIARELLA*** Maas, 1897

Fig. 77A

Hydroid: unknown.
Medusa: tentacles in 8 groups (4 perradial and 4 interradial), exumbrella with 8 marginal swellings, and 8 grooves; 4 oral tentacles dichotomously branched, with cnidocyst batteries at the tips; with adaxial ocelli.

Chiarella centripetalis Maas, 1897 [syn. *Rathkea jaschnowi* Naumov, 1956]

Genus ***DICORYNE*** Allman, 1859

Fig. 77B-D

Hydroid: hydrocaulus erect, branched or unbranched; perisarc conspicuous, terminating on or below hydranth body, never continued over base of tentacles; hydranths with one distal whorl of filiform tentacles; gonophores on gonozooids (blastostyles) and released as free-swimming styloid sporosacs, flagellated and provided with one or two tentacles arising from their proximal, originally attached end.
Recent references: Schuchert (1996); Schuchert (2001a).

Dicoryne conferta (Alder, 1856a)
Dicoryne conybeari (Allman, 1864)
Dicoryne flexuosa Sars, 1874

Genus ***GARVEIA*** Wright, 1859

Fig. 77E-J

Hydroid: hydrocaulus erect and branched, monosiphonic or polysiphonic; hydranth fusiform, hypostome dome-shaped, conical, surrounded by one distal whorl of tentacles; pseudohydrothecae covering polyp base but not extending over tentacles; gonophores as fixed sporosacs, borne on pedicels, hydrocauli, or hydrorhiza.
Recent references: Calder (1988a), Schuchert (2003).

Garveia annulata Nutting, 1901a
Garveia arborea (Browne, 1907a)
Garveia brevis (Fraser, 1918)
Garveia clevelandensis Pennycuik, 1959
Garveia crassa (Stechow, 1923a) [as *Bimeria*]
Garveia formosa (Fewkes, 1889)
Garveia franciscana (Torrey, 1902)
Garveia gracilis (Clark, 1876a)
Garveia grisea (Motz-Kossowska, 1905)
Garveia laxa (Fraser, 1938a) [as *Bimeria*]
Garveia nutans Wright, 1859
Garveia pusilla (Fraser, 1925)
Garveia robusta (Torrey, 1902)
Garveia tenella (Fraser, 1925)

Genus ***KOELLIKERINA*** Kramp, 1939

Figs 77K-O, 78A

Hydroid: known only for *K. fasciculata*; colonies arising from a creeping hydrorhiza formed by tubular stolons; hydrocauli erect, branched and covered by perisarc, encrusted with mud and various detritus; perisarc forming wrinkled pseudo-hydrothecae covering hydranth and base of tentacles, leaving hypostome free; hydranth fusiform to pear-shaped, hypostome conical, an irregular distal whorl of up to 14 tentacles; medusa buds stalked, borne singly on hydrocauli and hydrocladia.

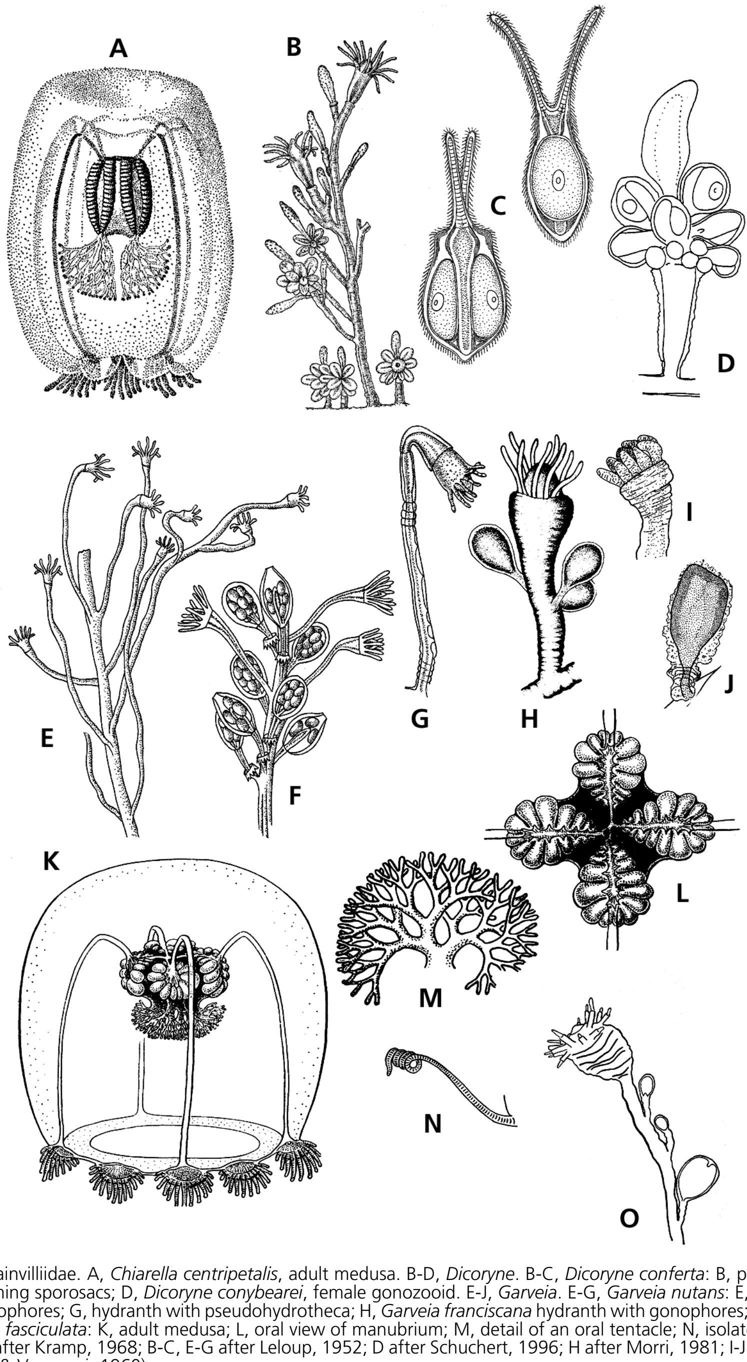


FIG. 77. Anthomedusae, Bougainvilliidae. A, *Chiarella centripetalis*, adult medusa. B-D, *Dicoryne*. B-C, *Dicoryne conferta*: B, part of a colony with hydranths and gonozooids; C, free swimming sporosacs; D, *Dicoryne conybearei*, female gonozooid. E-J, *Garveia*. E-G, *Garveia nutans*: E, part of a colony; F, detail of a branch with hydranths and gonophores; G, hydranth with pseudohydrotheca; H, *Garveia franciscana* hydranth with gonophores; I-J, *Garveia crassa*: I, hydranth; J, gonophore. K-O, *Koellikerina fasciculata*: K, adult medusa; L, oral view of manubrium; M, detail of an oral tentacle; N, isolated perradial marginal tentacle; O, polyp with medusa buds (A after Kramp, 1968; B-C, E-G after Leloup, 1952; D after Schuchert, 1996; H after Morri, 1981; I-J after Millard, 1977a; K-N after Mayer, 1910; O after Petersen & Vannucci, 1960).

***FIG. 77.** Anthomedusae, Bougainvilliidae. A,* Chiarella centripetalis *: méduse adulte. B-D,* Dicoryne. *B-C,* Dicoryne conferta *: B, portion d'une colonie montrant les hydranthes et des gonozoïdes ; C, sporosacs libres et nageurs ; D,* Dicoryne conybearei, *gonozoïde femelle. E-J,* Garveia. *E-G,* Garveia nutans *: E, portion d'une colonie ; F, détail d'une branche d'une colonie avec des hydranthes et des gonophores ; G, hydranthe avec pseudohydrothèque ; H,* Garveia franciscana, *hydranthe et gonophores ; I-J,* Garveia crassa *: I, hydranthe ; J, gonophore. K-O,* Koellikerina fasciculata *: K, méduse adulte ; L, vue orale du manubrium ; M, détail d'un tentacule oral ; N, tentacule marginal perradial isolé ; O, branche avec polype et bourgeons médusaires (A d'après Kramp, 1968 ; B-C, E-G d'après Leloup, 1952 ; D d'après Schuchert, 1996 ; H d'après Morri,1981 ; I-J d'après Millard, 1977a ; K-N d'après Mayer, 1910 ; O d'après Petersen & Vannucci, 1960).*

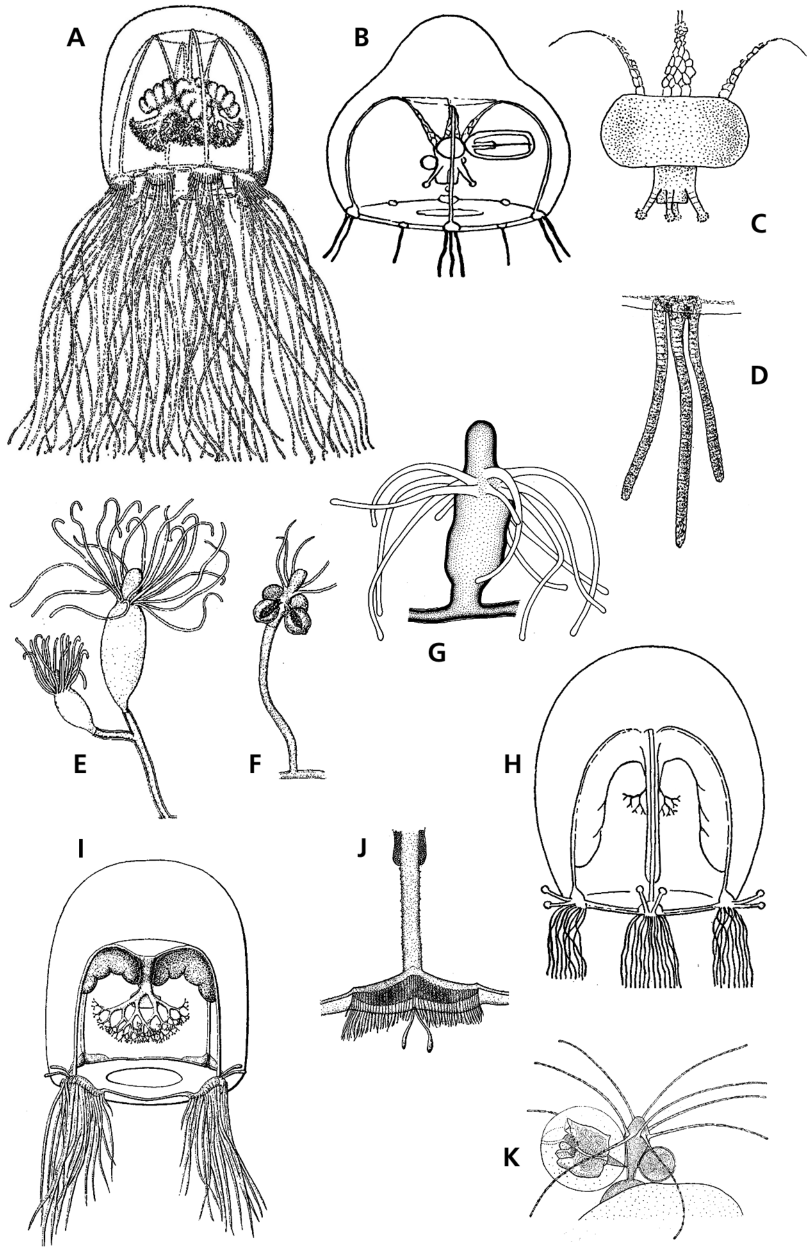


FIG. 78. Anthomedusae, Bougainvilliidae. A, *Koellikerina constricta*, adult medusa. B-D, *Lizzia blondina*: B, adult medusa with medusa buds; C, manubrium with male ''gonad''; D, perradial marginal tentacle group. E-G, *Millardiana longitentaculata*: E, two gastrozooids; F, a gonozooid with sporosacs; G, sterile hydranth. H-K, *Nemopsis*. H, *Nemopsis bachei* fully grown medusa; I-J, *Nemopsis dofleini*: I, adult medusa; J, abaxial view of a cluster of marginal tentacles showing the paired club-shaped tentacles; K, polyp with medusa buds (A after Bouillon, 1980; B & H after Kramp, 1959b; C-D after Russell,1953; E-F after Wedler & Larson, 1986; G after Calder, 1988a; I after Kramp, 1968; J after Uchida, 1925; K after Nagao, 1964).

FIG. 78. *Anthomedusae, Bougainvilliidae. A,* Koellikerina constricta, *méduse adulte. B-D,* Lizzia blondina : *B, méduse adulte avec des bourgeons médusaires ; C, manubrium développant des ''gonades'' mâles ; D, groupe de tentacules marginaux perradiares. E-G,* Millardiana longitentaculata : *E, deux gastérozoïdes ; F, un gonozoïde avec des sporosacs ; G, hydranthe stérile. H-K,* Nemopsis. *H,* Nemopsis bachei : *méduse adulte ; I-J,* Nemopsis dofleini : *I, méduse adulte ; J, vue abaxiale d'un groupe de tentacules marginaux montrant la paire de tentacules capités en forme de massue ; K, polype et bourgeons médusaires (A d'après Bouillon, 1980 ; B & H d'après Kramp, 1959b ; C-D d'après Russell,1953 ; E-F d'après Wedler & Larson, 1986 ; G d'après Calder, 1988a ; I d'après Kramp, 1968 ; J d'après Uchida , 1925 ; K d'après Nagao, 1964).*

Medusa: 8 groups of marginal tentacles of identical structure, 4 perradial and 4 interradial; 4 oral tentacles, perradial, dichotomously branched; "gonads" on manubrium, adradial, interradial, or perradial; with or without ocelli; endoderm of gastric cavity with numerous conspicuous expansions.
Recent reference: Bouillon *et al.* (1988).
Remarks: the hydroids described as *Thamnostoma* probably belong to the genus *Koellikerina*, see Petersen & Vannucci (1960).

Koellikerina constricta (Menon, 1932)
Koellikerina diforficulata Xu & Zhang, 1978
Koellikerina elegans (Mayer, 1900a)
Koellikerina fasciculata (Péron & Lesueur, 1810a)
Koellikerina maasi (Browne, 1910)
Koellikerina multicirrata (Kramp, 1928)
Koellikerina octonemalis (Maas, 1905)
Koellikerina ornata Kramp, 1959a
Koellikerina taiwanensis Xu, Huang & Chen, 1991

Genus ***LIZZELLA*** Haeckel, 1879

Hydroid: unknown.
Medusa: oral tentacles simple, unbranched; with gastric peduncle; 4 perradial and 4 interradial marginal bulbs, bearing the same number of tentacles. Systematic position uncertain, doubtful taxon.

Lizzella hyalina (Van Beneden, 1867) [doubtful status]
Lizzella octella Haeckel, 1879 [doubtful status]

Genus ***LIZZIA*** Forbes, 1846

Figs 25O, 78B-D

Hydroid: unknown.
Medusa: oral tentacles simple, unbranched; with gastric peduncle; usually 8 marginal bulbs (exceptionally 16, *Lizzia fulgurans*) each with one tentacle or with unequal groups of marginal tentacles; "gonads" surrounding manubrium; no ocelli.

Lizzia alvarinoae Segura, 1980
Lizzia blondina Forbes, 1848
Lizzia elisabethae Haeckel, 1879 [doubtful status]
Lizzia ferrarii Segura, 1980
Lizzia fulgurans (Agassiz, 1865)
Lizzia gracilis (Mayer, 1900a)
Lizzia octostyla (Haeckel, 1879)

Genus ***MILLARDIANA*** Wedler & Larson, 1986

Fig. 78E-G

Hydroid: colonies mostly stolonal, with perisarc terminating at hydranth base; hydranth thick, clavate; tentacles filiform, in 2-3 whorls below hypostome, those of one whorl more or less alternating with those of adjacent whorls, hypostome proboscis-like, extensible; gonophores as fixed sporosacs, borne on gonozooids beneath tentacles.
Recent reference: Calder (1988a).

Millardiana longitentaculata Wedler & Larson, 1986

Genus ***NEMOPSIS*** L. Agassiz, 1849

Fig. 78H-K

Hydroid: colonies similar to *Bougainvillia*, with gonophores on polyps (*N. bachei*) or solitary polyps, pedicellate, encrusted by perisarc until tentacular level, and with gonophores on pedicel (*N. dofleini*).
Medusa**:** 4 clusters of marginal tentacles, each with a median pair of club-shaped tentacles and, on both sides, a number of simple filiform tentacles; ocelli adaxial; 4 oral tentacles, perradial dichotomously branched; manubrium with 4 radial lobes extending towards radial canals; "gonads" on manubrial lobes.

Nemopsis bachei Agassiz, 1849
Nemopsis crucifera (Forbes & Goodsir, 1851)
Nemopsis dofleini Maas, 1909
Nemopsis heteronema Haeckel, 1879 [probably a syn. of *N. bachei*]
Nemopsis hexacanalis Huang & Xu, 1994
Nemopsis sp. Ganapati & Nagabhushanam, 1958

Genus ***NUBIELLA*** Bouillon, 1980

Fig. 79A

Hydroid: unknown.
Medusa: oral tentacles simple, unbranched; 4 solitary marginal tentacles.

Nubiella mitra Bouillon, 1980

Genus ***PACHYCORDYLE*** Weismann, 1883

Fig. 79B-E

Synonyms: *Clavopsella* Stechow, 1919a in part; *Thieliana* Stepanjants, Timoshkin, Anokhin & Napara, 2000.
Hydroid: Bougainvilliidae with well developed creeping colonies, with branched or unbranched hydrocauli; perisarc terminating at base of hydranth; hydranths club-shaped to spindle-shaped, with 2-4 alternating close whorls of filiform tentacles beneath hypostome, hypostome dome-shaped. Gonophores borne on stem, as fixed sporosacs or free eumedusoids without marginal tentacles, mouth or oral tentacles, radial canals or ring canal, seldom with velum, manubrium simple surrounded by gonads, no sense organs; they correspond to highly reduced medusae, resembling medusoid forms of siphonophores.
Recent references: Calder (1988a); Stepanjants *et al.* (2000); Schuchert (2004).

Pachycordyle conica Kramp, 1959a
Pachycordyle degenerata (Mayer, 1904) [probably gonophores of siphonophores]
Pachycordyle fusca Muller, 1913 [probably a syn. of *P. pusilla*]
Pachycordyle globulosa Kramp, 1959a [probably gonophores of siphonophores]
Pachycordyle kubotai Stepanjants, Timoshkin, Anokhin & Napara, 2000
Pachycordyle lineata Kramp, 1959a [probably gonophores of siphonophores]
Pachycordyle napolitana Weismann, 1883 [syn. *Pachycordyle weismanni* Hargitt, 1904]
Pachycordyle navis (Millard, 1959a) [syn. *Cordylophora inkermanica* Marfenin, 1983]
Pachycordyle pusilla (Motz-Kossowska, 1905) [as *Cordylophora*]

Genus ***PARAWRIGHTIA*** Warren, 1907

Fig. 79F-H

Hydroid: colony stolonal or erect, with irregularly branched or unbranched hydrocaulus; perisarc extending as a distinct pseudohydrotheca over base of hydranth, nearly to tentacles; hydranth vasiform, tentacles in several close, alternating distal whorls, hypostome nipple-shaped; gonophores as fixed sporosacs, enveloped in perisarc, borne on hydrocaulus and hydrocladia.
Recent references: Calder (1988a); Schuchert (1996).

Parawrightia robusta Warren, 1907

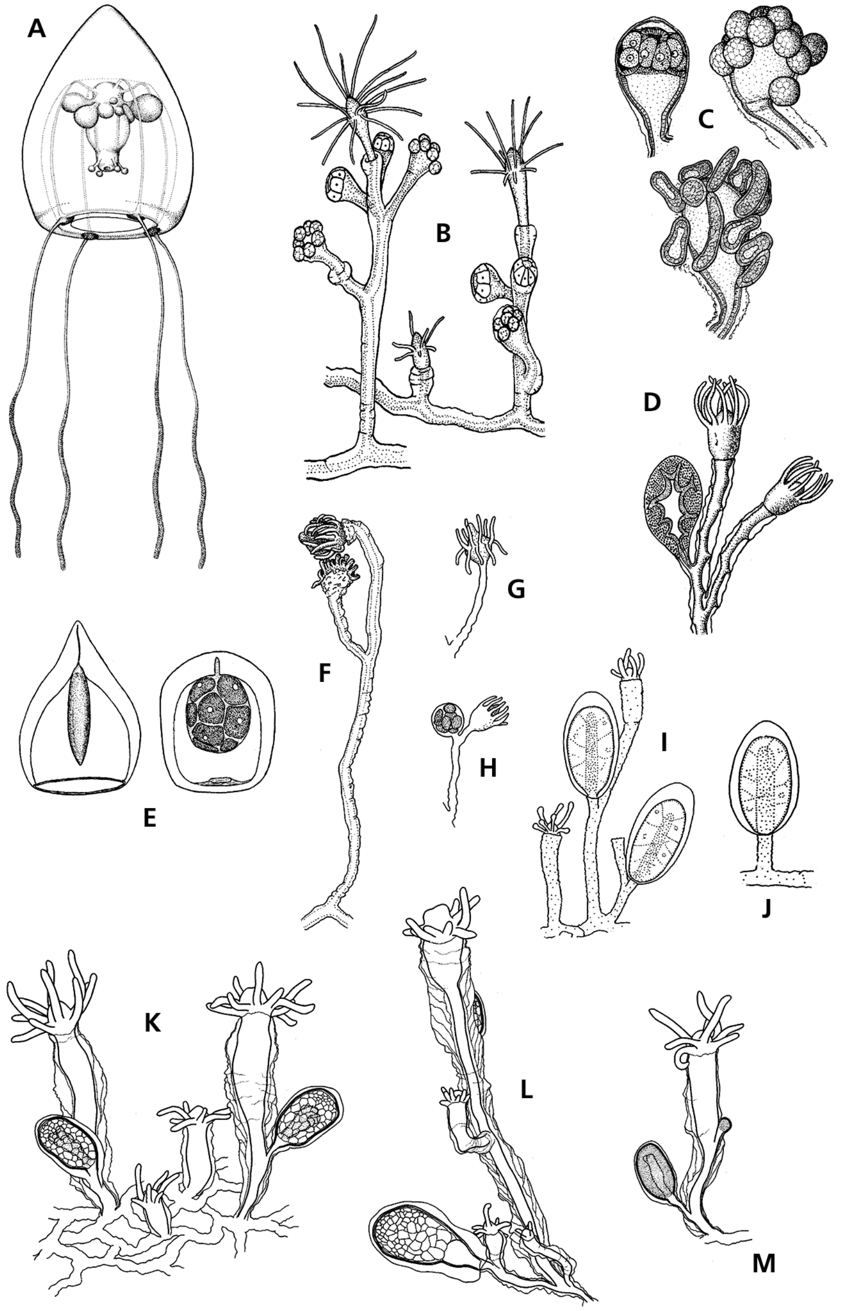


FIG. 79. Anthomedusae, Bougainvilliidae. A, *Nubiella mitra*, adult medusae with medusa buds on manubrium. B-E, *Pachycordyle*. B-C, *Pachycordyle navis*: B, fragment of a female colony with hydranths and gonophores; C, female gonophores at different stages of development, below with advanced planulae; D, *Pachycordyle napolitana* portion of a colony; E, *Pachycordyle conica* medusoid form (left), *Pachycordyle globulosa* medusoid form (right). F-H, *Parawrightia robusta*: F, stem with two hydranths; G, hydranth; H, hydranth with sporosac. I-M, *Rhizorhagium*. I-J, *Rhizorhagium antarcticum*: I, part of a colony with gonophores arising from cauli; J, gonophore arising from stolon; K-M, *Rhizorhagium sagamiense*: K, part of a female colony with unbranched stems and female gonophores; L, branched stem with hydranths and female gonophore; M, unbranched stem with male gonophore (A after Bouillon, 1980; B-C, F-H after Millard, 1975; D after Motz-Kosswska, 1905; E after Kramp, 1968; I-J after Schuchert, 1996; K-M after Hirohito, 1988).

FIG. 79. *Anthomedusae, Bougainvilliidae. A,* Nubiella mitra : *méduse adulte développant des bourgeons médusaires manubriaux. B-E,* Pachycordyle : *B-C,* Pachycordyle navis : *B, fragment d'une colonie femelle avec hydranthes et gonophores ; C, gonophores femelles à différents stades de développement, au-dessous, avec des planulas avancées ; D,* Pachycordyle napolitana : *portion d'une colonie ; E,* Pachycordyle conica *forme médusoïde (à gauche),* Pachycordyle globulosa *forme médusoïde (à droite). F-H,* Parawrightia robusta : *F, portion de branche avec deux hydranthes ; G, hydranthe ; H, hydranthe avec sporosac. I-M,* Rhizorhagium. *I-J,* Rhizorhagium antarcticum : *I, portion d'une colonie avec des gonophores issus de l'hydroclade ; J, gonophore issus du stolon ; K-M,* Rhizorhagium sagamiense : *K, portion d'une colonie non ramifiée présentant des gonophores femelles ; L, branche de colonie ramifiée montrant les hydranthes et des gonophores femelles ; M, branche de colonie non ramifiée portant des gonophores mâle (A d'après Bouillon, 1980 ; B-C, F-H d'après Millard, 1975 ; D d'après Motz-Kosswska, 1905 ; E d'après Kramp, 1968 ; I-J d'après Schuchert, 1996 ; K-M d'après Hirohito, 1988).*

Genus ***RHIZORHAGIUM*** M. Sars, 1874

Fig. 79I-M

Synonyms: *Aselomaris* Berrill, 1948; *Clavopsella* Stechow, 1919a in part; *Gravelya* Totton, 1930.
Hydroid: hydrocauli erect, unbranched, bearing a single terminal hydranth and, rarely, one or two lateral ones as well; perisarc firm, continued over polyp base as a pseudohydrotheca, but never investing tentacle bases; hydranth with one distal whorl of filiform tentacles, hypostome nipple-shaped or dome-shaped; gonophores as fixed sporosacs, borne on hydrorhiza and stems.
Recent references: Hirohito (1988); Calder (1991); Schuchert (1996); Schuchert (2001a).

Rhizorhagium album Rees, 1938
Rhizorhagium antarcticum (Hickson & Gravely, 1907)
Rhizorhagium arenosum (Alder, 1862a)
Rhizorhagium formosum (Fewkes, 1889)
Rhizorhagium michaeli (Berrill, 1948)
Rhizorhagium palori Mammen, 1963
Rhizorhagium roseum G.O. Sars, 1874
Rhizorhagium sagamiense Hirohito, 1988
Rhizorhagium sarsii (Bonnevie, 1898a)

Genus ***SILHOUETTA*** Millard & Bouillon, 1973

Fig. 80D-F

Hydroid: colony stolonal or erect, with firm perisarc terminating at hydranth base; hydranths large amphora-shaped, with 2 or more alternating, close-set distal whorls of tentacles; gonophores in clusters on hydrocauli and hydrocladia, giving off free medusae.
Medusa: only juvenile medusae known, with 4 marginal bulbs, each with one tentacle and an ocellus; manubrium with 4 simple or dichotomously branched oral tentacles.
Recent references: Wedler & Larson (1986); Calder (1988a); Schuchert (2004).

Silhouetta uvacarpa Millard & Bouillon, 1973 [Syn. *Silhouetta puertoricensis* Wedler & Larson, 1986]

Genus ***THAMNOSTOMA*** Haeckel, 1879

Fig. 80A

Hydroid: *Koellikerina*-like; see *Koellikerina.*
Medusa: 4 oral tentacles, dichotomously branched; 4, 8 or more solitary marginal tentacles; "gonads" interradial; with or without ocelli.
Recent reference: Hirohito (1988)

Thamnostoma dibalia (Busch, 1851)
Thamnostoma eilatensis Schmidt, 1972
Thamnostoma macrostomum Haeckel, 1879
Thamnostoma russelli Rees, 1938
Thamnostoma tetrellum (Haeckel, 1879)

Genus ***VELKOVRHIA*** Matjasic & Sket, 1971

Fig. 80B-C

Hydroid: freshwater colonies, erect, covered by perisarc; hydranths with two whorls of filiform tentacles, no pseudohydrothecae; gonophores on hydrocauli, as styloid fixed sporosacs.
Velkovrhia enigmatica Matjasic & Sket, 1971

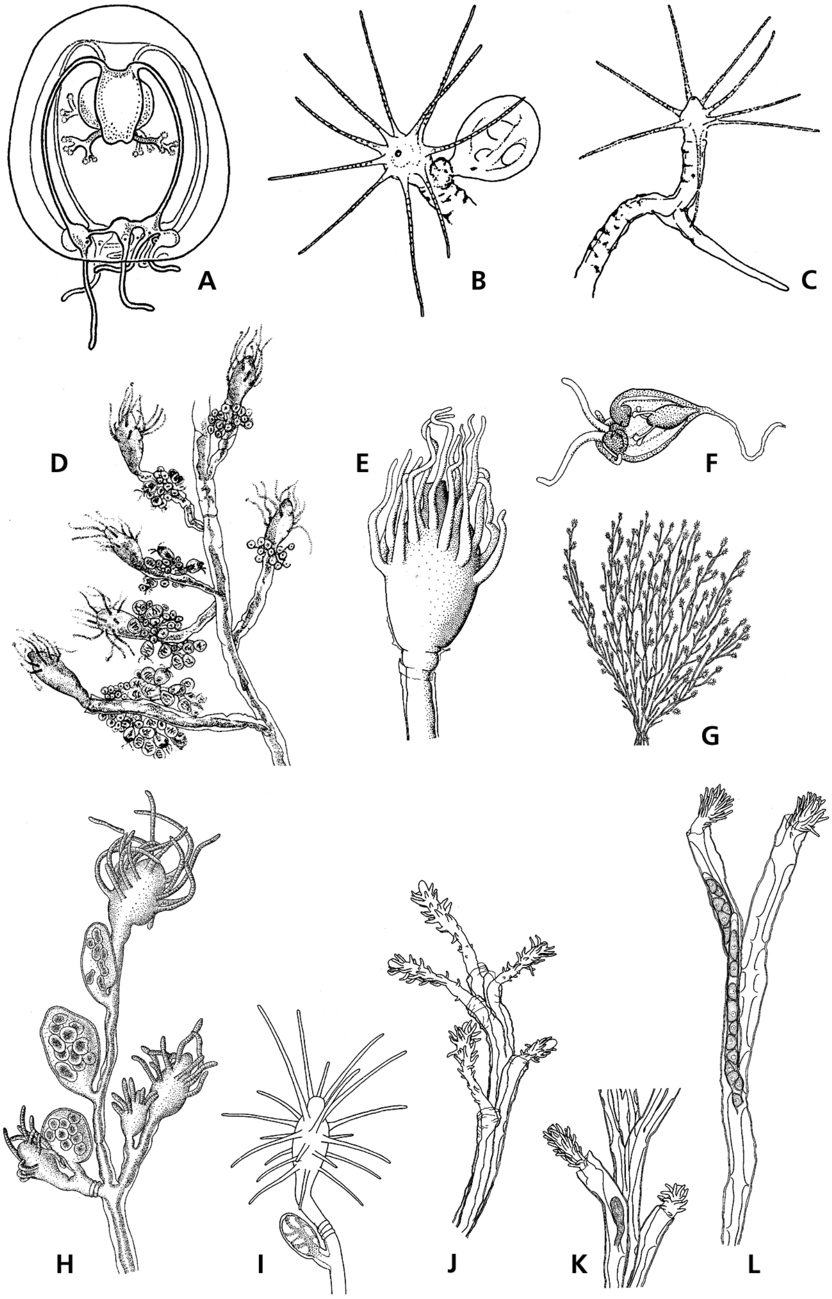


FIG. 80. Anthomedusae, Bougainvilliidae. A, *Thamnostoma dibalia*, adult medusa. B-C, *Velkovrhia enigmatica*: B, hydranth with fixed sporosac; C, part of colony with hydranth. D-F, *Silhouetta uvacarpa*: D, complete stem with hydranths and medusa buds; E, hydranth; F, medusa bud. G-K, Clavidae. G-I, *Cordylophora caspia*: G, general view of a colony; H, detail of a stem showing hydranths and female gonophores; I, hydrocladium with hydranth and young female gonophore. J-L, *Corydendrium*. J-K, *Corydendrium parasiticum*: J, part of stem with hydranths; K, part of stem with hydranths and male gonophores within perisarcal tubes; L, *Corydendrium brevicaulis*, branched stem with hydranths and female gonophores within perisarcal tubes (A after Kramp, 1959b; B-C after Clausen & Salvini-Plawen, 1986; D-F after Millard & Bouillon, 1973; G-H after Leloup, 1952; I after Schuchert, 1996; J-L after Hirohito, 1988).

***FIG. 80.** Anthomedusae, Bougainvilliidae. A,* Thamnostoma dibalia : *méduse adulte. B-C,* Velkovrhia enigmatica : *B, hydranthe avec sporosac ; C, portion de colonie avec un hydranthe. D-F,* Silhouetta uvacarpa *: D, fragment de colonie avec des hydranthes et des bourgeons médusaires ; E, hydranthe ; F, bourgeon médusaire. G-K, Clavidae. G-I,* Cordylophora caspia *: G, vue générale d'une colonie ; H, détail d'une portion de colonie montrant les hydranthes et des gonophores femelles ; I, hydroclade avec un hydranthe et un jeune gonophore femelle. J-L,* Corydendrium. *J-K,* Corydendrium parasiticum *: J, portion de colonie montrant les hydranthes ; K, portion de branche avec hydranthes et gonophores mâles dans leur tubes perisarcaux ; L,* Corydendrium brevicaulis*, branche ramifiée portant des hydranthes et des gonophores femelles inclus dans leurs tubes perisarcaux (A d'après Kramp, 1959b ; B-C d'après Clausen & Salvini-Plawen, 1986 ; D-F d'après Millard & Bouillon, 1973 ; G-H d'après Leloup, 1952; I d'après Schuchert, 1996; J-L d'après Hirohito, 1988).*

Family CLATHROZOELLIDAE Peña Cantero, Vervoort & Watson, 2003

Hydroid: Colonies erect and branched, unbranched when young. Skeleton formed by adherent perisarc tubes and cores of coenosarc. Stem resulting from addition of successive pseudohydrothecae, each inserting on previous one; base of pseudohydrotheca consisting of external wall of previous pseudohydrotheca, without direct communication between successive pseudohydrothecae. External surface provided with nematothecae. Hydranth with conical hypostome, surrounded by one whorl of filiform tentacles. Gonophores ovoid, located at the base of pseudohydrothecae beside hydranth, blastostyle completely reduced. Cnidome: microbasic mastigophores, microbasic euryteles, desmonemes and perhaps atrichous haplonemes.

Remarks: Following Peña Cantero *et al.* (2003) this family could present affinities with the Hydractinoidea (Bouillon, 1985) but the authors suggest some phylogenetic analyses are needed before establishing the affinities of the Clathrozoellidae with the other Filifera.

Genus ***CLATHROZOELLA*** Stechow, 1921

Fig. 127F

See family characters.

Clathrozoella abyssalis Peña Cantero, Vervoort & Watson, 2003
Clathrozoella bathyalis Peña Cantero, Vervoort & Watson, 2003
Clathrozoella drygalskii (Vanhöffen, 1910)
Clathrozoella medeae Peña Cantero, Vervoort & Watson, 2003

Family CLAVIDAE McCrady, 1859

Hydroid: hydrorhiza tubular, ramified or anastomosed; colony stolonal or erect; stem branched, mono- or polysiphonic; hydranths sessile or pedicellate, naked, occasionally covered by or retractable into a thin perisarc cone or tube (*Merona*, *Rhizogeton*, *Tubiclava*); tentacles filiform, scattered over oral and distal part of hydranth body; nematophores present or absent; gonophores as free medusae or sporosacs developing from hydrorhiza, hydrocaulus, or from reduced hydrants (blastostyles).

Medusae: umbrella bell-shaped; manubrium short; gastric peduncle gelatinous, or pseudo-peduncle formed by vacuolated endodermal cells; continuous row of sessile cnidocyst clusters along oral margin; 4 radial canals and circular canal; tentacles solitary, solid, numerous in adults; "gonads" on manubrium, interradial; ocelli adaxial.

Recent references: Wedler and Larson (1986); Calder (1988a; b); Migotto (1996); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2004).

Remarks: The genus *Clava* presents undeniable relations with the hydractiniids (see Bouillon *et al.* 1997) and has been included in this family by Schuchert (2001a) who reintroduced the name Cordylophoridae von Ledenfeld, 1885 for the remaining genera of the former family Clavidae. Later, Schuchert (2004) proposed to replace the nominal family Cordylophoridae with the nominal family Oceanidae Eschscholtz 1829. Furthermore, Schuchert (2004) underlied that the macrotaxonomy of the Oceanidae must be regarded as provisional and that the taxonomic validity of the genus *Oceania* has to be confirmed. To complicate the issue, the name Clavidae Mc Crady 1859 predates the Hydractiniidae Agassiz, 1862 threatening the latter name if the two are considered synonyms. Presently, we prefer to maintain the current use until more information, like molecular phylogenetic investigations, will become available.

KEYS TO POLYPS

1. colony erect and freely branched 2
– colony stolonal, hydroids at most slightly branched 4

2. branches not adnate to stem; gonophores as fixed sporosacs .... *Cordylophora*
– branches adnate to stem for some distance; gonophores as fixed sporosacs or free medusae........ 3

3. gonophores producing free medusae .... *Turritopsis*
– gonophores as fixed sporosacs .... *Corydendrium*

4. hydranth, or at least its pedicel or perisarcal tube, surrounded by perisarc 5
– hydranth naked, perisarc limited to hydrorhiza 8

5. hydranth retractable into perisarcal tube... 6
– hydranth not retractable into perisarcal tube; no nematothecae 7

6. gonophores on separate blastostyles; nematothecae present .... *Merona*
– gonophores on the stolons; naked nematophores .... *Similomerona*

7. gonophores on hydranth body .... *Tubiclava*
– gonophores on hydrorhiza and pedicels .... *Turritopsoides*

8. gonophores on hydranth body... *Clava*
– gonophores on hydrorhiza... *Rhizogeton*

KEY TO MEDUSAE

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

Genus ***CLAVA*** Gmelin, 1791

Fig. 3C

Hydroid: colonies stolonal; hydranths sessile, rising directly from hydrorhiza, naked except a low perisarcal collar around base, with conical hypostome, filiform tentacles scattered throughout the body; gonophores as fixed sporosacs (cryptomedusoids), below hydranth tentacles.
Recent references: Rossi *et al.* (2000); Schuchert (2001a).

Clava leptostyla Agassiz, 1862 [probably a syn. of *C. multicornis*]
Clava multicornis (Forskål, 1775)

Genus ***CORDYLOPHORA*** Allman, 1844

Fig. 80G-I

Hydroid: colony erect, hydrocaulus unbranched or monopodially branched with terminal hydranths; hydranth naked, fusiform, hypostome conical, tentacles filiform, scattered over much of body; gonophores as fixed sporosacs on hydranth pedicels, larvae and young polyps may develop within gonangia.
Recent references: Schuchert (1996, 2004); Stepanjants *et al.* (2000).

Cordylophora caspia (Pallas, 1771)
Cordylophora japonica Itô, 1951
Cordylophora solangiae Redier, 1967

Genus ***CORYDENDRIUM*** Van Beneden, 1844

Figs 80J-L, 81A

Hydroid: stolonal or branched; erect hydrocauli monosiphonic or polysiphonic, irregularly branched; branches completely or partly adnate to hydrocaulus, or to other branches; perisarc firm, covering up to hydranth base; hydranth elongate,

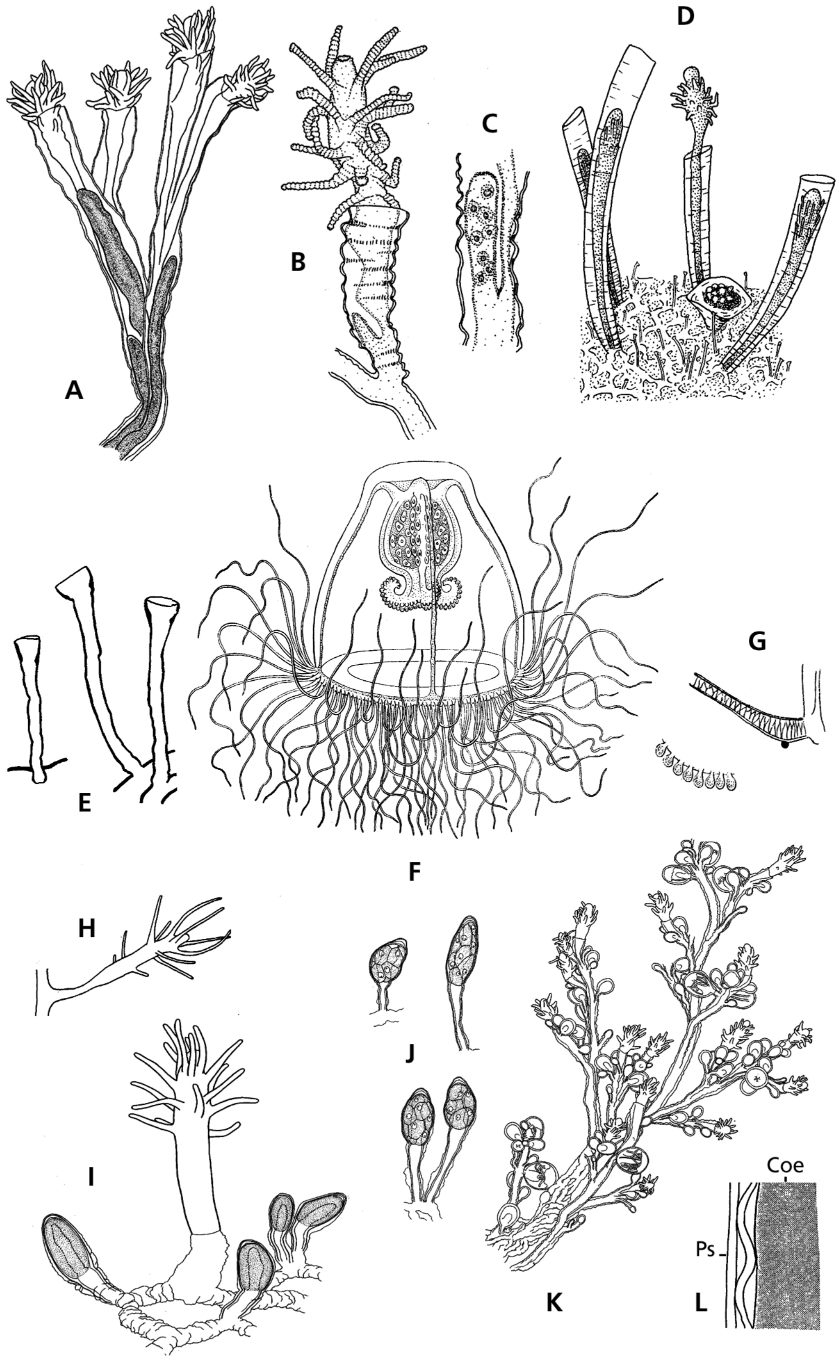


FIG. 81. Anthomedusae, Clavidae. A, *Corydendrium brevicaulis*, branched stem with hydranths and male gonophores within perisarcal tubes. B-C, *Corystolona annulata*: B, hydrorhiza, hydrocaulus and hydranth with young male gonophore; C, mature female gonophore with ova; D-E, *Merona cornucopiae*: D, part of colony growing on bivalve showing gastrozooids, one gonozooid and nematophores; E, nematothecae. F-H, *Oceania armata*: F, adult medusa; G, part of marginal tentacle showing the position of the ocellus (below), part of mouth lip showing the cnidocyst clusters (above); H, polyp stage. I-J, *Rhizogeton ezoense*: I, part of a colony with male gonophores; J, female gonophores. K-L, *Turritopsis nutricula*: K, part of stem of an erect colony with adnate branches, hydranths and medusa buds; L, drawing of the stem region showing the double layered structure of perisarc (A, I-K after Hirohito, 1988; B-C after Watson, 2002; D-E after Millard, 1975; F-G after Mayer, 1910; H & L after Schuchert, 1996). Coe = coenosarc, Ps = perisarc.

FIG. 81. *Anthomedusae, Clavidae. A,* Corydendrium brevicaulis, *branche ramifiée portant des hydranthes et des gonophores mâle inclus dans leurs tubes perisarcaux. B-C,* Merona cornucopiae *: B, portion de colonie poussant sur une coquille de bivalve et montrant des gastérozoïdes, un gonozoïde et des nematophores ; C, nematothecae. D-E,* Merona cornucopiae *: D, portion de colonie poussant sur une coquille de bivalve et montrant des gastérozoïdes, un gonozoïde et des nematophores ; E, nematothecae. F-H,* Oceania armata : *F, méduse adulte ; G, portion d'un tentacule marginal montrant la position de l'ocelle (au-dessous), portion de lèvre manubriale montrant les amas de cnidocystes (au-dessus) ; H, stade polype. I-J,* Turritopsis nutricula : *I, partie d'une colonie érigée présentant des branches adnées, des hydranthes et des bourgeons médusaires ; J, dessin d'une fraction de branche montrant la structure en double couche du périsarc (A, G-H d'après Hirohito, 1988 ; B-C d'après Watson, 2002 ; D-E d'après Mayer, 1910 ; F & J d'après Schuchert, 1996). Coe = coenosarc, Ps = périsarc.*

tubular, tentacles filiform and scattered over the body; gonophores as fixed sporosacs enclosed in perisarc, arising as blind, elongate sacs of coenosarc below hydranths and within perisarcal tubes of hydrocauli and hydrocladia branchlets.
Recent references: Calder (1988a); Schuchert (2004).

Corydendrium album Hirohito, 1988
Corydendrium brevicaulis Hirohito, 1988
Corydendrium corrugatum Nutting, 1905 [doubtful status]
Corydendrium dispar Kramp, 1935
Corydendrium flabellatum Fraser, 1938a
Corydendrium fruticosum Fraser, 1914a
Corydendrium parasiticum (Linnaeus, 1767)

Genus ***CORYSTOLONA*** (Watson, 1973)

Fig. 81B-C

Colonies stolonal; hydrocaulus simple, unbranched; perisarcal tube firm, terminating at hydranth base, no true pedicel; hydrantyh elongated, tubular with 26-30 scattered tentacles on body and an incipient ring of 4-5 oral tentacles around a dome-shaped hypostome; all tentacles armed with prominent rings of cnidocysts. Colonies dioecious, gonophores fixed sporosacs arising as blind sac laying below the hydranth within the hydrocaulus perisarcs, without spadix, female containing 10-12 eggs. Cnidocysts: Desmonemes and euryteles.
Recent references: Watson (2002).

Corystolona annulata (Watson, 1973)

Genus ***MERONA*** Norman, 1865

Fig. 81D-E

Hydroid: colony stolonal, polymorphic; gastrozooids unbranched, surrounded by a perisarc tube into which they can withdraw completely, tentacles filiform, scattered over much of body; gonozooids on stolon, without mouth and tentacles, with short perisarc tube around base, producing fixed sporosacs, dactylozooids on stolon, enclosed in a perisarc tube (nematotheca).
Recent references: Medel *et al.* (1993); Schuchert (2004).

Merona cornucopiae (Norman, 1864)
Merona ibera Medel, García-Gómez & Bouillon, 1993
Merona laxa (Fraser, 1938a) [as *Tubiclava*]
Merona operculata Watson, 1978

Genus ***OCEANIA*** Kölliker, 1853

Fig. 81F-H

Hydroid: not known from field, Metschnikoff (1886) obtained branched colonies with claviform hydranths having up to 13 filiform tentacles alternating in three whorls; gonophores unknown.
Medusa: peduncle short, pyramidal, gelatinous, without endodermal vacuolated cells.
Recent references: Schuchert (1996, 2004).

Oceania armata Kölliker, 1853a
Oceania tydemani Bleeker & van der Spoel, 1988

Genus *RHIZOGETON* Agassiz, 1862

Fig. 81I-J

Synonym: *Rhizodendrium* Calder, 1988.
Hydroid: colonies stolonal; hydrorhiza giving rise directly to naked and sessile hydranths or to hydranths on a short, unbranched, perisarc-covered hydrocaulus; tentacles filiform, scattered over much hydranth body; gonophores on hydrorhiza, as fixed sporosacs.
Recent references: Schuchert (2001a, 2004).

Rhizogeton fusiformis Agassiz, 1862
Rhizogeton conicum Schuchert, 1996
Rhizogeton ezoense Yamada, 1964
Rhizogeton nudum Broch, 1909
Rhizogeton sterreri (Calder, 1988a)

Genus *SIMILOMERONA* Schuchert, 2004

Hydroid: Colonies with polymorphic polyps, gastrozooids stolonal with scattered filiform tentacles, dactylozooids with rudimentary tentacles not in perisarc tubes, gonophores as fixed sporosacs on the stolons.
Recent reference: Schuchert (2004).

Similomerona nematophorum (Antsulevich & Polteva, 1986) [as *Merona*]

Genus *TUBICLAVA* Allman, 1863

Hydroid: colony stolonal; hydranth solitary, claviform, with scattered filiform tentacles, on perisarc-covered pedicel; gonophores as fixed sporosacs, in clusters on normal or reduced hydranths, under the inferior tentacles.
Remarks: poorly known genus, most species seem to belong to other genera of Clavidae often considered as congeneric with *Clava*, *Merona* or *Turritopsis.*
Recent references: Calder (1988a); Schuchert (1996, 2004).

Tubiclava lucerna Allman, 1863 [doubtful status]
Tubiclava triserialis Fraser, 1938a [doubtful status]

Genus *TURRITOPSIS* McCrady, 1857

Figs 25M, 64E, 81K-L, 82A-B

Hydroid: colony stolonal or erect; stem covered by a firm double-layered perisarc, often fouled by detritus and algae, monosiphonic in small colonies, polysiphonic in larger, irregularly branched ones and increasing in diameter from base to distal end; hydrocladia adnate and parallel to hydrocaulus or to other hydrocladia for some distance, before curving away at an acute angle and becoming free; hydranths terminal, naked, elongated, fusiform, with filiform tentacles irregularly scattered over distal three quarters of hydranth; gonophores giving rise to free medusae; buds arising mostly one by one from short stems or pedicels below hydranths, enclosed in perisarc.
Medusa: with family characters, with a pseudo-peduncle formed by large vacuolated endodermal cells.
Recent references: Calder (1988a); Schuchert (1996, 2004).

Turritopsis chevalense (Thornely, 1904) [doubtful status]
Turritopsis dohrnii (Weismann, 1883) [still refered to in many papers as *T. nutricula*]
Turritopsis fascicularis Fraser, 1943 [doubtful status]
Turritopsis lata Lendenfeld, 1885a
Turritopsis minor (Nutting, 1905) [doubtful status]
Turritopsis nutricula McCrady, 1857 [syn. *T. rubra* (Farqhar, 1895) and *T. pacifica* Maas, 1909]
Turritopsis policirrha (Keferstein, 1862)
Turritopsis pleurostoma (Péron & Lesueur, 1810) [doubtful status]

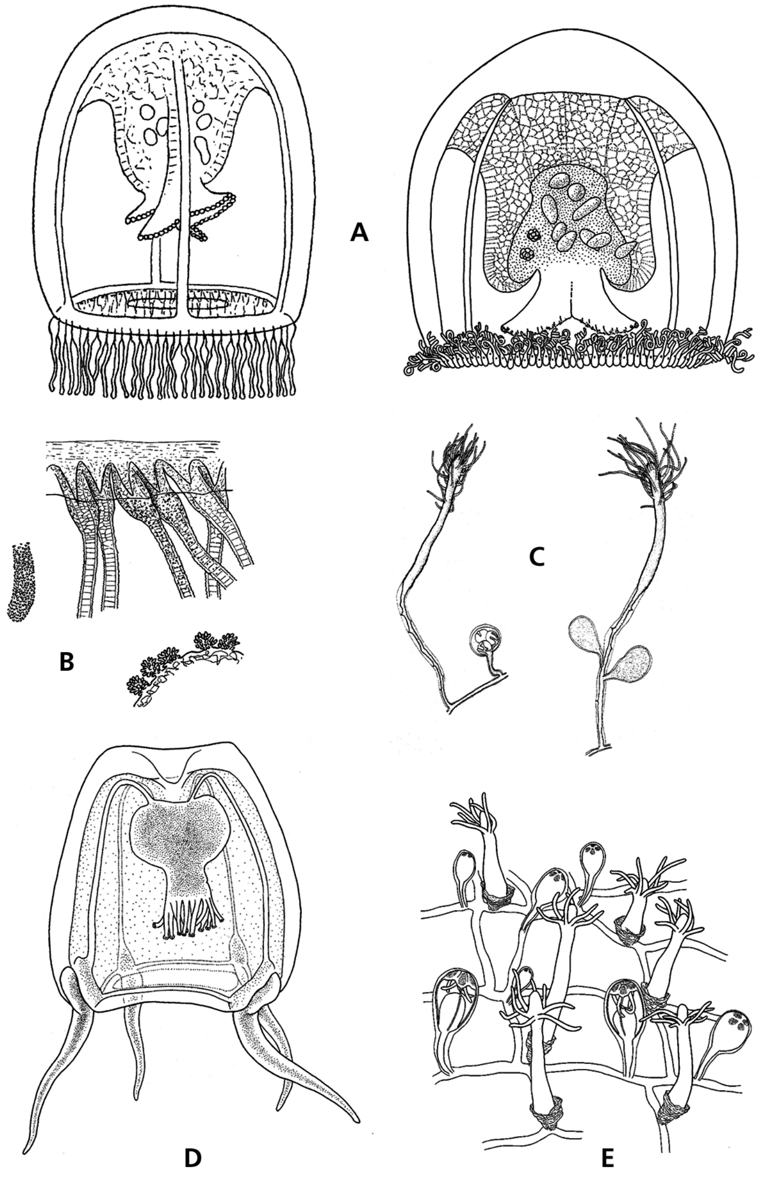


FIG. 82. Anthomedusae, Clavidae. A-B, *Turritopsis nutricula*: A, two adult medusae; B, base of marginal tentacles, ocelli omitted (above), tip of a marginal tentacle (left), margin of mouth lip showing the cnidocyst clusters (below). C, *Turritopsoides brehmeri*, hydranth and female gonophore (left), hydranth and male gonophores (right). D-E, Cytaedididae: D, *Cytaeis* sp., adult medusa; E, *Cytaeis uchidae*, part of colony showing the medusa buds and the cup-like perisarc at the base of the hydranths (A left: after Kramp, 1968, A right: after Shuchert, 1996; B after Russell, 1953; C after Calder, 1988b; D after Pagès *et al.*, 1992; E after Hirohito, 1988).

FIG. 82. *Anthomedusae, Clavidae. A-B,* Turritopsis nutricula : *A, deux méduses adultes ; B, base des tentacules marginaux, ocelles omis (au-dessus), extrémité d'un tentacule marginal (à gauche), bord d'une lèvre manubriale montrant les amas de cnidocystes (au dessous). C,* Turritopsoides brehmeri, *hydranthe et gonophore femelle (à gauche), hydranthe et gonophores mâles (à droite). D-E, Cytaedididae : D,* Cytaeis *sp., méduse adulte ; E,* Cytaeis uchidae, *portion de colonie montrant les bourgeons médusaires et le perisarc en forme de cupule à la base des hydranthes (A à gauche : d'après Kramp, 1968 ; A à droite: d'après Shuchert, 1996 ; B d'après Russell, 1953 ; C d'après Calder, 1988b ; D d'après Pagès et al., 1992 ; E d'après Hirohito, 1988).*

Genus *TURRITOPSOIDES* Calder, 1988

Fig. 82C

Hydroid: colony mostly stolonal, with irregular branches partly adnate to pedicels; hydrorhiza and pedicel perisarc moderately thick, extending over hydranth base as a thin film; hydranth elongate, tubular to clavate, with numerous scattered filiform tentacles; gonophores as fixed sporosacs, on short stalks from hydrorhiza and pedicel.
Turritopsoides brehmeri Calder, 1988b

Family CYTAEIDIDAE L. Agassiz, 1862

Hydroid: colony usually non-polymorphic, hydrorhiza reticulate, covered by perisarc, without spines; gastrozooid sessile, with one whorl of filiform tentacles below conical hypostome, naked, with a perisarc cup-shaped collar at base, sometimes of two sizes, smallest ones acting as dactylozooids; gonophores on hydrorhiza, as free medusae, medusoids with four radial canals, or as fixed sporosacs.
Medusa: umbrella bell-shaped; manubrium bulbous; mouth simple, circular, with 4 or more unbranched oral arms, either on or near mouth rim; 4 radial canals and circular canal; 4 or 8 marginal solid tentacles; "gonads" interradial or encircling manubrium; no ocelli.
Recent references: Calder (1988a); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bavestrello *et al.* (2000); Bouillon & Boero (2000).

KEY TO HYDROIDS

known only in the genus *Cytaeis*, with family characters.

KEY FOR MEDUSAE

1. 4 marginal tentacles . . . . *Cytaeis*
– 8 marginal tentacles . . . . *Paracytaeis*

Genus *CYTAEIS* Eschscholtz, 1829

Figs 82D-E, 83A-C

Synonyms: *Perarella Stechow*, 1922; *Stylactella* Haeckel, 1889 in part
Hydroid: see family characters.
Medusae: with family characters, 4 radial canals.
Remarks: Rees (1956; 1962) re-established the genus *Perarella* for species with fixed sporosacs or degenerated medusae. Since generic classification based exclusively on medusa reduction is presently rejected, *Perarella* is considered as congeneric with *Cytaeis*.
Recent references: Calder (1988a); Bouillon *et al.* (1991); Bavestrello (1987); Bavestrello *et al.* (2000).

Cytaeis abyssicola (Haeckel, 1889)
Cytaeis adherens Bouillon, Boero & Seghers, 1991
Cytaeis affinis (Jäderholm, 1904a) [doubtful status]
Cytaeis clavata (Jäderholm, 1905)
Cytaeis imperialis Uchida, 1964a
Cytaeis indica (Stechow, 1920)
Cytaeis nassa Millard, 1959b
Cytaeis niotha (Pennycuik, 1959)
Cytaeis nuda Rees, 1962
Cytaeis parastichopae Hirohito, 1988
Cytaeis propagulata (Bavestrello, 1987)
Cytaeis schneideri (Motz-Kossowska, 1905)
Cytaeis spongicola (Haeckel, 1889)
Cytaeis pusilla Gegenbaur, 1857
Cytaeis tetrastyla Eschscholtz, 1829
Cytaeis uchidae Rees, 1962
Cytaeis vulgaris Agassiz & Mayer, 1899

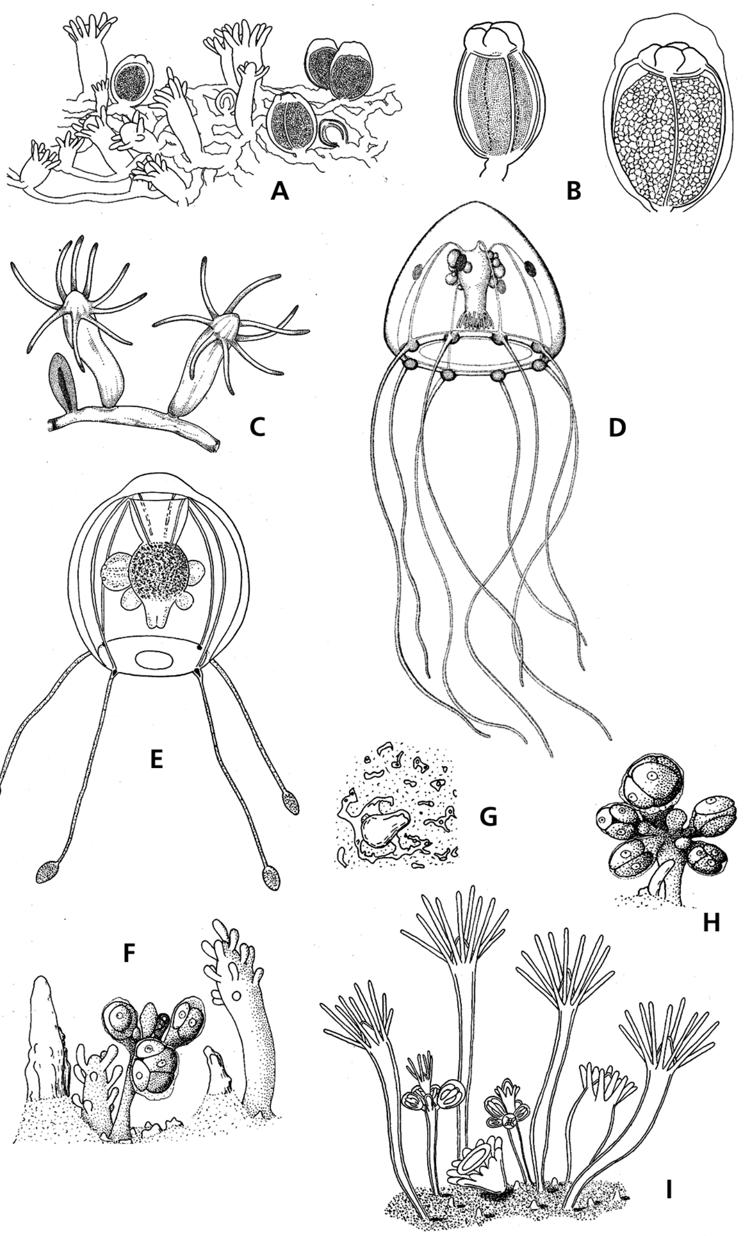


FIG. 83. Anthomedusae, Cytaeididae. A-C, *Cytaeis*. A-B, *Cytaeis* (*Perarella*) *parastichopae*: A, part of colony with hydranths and gonophores; B, male and female eumedusoids; C, *Cytaeis* (*Perarella*) *propagulata*, part of colony with hydranths and a sporosac. D, *Paracytaeis octona*, adult medusa with medusa buds. E, Eucodoniidae, *Eucodonium brownei*, adult medusa with medusa buds on manubrium. F-H, Hydractiniidae, *Clavactinia gallensis*: F, part of a colony showing gastrozooids, gonozooids, and spines; G, surface view of hydrorhiza with one large spine, many small ones and parts of trabeculae seen trough coenosarc; H, detail of female gonophore and spine. I, *Hydractinia carnea,* portion of hydroid colony (A-B after Hirohito, 1988; C after Bavestrello, 1987: p. 21, fig. 5.1 B; D after Bouillon, 1978; E & I after Russell, 1953; F-H after Millard & Bouillon, 1973).

FIG. 83. *Anthomedusae, Cytaeididae. A-C,* Cytaeis. *A-B,* Cytaeis *(*Perarella*)* parastichopae : *A, partie de colonie avec hydranthes et gonophores ; B, eumedusoides mâle et femelle ; C,* Cytaeis *(*Perarella*)* propagulata*, portion de colonie avec hydranthes et sporosacs. D,* Paracytaeis octona*, méduse adulte présentant des bourgeons médusaires manubriaux. E, Eucodoniidae,* Eucodonium brownei*, méduse adulte possédant des bourgeons médusaires manubriaux. F-H, Hydractiniidae,* Clavactinia gallensis : *F, portion de colonie montrant des gastérozoïdes, un gonozoïde et des épines ; G, vue superficielle de l'hydrorhize montrant une des larges épines, plusieurs petites et des parties du perisarc trabéculaire vu au travers du coenosarc ; H, détail d'un gonophore femelle et d'une épine. I,* Hydractinia carnea*, portion d'une colonie (A-B d'après Hirohito, 1988 ; C d'après Bavestrello, 1987 : p. 21, fig. 5.1 B; D d'après Bouillon, 1978; E & I d'après Russell, 1953; F-H d'après Millard & Bouillon, 1973).*

Genus ***PARACYTAEIS*** Bouillon, 1978

Fig. 83D

Hydroid: unknown.
Medusa: with family characters, 8 marginal tentacles; 4 interradial exumbrellar opaque oval spots of special vacuolated cells located midway of umbrella.

Paracytaeis octona Bouillon, 1978a

Family EUCODONIIDAE Schuchert, 1996

Hydroid: unknown.
Medusae: umbrella bell-shaped, no pointed apical projection; no exumbrellar cnidocyst tracks; manubrium quadrangular, on conical gastric peduncle; mouth quadrangular, with 4 inconspicuous cnidocyst-armed lips; 4 radial canals and circular canal; "gonads" encircling manubrium; 4 solid marginal tentacles with terminal swelling; marginal bulbs small; no ocelli.
Recent reference: Schuchert (1996).

Genus ***EUCODONIUM*** Hartlaub, 1907

Fig. 83E

With family characters.

Eucodonium brownei Hartlaub, 1907

Family HYDRACTINIIDAE L. Agassiz, 1862

Hydroid: colony stolonal, polymorphic, usually epizootic; hydrorhiza either as a reticulum formed by perisarc-covered stolonal tubes (sometimes with protective tubes: *Clavactinia protecta*), or as an encrusting mat issued from the coalescence of the stolonal system and either covered by a common layer of perisarc or with naked coenosarc; in some genera the hydrorhizal mat is invested by a calcareous skeleton; frequently with chitinous or calcareous spines forming sometimes pillars and branches; polyps sessile, naked; gastrozooids either with one whorl or with several closely alternating whorls of oral filiform tentacles or with scattered tentacles on the distal half of column, exceptionally with one or two tentacles; dactylozooids, when present, with no tentacles; ectodermal vesicles of unknown function present or not in hydrorhiza (*Hydrocorella, Janaria*); gonophores typically borne on gonozooids with one or more whorls of oral tentacles or without tentacles and mouth (= blastostyles), exceptionally on or in the hydrorhiza (*H. cryptogonia*), giving rise to fixed sporosacs, eumedusoids, or free medusae.
Medusa: umbrella more or less bell-shaped, with or without slight apical process; manubrium tubular to sac-shaped, not extending beyond bell margin; with or without gastric peduncle; mouth with 4 simple or branched oral lips elongated to form arms with terminal cnidocyst clusters (exceptionally mouth rim simple and armed with a cnidocysts ring: *Kinetocodium*); 4, 8, or more, solitary, solid, marginal tentacles; 4 radial canals and circular canal; "gonads" on manubrium, interradial, sometimes extending along the proximal portions of radial canals; with or without ocelli.
Recent references: Wedler & Larson (1986); Calder (1988a); Migotto (1996); Schuchert (1996); Bouillon *et al.* (1997); Boero *et al.* (1997); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2001a).

KEY TO HYDROIDS

1. colonies living on pteropods . . . . *Kinetocodium*
– colonies not living on pteropods 2

2. hydrorhiza with calcareous skeleton. 3
– hydrorhiza without calcareous skeleton 4

3. hydrorhiza forming conspicuous longitudinal ridges developing small spines and large pillar-shaped processes; gastrozooids on largest calcareous processes, with 1 or 2 extra long tentacles; gonozooids with tentacles . . . . *Hydrocorella*
– hydrorhiza with ectodermal vesicles, forming crenulated, sinuous crests; gastrozooids between crests, with a whorl of uniform tentacles; gonozooids without tentacles . . . . *Janaria*

4. gastrozooids with several whorls of tentacles scattered on distal half . . . . *Clavactinia*
– gastrozooids with one or more whorls of tentacles closely set around hypostome. . . . . *Hydractinia*

KEY TO MEDUSAE

Only one genus with known adult medusae: *Hydractinia* [medusae known as *Podocoryna*].

Genus ***CLAVACTINIA*** Thornely, 1904

Fig. 83F-H

Synonym: *Fiordlandia* Schuchert, 1996.
Hydroid: colony stolonal; hydrorhiza forming anastomosing perisarc-covered tubes that may coalesce into a basal encrusting layer covered by naked coenosarc, often bearing spines; gastrozooids with tentacles scattered on distal body half; gonozooid with reduced number of tentacles, bearing gonophores below tentacles; gonophores as fixed sporosacs, sometimes protected by hydrorhizal tubes.
Recent references: Schuchert (1996); Bouillon *et al.* (1997).

Clavactinia gallensis Thornely, 1904

Clavactinia protecta (Schuchert, 1996)

Genus ***HYDRACTINIA*** van Beneden, 1841

Figs 3D, 5D, 18, 25N, 27G-H, 56A, 83I, 84A-H

Synonyms: *Cnidostoma* Vanhöffen, 1911; *Podocoryna* Sars, 1846; *Stylactella* Haeckel, 1889 in part; *Stylactaria* Stechow, 1921.
Hydroid: colony stolonal, either with a reticular hydrorhiza, formed by perisarc-covered stolonal tubes, or with an encrusting mat issued through the coalescence of stolonal system, covered either by a common layer of perisarc or by naked coenosarc; hydrorhizal mat secretes a calcareous skeleton in some genera; frequently with chitinous or calcareous spines, sometimes forming pillars and branches; polyps sessile, naked, polymorphic; gastrozooids with one or more whorls of oral filiform tentacles, or with scattered tentacles on the distal half of body; dactylozooids, when present, with no tentacles; gonophores typically borne on gonozooids, exceptionally on or in hydrorhiza; gonozooids with one or more whorls of oral tentacles, or without tentacles and mouth (= blastostyles), giving rise to fixed sporosarcs, eumedusoids, or free medusae.
Medusa: umbrella more or less bell-shaped; with or without slight apical process; manubrium tubular to sac-shaped, not extending beyond bell margin; with or without gastric peduncle; mouth with 4 simple or branched oral lips, elongated to form arms with terminal cnidocyst clusters; 4, 8, or more, solitary, solid, marginal tentacles; 4 radial canals and circular canal; “gonads” on manubrium, interradial, sometimes extending along the proximal portions of radial canals; with or without ocelli.

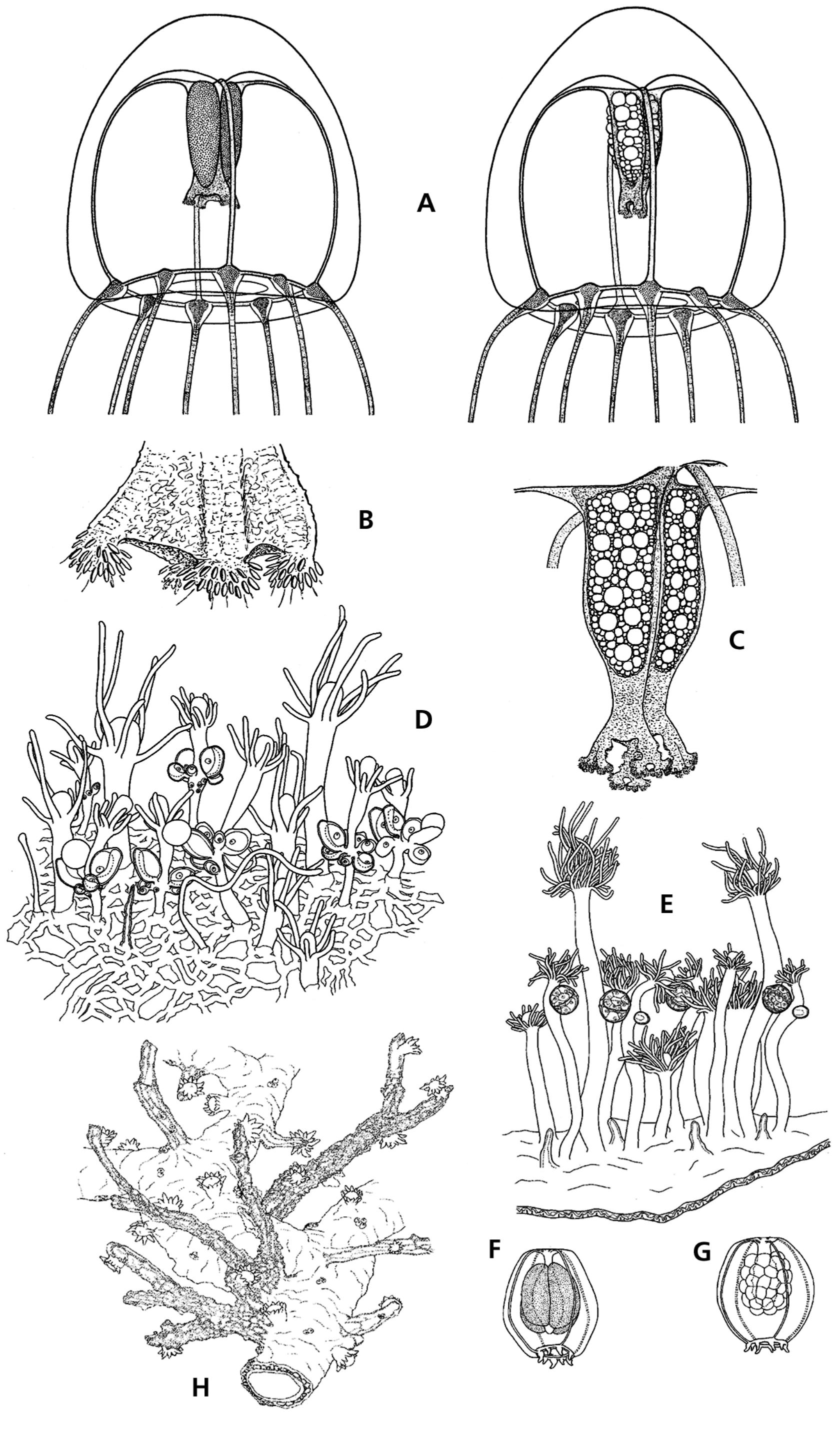


FIG. 84. Anthomedusae, Hydractiniidae. A-H, *Hydractinia*. A-B, *Hydractinia carnea*: A, male adult medusa (left), female adult medusa (right); B, mouth of newly liberated medusa. C, *Hydractinia borealis*, manubrium and mouth of an adult female medusa; D, *Hydractinia monoon*, part of a female colony showing the gastrozooids, the gonozooids with their fixed sporosacs, the spines and tentaculozooids; E-G, *Hydractinia epiconcha*: E, part of a female colony with gastrozooids, gonozooids and spines; F, male eumedusoid; G, female eumedusoid; H, *Hydractinia cryptogonia*, part of colony supported by a chitinous skeleton formed by reticular meshes and growing on and incrusting a polychaete tube, notice the groups of 2 to 5 eggs at the outer surface of the perisarc (A & C after Edwards, 1972; B after Russell, 1953; D-H after Hirohito, 1988).

FIG. 84. *Anthomedusae, Hydractiniidae. A-H,* Hydractinia. *A-B,* Hydractinia carnea : *A, méduse adulte mâle (à gauche), méduse adulte femelle (à droite) ; B, bouche d'une jeune méduse venant de se libérer. C,* Hydractinia borealis, *manubrium et bouche d'une méduse adulte femelle ; D,* Hydractinia monoon, *portion d'une colonie femelle montrant des gastérozoïdes, des gonozoïdes différenciant des sporosacs fixés, des épines et de tentaculozooides ; E-G,* Hydractinia epiconcha : *E, fragment d'une colonie femelle avec des gatérozooïdes, des gonozoïdes et des épines ; F, eumédusoïde mâle ; G, eumédusoïde femelle ; H,* Hydractinia cryptogonia, *partie d'une colonie supportée par un squelette chitineux, formé par des mèches réticulaires, croissant sur et incrustant un tube de polychète, noter les groupes de 2 à 5 œufs disposés à la surface externe du périsarc (A & C d'après Edwards, 1972 ; B d'après Russell, 1953; D-H d'après Hirohito, 1988).*

Recent references: Schuchert (1996); Bouillon *et al.* (1997); Boero *et al.* (1997); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2001a, 2003).

Hydractinia aculeata (Wagner, 1833)
Hydractinia aggregata Fraser, 1911
Hydractinia allmani Bonnevie, 1898b [syn. *H. Ornata* Bonnevie, 1898]
Hydractinia altispina Millard, 1955
Hydractinia angusta Hartlaub, 1904
Hydractinia americana Edwards, 1972
Hydractinia apicata Kramp, 1959a
Hydractinia arctica (Jäderholm, 1902a)
Hydractinia areolata (Alder, 1862a)
Hydractinia arge (Clarke, 1882)
Hydractinia armata Fraser, 1940a
Hydractinia australis (Schuchert, 1996)
Hydractinia bayeri Hirohito, 1984
Hydractinia bella (Hand, 1961)
Hydractinia betkensis (Watson, 1978)
Hydractinia borealis (Mayer, 1900b)
Hydractinia brachyurae (Hirohito, 1988)
Hydractinia calderi (Bouillon, Medel & Peña Cantero, 1997)
Hydractinia californica Torrey, 1904
Hydractinia canalifera Millard, 1957
Hydractinia carcinicola (Hiro, 1939)
Hydractinia carica Bergh, 1887
Hydractinia carnea (M. Sars, 1846) [syn. *H. exigua* (Haeckel, 1880) in part]
Hydractinia carolinae Fraser, 1912
Hydractinia claviformis (Bouillon, 1965)
Hydractinia conchicola (Yamada, 1947)
Hydractinia cryptogonia Hirohito, 1988
Hydractinia dendritica Hickson & Gravely, 1907
Hydractinia diogenes Millard, 1959b
Hydractinia disjuncta Fraser, 1938
Hydractinia dubia (Mayer, 1900)
Hydractinia echinata (Fleming, 1828)
Hydractinia epiconcha Stechow, 1907
Hydractinia epispongia Fraser, 1938a
Hydractinia fallax Broch, 1914
Hydractinia fucicola (M. Sars, 1857)
Hydractinia granulata Hirohito, 1988
Hydractinia hancocki Fraser, 1938a
Hydractinia hayamaensis Hirohito, 1988
Hydractinia hooperi (Sigerfoos, 1899)
Hydractinia humilis Bonnevie, 1898b
Hydractinia inabai (Hirohito, 1988)
Hydractinia inermis (Allman, 1872)
Hydractinia ingolfi Kramp, 1932a [probably a syn. of *Hydractinia arctica*]
Hydractinia kaffaria Millard, 1955
Hydractinia laevispina Fraser, 1911
Hydractinia longispina Fraser, 1938a
Hydractinia mar (Gasca & Calder, 1993)
Hydractinia marsupialia Millard, 1975
Hydractinia meteoris Thiel, 1938a
Hydractinia milleri Torrey, 1902
Hydractinia minima (Trinci, 1903) [syn. *H. simplex* Kramp, 1928]
Hydractinia minoi (Alcock, 1892)
Hydractinia minuta (Mayer, 1900a)
Hydractinia misakiensis (Iwasa, 1934a)
Hydractinia monocarpa Allman, 1876a
Hydractinia monoon (Hirohito, 1988)
Hydractinia multigranosi (Namikawa, 1991)
Hydractinia multispina Fraser, 1938a
Hydractinia multitentaculata (Millard, 1975)
Hydractinia nagaoensis Bouillon, Medel & Peña Cantero, 1997
Hydractinia ocellata (Agassiz & Mayer, 1902)
Hydractinia otagoensis (Schuchert, 1996)
Hydractinia novaezelandiae Schuchert, 1996
Hydractinia pacifica Hartlaub, 1905
Hydractinia parvispina Hartlaub, 1905
Hydractinia piscicola (Komai, 1932)
Hydractinia polycarpa Fraser, 1938a
Hydractinia polyclina Agassiz, 1862
Hydractinia proboscidea Hincks, 1869
Hydractinia prolifica Fraser, 1948
Hydractinia pruvoti Motz-Kossowska, 1905
Hydractinia quadrigemina Fraser, 1938a
Hydractinia reticulata (Hirohito, 1988)
Hydractinia rubricata Schuchert, 1996
Hydractinia rugosa Fraser, 1938b
Hydractinia sandrae (Wedler & Larson, 1986)
Hydractinia sarsii Steenstrup, 1850
Hydractinia sagamiensis (Hirohito, 1988) [juvenile medusa; doubtful status]
Hydractinia selena (Mills, 1976)
Hydractinia serrata Kramp, 1943
Hydractinia sodalis Stimpson, 1858
Hydractinia siphonis (Stechow, 1921a) [doubtful status]
Hydractinia spinipapillaris (Hirohito, 1988)
Hydractinia spiralis Goto, 1910
Hydractinia symbiolongicarpus Buss & Yund, 1989
Hydractinia symbiopollicaris Buss & Yund, 1989
Hydractinia tenuis (Browne, 1902)
Hydractinia tournieri (Picard & Rahm, 1954)
Hydractinia uchidai Nagao, 1961
Hydractinia valens Fraser, 1941
Hydractinia vallini Jäderholm, 1926
Hydractinia vermicola Allman, 1888 [doubtful status]
Hydractinia yerii (Iwasa, 1934b)

Genus ***HYDROCORELLA*** Stechow, 1921

Fig. 85A-E

Synonym: *Polyhydra* Stechow, 1962.

Hydroid: colony polymorphic, epizootic on hermit crab-inhabited gastropods shells; calcareous skeleton (coenosteum) covered by a layer of naked coenosarc and developing conspicuous longitudinal ridges covered by small spines and large pillar-shaped structures; numerous ectodermal vesicles buried in the coenosteum, identical to those of *Janaria* (see below); gastrozooids with one whorl of 5-12 tentacles, 1-2 of which longer than the others; dactylozooids as tentaculozooids situated around shell aperture and usually with a terminal battery of cnidocysts; gonophores on reduced gonozooids with about 6 rudimentary tentacles bearing several fixed sporosacs.

Remarks: very similar to *Hydractinia*, the main difference being the calcified skeleton.

Recent references: Cairns & Barnard (1984); Bouillon *et al.* (1997); Boero *et al.* (1997).

Hydrocorella africana Stechow, 1921b
Hydrocorella calcarea (Carter, 1877)
Hydrocorella spinifera (Stechow, 1962)

Genus ***JANARIA*** Stechow, 1921

Fig. 85F

Hydroid: colony polymorphic, epizootic on crustacean-inhabited gastropod shells; hydrorhiza with a calcareous skeleton (coenosteum) covered by a layer of naked coenosarc; coenosteum covering entire shell, including the internal cavity, often enlarging domain of hermit crab and forming series of calcareous branches radiating outwards the peripheral whorl of gastropod shell; skeleton producing low spines coalescing in meandering ridges; coenosteum with several layers of numerous internal hemispherical vesicles with apical pore; vesicles buried deeper below surface with age and maintained in contact with surface by narrow ducts, inside of vesicles lined with chitin and not in contact with coenosarc, identity and function of vesicles unknown (symbionts?); gastrozooids variable in size and form, hypostome with one whorl of identical filiform tentacles, dactylozooids uncommon, slender, cylindrical, solid; male gonozooids without tentacles (blastostyles), bearing several round fixed sporosacs; female gonozooids unknown.

Recent references: Cairns & Barnard (1984).

Janaria mirabilis Stechow, 1921b

Hydractiniidae *incertae sedis*:

Genus ***KINETOCODIUM*** Kramp, 1921

Fig. 85G-I

Hydroid: colony stolonal, living on Pteropods; gastrozooids with 0-6 short, oval, oral tentacles; dactylozooids filiform, entirely covered by cnidocysts; gonophores peduncled, on stolon, each with one medusa.

Medusa: only juvenile medusae known; manubrium flask-shaped; mouth quadrate with oral cnidocyst ring; 4 radial canals; three marginal tentacles and a rudimentary marginal bulb.

Kinetocodium danae Kramp, 1921

Family PTILOCODIIDAE Coward, 1909

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

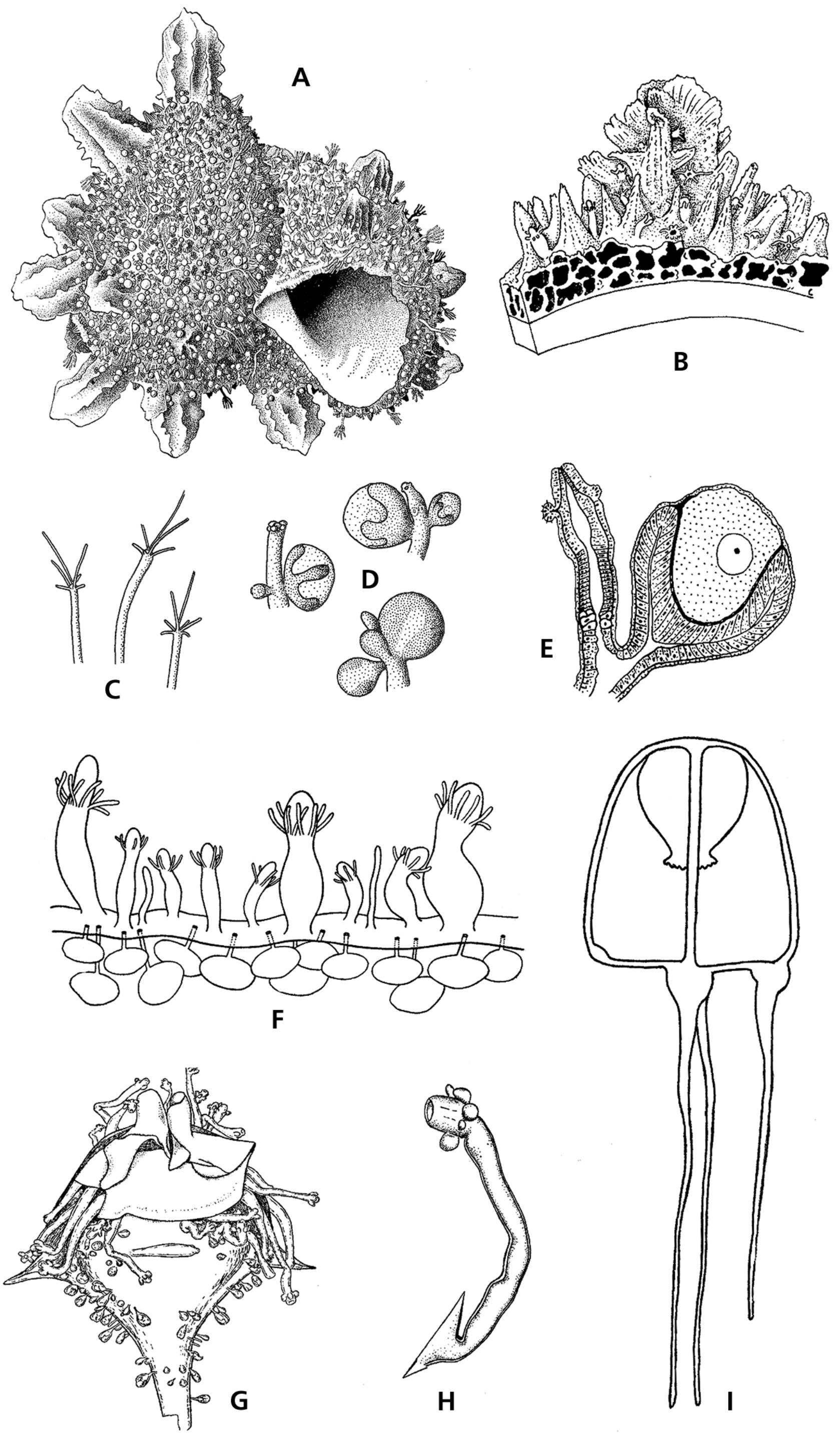


FIG. 85. Anthomedusae, Hydractiniidae. A-E, *Hydrocorella africana*: A, colony completely covering a shell of hermit-crab; B, section through colony and host shell showing skeleton calcareous processes and contracted hydranths; C, gastrozooids; D, gonozooids; E, detail of a gonozooid. F, *Janaria mirabilis*, diagrammatic view of a section trough a colony. G-I, *Kinetocodium danae*: G, colony living on the pteropod *Hylaea trispinosa*, ventral view; H, gastrozooid; I, newly liberated medusa (A after Bouillon, 1995a: p. 50, fig. 20; B-E after Millard, 1975; F after Stechow, 1962; G-I after Kramp, 1957).

FIG. 85. *Anthomedusae, Hydractiniidae. A-E,* Hydrocorella africana : *A, colonie couvrant complètement une coquille habitée par un bernard l'hermite ; B, section au travers d'une colonie et de la coquille hôte montrant les processus squelettiques calcaires et les hydranthes contractés ; C, gastérozoïdes ; D, gonozoïdes ; E, détail d'un gonozoïde. F,* Janaria mirabilis*, vue diagrammatique d'une section au travers d'une colonie. G-I,* Kinetocodium danae : *G, colonie vivant sur le ptéropode* Hylaea trispinosa*, vue ventrale ; H, gastérozoïde ; I, jeune méduse venant de se libérer (A d'après Bouillon, 1995a : p. 50, fig. 20 ; B-E d'après Millard, 1975 ; F d'après Stechow, 1962 ; G-I d'après Kramp, 1957).*

Medusa: umbrella more or less bell-shaped; with or without radial exumbrellar furrows; didermic centripetal tracks or exumbrellar rows of refringent spots; with marginal cnidocyst ring; when present, marginal tentacles solid, with tips armed with cnidocysts; 4 radial canals and circular canal; manubrium tubular or bottle-shaped, with mouth arms with terminal cnidocyst clusters, "gonads" adradial or interradial.

Recent references: Jarms (1987); Bouillon *et al.* (1997); Bouillon & Boero (2000).

Key to hydroids

1. colony polymorphic, dactylozooids of two types. . . . . *Hydrichthella*
– colony dimorphic, dactylozooids of one type 2
2. hydrorhiza crust-like, covered by naked coenosarc. . . . . *Ptilocodium*
– Hydrorhiza as a network of perisarc-protected tube-like stolons . . . . *Thecocodium*

Key to medusae

1. no marginal tentacles. . . . . *Tregoubovia*
– Marginal tentacles 2
2. "gonads" adradial. . . . . *Hansiella*
– "gonads" interradial . . . . *Thecocodium*

Genus ***HANSIELLA*** Bouillon, 1980

Fig. 86A

Hydroid: unknown.

Medusa: conspicuous marginal cnidocyst ring from which several centripetal didermic processes arise; 4 stiff marginal tentacles with cnidocyst-armed tips; manubrial mouth arms with terminal clusters of cnidocysts; short mesenteries; "gonads" adradial; no ocelli.

Recent reference: Bouillon *et al.* (1997).

Hansiella fragilis Bouillon, 1980

Genus ***HYDRICHTHELLA*** Stechow, 1909

Fig. 86B-D

Synonym: *Hydrichthelloides* Bouillon, 1978.

Hydroid: colony usually growing on sea fans, hydrorhiza encrusting, covered by naked coenosarc, or consisting of perisarc-covered reticular stolons pending substrate; gastrozooid tubular, without tentacles, hypostome studded by cnidocysts; dactylozooids hollow, without mouth, of two types: one with many capitate tentacles and the other filiform, with capitate tip; gonozooid similar to gastrozooid, bearing eumedusoids with four radial canals, 8 tentacles, velum, "gonads" on manubrium.

Recent references: Hirohito (1988); Bouillon *et al.* (1997).

Hydrichthella epigorgia Stechow, 1909 [syn. *H. doederleini* Stechow, 1926]

Hydrichthella reticulata (Bouillon, 1978b)

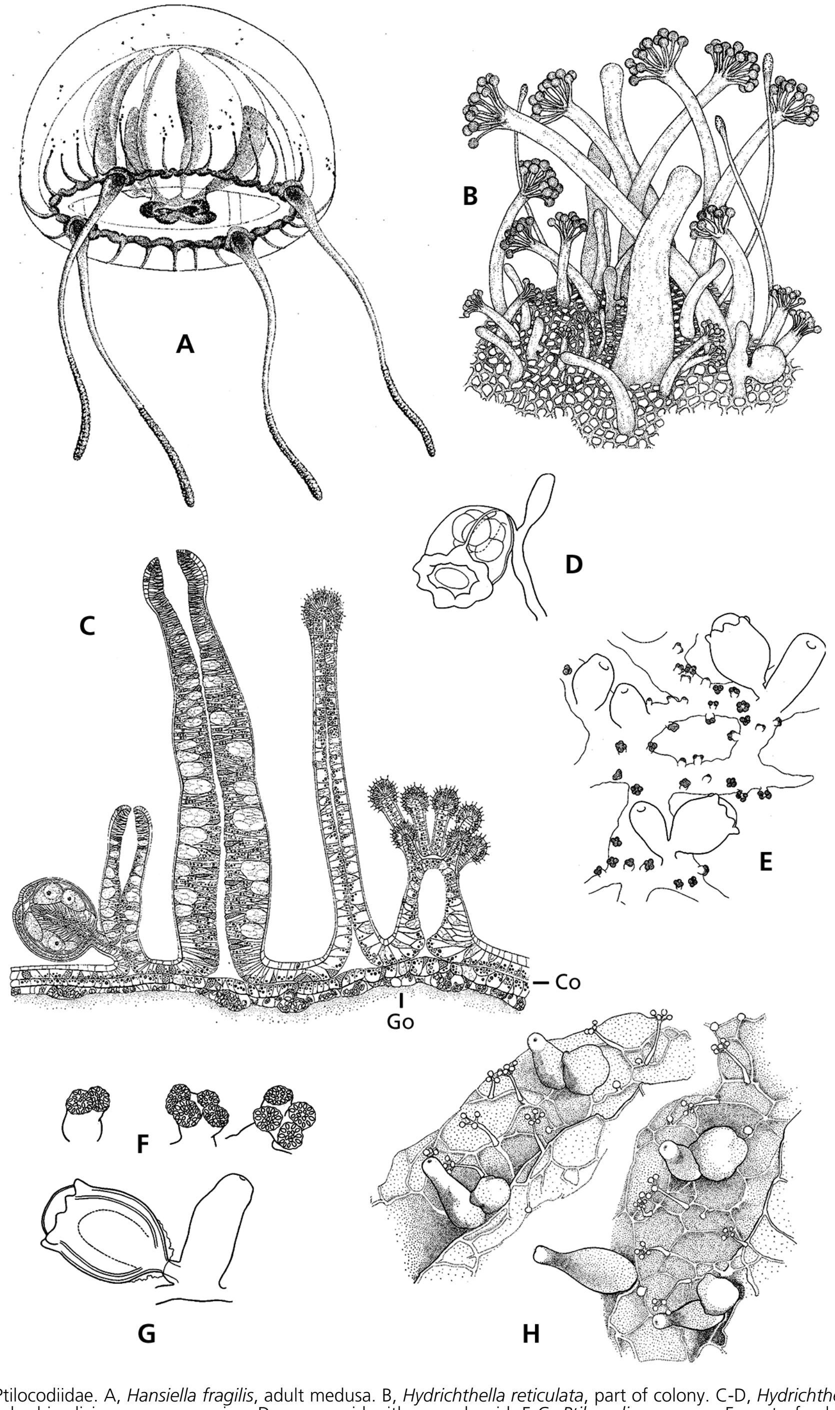


FIG. 86. Anthomedusae, Ptilocodiidae. A, *Hansiella fragilis*, adult medusa. B, *Hydrichthella reticulata*, part of colony. C-D, *Hydrichthella epigorgia*: C, part of a colony with crust-like hydrorhiza living on a gorgonian; D, gonozooid with eumedusoid. E-G, *Ptilocodium repens*: E, part of colony; F, dactylozooids; G, gastrozooid bearing an eumedusoid. H, *Thecocodium brieni*, two colonies (A after Bouillon, 1985b; B after Bouillon, 1987; C & H after Bouillon, 1967; D-G after Hirohito, 1988). Co = coenosarc; Go = gorgonian.

FIG. 86. *Anthomedusae, Ptilocodiidae. A, Hansiella fragilis*, méduse adulte. B, *Hydrichthella reticulata*, portion d'une colonie. C-D, *Hydrichthella epigorgia*: C, portion de colonie à hydrorhize encroûtante vivant sur une gorgone ; D, gonozoïde developpant un eumedusoide. E-G, *Ptilocodium repens :* E, fragment d'une colonie ; F, dactylozoïdes ; G, gastérozoïde portant un eumedusoide. H, *Thecocodium brieni,* deux colonies (A d'après Bouillon, 1985b ; B d'après Bouillon, 1987 ; C & H d'après Bouillon, 1967 ; D-G d'après Hirohito, 1988). Co = coenosarc; Go = gorgone.

Genus ***PTILOCODIUM*** Coward, 1909

(Fig. 86: E-G)

Hydroid: colony growing usually on pennatulids; hydrorhiza formed by closely anastomosed stolons covered by naked coenosarc; gastrogonozooid cylindrical, without tentacles, hypostome not armed with cnidocysts; dactylozooids solid, with 4-5 capitate tentacles on distal end; gonophores at base of gastrogonozooid, developing into eumedusoids with four radial canals and 4-8 tentacles, "gonads" on manubrium.
Recent references: Hirohito (1988); Bouillon *et al.* (1997).

Ptilocodium repens Coward, 1909

Genus ***THECOCODIUM*** Bouillon, 1967

(Fig. 86: H; Fig. 87: A, B)

Hydroid: hydrorhiza stolonal, formed by reticular, perisarc-covered tubes, gastrozooid cylindrical or club-shaped, without tentacles, hypostome armed by cnidocysts; dactylozooids solid, with 4-5 capitates tentacles; gonozooid similar to gastrozooid; gonophores as fixed sporosacs or free medusae.
Medusa: marginal cnidocyst ring from which either several centripetal endodermic processes or exumbrellar rows of cnidocysts arise; 4 stiff marginal tentacles embedded in exumbrellar furrows; short mesenteries; manubrium with mouth arms with terminal clusters of cnidocysts; "gonads" interradial; no ocelli.
Recent references: Jarms (1987); Hirohito (1988); Bouillon *et al.* (1997).

Thecocodium brieni Bouillon, 1967
Thecocodium penicillatum Jarms, 1987
Thecocodium quadratum (Werner, 1965)

Genus ***TREGOUBOVIA*** Picard, 1958

Fig. 87C

Hydroid: unknown.
Medusa: no exumbrellar furrows; with didermic centripetal tracks; no marginal tentacles or marginal tentacular bulbs; "gonads" interradial.
Recent reference: Bouillon *et al.* (1997).

Tregoubovia atentaculata Picard, 1958

Family RATHKEIDAE Russell, 1953

Hydroid: colony stolonal, with hydranths arising from ramified, creeping stolons; hydranth monomorphic, sessile, with one whorl of filiform tentacles surrounding a rounded hypostome; hydranth base with thin gelatinous perisarc; medusa buds developing on hydrorhiza or more rarely at hydranth base.
Medusa: umbrella somewhat globular, with slight apical process; manubrium short, cylindrical; with gastric peduncle; mouth with 4 lips elongated to form either simple or branched oral arms, with terminal and usually also lateral cnidocyst clusters; 4 to 8 radial canals and circular canal; "gonad" generally completely surrounding manubrium; 8 groups of solid marginal tentacles; no ocelli.
Recent references: Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

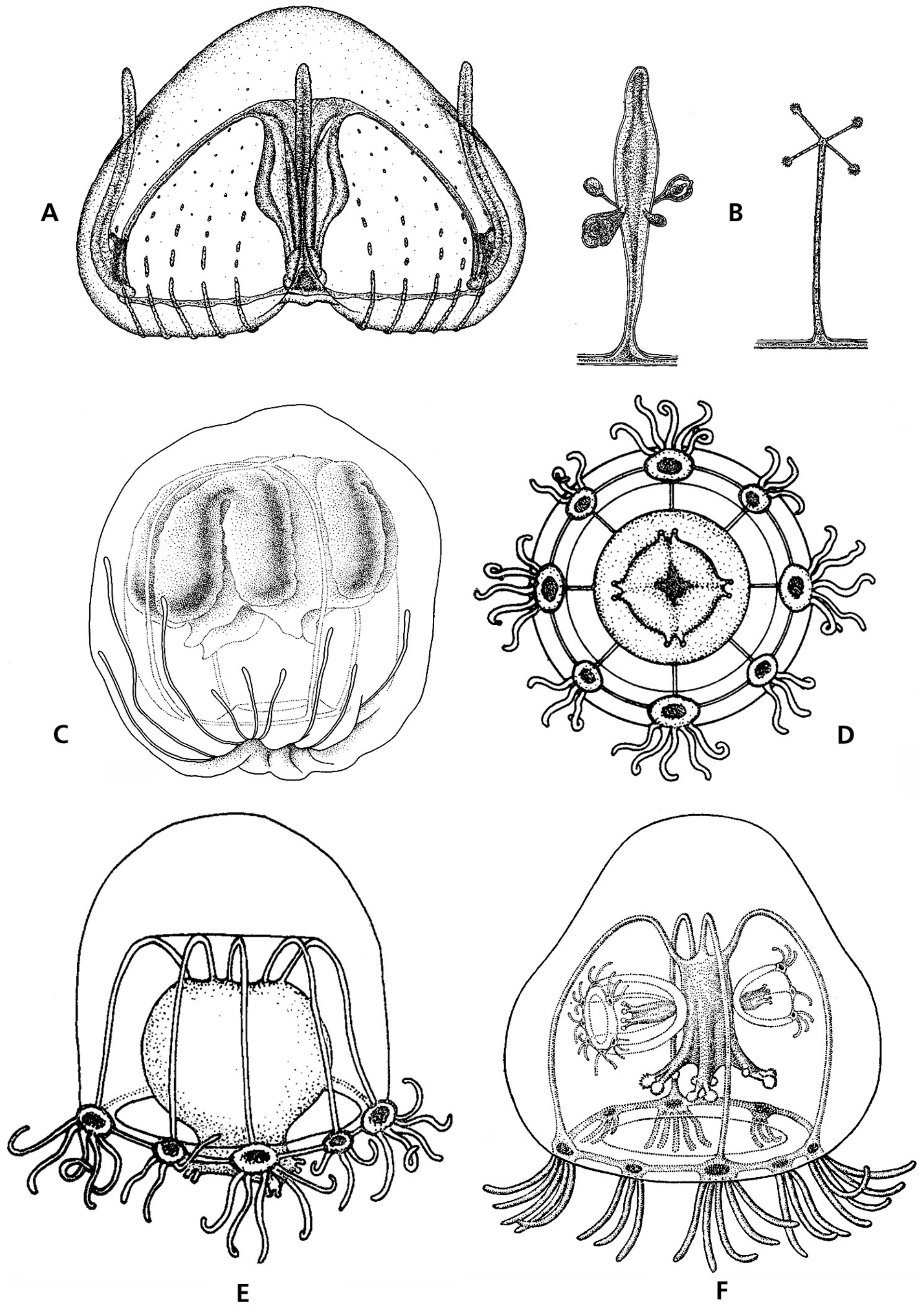


FIG. 87. Anthomedusae, Ptilocodiidae (end). A-B, *Thecocodium quadratum*: A, mature medusa; B, gastro-gonozooid (left), dactylozooid (right). C, *Tregoubovia atentaculata,* adult medusa. D-F, Rathkeidae. D-E, *Allorathkea macrogastrica*: D, oral view of an adult medusa; E, lateral view of an adult medusa; F, *Rathkea octopunctata*, adult medusa with manubrial medusa buds (A-B after Jarms, 1987: p. 60, figs 8.1, 8.2; C original figure; D-E after Xu Zhen-zu & Huang Jia-qi, 1990a; F after Naumov, 1969).

FIG. 87. *Anthomedusae, Ptilocodiidae (fin). A-B,* Thecocodium quadratum : *A, méduse mature ; B, gastro-gonozoïde (à gauche), dactylozoïde (à droite). C,* Tregoubovia atentaculata*, méduse adulte. D-F, Rathkeidae. D-E,* Allorathkea macrogastrica : *D, vue orale d'une méduse adulte ; E, vue latérale d'une méduse adulte ; F,* Rathkea octopunctata*, méduse adulte développant des bourgeons médusaires manubriaux (A-B d'après Jarms, 1987 : p. 60, figs 8.1, 8.2 ; C figures originales ; D-E d'après Xu Zhen-zu & Huang Jia-qi, 1990a ; F d'après Naumov, 1969).*

KEY TO HYDROIDS

Known only in *Rathkea*, see family characters.

KEY TO MEDUSAE

1. 4 radial canals . . . . *Rathkea*
– 8 radial canal . . . . *Allorathkea*

Genus *ALLORATHKEA* Schmidt, 1972

Fig. 87D-E

Synonym: *Pseudorathkea* Xu & Huang, 1990.
Hydroid: unknown.
Medusa: 8 radial canals; mouth arms divided once or dichotomously several times and ending in cnidocyst clusters.
Allorathkea ankeli Schmidt, 1972
Allorathkea macrogastrica (Xu & Huang, 1990a)

Genus *RATHKEA* Brandt, 1838

Figs 87F, 88A-D

Hydroid: See family characters.
Medusa: 4 radial canals and 4 elongated oral arms, simple or divided and armed with a various number of cnidocyst clusters.

Rathkea africana Kramp, 1957
Rathkea antarctica Uchida, 1971
Rathkea formosissima (Browne, 1902)
Rathkea lizzioides O'Sullivan, 1984
Rathkea octopunctata (M. Sars, 1835)
Rathkea rubence Nair, 1951

Family RHYSIIDAE Brinckmann, 1965

Hydroid: colony stolonal, polymorphic; hydrorhiza covered with perisarc; gastrozooid naked, columnar, with either one whorl of filiform tentacles or with cnidocyst clusters and a few thick filiform tentacles around hypostome; dactylozooids, when present, covered with perisarc up to capitate apical extreme; "gonads" on hydranth resembling gastrozooid, on one side of the body, no gonophores; male hydranth with 3 or 4 filiform tentacles, female hydranths with or without tentacles and transforming into a sporosac-like structure with the endoderm forming a spadix feeding one egg, developing into a planula.

Genus *RHYSIA* Brinckmann, 1965

Fig. 88E-H

See family characters.
Recent references: Hirohito (1988); Brinckmann-Voss *et al.* (1993).

Rhysia autumnalis Brinckmann, 1965a
Rhysia fletcheri Brinckmann-Voss, Lickey & Mills, 1993
Rhysia halecii (Hickson & Gravely, 1907)

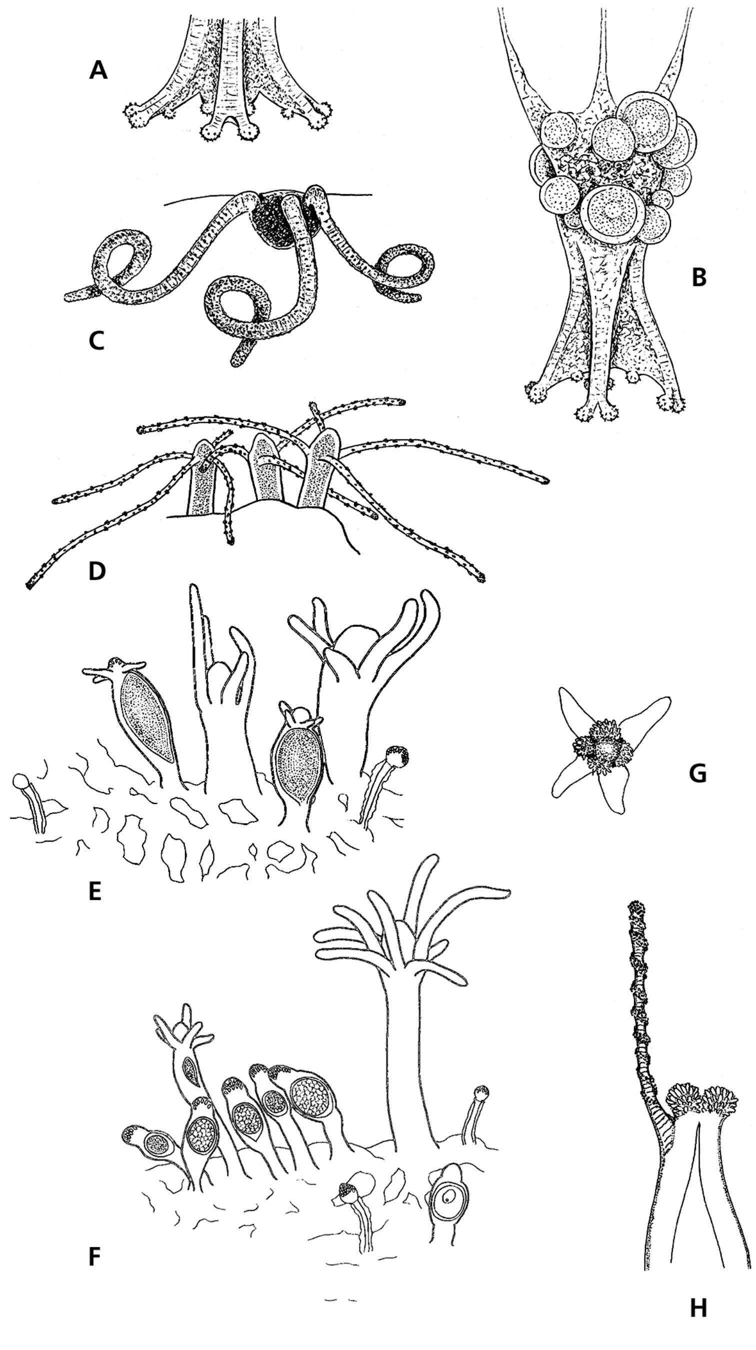


FIG. 88. Anthomedusae, Rathkeidae. A-D, *Rathkea octopunctata*: A, view of the mouth showing the disposition of the lips; B, manubrium showing the ''gonads'' and the lips; C, interradial marginal tentacle group; D, hydroid colony. E-F, Rhysiidae, *Rhysia halecii*: E, part of a male colony; F, part of a female colony. G-H, *Rhysia fletcheri*: G, oral view of the hypostome of a gastrozooid showing the oral cnidocyst clusters and the contracted tentacles; H, lateral view of the oral half of a gastrozooid showing the oral cnidocyst clusters and one extended tentacle (A-D after Russell, 1953; E-F after Hirohito, 1988; G-H after Brinckmann-Voss *et al*., 1993).

FIG. 88. *Anthomedusae, Rathkeidae. A-D,* Rathkea octopunctata : *A, vue de la bouche montrant la disposition des lèvres ; B, manubrium montrant les ''gonades'' et les lèvres buccales ; C, groupe de tentacules marginaux interradiaires ; D, colonie d'hydroïdes. E-F, Rhysiidae,* Rhysia halecii : *E, partie d'une colonie mâle ; F, portion d'une colonie femelle. G-H,* Rhysia fletcheri : *G, vue orale de l'hypostome d'un gastérozooide montrant les amas oraux de cnidocystes et les tentacules contractés ; H, vue latérale de la moitié orale d'un gastérozoïde montrant les amas cnidocytaires oraux et un tentacule étendu (A-D d'après Russell, 1953 ; E-F, d'après Hirohito, 1988 ; G-H d'après Brinckmann-Voss* et al.*, 1993).*

Family RUSSELLIDAE Kramp, 1957

Hydroid: unknown.
Medusa: umbrella with apical projection; manubrium on gastric peduncle, 4 small perradial manubrial pouches along the proximal part of 4 radial canals; 4 unbranched oral filiform tentacles attached above mouth margin; mouth with 4 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 sunk into deep furrows of umbrella margin; 8 adradial "gonads"; adaxial red ocellus at base of free portion of each tentacle.
Recent references: Bouillon (1999); Pagès *et al.* (1999); Bouillon & Boero (2000).

Genus ***RUSSELLIA*** Kramp, 1957

Fig. 101I

See family characters.

Russellia mirabilis Kramp, 1957

Family STYLASTERIDAE Gray, 1847

Hydroid: colony generally erect, branched, usually flabellate, more rarely encrusting, with a thick calcareous exoskeleton (coenosteum); polyps polymorphic and retractile; gastrozooids with one whorl of filiform tentacles, exceptionally without tentacles; bottom of gastric cavity containing usually an upright pointed or rounded toothed spine: the central style or gastrostyle; dactylozooids filiform, without tentacles, with or without style: the dactylostyle; gastrozooids and dactylozooids retractable into special skeletal depressions: gastropores and dactylopores; gastro- and dactylozooids either irregularly distributed over colony, or limited to certain regions of colony, or often arranged in circles (cyclosystems) where one gastrozooid is surrounded by several dactylozooids; gonophores as reduced fixed sporosacs and developed inside the "ampullae", internal or superficial globose exoskeletal structures; most species dioecious.
Remarks: The Stylasteridae present close affinities with the Hydractiniidae with which the are often united in a superfamily the Hydractinioidea.
Recent references: Cairns (1983; 1987; 1991a; b; c).

KEY TO GENERA, SUBGENERA, AND SPECIES GROUPS OF THE STYLASTERIDAE (AFTER CAIRNS 1983; 1991A; B; C)

1. distinct cyclosystems present 2
– distinct cyclosystems absent: coordination of gastro- and dactylopores random or arranged in rows but never in cyclosystems 12

2. gastrostyles absent 3
– gastrostyles present 6

3. cyclosystems unifacial 4
– cyclosystems not unifacial: arranged randomly or sympodially. . . . . 5 (*Conopora*)

4. Fixed lid partially covers gastropore . . . . *Crypthelia*
– lid absent, but small prong projects into gastropore ring constriction. . . . . *Astya*

5. Cyclosystems randomly arranged on branch . . . . *Conopora* A
– cyclosystems sympodially arranged on branch . . . . *Conopora* B

6. gastrostyles rudimentary; gastropore tube double-chambered; dactylostyles absent . . *Pseudocrypthelia*
– gastrostyles well-developed; gastropore tube single-chambered (cylindrical, constricted, or bent); dactylostyles present. 7

7. corallum encrusting, purple or pink; often more than 1 gastrostyle per cyclosystem . . . . . . *Stylantheca*
– corallum branching, variable in colour but most often white; 1 gastrostyle per cyclosystem 8

8. cyclosystems unifacial 9
– cyclosystems not unifacial: occur randomly or primarily sympodially . . . . 10 (*Stylaster* s.l.)

9. rudimentary fixed lids cover part of cyclosystem; coenosteum reticulate granular . . . . *Calyptopora*
– cyclosystems without lids; coenosteum linear-imbricate. . . . . *Stenohelia*

10. cyclosystems uniformly spaced on all sides of branches; number of dactylopores per cyclosystem low, e.g., 7-9; colony massive, branches usually blunt tipped; dactylostyles robust . . *Stylaster* A (=*"Allopora"*)
– cyclosystems primarily sympodially arranged; number of dactylopores per cyclosystem relatively high, e.g., 10-15; colony delicate, branches usually slender; dactylostyles rudimentary 11

11. cyclosystems exclusively sympodially arranged. . . . . *Stylaster* C
– cyclosystems primarily sympodially arranged but with additional cyclosystems on anterior and posterior faces . . . . *Stylaster* B

12. gastrostyles present 13
– gastrostyles absent 28

13. dactylostyles present 14
– dactylostyles absent 16

14. dactylostyles robust; dactylopore spines oriented randomly, linear, or as pseudocyclosystems . . . . *Errinopora*
– dactylostyles rudimentary; dactylopore spines abcauline 15

15. one to four dactylostyles per dactylopore; coenosteum reticulate-imbricate; dactylopore spines tall. . . . . *Inferiolabiata*
– one very rudimentary dactylostyle per dactylopore; coenosteum reticulate granular; dactylopore spines absent or very short. . . . . *Paraerrina*

16. gastro- and dactylopores linearly arranged in pore rows: the gastropores aligned in a sunken sulcus flanked on both sides by U-shaped dactylopore spines, their openings (slits) directed toward the gastropores 17
– Gastro- and dactylopores not arranged in pore rows: pores usually randomly arranged, but if dactylopores are linear, they are conical in shape (*Lepidopora*) or abcauline (*Phalangapora*) or adcauline (*Systematopora*) and not intimately associated with a gastropore row 19

17. gastro- and dactylopores and gastrostyles extremely long (height/width ratio of gastrostyle often over 10), often stabilized by transverse tabulae; pore rows usually restricted to branch edges; gastrostyle spines pointed. . . . . 18 (*Distichopora*)
– gastro- and dactylopores and gastrostyles short (height/width ratio of gastrostyle 1.5-4.0); pore rows meander over branch faces; spines on gastrostyle blunt, clavate . . . . *Gyropora*

18. corallum branching (flabellate or bushy) . . . . *Distichopora* (*Distichopora*)
– corallum flabellate, bilobate . . . . *Distichopora (Haplomerismos)*

19. corallum fenestrate. 20
– corallum freely branching with little or no anastomosis 21

20. gastropores aligned, coenosteum smooth, dactylopore spines conical; gastrostyles squat (H/W =1.5) with pointed tip . . . . *Cheiloporidion*
– gastropores randomly arranged; coenosteum granular or imbricate; dactylopore spines conical and adcauline; gastrostyles lanceolate (H/W = 3-4). . . . . *Errinopsis*

21. gastropore stellate . . . . *Stellapora*
– gastropores round to elliptical 22

22. dactylopores flush with coenosteal surface, not raised as spines 23
– dactylopores flanked by dactylopore spines (abcauline, adcauline, or conical), ampullae superficial. 24

23. colony branching dichotomously; ampullae internal. . . . . *Sporadopora*
– colony branching polychotomously; ampullae superficial, male with ampullar spines . . . *Stephanohelia*

24. dactylopore spines elliptical or circular, rimmed on all sides; walls serrate, apically; having ring palisades . . . . *Cyclonelia*
– dactylopores different 25

25. dactylopore spines conical; dactylopore tubes axial . . . . *Lepidopora*
– dactylopore spines U-shaped (abcauline or adcauline); dactylopore tubes peripheral 26

26. dactylopores adcauline 27
– dactylopore spines abcauline, with thin walls . . . . *Lepidotheca*

27. gastropores and dactylopores unilinearly arranged, dactylopore spines adcauline, with thin walls, short . . . . *Systematopora*
– no coordination of gastrozooids and dactylozooids; dactylopore spines adcauline, with thick walls, tall . . . . *Errina*

28. dactylopore spines conical; gastro- and dactylopores randomly arranged; dactylopore tubes axial 29
– dactylopore spines U-shaped; gastro- and dactylopores linearly arranged; dactylopore tubes peripheral- . . . . *Phalangapora*

29. hinged operculum covering gastropore; coenosteal pores small; ampullae superficial . . . . . *Adelopora*
– opercula absent; large, elongate coenosteal pores common between coenosteal strips; ampullae superficial . . . . *Pliobothrus*

Genus *ADELOPORA* Cairns, 1982

see photographs in Cairns (1983; 1991a)

Hydroid: colony flabellate or bushy; branches round in cross section, occasionally anastomosing, especially in flabellate colonies; coenosteum linear-imbricate, composed of broad, flat platelets; no granules; gastropores at branch tips, branching axils, and, in thicker branches, on lateral surfaces; gastropore tube cigar-shaped, with no style or tabulae; pore covered by a hinged operculum, which, when closed, is flushed with the coenosteal surface; dactylopores randomly arranged, apically perforate mounds; no dactylostyles; ampullae large and superficial, some with a lateral- tubular efferent canal.

Adelopora crassilabrum Cairns, 1991a
Adelopora fragilis Cairns, 1991a
Adelopora moseleyi Cairns, 1991a
Adelopora pseudothyron Cairns, 1982

Genus *ASTYA* Stechow, 1921

Fig. 89A

Hydroid: colony small, delicate, and flabellate; branches round in cross section and very thin, dista1 branches usually thinner in diameter than the cyclosystems they support; coenosteum linear-imbricate, white; all cyclosystems originate on the anterior side of the colony and project at right angles to the branch; cyclosystems slightly exsert, round to elliptical in cross section, up to 1.9 mm in greater diameter; gastropore composed of two chambers, with a short, blunt pillar projecting into the constricted aperture that separates the chambers; seventeen to 19 dactylopores per cyclosystem; the upper, outer edge of each pseudoseptum bears a nematopore; no gastro- or dactylostyles; ampullae restricted to a ring encircling the base of each cyclosystem, causing the cyclosystems to appear globose; the gastrozooid fills the crescent-shaped lower chamber and also projects upward as a cylindrica1 tube; mouth cruciform, no tentacles; dactylozooids adnate, with long free tentacles.

Astya aspidopora Cairns, 1991a
Astya subviridis (Moseley, 1879)

Genus ***CALYPTOPORA*** Boschma, 1968

Fig. 89B

Hydroid: colony flabellate; branches round to elliptical in cross section, sometimes posteriorly carinate; branch anastomosis may occur; coenosteum reticulate-granular and white, bearing numerous small papillae (nematopores), especially on larger branches; cyclosystems unilinearly or sometimes slightly sympodially arranged, all on the anterior side, usually with one or more diastemÚs and one or more fixed lids of variable size; lids broad, either as tongue-shaped projections, or simply the result of over development of several adjacent pseudosepta overhanging the gastropore; lids predominantly abcauline; gastropores broad and deep, with a small gastrostyle chamber containing a lanceolate, ridged gastrostyle of small-medium H/W ratio; a ring palisade is present; dactylostyles well developed; ampullae superficial, sometimes with an efferent duct.

Calyptopora complanata (Pourtalès, 1867) [as *Stylaster*]
Calyptopora pachypoma (Hickson & England, 1905)
Calyptopora reticulata Boschma, 1968a
Calyptopora sinuosa Cairns, 1991a

Genus ***CHEILOPORIDION*** Cairns, 1983

(see photographs in Cairns 1983)

Hydroid: colony uniplanar with a strong tendency toward branch anastomosis, producing a network or irregularly shaped fenestrae; branches elliptical, rectangular in cross section, the greater axis perpendicular to the plane of branching; branches ridged on both anterior and posterior faces; coenosteum reticulate, composed of short discontinuous smooth (not granulate) strips with rounded edges; dactylopores occur randomly on anterior and lateral branch surfaces; gastropores loosely aligned along lateral edges; gastro- and dactylopore tubes short, branches compact; gastropores flush with branch surface; gastrostyles ridged, bearing fused spines; dactylopores rimmed by two to four vertical platelets, forming a discontinuous collar around the pore; no dactylostyles; ampullae superficial; soft parts unknown.

Cheiloporidion pulvinatum Cairns, 1983

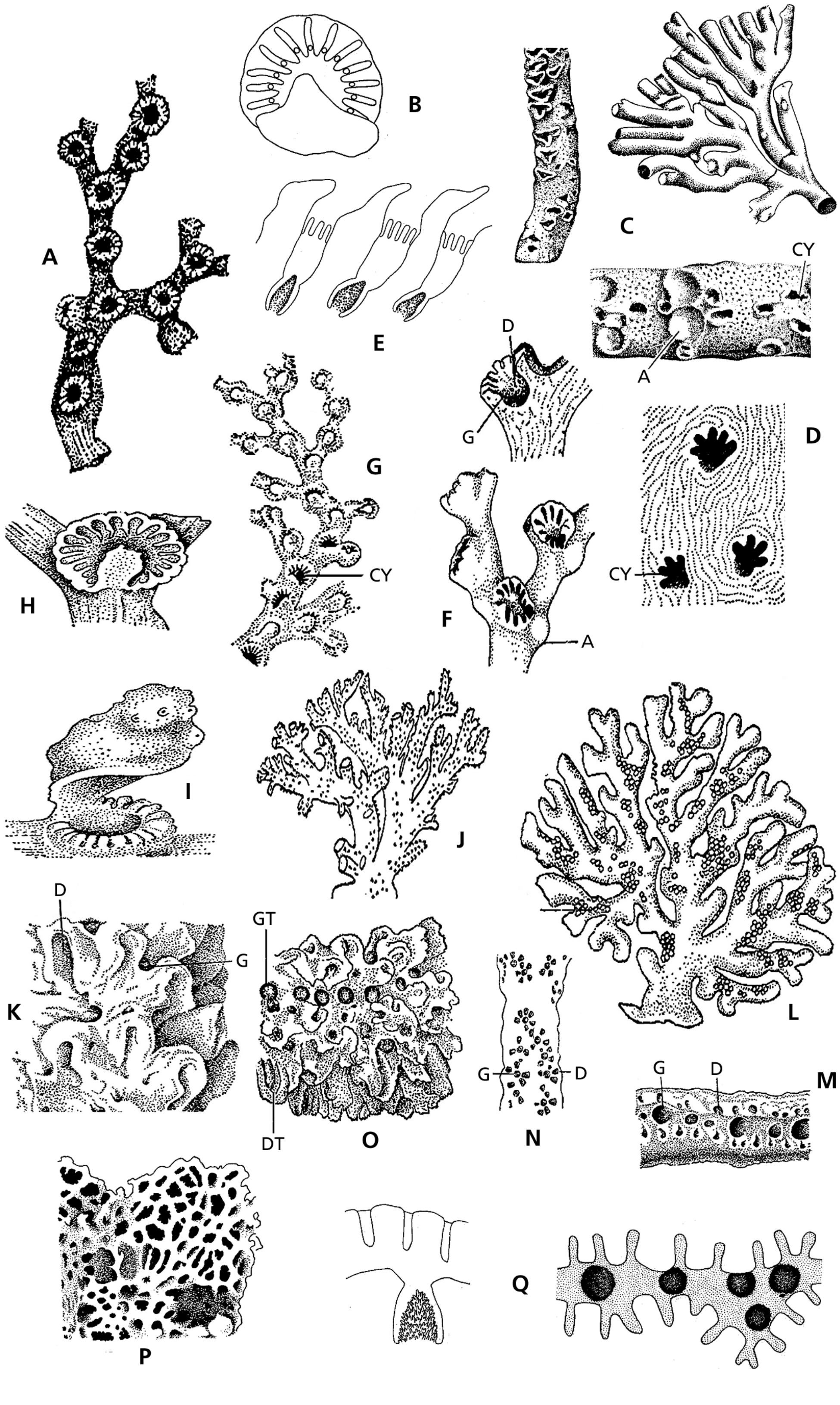
Genus ***CONGREGOPORA*** Nielsen, 1919

Fig. 89C

Hydroid: colony flabellate, up to 6 cm tall and 8 cm broad; branches round in cross section, and blunt; basal branches up to 5 mm in diameter; coenosteum covered by shallow pits that are equally spaced about 0.21 mm apart, perhaps the

FIG. 89. Anthomedusae, Stylasteridae. A, *Astya*. B, *Calyptopora*, cyclosystem in surface view (above), longitudinal section of three adjoining gastropores showing the gastrostyles (below). C, *Congregopora*, part of a colony (above right), branch of a colony showing the cyclosystems (above left), part of a colony showing the ampullae (below). D-F, *Conopora*: D, schematic view of a branch showing three cyclosystems; E, detail of a cyclosystem; F, part of a branch showing cyclosystems and ampullae. G-I, *Cryphtelia*: G, part of branch showing the disposition of the cyclosytems; H, cyclosytem seen from above; I, lateral view of a cyclosystem. J-K, *Errina*: J, general view of a colony; K, detail of a branch showing a gastropore and a dactylopore. L-M, *Distichopora*: L, general view of a colony showing the ampullae; M, detail of a branch showing the disposition of the gastropores and dactylopores. N-O, *Errinopora*: N, schematic view of a portion of branch showing the disposition of the cyclosystems; O, fragment of a ranch showing the gastrostyles and the dactylostyles. P, *Errinopsis*, fragment of a branch. Q, *Gyropora*, longitudinal section showing a gastropore with its gastrostyle and three dactylopores (left), part of a groove with five gastropores (right), (A, C-P, after Moore, 1956; B after Boschma, 1968a; Q after Boschma, 1960). Abbreviations for figs 89, 90, 91: A = ampullae; C = canal system; CY = cyclosystem; D = dactylopore; DT = dactylostyle; DZ = dactylozooid; G = gastropore, GT = gastrostyle; GZ = gastrozooid.

FIG. 89. *Anthomedusae, Stylasteridae. A,* Astya*. B,* Calyptopora*, vue superficielle d'un cyclosystème (au-dessus), coupe longitudinales de trois gastropores adjacents montrant les gastrostyles (au-dessous). C,* Congregopora*, partie d'une colonie (au-dessus à droite), branche d'une colonie montrant les cyclosystèmes (au-dessus à gauche), fragment de colonie montrant les ampoules sexuées (au-dessous). D-F,* Conopora *: D, vue schématique d'une branche montrant trois cyclosystèmes ; E, détail d'un cyclosystème ; F, portion d'une branche montrant les cyclosystèmes et les ampoules sexuées. G-I,* Cryphtelia *: G, portion d'une branche montrant la disposition des cyclosystèmes ; H, cyclosytème vu du dessus ; I, vue latérale d'un cyclosystème. J-K,* Errina *: J, vue générale d'une colonie ; K, détail d'une branche montrant un gastropore et un dactylopore. L-M,* Distichopora *: L, vue générale d'une colonie montrant les ampoules sexuées ; M, détail d'une branche montrant la disposition des gastropores et des dactylopores. N-O,* Errinopora *: N, vue schématique d'une portion de branche montrant la disposition de cyclosystèmes ; O, fragment d'une branche montrant les gastrostyles et les dactylostyles. P,* Errinopsis*, fragment d'une branche. Q,* Gyropora*, section longitudinale montrant un gastropore et son gastrostyle ainsi que trois dactylopores (à gauche), partie d'un sillon avec cinq gastropores (à droite), (A, C-P d'après Moore, 1956 ; B d'après Boschma, 1968a ; Q d'après Boschma, 1960). Abréviations des fig. 89, 90, 91 : A = ampoule sexuée ; C = système des canaux ; CY = cyclosystème ; D = dactylopore ; DT = dactylostyle ; DZ = dactylozoïde ; G = gastropore, GT = gastrostyle ; GZ = gastérozoïde.*


A
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preservation of coenosteal pores of a reticulate texture; cyclosystems triangular or elongate, the greater axis of the latter parallel to the branch; elongate cyclosystems about 0.7 mm long and 0.3 mm wide; one of the syntypes has cyclosystems arranged in three longitudinal rows; dactylopores difficult to detect in the cyclosystems, few in number and irregularly scattered around the gastropore; no gastro- or dactylostyles; craters of ruptured ampullae up to 1.34 mm in diameter.
Remarks: Cairns (1983) assigned this genus to incertae sedis.

Congregopora nasiformis, Nielsen 1919

Genus ***CONOPORA*** Moseley, 1879

Fig. 89D-F

Group A
Hydroid: colony flabellate unless modified by a commensal polychaete, which induces a somewhat bushy and more robust growth form; distal branches delicate and slightly compressed in the plane, of the colony, supporting sympodially arranged cyclosystems in alternating positions on the lateral branch edges, larger branches sometimes anastomose; coenosteum irregularly linear-imbricate, covered by broad, flat platelets; raised nematopores often present, sometimes in great density, especially on larger branches, the exterior of worm tubes, and the tops of pseudosepta; coenosteum white; distal cyclosystems oriented toward the branch tip, as in *Stylaster* (group C); gastropore two chambered, the upper, larger chamber separated from the lower, thinner one by a constricted aperture analogous (?homologous) to the ring palisade; adcauline diastemas common in some species; dactylotomes extend deeply into upper gastropore chamber; no gastro- or dactylostyles; female ampullae usually superficial; male ampullae usually internal, communicating with the upper gastropore chamber via an efferent duct.

Group B
Hydroid: colony robust; branches large and round in cross section, supporting randomly arranged cyclosystems on all branch surfaces, as in *Stylaster* (Group A); coenosteum reticulate-granular, nematopores common; no polychaete commensalism observed. Otherwise, similar to Group A.
Recent references: Schuchert (2003).

Conopora adeta Cairns, 1987
Conopora anthohelia Cairns, 1991a
Conopora candelabrum Cairns, 1991a
Conopora dura Hickson & England, 1909
Conopora gigantea Cairns, 1991a
Conopora laevis (Studer, 1878a)
Conopora major Hickson & England, 1905
Conopora tetrastichopora Cairns, 1991a
Conopora unifacialis Cairns, 1991a
Conopora verrucosa (Studer, 1878a)

Genus ***CRYPTHELIA*** Milne Edwards & Haim, 1849

Fig. 89G-I

Hydroid: colony flabellate, usually small and delicate; about one-quarter of species associated with a commensal polychaete, inducing more robust colonies; branches round in cross section, very thin; distal branches thinner in diameter than the cyclosystems they support; coenosteum linear-imbricate on distal branches, although this pattern is sometimes obscured on basal branches; coenosteum white; nematopores common on coenosteum, particularly on the lid and pseudosepta; all cyclosystems originate on the anterior side of the colony except in *C. trophostega,* which is bifacial; cyclosystems projecting at right angles to the branch, round to elliptical in cross section, 0.7-5.0 mm in diameter; gastropore composed of two chambers, the lower one very reduced; every cyclosystem bears a fixed lid usually attached at the abcauline position, which overhangs the gastropore to a variable degree; in the most extreme cases, the lid fuses to the coenosteum on the adcauline side, almost completely covering the cyclosystem and allowing the polyp to feed through only two lateral slits; multiple lids sometimes present; seven to 25 dactylopores per cyclosystem; tops of pseudosepta often concave; no gastro- or dactylostyles; ampullae superficial and large, usually associated with the lid, or encircling the cyclosystem; efferent ducts from both male and female ampullae open into the cyclosystem.

Crypthelia affinis Moseley, 1879
Crypthelia balia Hickson & England, 1905
Crypthelia clausa Broch, 1947
Crypthelia cryptotrema Zibrowius, 1981
Crypthelia curvata Cairns, 1991a
Crypthelia cymas Cairns, 1986a
Crypthelia dactylopoma Cairns, 1986a
Crypthelia eueides Cairns, 1986a
Crypthelia floridana Cairns, 1986b
Crypthelia formosa Cairns, 1983
Crypthelia fragilis Cairns, 1983
Crypthelia gigantea Fisher, 1938
Crypthelia glebulenta Cairns, 1986a
Crypthelia glossopoma Cairns, 1986b
Crypthelia insolita Cairns, 1986b
Crypthelia japonica (Milne Edwards & Haime, 1849)
Crypthelia lacunosa Cairns, 1986a
Crypthelia medioatlantica Zibrowius & Cairns, 1992
Crypthelia micropoma Cairns, 1985
Crypthelia papillosa Cairns, 1986b
Crypthelia peircei Pourtalès, 1867
Crypthelia platypoma Hickson & England, 1905
Crypthelia polypoma Cairns, 1991a
Crypthelia pudica Milne Edwards & Haime, 1849
Crypthelia robusta Cairns, 1991b
Crypthelia stenopoma Hickson & England, 1905
Crypthelia studeri Cairns, 1991a
Crypthelia tenuiseptata Cairns, 1986b
Crypthelia trophostega Fisher, 1938
Crypthelia vascomarquesi Zibrowius & Cairns, 1992

Genus ***CYCLOHELIA*** Cairns, 1991

(see photographs in Cairns 1991b)

Hydroid: gastro- and dactylopores uniformly distributed on corallum faces and edges; no coordination between types of pores; corallum a robust, solid lamella with smaller lamellae at right angles to it; coenosteal texture reticulate-granular. Gastropores flush with coenosteum; dactylopore tubes elongate (axial); gastrostyles ridged and quite elongate; no tabulae; dactylopore spines circular to elliptical, enclosed by a thin wall for entire perimeter; no dactylostyles; ampullae primarily internal.

Cyclohelia lamellata Cairns, 1991b

Genus ***DISTICHOPORA*** Lamarck, 1816

Fig. 89L-M

Distichopora (Distichopora)
Hydroid: colony usually flabellate, sometimes slightly bushy; branches closely spaced but rarely anastomotic, usually elliptical to rectangular in cross section, the greater branch axis in the plane of the colony; branch tips usually blunt; coenosteal texture tuberculate to reticulate, always covered by low granules; low, longitudinal supporting ridges sometimes present; colour of coenosteum highly variable; gastro- and dactylopores extend for a long distance down the centre of the branch; gastropores aligned or slightly staggered in pore rows, which run along the lateral branch edges, sometimes meandering over the branch faces; gastropores usually flanked on both sides by a row of dactylopores; however, sometimes only one side has pores or one side has a greater frequency and/or height of dactylopores; gastropores round to polygonal, sometimes sunken along a recessed sulcus or flush with the coenosteum; dactylopores oval to elliptical, their greater axis perpendicular to the pore row; dactylopores may be elevated (in which case a short dactylotome is present), conical, or flush with the surface; no dactylostyles; gastrostyles needle shaped (H/W often over 10) and very prominently ridged, the ridges bearing tall, pointed spines; a diffuse ring palisade is often present and tabulae sometimes stabilize the style; female ampullae superficial and often ridged in a stellate or longitudinal fashion; male ampullae smaller; ampullae often clustered.

Distichopora (Haplomerismos) Cairns, 1978

Hydroid: colony small and flabellate, the flabellum sometimes slightly curved; after initial bifurcation of main stem, no further branching occurs; instead, two vertically flattened lobes are produced which grow in opposite directions and parallel to the substrate; coenosteum flat and granular (not reticulate), bearing low longitudinal ridges; gastro- and dactylopores are both very long, extending for a great distance down the centre of the lobes; pore rows occur on lateral edges of lobes and main stem; dactylopores occur in about equal number on both sides of pore rows; gastrostyles have a very high H/W and are ridged, the ridges bearing tall, slender, often fused, spines; no ring palisade; ampullae internal, opening to surface by irregularly shaped pores.

Distichopora anceps Cairns, 1978
Distichopora anomala Cairns, 1986b
Distichopora barbadensis Pourtalès, 1874
Distichopora borealis Fisher, 1938
Distichopora cervina Pourtalès, 1871
Distichopora coccinea Gray, 1860
Distichopora contorta Pourtalès, 1878
Distichopora dispar Cairns, 1991a
Distichopora foliacea Pourtalès, 1868
Distichopora gracilis Dana, 1848
Distichopora irregularis Moseley, 1881
Distichopora laevigranulosa Cairns, 1986b
Distichopora livida Tenison-Woods, 1879a
Distichopora nitida Verrill, 1864
Distichopora profunda Hickson & England, 1909
Distichopora providentiae (Hickson & England, 1909)
Distichopora rosalindae Cairns, 1986b
Distichopora serpens Broch, 1942
Distichopora sulcata Pourtalès, 1867
Distichopora uniserialis Cairns, 1986b
Distichopora vervoorti Cairns & Hoeksema, 1998
Distichopora violacea (Pallas, 1766)
Distichopora yucatanensis Cairns, 1986b

Genus ***ERRINA*** Gray, 1835

Fig. 89J-K

Hydroid: colony usually flabellate but may be slightly bushy; branches robust to delicate, usually round in cross section, major may not anastomose; coenosteal texture usually reticulate with irregularly shaped granules, but may be linear and have low, rounded granules; the sides of dactylopore spines are sometimes imbricate; coenosteum white, orange, or pink; gastro- and dactylopores usually randomly arranged on branch; however, gastropores often more abundant on anterior side, sometimes aligned along the anterior or lateral branch edges; mayor gastropores may not bear an abcauline lip; gastrostyles usually of medium H/W; however, they range from 1.6-2.6 mm, the longer styles held in place by transverse tabulae; styles lanceolate, usually vertically ridged, the ridges bearing simple and fused spines; a ring palisade present in some species; dactylopore spines shaped as grooved tubercles, the grooves predominantly directed away from the branch tip (adcauline); walls of the dactylopore spines usually thick, such that the groove constitutes only one-third the width of the spine; spines vary greatly in size from rudimentary to over 1 mm tall; small dactylopores also occur as slits, flush with the branch surface; spines often clustered and sometimes composite; no dactylostyles; ampullae vary from internal to slightly submerged to fully superficial hemispheres.

Errina altispina Cairns, 1986b
Errina antarctica (Gray, 1872a)
Errina aspera (Linnaeus, 1767)
Errina atlantica Hickson, 1912a
Errina bicolor Cairns, 1991a
Errina boschmai Cairns, 1983
Errina capensis Hickson, 1912b
Errina chathamensis Cairns, 1991a
Errina cheilopora Cairns, 1983
Errina cochleata Pourtalès, 1867
Errina cooki Hickson, 1912b
Errina cruenta Boschma, 1968b
Errina dabneyi (Pourtalès, 1871) [syn. *E. amoena* Boschma, 1956]
Errina dendyi Hickson, 1912b
Errina fascicularis Cairns, 1983
Errina fissurata Gray, 1872b
Errina gracilis Marenzeller, 1903
Errina hicksoni Cairns, 1991a
Errina japonica Eguchi, 1968
Errina kerguelensis Broch, 1942
Errina laevigata Cairns, 1991a
Errina laterorifa Eguchi, 1964 [syn. *E. carnea* Boschma, 1965]

Errina macrogastra Marenzeller, 1904
Errina novaezelandiae Hickson, 1912b
Errina porifera Naumov, 1960 [doubtful status]
Errina reticulata Cairns, 1991a
Errina rubra Broch, 1942
Errina sinuosa Cairns, 1991a

Genus ***ERRINOPORA*** Fischer, 1931

Fig. 89N-O

Hydroid: colony uniplanar to slightly bushy, sometimes attached by a broad encrusting base; branches round, elliptical, or plate like in cross section; usually robust, with blunt or clavate tips; branch anastomosis sometimes occurs; coenosteal texture reticulate to spongy, covered by round to irregularly shaped granules; coenosteum orange, yellow, pink, or white; gastropores arranged in irregular vertical rows, short horizontal terraces, or randomly; no gastropore lips; gastrostyles of medium H/W, bearing vertical or oblique ridges; ridges bear tall, cylindrical, clavate spines, some of which are bifurcate; gastropores do not have tabulae or ring palisades; dactylopore spines robust, like those of *Errina* s.l., often fused laterally, forming chains flanking one or both sides of a line of gastropores, their grooves directed toward the pores; often, towards the base of a colony, several dactylopores are positioned around an isolated gastropore, so as to closely resemble a cyclosystem; sometimes there is no coordination of gastro- and dactylopores, the dactylopore spine grooves being uniformly abcauline; dactylostyles well developed, expressed as a spiny ridge extending most of the length of the dactylopore spine; ampullae superficial, sometimes clustered, and usually quite large; hemispherical or conical.

Errinopora cestoporina Cairns, 1983
Errinopora cyclopora (Cairns, 1983)
Errinopora latifundata Naumov, 1960
Errinopora nanneca Fisher, 1938
Errinopora pourtalesi (Dall, 1884)
Errinopora stylifera (Broch, 1935)
Errinopora zarhyncha Fisher, 1938

Genus ***ERRINOPSIS*** Broch, 1951

Fig. 89P

Hydroid: colony uniplanar, sometimes with accessory flabella projecting perpendicular to main flabellum; colony secondarily attached to substrate by numerous, relatively slender branches; branching highly anastomotic, producing fenestrate flabella; branches elliptical to rectangular in; cross section, the greater axis of the branch oriented perpendicular to the flabellum; ratio of branch edges as high as 1/4; coenosteal texture reticulate to slightly linear, covered by low, rounded granules, however, some dactylopore spines are coarsely imbricate; gastro- and dactylopores occur on all branch surfaces but tend to concentrate on anterior and anterolateral edges; gastrostyles lanceolate, attaining their greatest width at their midpoints; H/W ratio medium; styles ridged, the ridges bearing fused spines; no ring palisades or tabulae; dactylopore spines of two kinds: (1) low, apically perforate mounds, and (2) tall, thick, adcauline-grooved tubercles; the tall dactylopore spines sometimes add one or more extensions apically which serve as the forerunner of branch anastomosis; they may also have additional dactylopores producing large, usually bifurcate, composite spines; no dactylostyles; ampullae superficial and irregular in shape, sometimes with a lateral tubular efferent duct.

Errinopsis fenestrata Cairns, 1983
Errinopsis reticulum Broch, 1951

Genus ***GYROPORA*** Boschma, 1960 see Cairns, 1983

Fig. 89Q

Hydroid: colony flabellate and sparsely branched; small colonies columnar; branches thick, round to elliptical in cross section, blunt; coenosteum reticulate-granular and pale reddish purple; gastropores linearly arranged in sunken, meandering, and bifurcating valleys up to 30-40 pores long; shorter valleys and isolated pores also occur; gastrostyles longitudinally ridged and prominently spiny, of medium H/W; dactylopore spines similar to those of *Errina* s.s. and *Errinopora* in construction; however, the spines are fused laterally, often having common walls between them; grooves of spines always directed toward gastropores, forming a low, continuous perimeter on each side of a gastropore valley; a ring of dactylopore spines encircles isolated gastropores, producing pseudocyclosystems; no dactylostyles; ampullae not observed.

Gyropora africana Boschma, 1960

Genus ***INFERIOLABIATA*** Broch, 1951

Fig. 90A-C

Hydroid: colony flabellate to bushy; branches round in cross section and blunt tipped, sometimes anastomosing in response to a polychaete worm symbiosis; coenosteal texture reticulate-imbricate, the reticulation sometimes obscure away from base; no granules; gastro- and dactylopores randomly distributed; gastropores round and not lipped; gastrostyles cylindrical, gradually attenuate, and not ridged (H/W = 3-10); styles bear large individual spines and may be held in place by tabulae; dactylopore spines tall (up to 0.7 mm) and spout-like, with an abruptly truncated tip; dactylopore spines grooved along the side facing top of colony (abcauline), lower side of spine longitudinally ridged; adjacent spines often joined at their edges, forming a tier of 2-5 fused spines encircling part of the branch; dactylopores bear 1-4 rudimentary dactylostyles; ampullae large superficial hemispheres.

Inferiolabiata labiata (Moseley, 1879)
Inferiolabiata lowei Cairns, 1983
Inferiolabiata spinosa Cairns, 1991a

Genus ***LEPIDOPORA*** de Pourtalès, 1871

Fig. 90D

Hydroid: colony usually uniplanar but sometimes bushy; branches not coalescent, with pointed, blunt, or clavate branch tips; coenosteal texture quite variable, including: ornamented by tufts of calcium carbonate along longitudinal ridges; reticulate with tall, slender spines; reticulate with irregular granules; reticulate with rounded granules; linear with granules; and linear-imbricate; gastro- and dactylopores usually randomly arranged over coenosteum, but sometimes gastropores aligned on anterior branch face and dactylopores aligned on lateral branch edges; both gastro- and dactylopore tubes long, forming a cluster along each branch axis; gastropore tube may or may not have a ring palisade; gastropores sometimes have a lower lip; gastrostyles cylindrical, without ridges; usually long and slender, with tall, simple spines; H/W usually over 4 and up to 20; dactylopores usually elevated on small mounds which are apically perforate; pores sometimes linked by ridges; no dactylostyles; ampullae superficial, large, and hemispherical, sometimes with an efferent tube leading from side; soft parts unknown.

Lepidopora acrolophos Cairns, 1983
Lepidopora biserialis Cairns, 1986b
Lepidopora carinata (Pourtalès, 1867)
Lepidopora clavigera Cairns, 1986b
Lepidopora concatenata Cairns, 1991c
Lepidopora cryptocymas Cairns, 1985
Lepidopora decipiens Boschma, 1964a
Lepidopora dendrostylus Cairns, 1991a
Lepidopora diffusa Boschma, 1963a
Lepidopora eburnea (Calvet, 1903)
Lepidopora glabra (Pourtalès, 1867)
Lepidopora granulosa (Cairns, 1983)
Lepidopora hicksoni Boschma, 1963b
Lepidopora microstylus Cairns, 1991a
Lepidopora polystichopora Cairns, 1985
Lepidopora sarmentosa (Boschma, 1968c)
Lepidopora symmetrica Cairns, 1991a

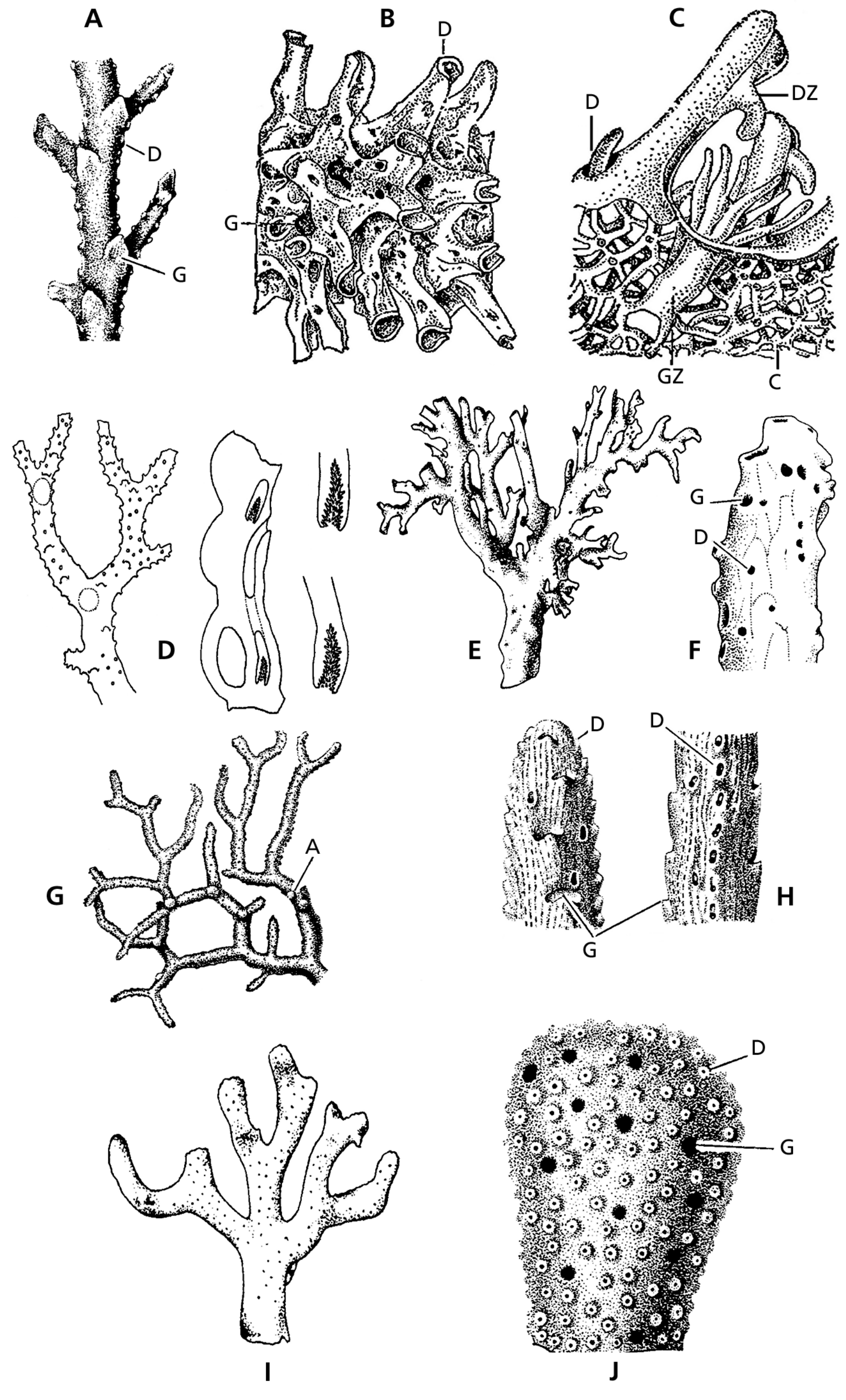


FIG. 90. Anthomedusae, Stylasteridae. A-C, *Inferiolabiata*: A, branch of a colony; B, fragment of a branch showing the gastropores and dactylopores; C, magnified view of gastropore and dactylopore showing the gastrozooid, dactylozooid and the canal system. D, *Lepidopora*, top of a branch showing the lips of gastropores, dactylopores and ampullae (left), section of a branchlet showing parts of two gastropores with gatrostyles and at left side three ampullae (middle), two gastropores with gastrostyles (right). E-F, *Paraerrina*: E, general view of a colony; F, detail of a fragment of a branch. G-H, *Phalangopora*: G, general view of a part of colony; H, terminal part of a branch (left), middle part of a branch (right). I-J, *Pliobothrus*: I, general view of a colony; J, detail of the end of a branch (A-C, E-J after Moore, 1956; D after Boschma, 1963b). Abbreviations, see fig. 89.

FIG. 90. *Anthomedusae, Stylasteridae. A-C,* Inferiolabiata : *A, branche d'une colonie; B, fragment d'une branche montrant les gastropores et dactylopores ; C, vue agrandie d'un gastropore et d'un dactylopore, montrant un gastérozoïde, un dactylozoïde et le système de canaux. D,* Lepidopora, *extrémité d'une branche montrant les lèvres des gastropores, dactylopores et des ampoules sexuées (à gauche), section d'une branche montrant des parties de deux gastropores avec leurs gatrostyles et trois ampoules sexuées (au milieu), deux gastropores avec leur gastrostyles (à droite). E-F,* Paraerrina : *E, vue générale d'une colonie ; F, détail d'un fragment de branche. G-H,* Phalangopora : *G, vue générale d'une partie d'une colonie ; H, partie terminale d'une branche (à gauche), partie médiane d'une branche (à droite). I-J,* Pliobothrus : *I, vue générale d'une colonie ; J, détail de l'extrémité d'une branche (A-C, E-J d'après Moore, 1956 ; D d'après Boschma, 1963b). Abréviations, voir fig. 89.*

Genus ***LEPIDOTHECA*** Cairns, 1983

(see photographs in Cairns 1983; 1991a)

Hydroid: colony flabellate and usually delicate; branches do not anastomose; coenosteal texture linear-imbricate; gastro- and dactylopores randomly distributed, but predominantly on the anterior side, or with gastropores located at or near branching axils; gastropores round to elliptical, sometimes bordered by an abcauline lip; gastrostyles long and slender (H/W = 4-9) and usually not ridged, resembling those of *Lepidopora;* however, the styles of several species are slightly ridged; ring palisade usually present; dactylopore spines low, horseshoe-shaped structures usually strongly inclined toward the distal branch tip; walls of dactylopore spines thin, the slit usually occupying over half the width of the spine; slits of spines abcauline, always facing the top of the colony; spines well separated from one another, never clustered or composite, and never ridged; dactylostyles usually absent; only *L. tenuistylus* has dactylostyles; ampullae large superficial hemispheres.

Lepidotheca altispina Cairns, 1991a
Lepidotheca brochi Cairns, 1986b
Lepidotheca cervicornis (Broch, 1942)
Lepidotheca chauliostylus Cairns, 1991a
Lepidotheca fascicularis (Cairns, 1983)
Lepidotheca hachijoensis (Eguchi, 1968)
Lepidotheca horrida (Hickson & England, 1905)
Lepidotheca inconsuta Cairns, 1991
Lepidotheca japonica (Eguchi, 1968)
Lepidotheca macropora Cairns, 1986a
Lepidotheca pourtalesi Cairns, 1986b
Lepidotheca ramosa (Hickson & England, 1905)
Lepidotheca robusta Cairns, 1991a
Lepidotheca tenuistylus (Broch, 1942)

Genus ***PARAERRINA*** Broch, 1942

Fig. 90E-F

Hydroid: colony flabellate; branches round in cross section and blunt tipped; branch anastomosis rare; coenosteal texture reticulate, covered by small, sharp granules; gastro- and dactylopores randomly arranged; gastropores round and flush with surface or very slightly rimmed; gastrostyles of medium height, not ridged, and bear extremely long, robust, branching spines; horizontal and vertical tabulae stabilise proximal end of gastrostyle; dactylopores flush with surface, except near branch tips where they are bordered by low dactylopore spines with abcauline slits; rudimentary dactylostyles present; ampullae superficial hemispheres, female twice the diameter of male.

Paraerrina decipiens Broch, 1942

Genus ***PHALANGOPORA*** Kirkpatrick, 1887

Fig. 90G-H

Hydroid: colony branching uniplanar and nonanastomosing; branches round in cross section and blunt tipped; coenosteum composed of longitudinal strips covered by narrow, imbricate platelets of relatively uniform width; strips delimited by narrow, elongate pores; gastropores linearly arranged on both flabellar faces, each bordered by a broad abcauline lip; elongate dactylopores linearly arranged on branch edges, and more highly raised on abcauline side; branch core dense, permeated by narrow diameter coenosteal canals; gastropore tubes short; dactylopore tubes long and slender, but do not form clusters of tubes in branch axis; no tabulae present; no gastro-or dactylopores; female ampullae, superficial; male colonies unknown.

Phalangopora regularis Kirkpatrick, 1887

Genus *PLIOBOTHRUS* de Pourtalès, 1868

Fig. 90I-J

Hydroid: colony branching uniplanar and nonanastomosing; branches round in cross section or flattened in flabellar plane; coenosteum composed of longitudinal strips covered by imbricated platelets of variable width; strips bordered by large; elongate coenosteal pores; dactylopore coenosteum may be coarsely granulate; gastro- and dactylopores irregularly scattered; however, usually slightly more abundant on anterior side; gastropores round to slightly elliptical, flush with surface, opening into a larger, roughly hemispherical chamber below; rudimentary perforate tabulae sometimes occur in the gastropore tube; dactylopores apically located on tall tubes or low mounds; dactylopore tubes extend along centre of branch axis for a considerable distance; no gastro- or dactylostyles; ampullae usually internal and hemispherical, opening to surface by a small efferent pore; no sexual dimorphism in size.

Pliobothrus echinatus Cairns, 1986b
Pliobothrus dispergens Nielsen, 1919
Pliobothrus fistulosus Cairns, 1991c
Pliobothrus gracilis Zibrowius & Cairns, 1992
Pliobothrus laevis Nielsen, 1919
Pliobothrus spinosa (Hickson & England, 1905)
Pliobothrus symmetricus Pourtalès, 1868
Pliobothrus tubulatus (Pourtalès, 1867)

Genus *PSEUDOCRYPTHELIA* Cairns, 1983

(see photographs in Cairns 1983; 1991a)

Hydroid: colony small, delicate, and primarily uniplanar; coenosteal texture linear imbricate; nematopnres round a rid slightly raised, occurring on pseudosepta, ampullae, coenosteal surface, and even within the gastropore; cyclosystems unifacial, each covered by a massive fixed lid; gastropore tube double chambered; small, rudimentary gastrostyle present; dactylostyles absent; ampullae contained in lids of cyclosystem.

Pseudocrypthelia pachypoma (Hickson & England, 1905)

Genus *SPORADOPORA* Moseley, 1879

Fig. 91A-B

Hydroid: colony uniplanar with occasional anastomosis of branches; branches stout, bluntly tipped and round in cross section; branch axils u-shaped; coenosteum irregularly porous to reticulate; if reticulate, coenosteal strips short, discontinuous, and not granular; gastro- and dactylopores scattered randomly over coenosteum, both usually flush with the surface; both gastro- and dactylopore tubes long, forming clusters along the branch axis; long gastropore tubes have multiple, thin, complete tabulae or very fine bridges, which support the gastrostyle; gastrostyles very long and slender (H/W up to 21) and prominently ridged; dactylostyles absent; ampullae internal, opening to branch surface by small efferent ducts.

Sporadopora dichotoma (Moseley, 1876)
Sporadopora micropora Cairns, 1991a
Sporadopora mortenseni Broch, 1942

Genus *STELLAPORA* Cairns, 1983

(see photographs in Cairns 1983)

Hydroid: colony robust, flabellate to slightly bushy; branches thick, anastomotic, and bluntly tipped; coenosteal texture reticulate, covered by irregularly shaped granules; gastro- and dactylopores randomly distributed over coenosteum; gastropores large, round, or stellate in shape; gastrostyle slender with longitudinal ridges and a pointed tip, fused spines

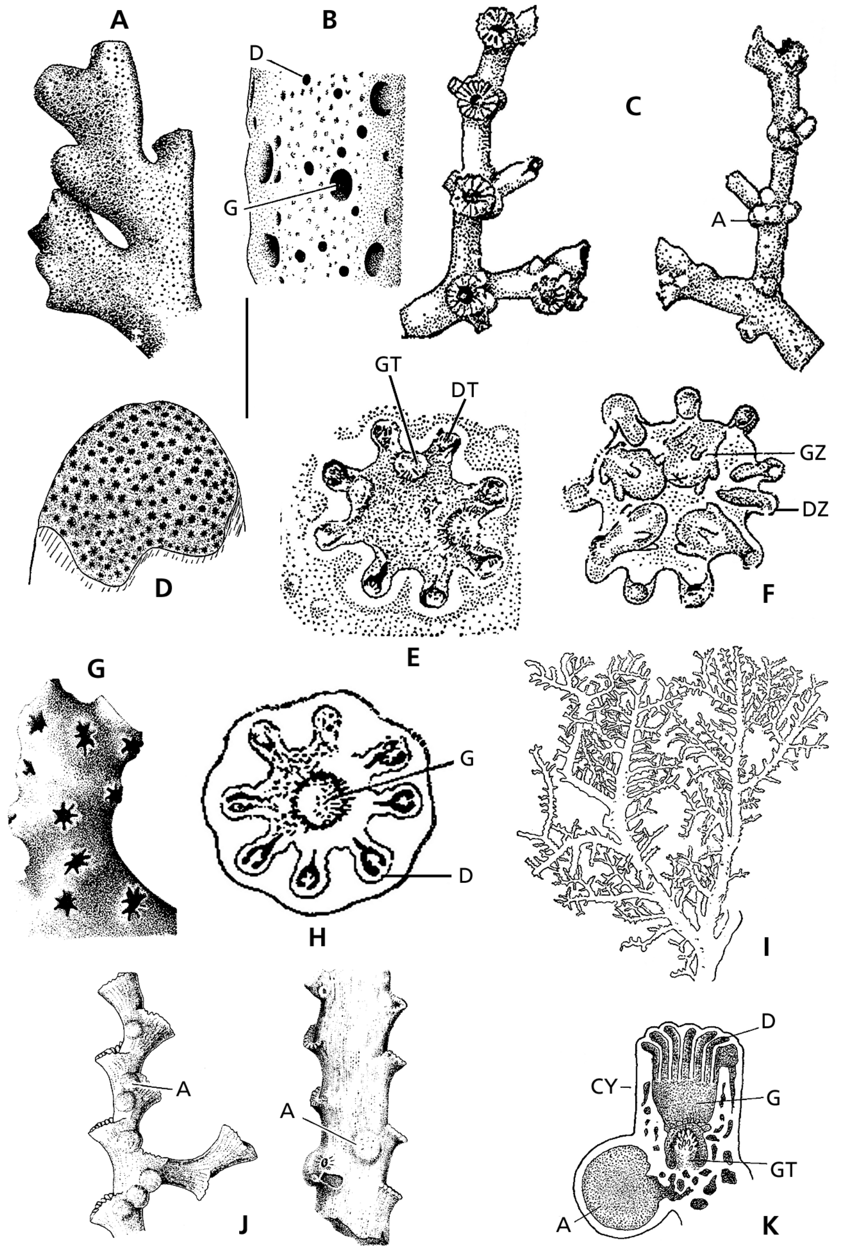


FIG. 91. Anthomedusae, Stylasteridae. A-B, *Sporadopora*: A, view of a part of colony; B, portion of a branch. C, *Stenohelia*, part of colony showing the cyclosytems (left), part of colony showing the ampullae (right). D-F, *Stylantheca*: D, general view of an incrusting colony; E, detail of a cyclosystem showing the gastrostyles and dactylostyles; G, detail of cyclosystem showing the gastrozooids and dactylozooids. G-H, *Stylaster* (*Allopora* group): G, part of a colony; H, schematic view of a cyclosystem. I-K, *Stylaster* (*Stylaster* group): I, general view of a colony; J, part of branch showing cyclosytems (left), part of branch showing cyclosystems and an ampullae (right); K, longitudinal section trough a cyclosystem with an attached ampullae (A-C, E-H, J-K after Moore, 1956, D & I after Hyman, 1940). Abbreviations, see fig. 89.

***FIG. 91.** Anthomedusae, Stylasteridae. A-B,* Sporadopora : *A, vue d'une partie de colonie ; B, portion d'une branche. C,* Stenohelia, *portion de colonie montrant les cyclosytèmes (à gauche), partie d'une colonie montrant les ampoules sexuées (à droite). D-F,* Stylantheca : *D, vue générale d'une colonie encroûtante ; E, détail d'un cyclosystème montrant les gastrostyles et les dactylostyles ; F,détail d'un cyclosystème montrant les gastérozoïdes et dactylozoïdes ; G-H,* Stylaster *(*Allopora *group) : G, fragment d'une colonie ; H, vue schématique d'un cyclosystème ; I-K,* Stylaster *(*Stylaster *group) : I, vue générale d'une colonie ; J, portion d'une branche montrant les cyclosystèmes (à gauche), détail d'une portion de branche montrant les cyclosystèmes et une ampoule sexuée (à droite) ; K, section longitudinale d'un cyclosystème et d'une ampoule sexuée (A-C, E-H, J-K d'après Moore, 1956 ; D & I d'après Hyman, 1940). Abréviations, voir fig. 89.*

ornament the ridges; no ring palisades; dactylopore spines dimorphic: the larger ones very tall, thin-walled, and spout-like with an abruptly truncated tip, grooved along the side facing the top of the colony (abcauline), not ridged on their lower sides, often clustered, some appearing composite; smaller ones small, raised, elliptical slits or apically perforated mounds; no dactylostyles; ampullae superficial, hemispherical.

Stellapora echinata (Moseley, 1879)

Genus *STENOHELIA* Kent, 1870

Fig. 91C

Hydroid: colony flabellate and delicate; distal branches round in cross section and usually very thin, sometimes half the diameter of a cyclosystem in thickness; sometimes polychaete commensals induce perforated tubes to be produced, which usually lead to a more robust and slightly bushy corallum; coenosteum white and usually longitudinally ridged, especially on distal branches; larger diameter branches either ridged or reticulate in texture; coenosteum usually covered by irregularly shaped granules but in one case *(S. robusta)* a linear-imbricate texture is present; nematopores often occur on the outside of worm tubes but are otherwise rare; coenosteal spines sometimes present; all cyclosystems originate on the anterior side and project perpendicular to the branch; cyclosystems usually unilinearly arranged on a branch and measure 0.8-2.0 mm in diameter; gastropores very long and invariably curved 90a along the branch axis, sometimes extending all the way to the wall of the more proximal cyclosystem; in the latter case, the gastrostyle is not visible from the outside; however, usually the gastropore is shorter and the tip of the style can be glimpsed projecting through a well-developed ring palisade; gastrostyle of medium to high H/W, irregularly ridged, and with fused spines; seven to 20 dactylopores per cyclosystem; no diastemas or lids; dactylostyles rudimentary; ampullae superficial hemispheres, usually clustered around a cyclosystem, but may also be scattered over the anterior and posterior surfaces.

Stenohelia concinna Boschma, 1964b
Stenohelia conferta Boschma, 1968d
Stenohelia echinata Eguchi, 1968
Stenohelia maderensis (Johnston, 1862)
Stenohelia minima (Hickson & England, 1905)
Stenohelia pauciseptata Cairns, 1986b
Stenohelia profunda Moseley, 1881
Stenohelia robusta Boschma, 1964b
Stenohelia tiliata (Hickson & England, 1905)
Stenohelia umbonata (Hickson & England, 1905)
Stenohelia yabei (Eguchi, 1941)

Genus *STEPHANOHELIA* Cairns, 1990

(see photographs in Cairns 1990; 1991a)

Hydroid: colony branching polychotomous, gastropores occurring exclusively at branch axils; irregular in shape; commensal polychaetes common; coenosteum linear-imbricate; gastrostyle massive, with a thick mid-section and pointed tip; dactylopore spines inconspicuous, elliptical, and flush with coenosteum; no dactylostyles; male ampullae superficial, each with several porous apical spines.

Stephanohelia praecipua Cairns, 1991a

Genus *STYLANTHECA* Fisher, 1931

Fig. 91D-F

Hydroid: colony encrusting, forming thin laminae on rocks and shells; coenosteum reticulate-granular; purple to light pink, and bears numerous small, apically perforate papillae; cyclosystems round to elliptical, each bearing 1-12 gastrozooids and gastrostyles; gastrostyles globose to conical, squat (H/W usually less than 2), and vertically ridged; the ridges bearing long, slender spines; a prominent ring palisade originates from the common spongy horizontal gastropore floor, below which the gastrostyles are housed in individual gastrostyle chambers; three to sixteen dactylopores per cyclosystem; isolated dactylopores uncommon; inner edge of dactylostome deep, revealing a well-developed dactylostyle; ampullae internal, often massed together or encircling a cyclosystem, alternating with the dactylopores.

Stylantheca papillosa (Dall, 1884)
Stylantheca petrograpta (Fisher, 1938)
Stylantheca porphyra Fisher, 1931

Genus ***STYLASTER*** Gray, 1831

Fig. 91G-K

Synonym: *Allopora* Ehrenberg, 1834.

Group A (”*Allopora*”)
Hydroid: colony flabellate to bushy, often massive; branches cylindrical to slightly compressed and blunt: branch anastomosis occurs in some species; coenosteum reticulate, covered by rounded or irregularly shaped granules; coenosteum white, orange, red, pink, purple, yellow, or blue; coenosteal papillae (small mounds) short; flattened coenosteal outgrowths present in some species; cyclosystems uniformly spaced on all sides of branches; gastrostyles quite variable in shape; ranging from almost hemispherical (H/W = 1), to bullet shaped (H/W = 2-5), to lanceolate (H/W up to 10); gastrostyles longitudinally ridged and usually highly spinose: ring palisade often present; tabulae rarely present; 3 to 17 dactylopores per cyclosystem, most commonly 7-9; diastemas rare; additional isolated dactylopores often present; sometimes in great numbers; dactylostyles well developed, composed of long cylindrical elements; but not present in isolated dactylopores; ampullae low superficial bulges sometimes ridged.

Group B (Annectant group)
Like group C, but in addition to the regularly sympodially arranged cyclosystems at the branch tips there are additional cyclosystems on the anterior and posterior branch faces, especially on the larger diameter branches; colony usually slightly more robust, sometimes bushy.

Group C (“*Stylaster*”)
Colony flabellate and delicate; branches usually slender, terminating in a characteristic zigzag, sympodial shape; branches elliptical in cross section and sometimes anastomose, even approaching the fenestrate growth form of *Errinopsis*; coenosteum variable in texture, including reticulate-granular, linear-imbricate and very irregular reticulate-imbricate papillae (nematopores?), sometimes with short ridges, orange, beige, purple, or white; cyclosystems occur in a regularly sympodial pattern resulting in two rows, one on each lateral branch edge; these rows may be displaced to the anterolateral edges of large diameter branches but cyclosystems do not occur on the anterior or posterior branch faces; cyclosystems usually slightly raised above the coenosteum, especially the abcauline side, which gives them an anteriorly projecting aspect; gastrostyles lanceolate and ridged, with a medium to high H/W ratio, and invariably with a well-developed ring palisade; usually 10-15 dactylopores per cyclosystem; adcauline diastemas common; dactylostyles rudimentary; ampullae large and superficial, sometimes ridged.

Stylaster alaskanus Fisher, 1938
Stylaster amphiheloides Kent, 1871
Stylaster antillarum Zibrowius & Cairns, 1982
Stylaster asper Kent, 1871
Stylaster atlanticus Cairns, 1986b
Stylaster aurantiacus Cairns, 1986b
Stylaster bellus (Dana, 1848)
Stylaster bilobatus Hickson & England, 1909
Stylaster bithalamus Broch, 1936a
Stylaster blatteus (Boschma, 1961)
Stylaster bocki Broch, 1936a
Stylaster boreopacificus Broch, 1932
Stylaster boschmai Eguchi, 1965
Stylaster brochi (Fisher, 1938)

Stylaster brunneus Boschma, 1970
Stylaster californicus (Verrill, 1866)
Stylaster campylecus (Fisher, 1938)
Stylaster cancellatus Fisher, 1938
Stylaster carinatus Broch, 1936a
Stylaster chibaensis Eguchi, 1968
Stylaster cocosensis Cairns, 1991c
Stylaster corallium Cairns, 1986b
Stylaster crassior Broch, 1936a
Stylaster densicaulis Moseley, 1879
Stylaster dentatus Broch, 1936a
Stylaster divergens Marenzeller, 1904
Stylaster duchassaingi Pourtalès, 1867
Stylaster echinatus Broch, 1936
Stylaster eguchii (Boschma, 1966a)
Stylaster elassotomus Fisher, 1938
Stylaster erubescens Pourtalès, 1868
Stylaster eximius Kent, 1871
Stylaster filogranus Pourtalès, 1871
Stylaster flabelliformis (Lamarck, 1816)
Stylaster galapagensis Cairns, 1986a
Stylaster gemmascens (Esper, 1794)
Stylaster gracilis Milne-Edwards & Haime, 1850 [doubtful status]
Stylaster granulosus Milne-Edwards & Haime, 1850
Stylaster hattorii (Eguchi, 1968)
Stylaster horologium Cairns, 1991a
Stylaster ibericus Zibrowius & Cairns, 1992
Stylaster imbricatus Cairns, 1991a
Stylaster incompletus (Tennison-Woods, 1883)
Stylaster incrassatus (Eguchi, 1941)
Stylaster inornatus Cairns, 1986b
Stylaster laevigatus Cairns, 1986
Stylaster lonchitis Broch, 1947
Stylaster marenzelleri Cairns, 1986a
Stylaster maroccanus Zibrowius & Cairns, 1992
Stylaster marshae Cairns, 1988
Stylaster microstriatus Broch, 1936a
Stylaster miniatus (Pourtalès, 1868)
Stylaster moseleyanus (Fisher, 1938)
Stylaster multiplex Hickson & England, 1905
Stylaster nobilis (Kent, 1871)
Stylaster norvegicus (Gunnerus, 1768)
Stylaster papillosa (Dall, 1884) [doubtful status]
Stylaster papuensis Zibrowius, 1981
Stylaster petrograpta (Fisher, 1938) [doubtful status]
Stylaster polymorphus Broch, 1936b
Stylaster polyorchis (Fisher, 1938) [syn. *S. abei* (Eguchi, 1968)]
Stylaster profundiporus Broch, 1936b
Stylaster profundus (Moseley, 1879)
Stylaster pulcher Quelch, 1884a
Stylaster punctatus Pourtalès, 1871
Stylaster purpuratus (Naumov, 1960)
Stylaster ramosus Broch, 1936a
Stylaster robustus (Cairns, 1983)
Stylaster rosaceus (Greeff, 1886)
Stylaster roseus (Pallas, 1766)
Stylaster sanguineus Milne Edwards & Haime, 1850
Stylaster scabiosus Broch, 1935
Stylaster solidus Broch, 1935
Stylaster spatula Cairns, 1986b
Stylaster stejnegeri (Fisher, 1938)
Stylaster stellulatus Stewart, 1878
Stylaster subviolacea (Kent, 1871)
Stylaster tenisonwoodsi Cairns, 1988
Stylaster venustus (Verrill, 1870)
Stylaster verrillii (Dall, 1884)

Genus ***SYSTEMAPORA*** Cairns, 1990

(see photographs in Cairns 1990; 1991a)

Hydroid: both gastro- and dactylopores relatively short and unilinearly arranged, the former on branch faces, the latter on branch edges; colony uniplanar or multiplanar and delicate; coenosteum linear-imbricate; gastropore bordered by a massive lower lip; gastropore tubes cylindrical, without a ring palisade; gastrostyles conical and usually ridged, each with a massive apical spine; dactylopores adcauline or flush; no dactylostyles; ampullae superficial and highly sculptured.

Systemapora ornata Cairns, 1991a

Family TRICHYDRIDAE Hincks, 1868

Hydroid: colony stolonal, stolon covered by thin perisarc; hydranth sessile, with a collar-like tube of perisarc at base, with one amphicoronate whorl of filiform tentacles; gonophores and cnidocysts unknown.
Medusa: no gastric peduncle; mesoglea especially thick in upper part of umbrella; 4 large, simple, pleated lips; 4 radial canals; numerous fine, lateral branched, anastomosing centripetal canals connecting non perradial marginal bulbs to radial canals; "gonads" interradial; marginal tentacles solid, with triangular marginal bulbs; no ocelli.

Remarks: the systematic position of this family remains uncertain. The medusae of *Trichydra* were previously included in the Proboscidactylidae (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 Campanulinidae, or as being next to the Lafœidae, and also tentatively as being the hydroid of *Lizzia blondina* (see Edwards 1973a and Brinckmann-Voss & Arai 1998 for reviews). The hydroids present great morphological affinities with those of *Halitiara inflexa* Bouillon, 1980 (see Bouillon 1985b). 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. One species *Pochella* (*Trichydra*) *oligonema* has been transferred by Schuchert (1996) to the genus *Fabienna* considered here as a Laingiomedusae, thus the family Trichydridae became monotypic including only *Trichydra pudica* Wright, 1858.

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

Recent reference: Brinckmann-Voss & Arai (1998).

Genus ***TRICHYDRA*** Wright, 1858

Fig. 92A-B

Medusae and hydroids with the characters of the family.

Trichydra pudica Wright, 1858

Margelina *incertae sedis*:

Family BALELLIDAE Stechow, 1922

Hydroids forming colonies with erect, irregularly branched, polysiphonic hydrocauli; hydranths irregularly on hydrocauli and hydrocladia, basally elongated, stalk-like, enclosed by cup-like perisarc on base; with two distinct and widely separated whorls of filiform tentacles, one oral under hypostome and one at aboral base; with digital, solid, dactylozooids on hydrocaulus and hydrocladia, surrounded or not by a thin perisarcal sheath on their base. Gonophores where known as juvenile medusae with four radial canals and four short marginal tentacles.

Recent references: Calder (1988a); Hirohito (1988); Schuchert (2003).

Genus ***BALELLA*** Stechow, 1919

Fig. 75A-C

With characters of the family.

Remarks: The genus *Balella* has been included in a subfamily Balellinae within the Clavidae by Stechow (1922a), afterwards it has been considered as a Bougainvilliidae by Millard (1975), Bouillon (1985a), and Hirohito (1988). Calder (1988a) regarded *Balella* to be closer to the Clavidae than the Bougainvilliidae but returned it to the family Balellidae which was considered as a valid taxon; we concur here with Calder (1988a) and keep the Balellidae as a separate family but as incertae sedis, awaiting more knowledge about the sexual stage.

Recent references: Calder *et al.* (2003); Schuchert (2003).

Balella mirabilis (Nutting, 1905) [syn. *Balella irregularis* (Fraser, 1938a)]

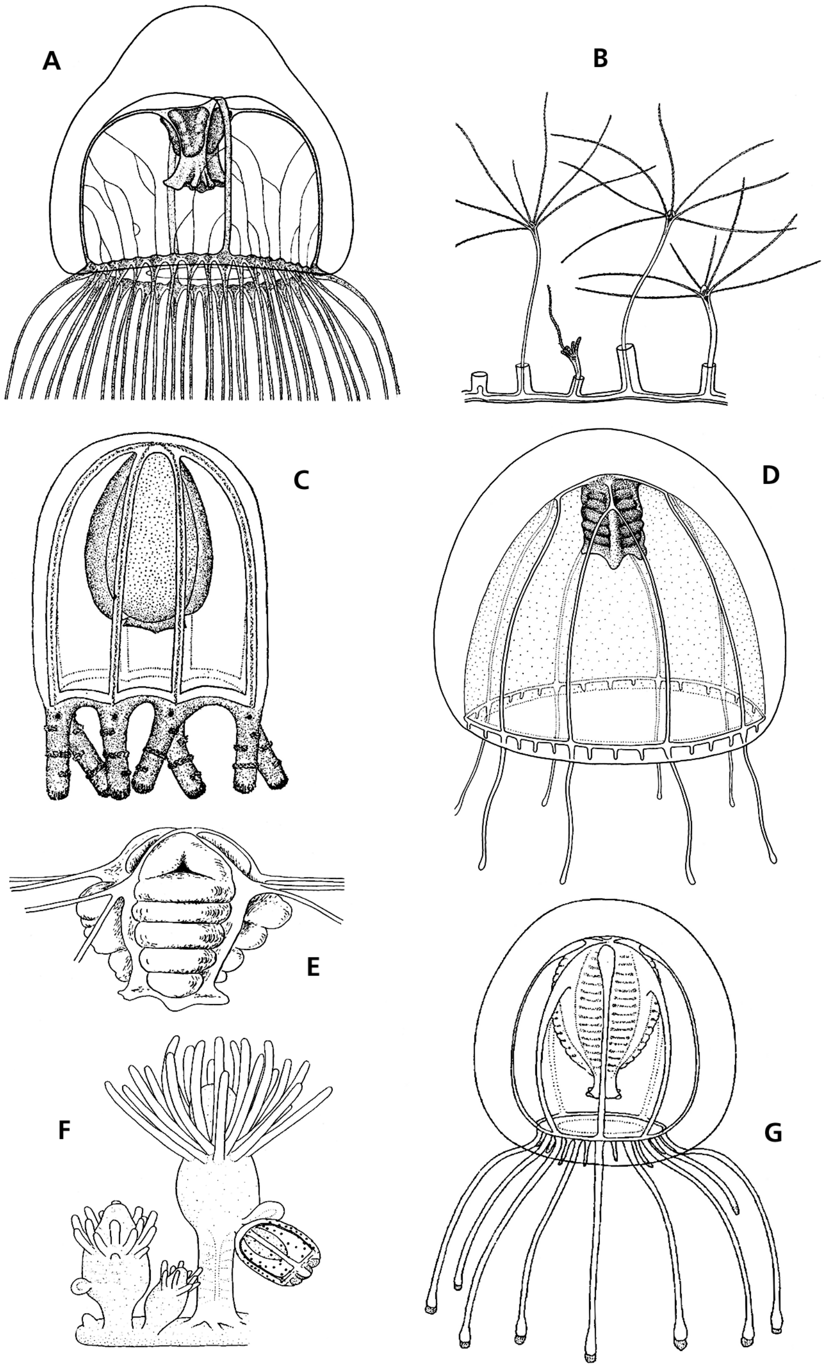


FIG. 92. Anthomedusae. A-B, Trichydridae, *Trichydra pudica*: A, adult medusa; B, hydroid colony. C-G, Bythotiaridae: C, *Bythocellata cruciformis*, adult medusa; D-E, *Bythotiara murrayi*: D, adult medusa; E, manubrium and ''gonad''; F, *Bythotiara parasitica*, polyp colony with medusa buds living in ascidians; G, *Calycopsis bigelowi*, fully grown medusa (A after Edwards, 1973; B & E after Russell, 1953; C after Kramp, 1968; D after Pagès *et al*., 1992; F-G, after Schuchert, 1996).

***FIG. 92.** Anthomedusae. A-B, Trichydridae,* Trichydra pudica *: A, méduse adulte ; B, colonie d'hydroïdes. C-G, Bythotiaridae : C,* Bythocellata cruciformis, *méduse adulte ; D-E,* Bythotiara murrayi *: D, méduse adulte ; E, manubrium et ''gonade'' ; F,* Bythotiara parasitica*, colonie de polypes présentant des bourgeons médusaires vivant dans une ascidie ; G,* Calycopsis bigelowi : *méduse adulte (A d'après Edwards, 1973 ; B & E d'après Russell, 1953 ; C d'après Kramp, 1968 ; D d'après Pagès et al., 1992; F-G d'après Schuchert, 1996).*

Suborder PANDEIDA Haeckel, 1879

Hydroid: Colonies generally stolonal, sometimes erect and branching (Eudendriidae), monomorphic; hydranths when known with conical hypostome except in the Eudendriidae; usually with one whorl of filiform tentacles exceptionally with two or three or scattered (Eudendriidae, *Stomotoca atra*). Gonophores as free medusae or sporosacs.
Medusa: Filifera medusae with hollow tentacles; ocelli, when present, abaxial; mouth simple, lips usually without specialised cnidocyst armed structures, without oral tentacles (except Russellidae).
Recent references: Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. marginal tentacles without basal bulbs or swellings, terminated in a terminal cnidocyst cluster .... Bythotiaridae
– marginal tentacles usually with basal bulbs, without terminal cnidocyst clusters or capitations 2

2. with branched or divided radial canals 3
– with undivided radial canals 4

3. with two simple and two bifurcated radial canals; tentacular bulbs develop into medusae . Niobiidae
with 4-6 branched radial canals, exumbrella with exumbrellar cnidocyst tracts; manubrium with radial gastric pouches; usually with no circular canal; without rudimentary bulbs .... Proboscidactylidae

4. with 4 unbranched oral tentacles, without terminal clusters of cnidocyst, situated above mouth opening .... Russellidae
– 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
– 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

Synonym: Calycopsidae Bigelow, 1913
Hydroid: hydrorhiza plate-like, giving rise to unbranched colonies living in ascidian prebranchial cavities; hydranths sessile, with up to five irregular whorls of filiform tentacles; medusa buds arising from polyps.
Medusa: 4 lips, simple or crenulated; with or without centripetal canals; "gonads" simple or folded, adradial or interradial, on manubrial wall; 4 or 8 radial canals, simple or branching; 4, 8 or more hollow marginal tentacles (mesoglea of distal part of tentacles often enlarged and strongly reducing endodermal axis), each terminating in a large cnidocyst cluster, with basal portion often adnate to exumbrella; marginal bulbs highly reduced or absent; with or without rudimentary or dwarf solid tentacles (*Eumedusa*); rarely with abaxial ocelli.
Recent references: Bouillon *et al.* (1988); Arai & Brinckmann-Voss (1998a); Pagès *et al.* (1992); Schuchert (1996); Brinckmann-Voss & Arai (1998); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO THE HYDROIDS
(see family characters)

KEY TO MEDUSAE

1. centripetal canals, blind or joining base of manubrium........ 2
– no centripetal canals 4

2. all tentacles hollow, cnidocysts only in the terminal knob .... *Calycopsis*
– two kinds of tentacles 3

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

4. radial canals simple, unbranched 5
– radial canals branched, "gonads" folded 7

5. "gonads" smooth interradial 6
– "gonads" smooth adradial . . . . *Pseudotiara*

6. 8 radial canals, marginal tentacles with abaxial basal ocelli . . . . *Bythocellata*
– 4 radial canals; no ocelli . . . . *Heterotiara*

7. radial canals bifurcated (some few additional branches may occur as abnormalities). . . . . . . *Bythotiara*
– radial canals branching repeatedly at various levels. . . . . *Sibogita*

Genus ***BYTHOCELLATA*** Nair, 1951

Fig. 92C

Hydroid: unknown.
Medusa: exumbrella with cnidocyst rows; 8 radial canals, unbranched; 8 marginal tentacles; abaxial ocelli on tentacle bases; no secondary tentacles.

Bythocellata cruciformis Nair, 1951

Genus ***BYTHOTIARA*** Günther, 1903

Fig. 92D-F

Hydroid: see family diagnosis.
Medusa: 4 radial canals, simple or branching; "gonads" interradial, with transverse furrows; with or without rudimentary or dwarf tentacles, entirely covered with cnidocysts; no ocelli.
Recent references: Pagès *et al.* (1991); Schuchert (1996); Brinckmann-Voss & Arai (1998).

Bythotiara capensis Pagès, Bouillon & Gili, 1991
Bythotiara depressa Naumov, 1960
Bythotiara drygalskii Vanhöffen, 1912
Bythotiara huntsmani (Fraser, 1911)
Bythotiara metschnikovii Bouillon, Boero & Seghers, 1988
Bythotiara murrayi Günther, 1903
Bythotiara parasitica (Kirk, 1915) [includes *Bythotiara* sp. of Schuchert, 1996]
Bythotiara stilbosa Mills & Rees, 1979

Genus ***CALYCOPSIS*** Fewkes, 1882

Fig. 92G

Hydroid: unknown.
Medusa: radial canals unbranched; 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; no ocelli.
Recent reference: Brinckmann-Voss & Arai (1998).

Calycopsis bigelowi Vanhöffen, 1911
Calycopsis borchgrewinki (Browne, 1910)
Calycopsis chuni Vanhöffen, 1911
Calycopsis gara Petersen, 1957
Calycopsis krampi Petersen, 1957
Calycopsis lipi Van der Spoel & Bleeker, 1988
Calycopsis nematophora Bigelow, 1913
Calycopsis papillata Bigelow, 1918
Calycopsis simplex Kramp & Damas, 1925
Calycopsis simulans (Bigelow, 1909)
Calycopsis typa Fewkes, 1882a

Genus *EUMEDUSA* Bigelow, 1920

Fig. 93A

Hydroid: unknown.
Medusa: 4 unbranched radial canals and 4 or more? centripetal canals arising from ring canal; “gonads” folded; tentacles of two kinds, large hollow ones with rings of cnidocysts and terminal knob, small solid ones without terminal knob; no ocelli.

Eumedusa birulai (Linko, 1913)

Genus *HETEROTIARA* Maas, 1905

Fig. 93B

Hydroid: unknown.
Medusa: umbrella thick; 4 simple radial canals; no centripetal canals; “gonads” interradial, no transverse folds; no secondary tentacles; no ocelli. See below under *Gymnogonium* and *Kanaka*.

Heterotiara anonyma Maas, 1905
Heterotiara minor Vanhöffen, 1911

Genus *MEATOR* Bigelow, 1913

Fig. 93C

Hydroid: unknown.
Medusa: 4 simple radial canals; no centripetal canals; 8 smooth adradial “gonads”, tentacles of different size, without terminal knob of cnidocysts; no ocelli.

Meator rubatra Bigelow, 1913 [doubtful status]

Genus *PSEUDOTIARA* Bouillon, 1980

Figs 63B, 93D

Hydroid: unknown.
Medusa: 4 marginal tentacles, with much reduced basal swellings; 4 small, simple lips; usually without centripetal canals; 4 radial canals, usually simple; 8 longitudinal “gonads” on perradial ridges of manubrium; no ocelli.

Pseudotiara tropica (Bigelow, 1912)

Genus *SIBOGITA* Maas, 1905

Fig. 93E-F

Hydroid: unknown.
Medusa: 4 primary radial canals, branching repeatedly at various levels; no centripetal canals; with or without secondary tentacles and warts; “gonads” transversely folded; no ocelli.

Sibogita geometrica Maas, 1905

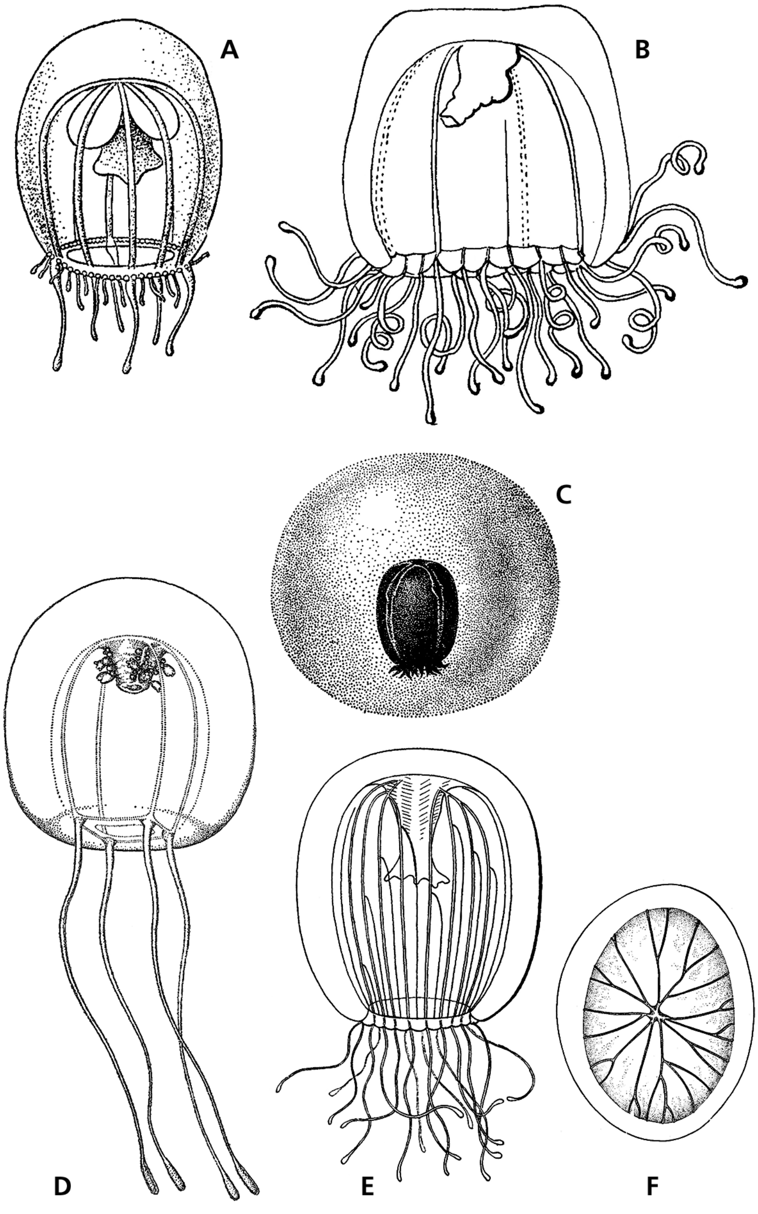


FIG. 93. Anthomedusae, Bythotiaridae. A, *Eumedusa birulai*, mature medusa. B, *Heterotiara minor*, adult medusa. C, *Meator rubatra*, fully-grown medusa. D, *Pseudotiara tropica*, adult medusa with medusa buds on the manubrium. E-F, *Sibogita geometrica*: E, adult medusa; F, exumbrellar diagram (A-C, E-F after Kramp, 1968; D after Bouillon, 1980).

FIG. 93. *Anthomedusae, Bythotiaridae. A,* Eumedusa birulai*, méduse mature. B,* Heterotiara minor*, méduse adulte. C,* Meator rubatra*, méduse adulte. D,* Pseudotiara tropica*, méduse adulte présentant des bourgeons médusaires manubriaux. E-F,* Sibogita geometrica : *E, méduse adulte ; F, diagramme exombrellaire (A-C, E-F d'après Kramp, 1968 ; D d'après Bouillon, 1980).*

Bythotiaridae *incertae sedis*:

Genus ***GYMNOGONIUM*** Xu & Huang, 1994

Fig. 94A-B

Hydroid: unknown.
Medusa: 2 simple and 2 bifurcated radial canals; no centripetal canals; gonads perradial; 6 hollow tentacles tipped by a spherical cnidocyst knob; marginal tentacles leaving umbrella at some distance from margin, with basal swellings embedded in mesoglea; no ocelli.
Remarks: Perhaps a juvenile *Heterotiara*.

Gymnogonium zhengzhongii Xu & Huang, 1994 [probably a syn. of *Heterotiara anonyma*]

Genus ***KANAKA*** Uchida, 1947

Fig. 94C

Hydroid: unknown.
Medusa: 4 radial canals with differentiated upper and lower halves; no centripetal canals; 8 tentacles, long, hollow, with terminal cnidocyst knob; no secondary tentacles; manubrium short; 4 well developed lips; "gonads" seem to develop on the lower part of radial canals; no ocelli.
Remarks: Perhaps *Heterotiara minor*.

Kanaka pelagica Uchida, 1947a

Family EUDENDRIIDAE L. Agassiz, 1862

Hydroid: colony with erect, usually branched, stem arising from a creeping hydrorhiza; hydrocaulus enclosed by firm perisarc either up to hydranth base, or sometimes enveloping lower half of hydranth in a cupuliform process (*E. vaginatum*); hydranth large, urn-shaped with peduncled hypostome and one (*Eudendrium*) or more (*Myrionema*) whorls of solid filiform tentacles immediately below it, sometimes with special cnidocyst-bearing processes erroneously called cnidophores; ectodermal groove at hydranth base, sometimes with a nettle ring immediately above; endoderm of oral part of hypostome thin and not differentiated; reproduction by fixed sporosacs borne on hydranth body, below tentacles, colonies usually gonochoric; reproductive hydranth often reduced to blastostyle, male gonophores usually with several chambers in linear series, female gonophores initially with curved spadix, each spadix with a single egg.
Remarks: the systematic position of the Eudendriidae is unclear; in spite of being a very uniform taxon, its phylogenetic affinities are not easy to establish and new criteria seem necessary to tackle this problem (Fig. 7: B).
Recent references: Calder (1988a); Schuchert (1996); Marques (1996); Marques *et al.* (2000a; b); Marques (2001); Watson (2000); Schuchert (2001a).

Genus ***EUDENDRIUM*** Ehrenberg, 1834

Fig. 3A, 7B, 94D-J

Hydroid: hydranth short, with a single whorl of tentacles.
Remarks: cnidome features are essential for species identification.
Recent references: Calder (1988a); Marinopoulos (1992); Marques (1996); Marques & Calder (2000); Marques *et al.* (2000a; b); Watson (2000); Schuchert (2001a, 2003); Calder *et al.* (2003).

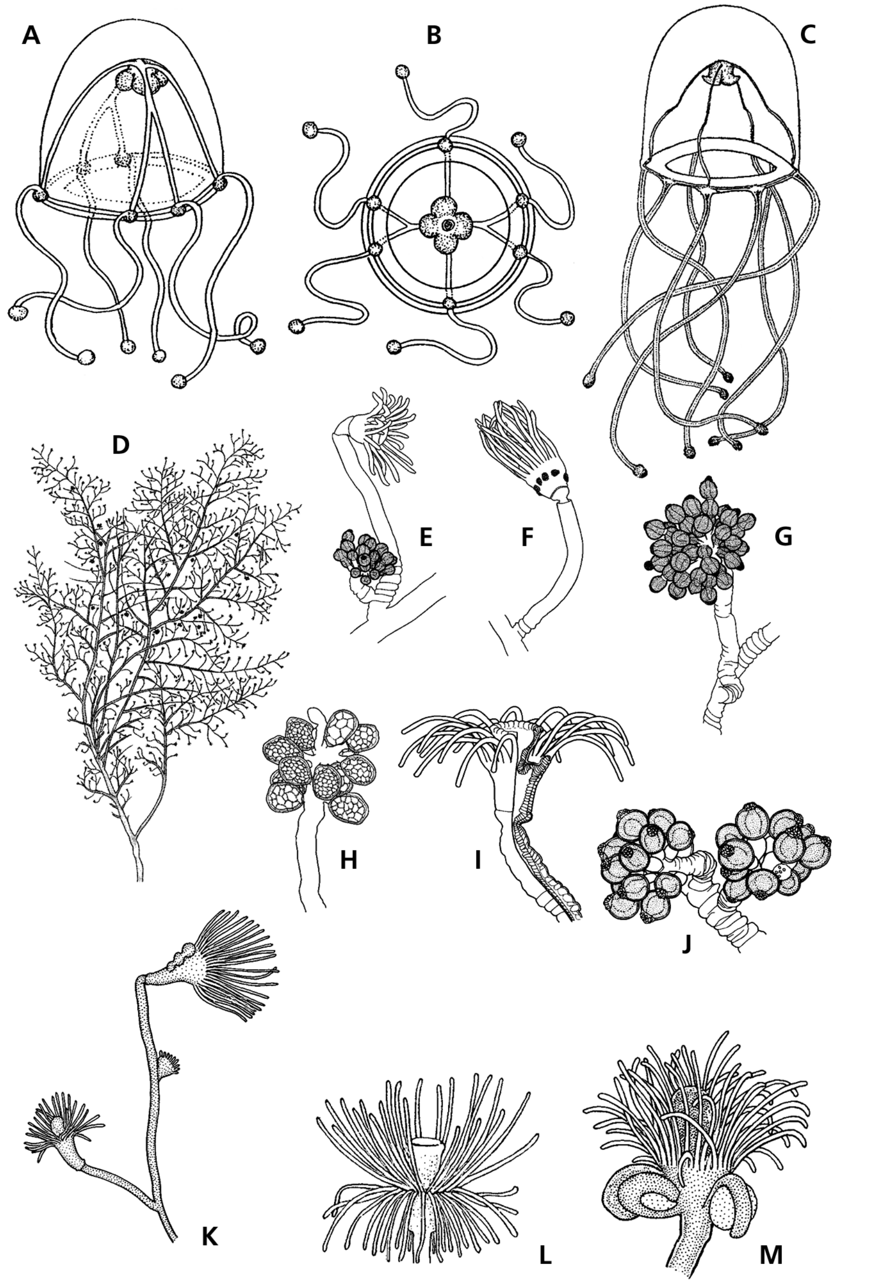


FIG. 94. Anthomedusae, Bythotiaridae. A-B, *Gymnogonium zhengzhongii*, medusae: A, lateral view; B, oral view. C, *Kanaka pelagica*, adult medusa. D-J, Eudendriidae, *Eudendrium*: D-H, *Eudendrium magnificum*: D, general view of a colony; E, part of stem with hydranth and male blastostyle; F, hydranth showing the large cnidocysts spots of the body; G, portion of branch with male blastostyle; H, female blastosyle; I-J, *Eudendrium biseriale*: I, hydranth, right part representing a longitudinal section; J, male blastotyle. K-M, *Myrionema amboinense*: K, hydrocaulus and hydranth with male gonophore; L, detail of hydranth; M, hydranth with female gonophores (A-B after Xu Zhenzu & Huang Jiaqui, 1994; C after Kramp, 1968; D-J after Hirohito, 1995; K & M after Calder, 1988a; L after Wedler & Larson, 1986).

FIG. 94. *Anthomedusae, Bythotiaridae. A-B,* Gymnogonium zhengzhongii*, méduses adultes : A, vue latérale ; B, vue orale. C,* Kanaka pelagica*, méduse adulte. D-J, Eudendriidae,* Eudendrium *: D-H,* Eudendrium magnificum *: D, vue générale d'une colonie ; E, partie d'une branche montrant un hydranthe et un blastostyle mâle ; F, hydranthe montrant les larges masses cnidocytaires du milieu du corps ; G, blastostyle mâle ; H, blastosyle femelle ; I-J,* Eudendrium biseriale *: I, hydranthe, la partie de droite représente une section longitudinale ; J, blastotyle mâle. K-M,* Myrionema amboinense *: K, hydrocaule et hydranthe développant un gonophore mâle ; L, détail d'un hydranthe ; M, hydranthes développant des gonophores femelles (A-B d'après Xu Zhenzu & Huang Jiaqui, 1994 ; C d'après Kramp, 1968 ; D-J d'après Hirohito, 1995 ; K & M d'après Calder, 1988a ; L d'après Wedler & Larson, 1986).*

Eudendrium album Nutting, 1898
Eudendrium angustum Warren, 1908
Eudendrium annulatum Norman, 1864
Eudendrium antarcticum Stechow, 1921a
Eudendrium arbusculum Wright, 1859
Eudendrium armatum Tichomiroff, 1887
Eudendrium armstrongi Stechow, 1909
Eudendrium attenuatum Allman, 1877
Eudendrium aylingae Watson, 1985
Eudendrium balei Watson, 1985
Eudendrium bathyalis Marques & Calder, 2000
Eudendrium bermudense Calder, 1988a
Eudendrium biseriale Fraser, 1935
Eudendrium boreale Yamada, 1954
Eudendrium breve Fraser, 1938a
Eudendrium calceolatum Motz-Kossowska, 1905
Eudendrium californicum Torrey, 1902
Eudendrium capillare Alder, 1856a [syn. *E. tenue* Agassiz, 1865]
Eudendrium carneum Clarke, 1882 [syn. *E. cunninghami* Kirkpatrick, 1910]
Eudendrium certicaule Fraser, 1938a
Eudendrium cingulatum Stimpson, 1854
Eudendrium cochleatum Allman, 1877
Eudendrium corrugatum Watson, 1985
Eudendrium currumbense Watson, 1985
Eudendrium cyathiferum Jäderholm, 1904a
Eudendrium deciduum Millard, 1957
Eudendrium deforme Hartlaub, 1905
Eudendrium dispar L. Agassiz, 1862a
Eudendrium distichum Clarke, 1879
Eudendrium elsaeoswaldae Stechow, 1921c
Eudendrium eximium Allman, 1877 [syn. *E. exiguum* Allman, 1877]
Eudendrium fragile Motz-Kossowska, 1905
Eudendrium generale von Lendenfeld, 1885a
Eudendrium glomeratum Picard, 1951
Eudendrium gracile Allman, 1877
Eudendrium imperiale Yamada, 1954
Eudendrium infundibuliforme Kirkpatrick, 1890a
Eudendrium insigne Hincks, 1861
Eudendrium irregulare Fraser, 1922
Eudendrium islandicum Schuchert, 2000
Eudendrium japonicum Yamada, 1954
Eudendrium kirkpatricki Watson, 1985
Eudendrium laxum Allman, 1877
Eudendrium lineale Yamada, 1954
Eudendrium magnificum Yamada, 1954
Eudendrium maldivense Borradaile, 1905
Eudendrium maorianus Schuchert, 1996
Eudendrium merulum Watson, 1985
Eudendrium minutum Watson, 1985
Eudendrium moulouyensis Marques, Cantero, Vervoort, 2000
Eudendrium nambuccense Watson, 1985
Eudendrium nodosum Fraser, 1938a
Eudendrium novazealandiae Marktanner-Turneretscher, 1890
Eudendrium parvum Warren, 1908
Eudendrium pennycuikae Watson, 1985
Eudendrium planum Bonnevie, 1898b
Eudendrium pocaruquarum Marques, 1995
Eudendrium racemosum (Cavolini, 1785)
Eudendrium rameum (Pallas, 1766)
Eudendrium ramosum (Linnaeus, 1758)
Eudendrium ritchiei Millard, 1975
Eudendrium rugosum Fraser, 1940b
Eudendrium sagaminum Yamada, 1954
Eudendrium simplex Pieper, 1884 [syn. *E. motzkossowskae* Picard, 1951]
Eudendrium speciosum Fraser, 1945
Eudendrium stratum Bonnevie, 1898b
Eudendrium tenellum Allman, 1877
Eudendrium terranovae Watson, 1985
Eudendrium tottoni Stechow, 1932
Eudendrium vaginatum Allman, 1863
Eudendrium vervoorti Marques & Migotto, 1998
Eudendrium wrighti (Hartlaub, 1905) [homonym *E. arbusculum* Wright, 1859, according to Marques & Vervoort, 1999]

Genus ***MYRIONEMA*** Pictet, 1893

Fig. 94K-M

Hydroid: hydranth elongated, with two or more whorls of tentacles.
Recent references: Calder (1988a); Marques *et al.* (2000a; b).

Myrionema amboinense Pictet, 1893 [syn. *M. hargitti* Congdon, 1906]

Family NIOBIIDAE Petersen, 1979

Hydroid: unknown.
Medusa: 2 simple and 2 bifurcated radial canals, so that six canals reach the circular canal; "gonads" on manubrium, interradial; marginal tentacular bulbs developing into medusae; no ocelli, gastric peduncle, and mesenteries.
Recent references: Bouillon (1999); Bouillon & Boero (2000).

Genus ***NIOBIA*** Mayer, 1900

Fig. 95A

See family characters.

Niobia dendrotentaculata Mayer, 1900a

Family PANDEIDAE Haeckel, 1879

Hydroid: colony usually stolonal, not branching; hydranth tentacles filiform, normally in one whorl, exceptionally in two or more whorls, or scattered, or absent; perisarc developed to a variable degree, occasionally forming a pseudohydrotheca or missing completely; reproduction mainly by free medusae, except in some modified genera of questionable affinity like *Nudiclava* = *Hydrichthys.*

Medusa: umbrella bell-shaped, with or without apical projection; manubrium quadratic, usually large; with or without gastric peduncle; 4 oral lips, simple, or crenulated, or complexly folded; 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 position, sometimes extending along radial canals, or completely perradial; 2 or more hollow marginal tentacles; bulbs mostly tapering, elongated, conical (almost carrot-shaped) and often laterally compressed; with or without rudimentary tentacles (tentaculae), or marginal warts; with or without abaxial ocelli; cnidome usually containing microbasic euryteles.

Recent references: Wedler & Larson (1986); Calder (1988a); Pagès *et al.* (1992); Migotto (1996); Schuchert (1996); Brinckmann-Voss & Arai (1998); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2001a).

KEY TO HYDROIDS

Many species of Pandeidae are known only as medusae and their hydroids are known only as juveniles or are completely unknown. In contrast to pandeid medusae, most pandeid hydroids, furthermore, are of so uniform architecture that it is almost impossible to identify them with a key. In hydroid-based classifications, they were once referred to the genus *Perigonimus*, a nominal taxon that proved unsound when accommodated into a unified classification, considering both hydroids and medusae (Rees, 1956).

1. hydroids parasitic on fish, or of copepods parasite of fish, hydrorhiza forming a naked encrusting plate; without tentacles . . . . *Hydrichthys* and *Larsonia*
– hydrorhiza as creeping stolons 2

2. hydranth sessile or almost sessile and naked 3
– hydranth on more or less developed hydrocaulus covered with perisarc 5

3. hydranth with one whorl of 4-6 oral tentacles . . . . *Codonorchis*
– hydranth with more than one whorl of oral tentacles 4

4. hydranth with 2 whorls of oral tentacles . . . . *Pandea*
– hydranth with 3 whorls of oral tentacles . . . . *Stomotoca*

5. hydranth without pseudohydrotheca 7
– hydranth with pseudohydrotheca. 6

6. pseudohydrotheca more or less gelatinous. . . . . *Leuckartiara*
– pseudohydrotheca not gelatinous . . . . *Neoturris*

7. hydrocaulus short, hydranth with a single row of 3-4 filiform tentacles. . . . . *Octotiara*
– hydrocaulus well developed; hydranth with an amphicoronate whorl of more than 8 filiform tentacles . . . . *Amphinema*

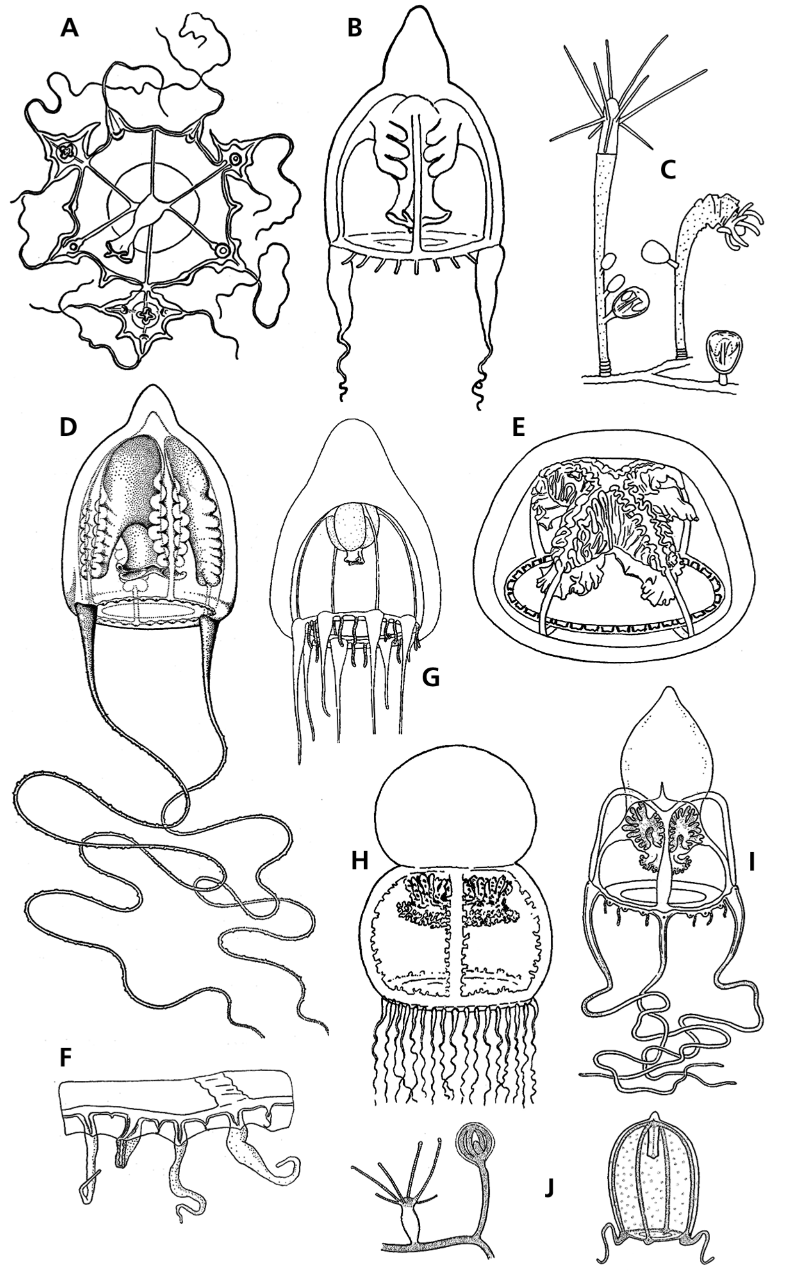


FIG. 95. Anthomedusae. A, Niobiidae, *Niobia dendrotentaculata*, adult medusa with medusa buds on tentacle bulbs. B-D, Pandeidae, *Amphinema*: B-C, *Amphinema rugosum*: B, adult medusa; C, hydroid with medusa buds on caulus and hydrorhiza; D, *Amphinema turrida*, adult medusa. E-F, *Annataria affinis*: E, mature medusa; F, portion of umbrella margin seen from abaxial side with four primary tentacles and four secondary tentacles. G, *Barnettia caprai*, fully grown medusa. H, *Catalbama vesicarium*, mature medusa. I, *Cirrhitiara superba*, fully grown medusa; J, *Codonorchis octaedrus*, portion of colony with hydranth and medusa bud (left), newly released medusa (right) (A-B, E, H-I after Kramp, 1968; C, G after Schuchert, 1996; D after Bouillon, 1980; F after Kramp, 1926; J after Boero *et al*., 1997).

FIG. 95. *Anthomedusae. A, Niobiidae,* Niobia dendrotentaculata*, méduse adulte présentant des bourgeons médusaires sur les bulbes tentaculaires. B-D, Pandeidae,* Amphinema : *B-C,* Amphinema rugosum : *B, méduse adulte ; C, colonies d'hydroïdes possédant des bourgeons médusaires sur les pédoncules et l'hydrorhize ; D,* Amphinema turrida*, méduse adulte. E-F,* Annataria affinis : *E, méduse mature ; F, portion du bord ombrellaire vu du côté abaxial et montrant quatre tentacules primaires et quatre tentacules secondaires. G,* Barnettia caprai*, méduse adulte. H,* Catalbama vesicarium*, méduse adulte. I,* Cirrhitiara superba*, méduse adulte. J,* Codonorchis octaedrus*, portion de colonie montrant un hydranthe un bourgeon médusaire (à gauche), jeune méduse venant de se libérer (à droite) (A-B, E, H-I d'après Kramp,1968 ; C, G d'après Schuchert, 1996 ; D d'après Bouillon, 1980 ; F d'après Kramp, 1926 ; J d'après Boero et al., 1997).*

KEY TO MEDUSAE:

Where only juvenile medusae known: see Pandeidae incertae sedis, or juveniles, or conspecific, below:

1. radial canals with long lateral diverticula; marginal tentacles numerous, with stalked cnidocyst knobs along most of their length . . . . . . *Zanclonia*
– radial canals without long lateral diverticula; marginal tentacles without stalked cnidocyst knobs . . 2

2. centripetal canals. 3
– no centripetal canals 4

3. 4 interradial centripetal canals; without gastric peduncle . . . . . . *Eutiara*
– up to 12 centripetal canals; with a very large peduncle. . . . . . *Timoides*

4. only two well developed marginal tentacles in adults 5
– more than two well developed tentacles in adults 8

5. no gastric peduncle 6
– gastric peduncle 7

6. “gonads” horseshoe-shaped . . . . . . *Codonorchis*
– “gonads” not horseshoe-shaped . . . . . . *Amphinema*

7. simple mouth rim, simple “gonads”; rudimentary tentacles. . . . . . *Stomotoca*
– complexly crenulated lips; complexly transversally folded “gonads”; rudimentary marginal warts . . . . . . *Larsonia*

8. more than two marginal tentacles and marginal cirri . . . . . . *Cirrhitiara*
– more than two marginal tentacles and no marginal cirri. 9

9. 4 perradial marginal bulbs with hollow tentacles and 4 broad interradial bulbs rimmed by a cluster of short solid tentaculae . . . . . . *Geomackiea*
– identical perradial and interradial bulbs, marginal tentacles hollow 10

10. no mesenteries 11
– mesenteries 13

11. 4 perradial manubrial lobes. . . . . . *Annatiara*
– no perradial manubrial lobes 12

12. “gonads” oval, smooth . . . . . . *Barnettia*
– “gonads” horseshoe-shaped, folded. . . . . . *Halitholus*

13. “gonads” not reticulated or folded, smooth, sometimes corrugated; 4 fairly simple lips 14
– “gonads” reticulate or folded, or both; oral lips more or less folded or crenulated. 16

14. - exumbrellar intertentacular longitudinal ridges . . . . . . *Janiopsis*
– no exumbrellar intertentacular longitudinal ridges 15

15. manubrium quadrangular, short and broad, with entire upper surface attached to subumbrella; “gonads” large, sheet-like, smooth, covering all interradial surface, with 3-4 dark red spots in living specimens . . . . . . *Pandeopsis*
– 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 . . . . . . *Hydrichthys*
– “gonads” reticulate. 17

17. “gonads” without isolated interradial pits, horseshoe-shaped, with diverging horizontal folds, connected by interradial transverse bridge. . . . . . *Leuckartiara*
– “gonads” with isolated interradial pits, with or without additional folds, not horseshoe-shaped . . . 18

18. “gonads” altogether reticulate without surrounding folds . . . . . . *Pandea*
– “gonads” with combined folds and pits 19

19. "gonads" in 8 vertical, adradial series of transverse folds, interradial portion of manubrium walls with isolated pits; no ocelli .... *Neoturris*
– "gonads" mainly in irregular, more or less vertical folds surrounding a reticulate area, with ocelli .... *Catablema*

Genus ***AMPHINEMA*** Haeckel, 1879

Figs 25G, 95B-D

Hydroid: colony stolonal, with creeping hydrorhiza; hydrocaulus well-developed, unbranched, covered by perisarc but not developing in a real pseudohydrotheca; hydranth elongate, with one whorl of amphicoronate, filiform, oral tentacles; polyps bending over when stressed; medusa buds on short peduncles arising from hydrorhiza, hydrocaulus, or both.
Medusa: generally with a large apical projection; sometimes with an apical chamber; typically with 2 opposite hollow marginal tentacles; with marginal warts or tentaculae; without gastric peduncle; manubrium with broad base; with or without mesenteries; 4 simple oral lips; "gonads" either adradial, interradial or perradial, occasionally extending along radial canals; with or without ocelli.
Recent references: Brinckmann-Voss & Arai (1998); Rees (2000); Schuchert (2001a).

Amphinema australis (Mayer, 1900a)
Amphinema biscayana (Browne, 1907a) [doubtful status]
Amphinema dinema (Péron & Lesueur, 1810a)
Amphinema krampi Russell, 1956a
Amphinema modernisme Bouillon, Gili, Pagès & Isla, 2000
Amphinema physophorum (Uchida, 1927a)
Amphinema platyhedos Arai & Brinckmann-Voss, 1983
Amphinema rubrum (Kramp, 1957)
Amphinema rugosum (Mayer, 1900) [syn. *A. shantungensis* Chow & Huang, 1958]
Amphinema tsingtauensis (Kao, Li, Chang & Li, 1958)
Amphinema turrida (Mayer, 1900a)

Genus ***ANNATIARA*** Russell, 1940

Fig. 95E-F

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

Annatiara affinis (Hartlaub, 1914)
Annatiara lempersi Bleeker & van der Spoel, 1988

Genus ***BARNETTIA*** Schuchert, 1996

Fig. 95G

Hydroid: unknown.
Medusa: sometimes with apical projection; 8 hollow, long tentacles, between each pair of which are cirri-like small tentacles without bulbs, with chordal endoderm, evenly spaced and not associated with the larger tentacles; manubrium small, with 4 simple perradial lips; "gonads" interradial, smooth; 4 radial canals, without mesenteries; no ocelli.

Barnettia caprai Schuchert, 1996

Genus ***CATABLEMA*** Haeckel, 1879

Fig. 95H

Hydroid: unknown.
Medusa: apical projection large, dome-shaped; with numerous tentacles, with or without marginal bulbs between adjoining tentacles; no gastric peduncle; manubrium large with broad base, with 4 short mesenteries; 4 large, crenulated oral 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.

Catablema multicirratum Kishinouye, 1910
Catablema nodulosum Bigelow, 1913
Catablema vescicarium (L. Agassiz, 1862)

Genus ***CIRRHITIARA*** Hartlaub, 1913

Fig. 95I

Hydroid: unknown.
Medusa: apical projection large, solid; 4 or 8 large hollow marginal tentacles and 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.

Cirrhitiara simplex Xu, Huang & Chen, 1991
Cirrhitiara superba (Mayer, 1900a)

Genus ***CODONORCHIS*** Haeckel, 1879

Figs 95J, 96A

Hydroid: colony stolonal, arising from a simple hydrorhiza; hydranth small (0,25 mm), sessile, naked, fusiform; hypostome short, conical; one whorl of 4-6 filiform tentacles; medusa buds on hydrorhiza, with a pedicel generally longer than hydranth.
Medusa: with apical projection; 2 opposite hollow marginal tentacles; marginal tentaculae; no gastric peduncle; manubrium with broad base; with mesenteries; mouth cruciform with 4 simple lips; “gonads” horseshoe-shaped; with ocelli.
Recent reference: Boero *et al.* (1997).

Codonorchis octaedrus Haeckel, 1879

Genus ***EUTIARA*** Bigelow, 1918

Fig. 96B

Hydroid: unknown.
Medusa: bell with exumbrellar longitudinal ribs; blind centripetal canals alternating with radial canals; radial canals large, with lateral diverticula, with well developed mesenteries; complex “gonads” forming eight series of adradial folds.

Eutiara mayeri Bigelow, 1918
Eutiara russelli Bouillon, 1981

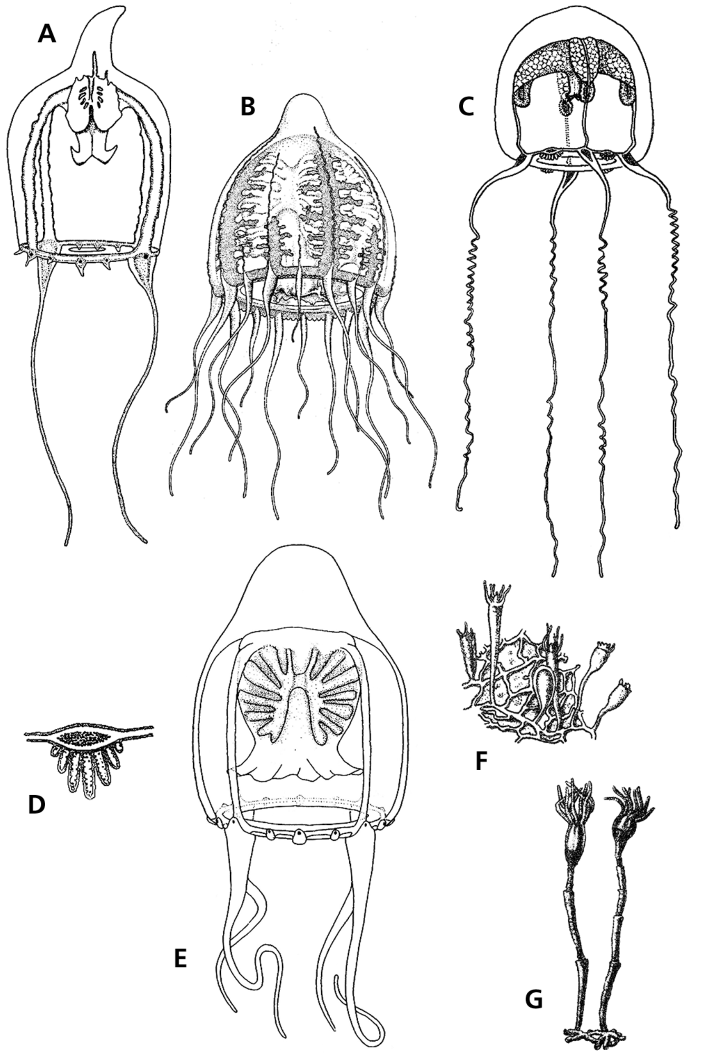


FIG. 96. Anthomedusae, Pandeidae. A, *Codonorchis octaedrus*, mature medusa. B, *Eutiara russelli*, adult medusa. C-D, *Geomackiea zephyrolata*: C, mature medusa; D, enlarged view of an interradial marginal bulb. E-G, *Halitholus*: E, *Halitholus pauper*, fully grown medusae; F-G, *Halitholus cirratus*, ''*Perigonimus*'' *yoldia-articae,* presumed hydroid stage (A after Boero *et al.*, 1997; B after Bouillon, 1981; C-D after Mills, 1985; E after Schuchert, 1996; F-G after Naumov, 1969).

FIG. 96. *Anthomedusae, Pandeidae. A, Codonorchis octaedrus,* méduse mature. B, *Eutiara russelli*, méduse adulte. C-D, *Geomackiea zephyrolata :* C, méduse mature ; D, vue élargie d'un bulbe marginal interradiare. E-G, *Halitholus :* E, *Halitholus pauper*, méduse adulte ; F-G, *Halitholus cirratus*, ''*Perigonimus*'' *yoldia-articae,* stades hydroïdes présumés (A d'après Boero *et al.*, 1997 ; B d'après Bouillon, 1981 ; C-D d'après Mills, 1985 ; E d'après Schuchert, 1996 ; F-G d'après Naumov, 1969).

Genus ***GEOMACKIEA*** Mills, 1985

Fig. 96C-D

Hydroid: unknown.
Medusa: no apical projection; 4 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; no peduncle; mouth simple, unarmed; "gonads" smooth, interradial, extending along half of radial canals; no ocelli.

Geomackiea zephyrolata Mills, 1985

Genus ***HALITHOLUS*** Hartlaub, 1913

Fig. 96E-G

Hydroid: colony reptant, "*Perigonimus* like" (see family definition); hydranths with 6-10 tentacles; medusa buds on hydrorhiza.

Medusa: apical projection large, dome-shaped; manubrium quadratic; "gonads" adradial, more or less horseshoe-shaped, folded; mouth rim faintly crenulated; radial canals narrow, not or very faintly jagged; no mesenteries; 4 or more hollow marginal tentacles; with or without ocelli.
Recent references: Arai & Brinckmann-Voss (1980); Schuchert (2001a).

Halitholus cirratus Hartlaub, 1913
Halitholus intermedius (Browne, 1902)
Halitholus pauper Hartlaub, 1913

Genus ***HYDRICHTHYS*** Fewkes, 1887

Fig. 97A-C

Synonyms: *Ichthyocodium* Jungersen, 1911; *Nudiclava* Lloyd, 1907.
Hydroid: parasite of fish or of parasitic copepods on fish, hydrorhiza reticular, or forming a naked encrusting plate; gastrozooid tubular, without tentacles; gonozooid branched or unbranched, with clusters of medusa buds or fixed gonophores.
Medusa: umbrella dome-shaped, with large apical projection; manubrium cruciform; mouth with 4 well developed slightly folded lips; 4 or more radial canals, jagged, some with lateral crest; with conspicuous mesenteries; up to 6 marginal tentacles with conical bulbs; "gonads" on interradial surface of manubrium, developed in 8 adradially folded masses; no ocelli.
Recent reference: Boero *et al.* (1991)

Hydrichthys boycei Warren, 1916
Hydrichthys cyclothonis Damas, 1934
Hydrichthys mirus Fewkes, 1887
Hydrichthys monocanthi (Lloyd, 1907)
Hydrichthys pacifica Miyashita, 1941
Hydrichthys pietschi Martin, 1975
Hydrichthys sarcotretis (Jungersen, 1911)

Genus ***JANIOPSIS*** Bouillon, 1980

Fig. 97D

Hydroid: unknown.
Medusa: apical projection conspicuous; numerous exumbrellar intertentacular meridional ridges ending at the origin of apical projection; long manubrial mesenteries; "gonads" smooth, covering interradial apical part of manubrium, at maturity extending adradially along mesenteries and radial canals; proximal part of manubrium elongated, with 4 crenulated lips; up to 16 marginal tentacles with laterally compressed bulbs; with ocelli.

Janiopsis costata Bouillon, 1980

Genus ***LARSONIA*** Boero, Bouillon & Gravili, 1991

(Fig. 97E, F)

Hydroid: parasitic on fish, with plate-like naked hydrorhiza, hydranth with no tentacles; gonozooid branched, giving rise to free medusae.
Medusa: thick apical mesoglea and usually sharply pointed apex; manubrium swollen on a broad gastric peduncle, extending beyond bell margin, mouth with crenulated lips; "gonads" in 8 adradial rows, complexly transversely folded; 2 opposite perradial tentacles, numerous rudimentary warts; no ocelli.

Larsonia pterophylla (Haeckel, 1879) [as *Stomotoca*]

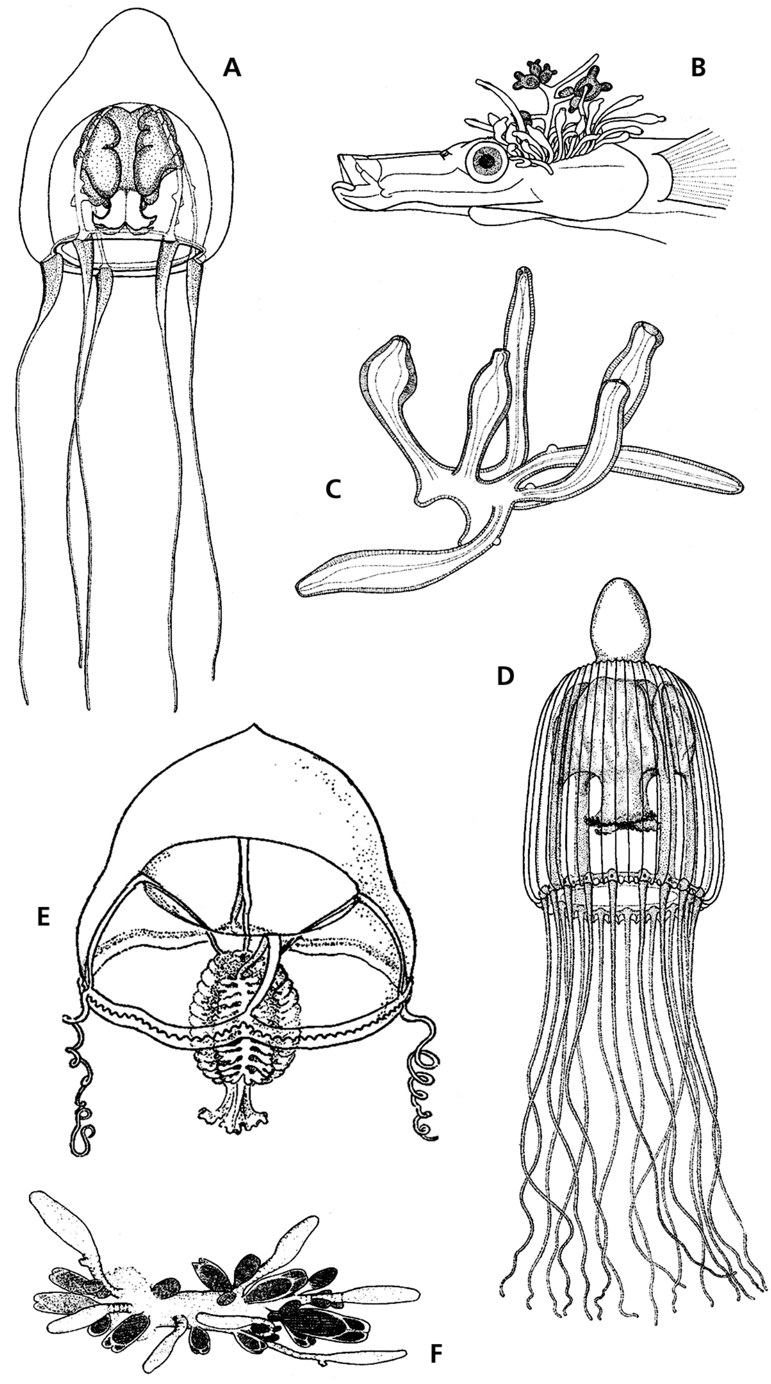


FIG. 97. Anthomedusae, Pandeidae. A-C, *Hydrichthys mirus*: A, mature medusa; B, hydroid colony parasitizing the head a syngnatid fish; C, detail of a colony. D, *Janiopsis costata*, mature medusa. E-F, *Larsonia pterophylla*: E, adult medusa; F, colony living on the skin of a larval fish (A-C after Boero *et al*., 1991; D after Bouillon, 1980; E after Kramp, 1968; F after Wedler & Larson, 1986).

FIG. 97. *Anthomedusae, Pandeidae. A-C,* Hydrichthys mirus : *A, méduse mature ; B, colonie d'hydroïdes parasitant la tête d'un poisson syngnatide ; C, détail d'une colonie. D,* Janiopsis costata*, méduse mature. E-F,* Larsonia pterophylla : *E, méduse adulte ; F, colonie vivant sur la peau d'une larve de poisson (A-C d'après Boero et al., 1991 ; D d'après Bouillon, 1980 ; E d'après Kramp, 1968 ; F d'après Wedler & Larson, 1986).*

Genus *LEUCKARTIARA* Hartlaub, 1914

Figs 24B, 26M, 35C, 98A-D

Hydroid: colonies mostly stolonal; hydrocaulus not or sparingly branched, covered by perisarc extending on hydranth body, forming a more or less gelatinous pseudohydrotheca; hydranth with one whorl of oral filiform tentacles; medusa buds on hydrocaulus or hydrorhiza, covered by thin perisarc.
Medusa: usually with apical projection of varying shape; manubrium large, connected to radial canals by mesenteries; mouth margin extensively folded or crenulated; "gonads" interradial, bipartite but connected interradially, horseshoe-shaped, with horizontal folds directed perradially; radial canals broad and ribbon-like, often with jagged edges; tentacles numerous, hollow, with elongated, laterally compressed basal bulbs; often with rudimentary tentacles; usually with ocelli.
Recent references: Schuchert (1996, 2001a).

Leuckartiara abyssi (G.O. Sars, 1874)
Leuckartiara adnata Pagès, Bouillon & Gili, 1991
Leuckartiara annexa Kramp, 1957
Leuckartiara brownei Larson & Harbison, 1990
Leuckartiara eckerti Bouillon, 1985b
Leuckartiara foersteri Arai & Brinckmann-Voss, 1980b
Leuckartiara gardineri Browne, 1916
Leuckartiara grimaldii Ranson, 1936
Leuckartiara hoepplii Hsu, 1928
Leuckartiara nobilis Hartlaub, 1913
Leuckartiara octona (Fleming, 1823)
Leuckartiara orientalis Xu, Huang & Chen, 1991
Leuckartiara simplex Bouillon, 1980
Leuckartiara zacae Bigelow, 1940
Leuckartiara sp. Arai & Brinckmann-Voss, 1980a

Genus *MERGA* Hartlaub, 1914

Fig. 98E-H

Hydroid: hydrorhiza ramified; hydrocaulus slightly branched or not; hydranth on hydrocaulus or almost sessile, with or without pseudohydrotheca, one whorl of filiform tentacles; medusa buds arising from hydrocauli and hydrorhiza.
Medusa: manubrium cruciform, never twisted, with perradial edges connected with radial canals by long mesenteries; "gonads" smooth or exceptionally slightly folded or weakly corrugated, generally adradial; oral lips simple or faintly crenulated; 4-8 or more marginal tentacles; with or without rudimentary bulbs or tentaculae; with or without ocelli.
Recent reference: Brinckmann-Voss & Arai (1998).

Merga bulbosa Bouillon, 1980
Merga galleri Brinckmann, 1962
Merga macrobulbosa Xu, Huang & Chen, 1991
Merga reesi Russell, 1956b
Merga tergestina (Neppi & Stiasny, 1912)
Merga tregoubovii Picard, 1960
Merga treubeli Schuchert, 1996
Merga violacea (A. Agassiz & Mayer, 1899)

Genus *NEOTURRIS* Hartlaub, 1914

Figs 3B, 35A, 98I-J

Hydroid: colony stolonal with terminal hydranth; perisarc of hydrocaulus forming a pseudohydrotheca; hydranth with one whorl of filiform oral tentacles; gonophores giving free medusae developing from hydrocauli, sometimes from hydrorhiza, completely covered with perisarc.
Medusa: apical projection varying much in shape and size, often reduced; manubrium 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"; 8 or more hollow marginal tentacles with laterally compressed basal bulbs; without rudimentary tentacles or marginal warts; mostly without ocelli.
Recent reference: Bouillon (1995b).

Neoturris bigelowi Kramp, 1959a
Neoturris breviconis (Murbach & Shaerer, 1902)
Neoturris crockeri Bigelow, 1940
Neoturris fontata (Bigelow, 1909)
Neoturris papua (Lesson, 1843)
Neoturris pelagica (A. Agassiz & Mayer, 1902)
Neoturris pileata (Forskål, 1775)

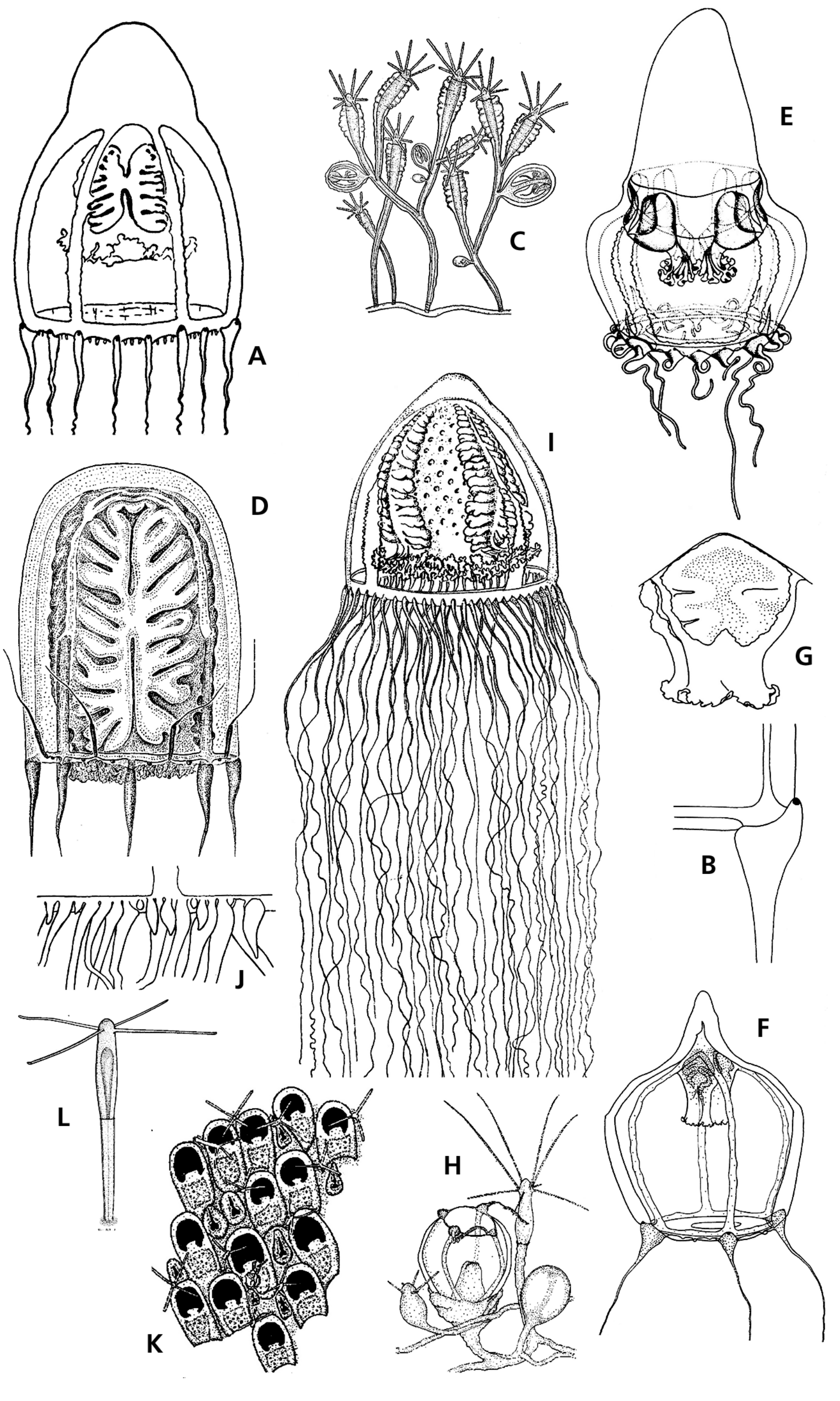


FIG. 98. Anthomedusae, Pandeidae. A-D, *Leuckartiara*: A-C, *Leuckartiara octona*: A, mature medusa; B, diagram of a lateral view of a marginal tentacle showing the abaxial spur and an ocellus; C, general view of a part of a hydroid colony; D, *Leuckartiara annexa*, adult medusa. E-H, *Merga*: E, *Merga galleri*, fully grown medusa; F-H, *Merga tergestina*: F, mature medusa; G, manubrium with ''gonad''; H, fragment of a hydroid colony with medusa buds. I-J, *Neoturris pileata*: I, adult medusa; J, portion of exumbrella. K-L, *Octotiara russelli*: K, colony with medusa buds fixed on a bryozoan; L, detail of a hydranth (A after Kramp, 1959b; B-C & J after Russell, 1953; D after Kramp, 1968; E after Brinckmann, 1962; F-H after Vannucci & Yamada, 1959; I after Hartlaub, 1914; K-L after Boero & Bouillon, 1989).

***FIG. 98.** Anthomedusae, Pandeidae. A-D,* Leuckartiara : *A-C,* Leuckartiara octona : *A, méduse mature ; B, diagramme d'une vue latérale d'un tentacule marginal montrant l'éperon abaxial et un ocelle ; C, vue générale d'une partie de colonie d'hydraires ; D,* Leuckartiara annexa, *méduse adulte. E-H,* Merga : *E,* Merga galleri, *méduse adulte ; F-H,* Merga tergestina : *F, méduse mature ; G, manubrium et ''gonade'' ; H, fragment d'une colonie d'hydroïdes présentant des bourgeons médusaires. I-J,* Neoturris pileata *: I, méduse adulte ; J, portion de l'exombrelle. K-L,* Octotiara russelli *: K, colonie d'hydroïdes développant des bourgeons médusaires et fixée sur un bryozoaire ; L, détail d'un hydranthe (A d'après Kramp, 1959b ; B-C & J d'après Russell, 1953 ; D d'après Kramp, 1968 ; E d'après Brinckmann, 1962 ; F-H d'après Vannucci & Yamada, 1959 ; I d'après Hartlaub, 1914 ; K-L d'après Boero & Bouillon, 1989).*

Genus ***OCTOTIARA*** Kramp, 1953

Figs 98K-L, 99A

Hydroid: symbiotic with bryozoans; hydrorhiza stolonal; hydrocaulus short, covered by thin perisarc; hydranth with a single row of 3-4 filiform tentacles; isolated medusa buds on hydrorhiza.
Medusa: 8 simple radial canals; gastric peduncle; manubrium extending beyond umbrellar margin; with transversely folded "gonads"; without mesenteries.
Recent reference: Boero & Bouillon (1989).

Octotiara russelli Kramp, 1953

Genus ***PANDEA*** Lesson, 1843

Fig. 99B-C

Hydroid: where known, stolonal, arising from branched hydrorhiza, epizoite on planktonic pteropod gastropods; hydranth naked, sessile or on a short pedicel, with filiform oral tentacles of variable length in two whorls; medusa buds on short pedicels covered by perisarc and arising directly from hydrorhiza.
Medusa: 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.
See also under *Campaniclava*.
Recent references: Alvariño (1988); Brinckmann-Voss & Arai (1998).

Pandea conica (Quoy & Gaimard, 1827) [syn. *Campaniclava cleodorae* (Gegenbaur, 1854)]
Pandea cybeles Alvariño, 1988
Pandea minima von Lendenfeld, 1885b [doubtful status]
Pandea rubra Bigelow, 1913

Genus ***PANDEOPSIS*** Kramp, 1959

Fig. 99D-F

Hydroid: known 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.
Medusa: manubrium large, quadratic, with long mesenteries; "gonads" smooth, sheet-like, covering interradial surface of manubrium and with 3-4 dark red spots in living or recently fixed specimens; mouth with 4 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.

Pandeopsis ikarii (Uchida, 1927a)

Genus ***STOMOTOCA*** L. Agassiz, 1862

Fig. 99G-H

Hydroid: colony stolonal; stem unbranched; hydranth with three rows of filiform tentacles, oral whorl held upwards, aboral rows perpendicular to column; gonophores on hydrorhiza.

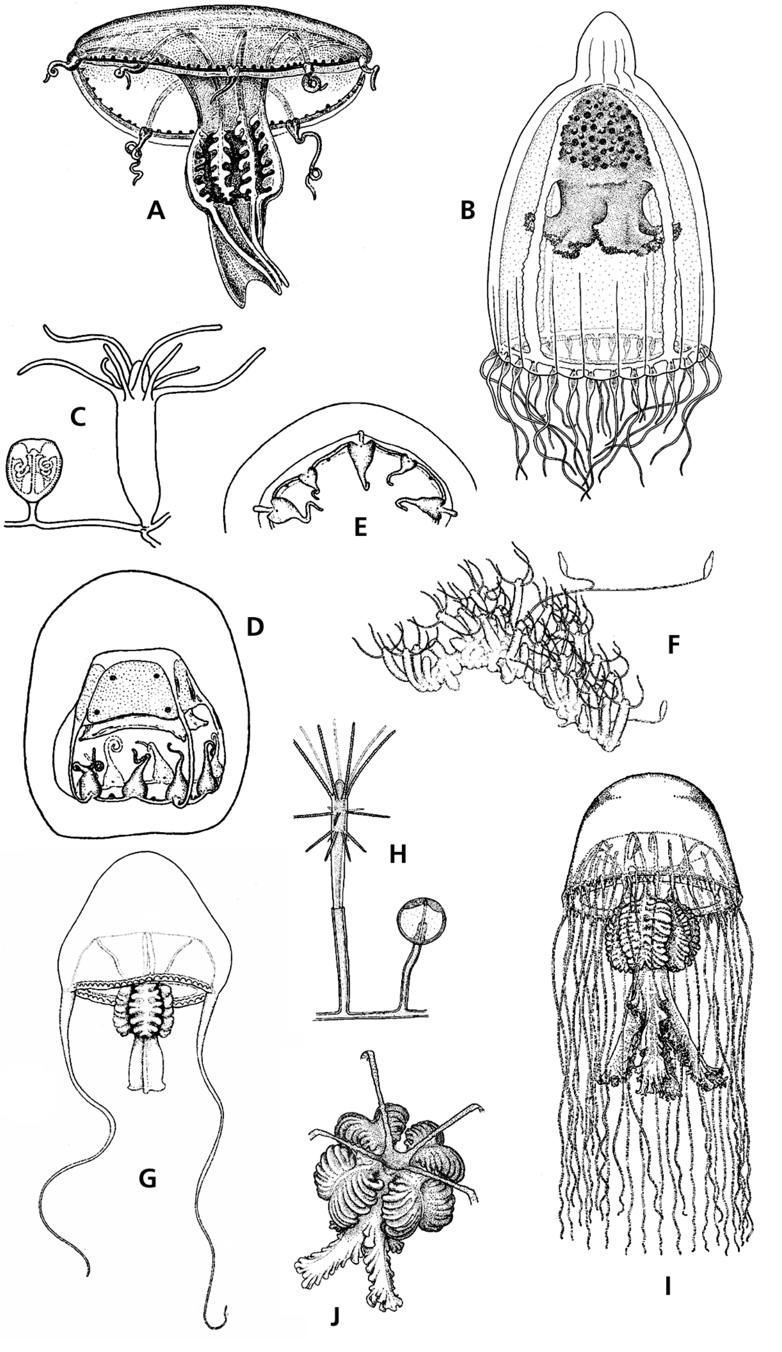


FIG. 99. Anthomedusae, Pandeidae. A, *Octotiara russelli*, mature medusa. B-C, *Pandea conica :* B, adult medusa; C, portion of a hydroid colony with a hydranth and a medusa bud. D-F, *Pandeopsis ikarii*: D, fully grown medusa; E, portion of exumbrella margin; F hydroid colony. G-H, *Stomotoca atra*: G, mature medusa; H, portion of a colony with hydranth and medusa bud. I-J, *Timoides agassizi*: I, adult medusa; J, apico-lateral view of manubrium, radial canals and ''gonads'' (A, D-E after Kramp, 1968; B after Pagès *et al*., 1992; C after Picard, 1956; F after Bouillon, 1985b; G after Bouillon *et al*., 1991; H after Boero & Bouillon, 1989; I-J after Bouillon, 1980).

***FIG. 99.** Anthomedusae, Pandeidae. A, Octotiara russelli*, méduse mature. B-C, *Pandea conica :* B, méduse adulte ; C, fragment d'une colonie d'hydroïdes montrant un hydranthe et un bourgeon médusaire. D-F, *Pandeopsis ikarii :* D, méduse adulte ; E, portion du bord exombrellaire ; F, colonie d'hydroïdes. G-H, *Stomotoca atra :* G, méduse mature ; H, portion d'une colonie avec un hydranthe et un bourgeon médusaire. I-J, *Timoides agassizi :* I, méduse adulte ; J, vue apico-latérale du manubrium, des canaux radiares et des ''gonades'' (A, D-E d'après Kramp, 1968 ; B d'après Pagès *et al*., 1992 ; C d'après Picard, 1956 ; F d'après Bouillon, 1985b ; G d'après Bouillon *et al*., 1991 ; H d'après Boero & Bouillon, 1989 ; I-J d'après Bouillon, 1980).

Medusa: umbrella bell-shaped; 2 marginal perradial tentacles, numerous marginal rudimentary tentacles; manubrium on broad peduncle extending beyond bell margin, mouth rim smooth; "gonads" in 8 well separated adradial rows, with simple transverse folds.
Recent references: Boero & Bouillon (1989), Boero *et al.* (1991).

Stomotoca atra L. Agassiz, 1862a

Genus ***TIMOIDES*** Bigelow, 1924

Fig. 99I-J

Hydroid: unknown
Medusa: Pandeidae with blindly ending centripetal canals, with large gastric peduncle twice as long as subumbrellar cavity; manubrium very long with 4 long lancet-shaped lips; "gonads" on lower part of peduncle, just above manubrium; with numerous tentacles and marginal cirri. No sense organs.

Timoides agassizi Bigelow, 1904

Genus ***ZANCLONIA*** Hartlaub, 1913

Fig. 100A
Hydroid: unknown.
Medusa: 20 long, transverse diverticula at right angles on both sides of 4 radial canals; 24-32 marginal tentacles, each with adaxial series of stalked cnidocyst knobs.

Zanclonia weldoni (Browne, 1910)

Pandeidae *incertae sedis*:

Genus ***CAMPANICLAVA*** Allman, 1864

(Only for *Campaniclava clionis*, Vanhöffen, 1910)
Fig. 100B

Hydroid: colony stolonal, living on pteropods; hydranths on a short pedicel, with 9-10 distally scattered filiform tentacles and one larger below them; gonophores peduncled, issued from hydrorhiza.
Medusa: only juvenile known, with 4 tentacles and conspicuous marginal bulbs; manubrium quadratic; mouth simple.

Campaniclava clionis Vanhöffen, 1910 [probably a syn. of *Pandea rubra*]

Genus ***DISSONEMA*** Haeckel, 1879

Fig. 100C

Hydroid: unknown.
Medusa: 2 or 4 perradial tentacles; tentaculae sometimes present; with abaxial ocelli; "gonads" extend from manubrium outwards along the radial canals.
Genus comprising doubtful species of doubtful affinity.

Dissonema gaussi Vanhöffen, 1912
Dissonema saphenella Haeckel, 1879

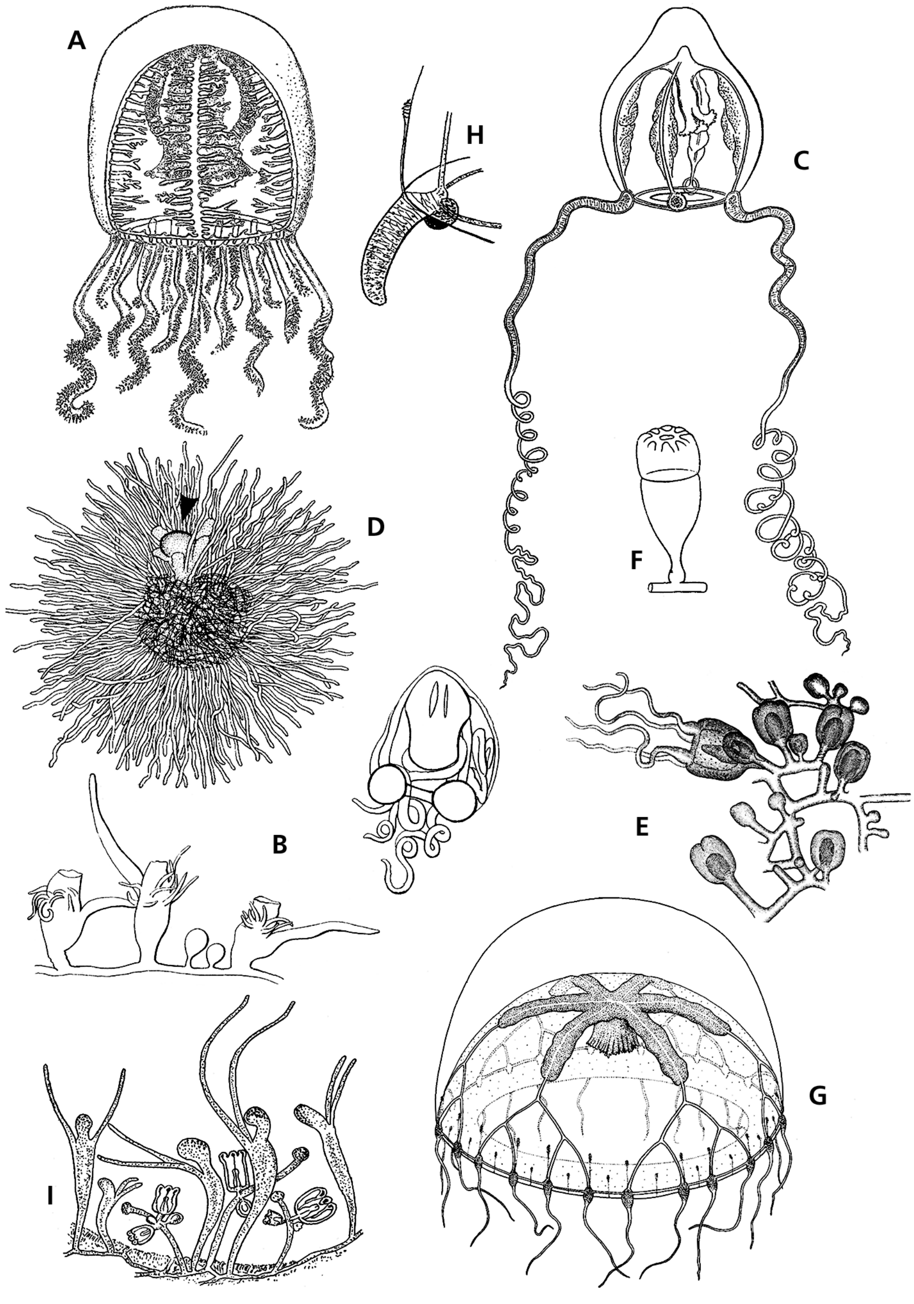


FIG. 100. Anthomedusae, Pandeidae (end). A, *Zanclonia weldoni*, mature medusa. B, *Campaniclava clionis*, medusa bud (above left), portion of a colony with hydranths and gonophores (below). C, *Dissonema saphenella*, adult medusa. D, *Pelagiana trichodesmiae*, polyp (see arrow). E-F, *Perigonella sulfura*: E, part of colony with medusa buds; F, hydranth. G-I, Proboscidactylidae, *Proboscidactyla stellata*: G, mature medusa; H, diagram showing the insertion of the marginal tentacles and the position of the adaxial cnidocyst pad; I, hydroid colony with medusa buds (A & C after Kramp, 1968; B after Vanhöffen, 1910; D after Calder, 1988a; E-F after Schulze, 1880; G after Pagès *et al*., 1992; H-I after Russell, 1953).

FIG. 100. *Anthomedusae, Pandeidae (fin). A,* Zanclonia weldoni*, méduse mature. B,* Campaniclava clionis*, bourgeon médusaire (au dessus à droite), portion d'une colonie montrant les hydranthes et les gonophores (au-dessous). C,* Dissonema saphenella*, méduse adulte. D,* Pelagiana trichodesmiae*, polype (voir flèche). E-F,* Perigonella sulfura *: E, portion d'une colonie montrant les hydranthes et les bourgeons médusaires ; F, hydranthe. G-I, Proboscidactylidae,* Proboscidactyla stellata *: G, méduse mature ; H, diagramme montrant l'insertion d'un tentacule marginal et la position d'un coussinet cnidocytaire adaxial ; I, colonie d'hydroïdes avec des bourgeons médusaires (A & C d'après Kramp, 1968 ; B d'après Vanhöffen, 1910 ; D d'après Calder, 1988a ; E-F d'après Schulze, 1880 ; G d'après Pagès* et al.*, 1992 ; H-I d'après Russell, 1953).*

Genus *PELAGIANA* Borstad & Brinckmann-Voss, 1979

Fig. 100D

Hydroid: colony living in the blue-green algae *Trichodesmium.*
Medusa: only juvenile medusae known, with 4 perradial marginal bulbs, 2 opposite ones tentacled.

Pelagiana trichodesmii Borstad & Brinckmann-Voss, 1979 [as *P. trichodesmiae*]

Genus *PERIGONELLA* Stechow, 1921

Fig. 100E-F

Hydroid: hydrorhiza stolonal, fixed on the pteropod *Cavolinia tridentata*; hydranth solitary, almost sessile, with one whorl of tentacles; gonophores pedicellate, borne on hydrorhiza, giving rise to free medusae.
Medusa: only young medusae known, with 4 conical marginal bulbs, 4 tentacles, a simple manubrium without oral formations.

Perigonella sulphurea (Chun, 1889)

Family PROBOSCIDACTYLIDAE Hand & Hendrickson, 1950

Hydroid: hydrorhiza as creeping naked stolons around rim of sabellid polychaete tubes; hydranths almost sessile, polymorphic; gastrozooid with rounded hypostome, separated from the body by a constriction; with large cluster of cnidocysts, or "cap", somewhat displaced onto one side of hypostome, 2 filiform tentacles arising close together, under hypostomial constriction, opposite to cnidocyst cluster; gonozooid and dactylozooid without tentacles, mouthless and smaller than gastrozooid; medusa buds very close to gonozooid tip.
Medusa: umbrella mostly hemispherical; manubrium with 4-6 or more radial gastric lobes, extending along proximal portions of radial canals; "gonads" surrounding manubrium and extending on gastric lobes; radial canals branched, obliterated canals sometimes present; usually no circular canal but with a solid endodermal marginal core; numerous exumbrellar cnidocyst clusters or bands alternating with tentacles; marginal tentacles hollow, with swollen hollow base connected to the lumen of radial canals.
Remarks: The systematic position of the Proboscidactylidae is unclear; they were included in the Limnomedusae, mostly for convenience. 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 this suggestion here.
Recent references: Pagès *et al.* (1991; 1992); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

Genus *PROBOSCIDACTYLA* Brandt, 1834

Figs 5E, 26U, 100G-I, 101A

Hydroid and medusa with the characters of the family.

Proboscidactyla abyssicola Uchida, 1947b
Proboscidactyla circumsabella Hand, 1954
Proboscidactyla flavicirrata Brandt, 1835 [probable syn. *P. occidentalis* (Fewkes, 1889) and *P. pacifica* (Maas, 1909)]
Proboscidactyla mutabilis (Browne, 1902)
Proboscidactyla ornata (McCrady, 1859) [syn. *P. conica* Menon, 1932]
Proboscidactyla stellata (Forbes, 1846) [syn. *P. brooksi* (Mayer, 1910) and *P. furcata* (Haeckel, 1879)]
Proboscidactyla sp. - Schuchert, 1996

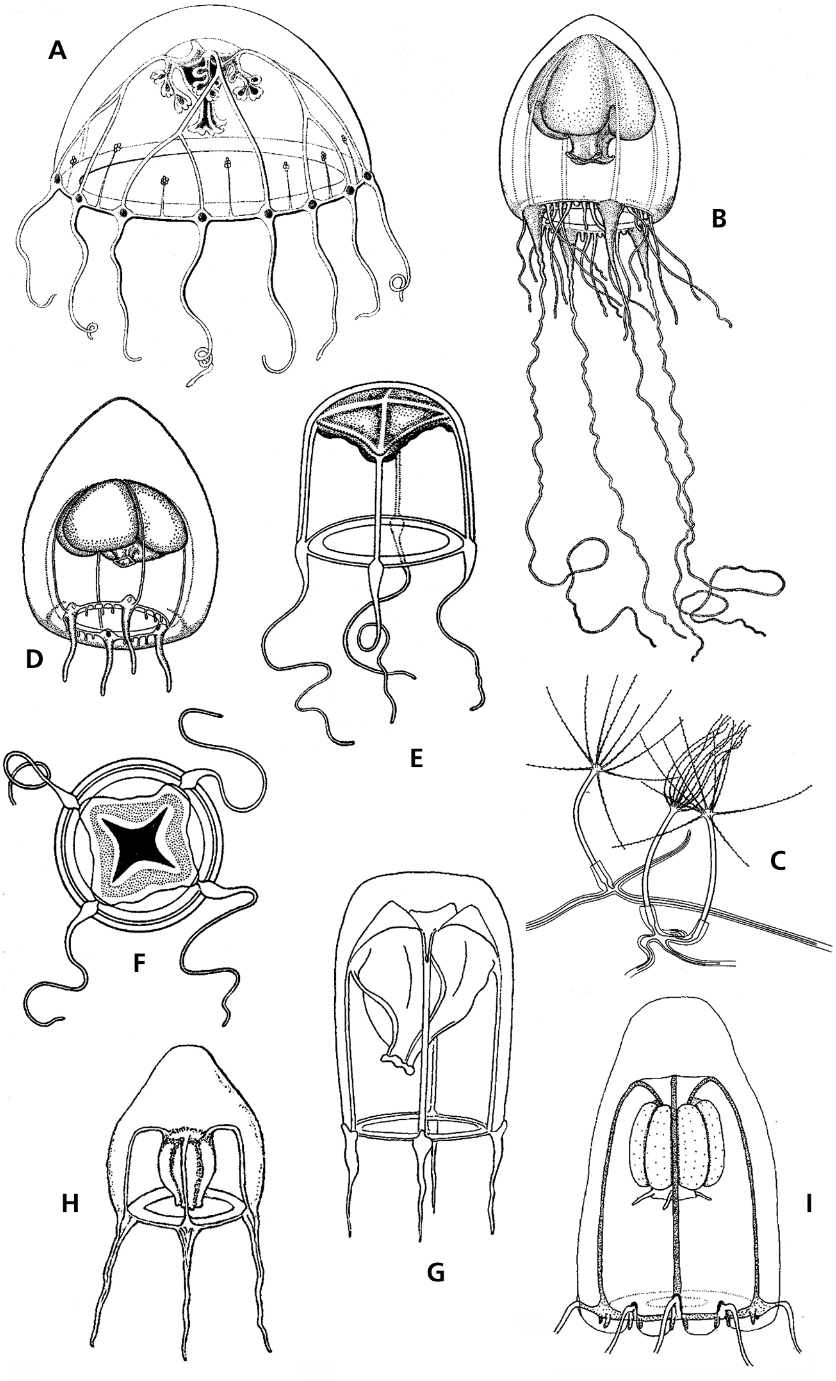


FIG. 101. Proboscidactylidae. A, *Proboscidactyla ornata*, adult medusa with medusa buds. Protiaridae. B-C, *Halitiara inflexa*: B, fully-grown medusa; C, portion of a hydroid colony. D, *Halitiarella ocellata*, adult medusa. E-F, *Latitiara orientalis*: E, adult medusa lateral view; F, adult medusa oral view. G, *Paratiara digitalis,* mature medusa; H, *Protiara haeckeli*, adult medusa. I, Russellidae, *Russellia mirabilis*, mature medusa (A after Mayer, 1910; B & D after Bouillon, 1980; C after Bouillon, 1985; E-F after Xu Zhenzu & Huang Jia-Chi, 1990; G after Kramp, 1959; H after Hartlaub, 1913; I after Pagès *et al*., 1999: p. 2432, fig. 1).

***FIG. 101.** Proboscidactylidae. A,* Proboscidactyla ornata*, méduse adulte présentant des bourgeons médusaires. Protiaridae. B-C,* Halitiara inflexa *: B, méduse adulte; C, portion d'une colonies d'hydroïdes. D,* Halitiarella ocellata*, méduse adulte. E-F,* Latitiara orientalis *: E, méduse adulte vue latérale ; F, méduse adulte vue orale. G,* Paratiara digitalis*, méduse mature. H,* Protiara haeckeli*, méduse adulte. I, Russellidae,* Russellia mirabilis *: méduse mature. (A d'après Mayer, 1910 ; B & D d'après Bouillon, 1980 ; C d'après Bouillon, 1985 ; E-F d'après Xu Zhenzu & Huang Jia-Chi, 1990 ; G d'après Kramp, 1959 ; H d'après Hartlaub, 1913 ; I d'après Pagès et al., 1999 : p. 2432, fig. 1).*

Family PROTIARIDAE Haeckel 1879

Hydroid: colony arising from creeping stolons; hydranth issued from short hydrocaulus; hydrorhiza and hydrocaulus covered by perisarc, which forms a cup at hydranth base; hydranth with one whorl of filiform tentacles, large cnidocysts alternating with tentacles; gonophores unknown.

Medusa: 4 fully developed marginal tentacles arising from large, hollow tentacular bulbs; 4 simple radial canals and a circular canal, mouth with 4 simple lips; "gonads" interradial, with smooth surface; with or without mesenteries; without rudimentary bulbs; margin with or without cirri-like tentacles; exceptionally with ocelli.

Remarks: the hydroids of *Halitiara inflexa* (Bouillon 1985b; Bouillon *et al.* 1988b) and *Halitiara formosa* (Brinckmann-Voss, pers. comm.) are very different from Pandeidae polyps, showing some resemblance with certain Campanulinidae hydroids and mainly with *Trichydra* polyps (Bouillon *et al.* 1988b). 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 that characterises normally only Leptomedusae families (i.e., Eirenidae, Eucheilotidae, Haleciidae, Lovenellidae, and Tiaropsidae).

Recent references: Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. marginal cirri 2
– no marginal cirri 3
2. adaxial ocelli . . . . *Halitiarella*
– no ocelli . . . . *Halitiara*
3. no mesenteries; 4 or 8 "gonads" on interradial walls of manubrium . . . . *Protiara*
– mesenteries 4
4. "gonads" interradial; marginal tentacles with abaxial spurs . . . . *Paratiara*
– "gonads" entirely surrounding manubrium; marginal tentacles without abaxial spurs . . . . *Latitiara*

Genus ***HALITIARA*** Fewkes, 1882

Fig. 101B-C

Hydroid: see family characters.

Medusa: 4 straight radial canals; 4 perradial marginal tentacles; marginal cirri; mouth simple, cruciform; with or without mesenteries; "gonads" interradial, smooth, sometimes extending over mesenteries; without ocelli; cnidome, when known, with merotrichous isorhizae.

Halitiara formosa Fewkes, 1882b
Halitiara inflexa Bouillon, 1980
Halitiara rigida Bouillon, 1980

Genus ***HALITIARELLA*** Bouillon, 1980

Fig. 101D

Hydroid: unknown.

Medusa: with 4 straight 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. Cnidome unknown.

Remarks: presumably congeneric with *Halitiara*

Halitiarella ocellata Bouillon, 1980
Halitiarella minuta Xu, Huang & Chen, 1991 [doubtful status]

Genus *LATITIARA* Xu and Huang, 1990
Fig. 101E-F

Hydroid: unknown.
Medusa: "gonad" entirely surrounding manubrium; gastric mesenteries; 4 radial canals; 4 marginal tentacles without abaxial spurs; no marginal cirri; no ocelli.

Latitiara orientalis Xu & Huang, 1990b

Genus *PARATIARA* Kramp and Damas, 1925
Fig. 101G

Hydroid: unknown.
Medusa: "gonads" smooth, interradial; manubrium more or less twisted, with well-developed mesenteries; 4 simple oral lips; marginal tentacles with abaxial spurs; no ocelli; no marginal cirri.

Paratiara digitalis Kramp & Damas, 1925

Genus *PROTIARA* Haeckel, 1879
Fig. 101H

Hydroid: unknown.
Medusa: 4 or 8 longitudinal "gonads", interradial or perradial?; 4 marginal tentacles, no marginal cirri or tentaculae; no mesenteries; mouth with 4 simple lips; with or without ocelli.

Protiara haeckeli Hargitt, 1902
Protiara tetranema (Péron & Lesueur, 1810a)
Protiara sp. Bouillon & Barnett, 1999

Order CAPITATA Kühn, 1913

Hydroid: hydranths usually with capitate tentacles either in the adult polyps or during their larval life; gonophores generally borne on hydranth body.
Medusa: "gonads" usually completely surrounding the manubrium; mouth simple and circular; marginal tentacles usually hollow (solid in Margelopsidae and Porpitidae); cnidome characterised by the presence of stenoteles; sexual reproduction leading to planulae or actinulae; planulae with usually two types of ectodermal embryonic glandular cells: spumous and spheroulous ones.
Recent references: Petersen (1990); Schuchert (1996).

KEY TO HYDROIDS

1. hydranths with aboral tentacles only 2
– hydranths with oral and aboral tentacles 3

2. hydranth with numerous capitate tentacles arranged in 3-6 irregular aboral whorls around middle part of the hydranth body and with creeping stolonal hydrorhiza or with tentacles in 1 or 5-6 close alternate aboral whorls surrounding base of hypostome and with mat-like hydrorhiza, forming a basal plate . . . . Sphaerocorynida

– hydranth claviform; with long hypostome; tentacles scattered in one or more aboral whorls under hypostome, hydrocaulus not clearly demarcated, short, ending in pedal disc or creeping stolon . . . . Moerisiida

3. hydranth with solid or parenchymatic oral tentacles in one whorl around hypostome or spreading down over hydranth body; with solid or parenchymatic aboral tentacles in one or three whorls or absent . . . . Tubulariida

– hydranths mono- or polymorphic, oral tentacles capitate or moniliform, aboral tentacles in whorls or scattered, either capitate, moniliform, ramified capitate, reduced, or without tentacles; hydroids as floating or fixed colonies; fixed colonies arising either from simple creeping stolonal tubes, from an encrusting basal mat, from upright branched hydrorhiza consisting of a central axis of perisarc covered by coenosarc, or from a calcified exoskeleton . . . . Zancleida

KEY TO MEDUSAE

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

– marginal tentacles developed at junctions between radial canals and circular canal and along entire circular canal (except *Tiaricodon*); manubrium quadrate; mouth cruciform; interradial "gonads" on manubrium and radial lobes or on radial lobes only. . . . . Moerisiida

2. Manubrium with quadrate or octagonal base and cylindrical mouth tube; interradial "gonads"; usually with exumbrellar cnidocyst pouches or tracks; tentacles with cnidophores (except the Porpitidae). . . . . Zancleida

– generally with cylindrical manubrium with circular base; mouth usually simple and circular; "gonads" normally completely surrounding manubrium . . . . Tubulariida

Suborder MOERISIIDA Poche, 1914

Hydroid: hydranth claviform, with long hypostome; tentacles aboral, scattered, or in one or more whorls under hypostome base; hydrocaulus not clearly demarcated, short, ending in pedal disc or in a creeping stolon; free medusae or reduced gonophores.

Medusa: manubrium quadrate, forming radial lobes; mouth cruciform; "gonads" interradial, 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 spherulous ones.

Recent references: Petersen (1990); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. hydranth with tentacles 2

– hydranth without tentacles . . . . Protohydridae

2. perisarcal base and protective perisarcal spine above hydranth; 3-8, generally 4 distal whorls of capitate tentacles with a few scattered cnidocysts along their length . . . . Halimedusidae

– hydranth without protective perisarcal spine. 3

3. hydranth with filiform or modified moniliform tentacles, in one in one whorl under hypostome; living in freshwater. . . . . Hydridae

– hydranth with moniliform or modified moniliform tentacles scattered or in one whorl around middle part of body; living in brackish or sea water . . . . Moerisiidae

KEY TO MEDUSAE

1. without gastric peduncle 2
– with gastric peduncle 4

2. with perradial manubrial lobes along proximal parts of radial canals; "gonads" on manubrium and perradial lobes . . . . Moerisiidae
– without perradial manubrial lobes 3

3. with "gonads" in four pedunculate pendulous perradial pouches hanging into subumbrellar cavity. . . . . Boeromedusidae
– "Gonads" on manubrium, in 8 -16 adradial pouches . . . . Urashimeidae

4. gastric peduncle conspicuous; "gonads" on perradial manubrial pouches on gastric peduncle. . . . . Polyorchidae
– gastric peduncle short; "gonads" either on manubrium or on manubrium and perradial manubrium lobes. . . . . Halimedusidae

Family BOEROMEDUSIDAE Bouillon, 1995

Hydroid: unknown.
Medusa: with apical projection; manubrium cylindrical; mouth simple, tubular; 4 radial canals and circular canal; 4 conical marginal bulbs; four simple, hollow tentacles with many cnidocyst clusters including a terminal ovoid cluster; "gonads" on manubrium as 4 large perradial pouches hanging freely in subumbrellar cavity; no ocelli.
Recent references: Bouillon (1995b); Schuchert (1996); Bouillon & Barnett (1999); Mills (2000).

Genus ***BOEROMEDUSA*** Bouillon, 1995

Fig. 102A-B
With characters of the family.

Boeromedusa auricogonia Bouillon, 1995b

Family HALIMEDUSIDAE Arai & Brinckmann-Voss, 1980

Hydroid: polyps small (150-200 μm), solitary, with a small circular perisarcal base with a short finger like protective perisarcal extension or spine above hydranth; 3-8, generally 4 distal whorls of capitate tentacles, with a few scattered cnidocysts along their length; medusa buds single, just below tentacles.
Medusa: usually with a low gastric peduncle and with distinct interradial peaks in jelly above manubrium base; manubrium cruciform, with perradial lobes; mouth quadratic to cruciform, with lips lined by cnidocysts; 4 radial canals; 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; no mesenteries; marginal bulbs cylindrical, with abaxial ocelli.
Recent references: Bouillon (1995); Bouillon (1999); Brinckmann-Voss & Arai (1998); Bouillon & Barnett (1999); Bouillon & Boero (2000); Mills (2000).

KEY TO MEDUSAE

1. 4 perradial marginal tentacles 2
– 4 perradial marginal tentacles and 4 interradial groups of marginal tentacles. . . . . *Halimedusa*

2. imperfectly moniliform tentacles . . . . *Tiaricodon*
– tentacles with stalked knobs of cnidocysts . . . . *Urashimea*

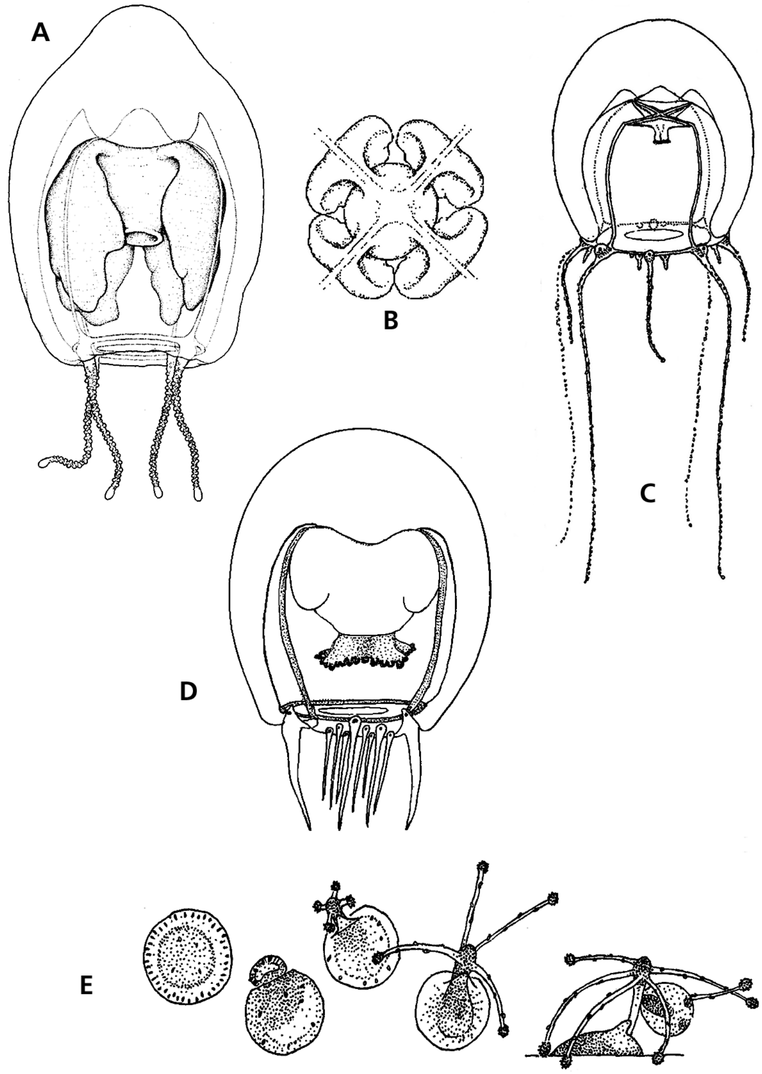


FIG. 102. Anthomedusae. A-B, Boeromedusidae, *Boeromedusa auricogonia*: A, mature medusa; B, apical view of a mature medusa. C-E, Halimedusidae, *Halimedusa typus*: C, developing medusa; D, mature medusa; E, developing stages from planula to a polyp with a medusa bud (A-B after Bouillon, 1995; C & E after Mills, 2000; D after Arai & Brinckmann-Voss, 1980a).

FIG. 102. *Anthomedusae. A-B, Boeromedusidae,* Boeromedusa auricogonia : *A, méduse mature ; B, vue apicale d'une méduse mature. C-E, Halimedusidae,* Halimedusa typus : *C, méduse en voie de développement ; D, méduse mature ; E, divers stades de développement allant de la planula au polype pourvu d'un bourgeon médusaire (A-B d'après Bouillon, 1995 ; C & E d'après Mills, 2000 ; D d'après Arai & Brinckmann-Voss, 1980).*

Genus ***HALIMEDUSA*** Bigelow, 1916

Fig. 102C-E

Hydroid: see family characters.

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

Halimedusa typus Bigelow, 1916

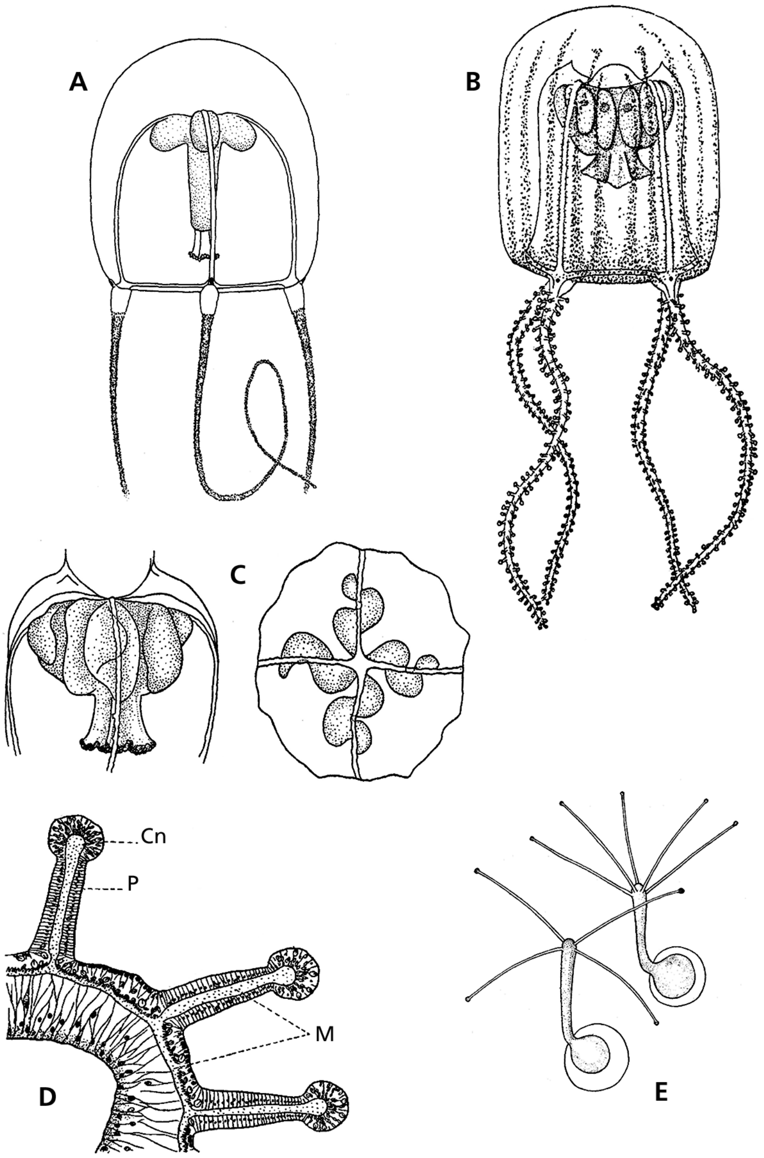


FIG. 103. Anthomedusae, Halimedusidae. A, *Tiaricodon coeruleus*, medusa; B-E, *Urashimea globosa*: B, adult medusa; C, lateral and aboral view of a well-developed medusa; D, cross section of a quadrant of a tentacle; E, young polyps (A after Schuchert, 1996; B after Uchida, 1927a; C-E after Uchida & Nagao, 1961). Cn = cnidocyst knob; M = mesoglea; P = stalk of the cnidocyst knob.

FIG. 103. *Anthomedusae, Halimedusidae. A,* Tiaricodon coeruleus*, méduse. B-E,* Urashimea globosa *: B, méduse adulte ; C, vues latérale et aborale d'une méduse adulte ; D, coupe transversale d'un quadrant de tentacule ; E, jeunes polypes (A d'après Schuchert, 1996 ; B d'après Uchida, 1927a ; C-E d'après Uchida & Nagao, 1961). Cn = bouton de cnidocystes ; M = mésoglée ; P = pédoncule du bouton cnidocytaire.*

Genus ***TIARICODON*** Browne 1902

Fig. 103A

Hydroid: described by Xu and Chen, 1998, resembling a solitary *Coryne*.

Medusa: 4 imperfectly moniliform marginal tentacles; stout, elongated marginal bulbs surrounded by thickened, cnidocyst-studded epidermis; manubrium prismatic with quadratic base, with short sac-like perradial pouches; gastric peduncle small or absent; mouth with 4 distinct frilled lips, thickened with cnidocyst; "gonads" on manubrium surface and manubrial pouches; 4 radial canals without diverticula; abaxial ocelli.

Tiaricodon coeruleus Browne, 1902
Tiaricodon sp. Schuchert, 1996

Genus ***URASHIMEA*** Kishinouye, 1910

Fig. 103B-E

Hydroid: only young stage known, small, solitary, without periderm; hydranth cone-shaped, not distinctly demarcated from hydrocaulus, 4-5 oral tentacles, long, capitate.

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

Urashimea globosa Kishinouye, 1910

Family HYDRIDAE Dana, 1846

Hydroid: solitary, with hollow filiform tentacles, but often moniliform distally, in one whorl under hypostome; eggs and sperm

developed directly in ectoderm of polyps in wart-like protuberances; in hermaphroditic species, "testis" develop on upper part of hydranth, "ovaries" on lower part; asexual reproduction by lateral buds, leading to temporary colonies; lower part of hydranth with simple pedal disc and with central pore, no perisarc except on encysted embryos.
Remarks: The Hydridae are here included in the Moerisiida (see Bouillon 1985a and Petersen 1990 for comments) but it is not excluded that they may form an order by themselves.

Genus ***HYDRA*** Linné, 1758

Fig. 104A-C

Synonyms: *Chlorohydra* Schulze, 1917; *Pelmatohydra* Schulze, 1917.
Hydroid: see family characters.
Recent reference on phylogeny: Petersen (1990).

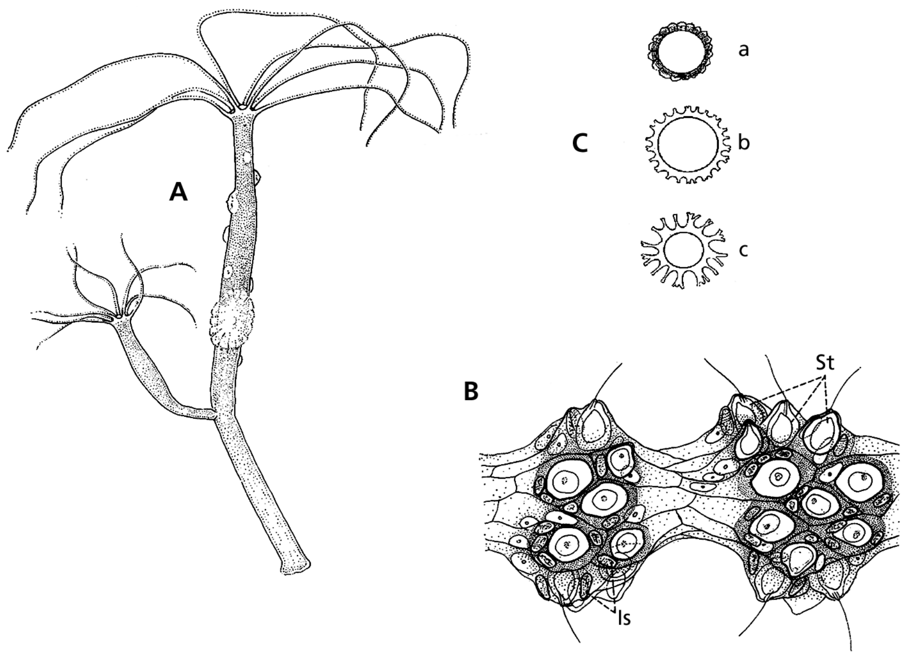
Hydra americana Hyman, 1929
Hydra canadensis Rowan, 1930
Hydra carnea Hyman, 1931
Hydra cauliculata Hyman, 1938
Hydra circumcincta Schulze, 1914
Hydra graysoni Maxwell, 1972
Hydra hadleyi (Forrest, 1959)
Hydra hymanae Hadley & Forrest, 1949
Hydra intaba Ewer, 1948
Hydra iheringi Cordero, 1941
Hydra intermedia de Carvalho Wolle, 1978
Hydra japonica Itô, 1947a
Hydra liriosoma Campbell, 1987
Hydra littoralis Hyman, 1931
Hydra madagascariensis Campbell, 1999
Hydra magnipapillata Itô, 1947b
Hydra mariana Cox & Young, 1973
Hydra minima Forrest, 1963
Hydra mohensis Fan & Shi, 1999
Hydra oligactis Pallas, 1766
Hydra oregona Griffin & Peters, 1939
Hydra oxycnida Schulze, 1914
Hydra paludicola Itô, 1947a
Hydra parva Itô, 1947c
Hydra plagiodesmica Dioni, 1968
Hydra pseudoligactis (Hyman, 1931)
Hydra robusta (Itô, 1947d)
Hydra rutgersensis Forrest, 1963
Hydra salmacidis Lang da Silveira, Souza-Gomes & de Souza Silva, 1997
Hydra umfula R.F. Ewer, 1948
Hydra utahensis Hyman, 1931
Hydra viridissima Pallas, 1766
Hydra vulgaris Pallas, 1766 [syn. *Moerisia alberti* Leloup, 1938]

Family MOERISIIDAE Poche, 1914

Hydroid: aboral tentacles moniliform or modified moniliform, scattered or in one whorl around middle part of the hydranth body; medusa buds on short pedicels between or just under the tentacles; polyp buds produced from lower part of hydranth; hydrocaulus short, ending in pedal disc forming podocysts, or with short stolon-like tubes ending in podocysts or hydranths.
Medusa: manubrium prismatic, with radial lobes on proximal parts of the 4 radial canals; no gastric peduncle; with or without centripetal canals; mouth simple, cruciform; usually without lips except in oldest specimens; "gonads" on manubrium and surrounding manubrial lobes or only on manubrial lobes overlying the radial canals; with either 4, or 16-32, or several hundreds moniliform or modified moniliform hollow marginal tentacles with adnate bulbs; abaxial ocelli; no statocysts.
Recent references: Petersen (1990); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. Tentacles solid, scattered under long hypostome; tentacles with cnidocysts in a terminal knob and several adaxial knobs . . . . *Odessia*
– tentacles hollow, in one whorl or scattered; tentacles moniliform. . . . . *Moerisia*



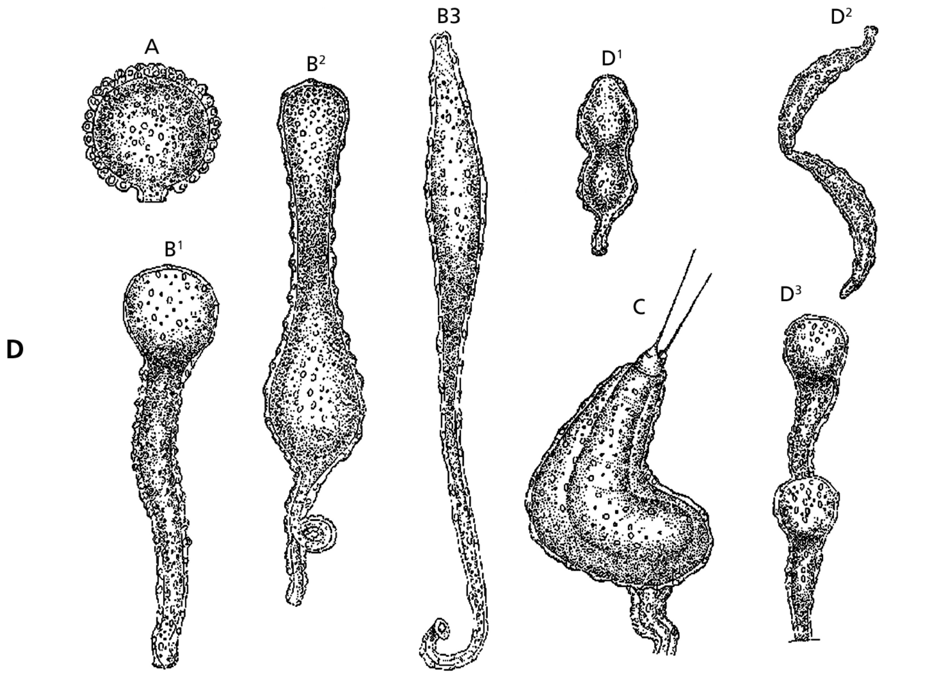


FIG. 104. Anthomedusae, Hydridae. A-C, *Hydra*: A, *Hydra viridis*, hydranth with bud and gonads; B, terminal moniliform portion of a tentacle of *Hydra pirardi*; C, encysted eggs of *Hydra viridissima* (a), *Hydra attenuata* (b), *Hydra vulgaris* (c). Protohydridae. D, *Protohydra leuckarti*: contracted specimen (A), expended specimens (B1, B2, B3), specimen engulfing a copepod (C), various stages of transversal division (D1, D2, D3) (A after Brien, 1950; B after Brien, 1961; C after Steche, 1911; D after Greef, 1869). Is = isorhiza; St = stenoteles.

FIG. 104. *Anthomedusae, Hydridae. A-C,* Hydra : *A,* Hydra viridis, *hydranthe avec un bourgeon polypodial et des gonades ; B, portion terminale moniliforme d'un tentacule de* Hydra pirardi *; C, œufs encystés de* Hydra viridissima *(a),* Hydra attenuata *(b),* Hydra vulgaris *(c). D, Protohydridae,* Protohydra leuckarti : *spécimen contracté (A), spécimens en extension (B1, B2, B3), spécimen mangeant un copepod (C), stades variés de division transversale (D1, D2, D3) (a d'après Brien, 1950 ; B d'après Brien, 1961 ; C d'après Steche, 1911 ; D d'après Greef, 1869). Is = isorhizes ; St = sténotèles.*

KEY TO MEDUSAE

1. radial lobes of manubrium twisted; "gonads" lobed . . . . *Halmomises*
– radial lobes of manubrium not twisted; "gonads" smooth 2
2. marginal tentacles moniliform; "gonads" on manubrium continuous with those on manubrium lobes . . . . *Moerisia*
– marginal tentacles with irregularly transverse cnidocyst claps or bands; "gonads" on manubrium, usually separated from those on manubrial lobes in adults . . . . *Odessia*

Genus ***HALMOMISES*** von Kennel, 1891

Hydroid: unknown.
Medusa: manubrium with radial lobes; "gonads" twisted and folded, extending along proximal portion of radial canals; marginal tentacles with cnidocyst rings throughout their length.
Recent references: Petersen (1990) considered the genus as doubtful due to insufficient description; Jankowski (2001).

Halmomises ancestries Kennel, 1891a [doubtful status]

Genus ***MOERISIA*** Boulenger, 1908

Figs 57E, 105A-C

Synonym: *Ostroumovia* Hadzi, 1928.
Hydroid: with the general characters of the family, tentacles moniliform.
Medusa: either 4, or 16-32 moniliform marginal tentacles; no centripetal canals; "gonads" on manubrium, interradial, continuous with those on manubrial lobes.
Recent references: Petersen (1990); Jankowski (2001).

Moerisia carine Bouillon, 1978c
Moerisia gangetica Kramp, 1958
Moerisia gemmata (Ritchie, 1915)
Moerisia horii (T. & S. Uchida, 1929)
Moerisia inkermanica Paltschikowa-Ostroumova, 1925
Moerisia lyonsi Boulenger, 1908
Moerisia pallasi (Derzhavin, 1912)

Genus ***ODESSIA*** Paspaleff, 1937

Fig. 105D-E

Hydroid: tentacles scattered under hypostome, each with one large terminal knob of cnidocysts and several adaxial knobs.
Medusa: "gonads" on perradial manubrial lobes, usually separated from those on manubrium walls in adults; no centripetal canals; 16-32 marginal tentacles with cnidocysts in irregular transverse claps or bands.
Recent reference: Petersen (1990).

Odessia maeotica (Ostroumoff, 1896)
Odessia multitentaculata Xu, Huang & Chen, 1991 [doubtful status]

Family POLYORCHIDAE Agassiz, 1862

Hydroid: unknown.
Medusa: gastric peduncle usually well developed; manubrium prismatic, with perradial pouches, 4 oral lips crowded with cnidocysts; 4 radial canals with or without blind side branches; "gonads" either spiral or sausage-shaped on perradial manubrial pouches only; tentacles

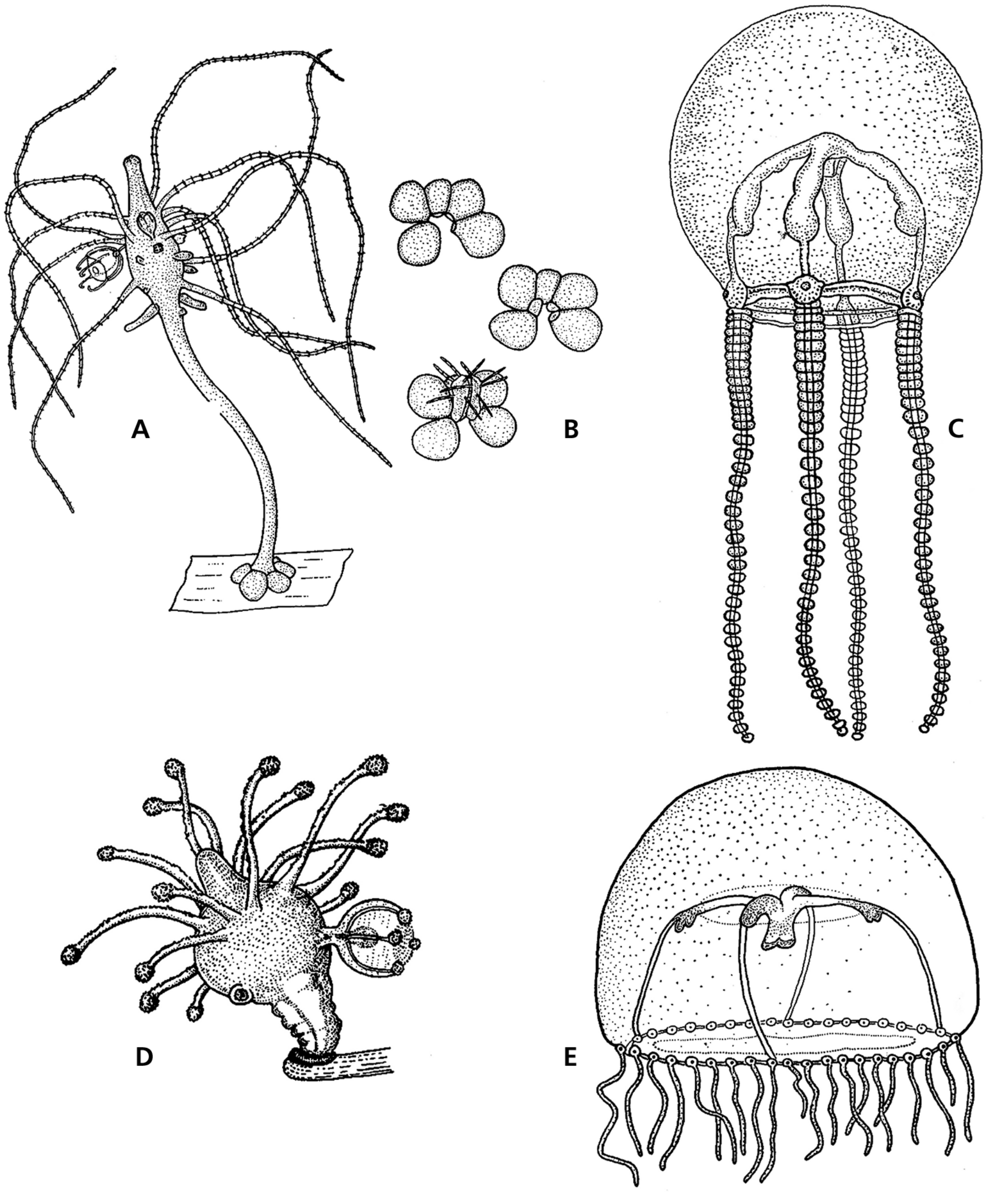


FIG. 105. Anthomedusae, Moerisiidae. A-B, *Moerisia horii*: A, hydroid with podocysts and medusa buds; B, developing podocysts. C, *Moerisia lyonsi*, medusa. D-E, *Odessia maoetica*: D, hydroid with medusa bud; E, adult medusa (A-B after Uchida & Nagao, 1959; C after Rees, 1953; D after Rees, 1958: p. 541, fig. 5; E after Morri, 1981).

FIG. 105. *Anthomedusae, Moerisiidae. A-B,* Moerisia horii : *A, hydroïde avec des podocystes et des bourgeons médusaires ; B, podocystes en développement. C,* Moerisia lyonsi*, méduse mature. D-E,* Odessia maoetica : *D, hydroïde portant un bourgeon médusaire ; E, méduse adulte (A-B d'après Uchida & Nagao, 1959 ; C, d'après Rees, 1953 ; D d'après Rees, 1958 : p. 541, fig. 5 ; E d'après Morri, 1981).*

numerous (24-260) with stout elongate bulbs; abaxial ocelli.

Remarks: the known 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 peduncle and the perradial manubrial pouches become so attached along the gastric peduncle between manubrium and the proximal parts of the radial canals. In most 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.

Recent references: Petersen (1990); Schuchert (1996); Bouillon & Barnett (1999); Bouillon & Boero (2000); Mills (2000).

KEY TO MEDUSAE

1. marginal tentacles in 8 marginal clusters; "gonads" spirally twisted on peduncular manubrium pouches . . . . *Spirocodon*
– marginal tentacles not in clusters; "gonads" sausage-shaped on peduncular manubrium pouches, pendulous 2

2. radial canals with lateral branches . . . . *Polyorchis*
– radial canals without lateral branches. . . . . *Scrippsia*

Genus ***POLYORCHIS*** A. Agassiz, 1862

Fig. 106A

Hydroid: unknown.

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

Polyorchis haplus Skogsberg, 1948
Polyorchis karafutoensis Kishinouye, 1910
Polyorchis penicillatus (Eschscholtz, 1829) [syn. *P. montereyensis* Skogsberg, 1948]

Genus ***SCRIPPSIA*** Torrey, 1909

Fig. 106B

Hydroid: unknown.

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

Scrippsia pacifica Torrey, 1909

Genus ***SPIROCODON*** Haeckel, 1880

Fig. 106C-D

Hydroid: unknown.

Medusa: bell margin drawn up in 8 broad lobes making tentacles appear to be arranged in 8 clusters; tentacles hollow; marginal tentacular bulbs adnate, with abaxial ocelli; 4 radial canals with dendritic side branches; 4 interradial arborescent

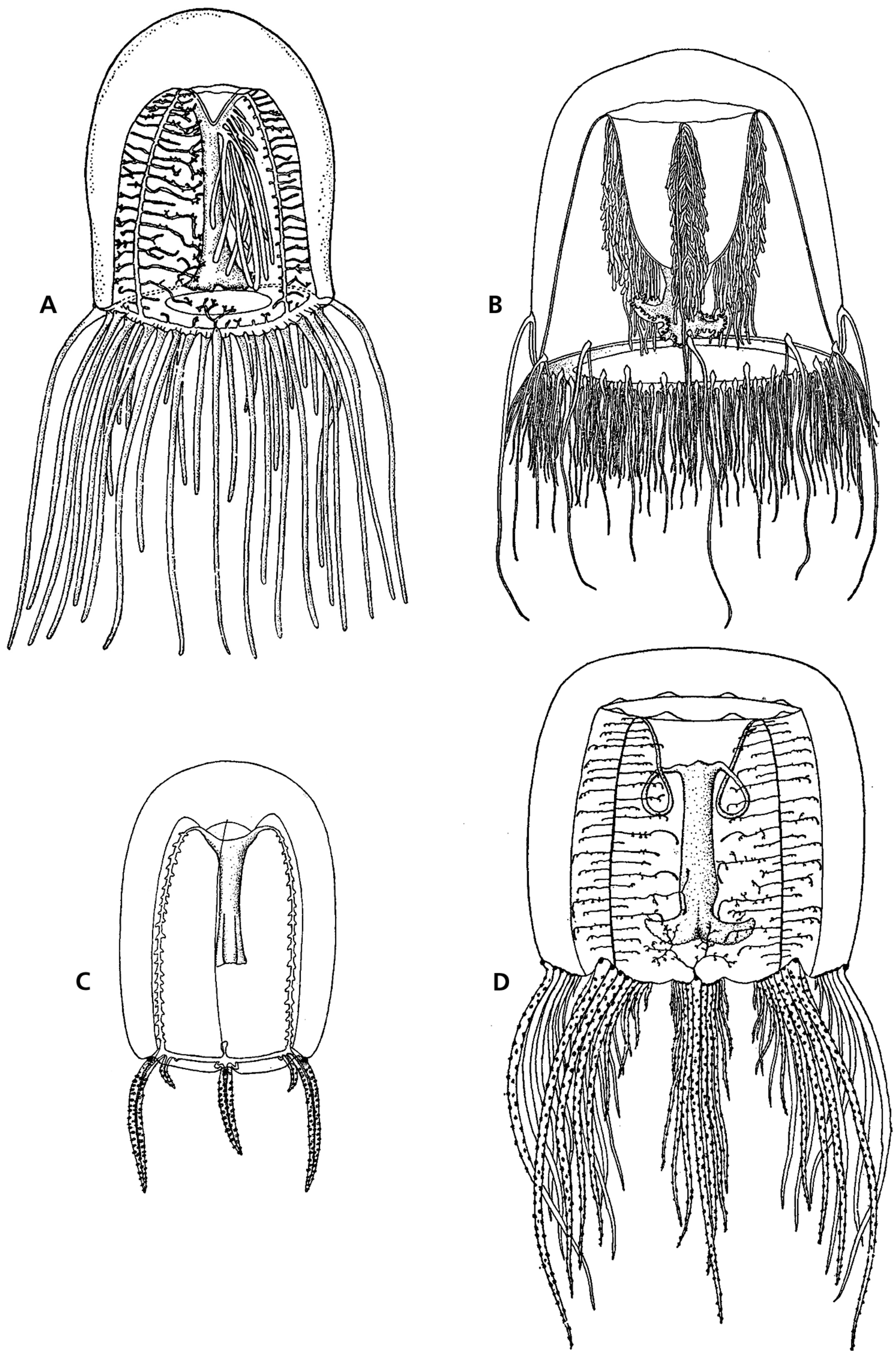


FIG. 106. Anthomedusae, Polyorchidae. A, *Polyorchis karafutoensis*, adult medusa. B, *Scrippsia pacifica*, adult medusa. C-D, *Spirocodon saltator*: C, young medusa; D, adult medusa (A after Nagao, 1970; B after Mayer, 1910; C-D after Uchida, 1927a).

FIG.106. *Anthomedusae, Polyorchidae. A,* Polyorchis karafutoensis*, méduse adulte. B,* Scrippsia pacifica*, méduse adulte. C-D,* Spirocodon saltator : *C, jeune méduse ; D, méduse adulte (A d'après Nagao, 1970 ; B d'après Mayer, 1910 ; C-D d'après Uchida, 1927a).*

centripetal canals in each interradius; gastric peduncle broad, manubrium prismatic, with elongated, spirally twisted, perradial, peduncular pouches, with long frilled lips with a row of cnidocysts; "gonads" along peduncular manubrial pouches.

Spirocodon saltator (Tilesius, 1818)

Family PROTOHYDRIDAE Allman, 1888

Hydroid: paedomorphic, usually living in brackish-waters; hydranth solitary, spindle-shaped, without tentacles but with scattered cnidocyst warts, moving as caterpillars; ectodermal pedal disc; sexual products differentiated in endoderm, reproductive cycle unknown, asexual reproduction by transverse fission.

Genus ***PROTOHYDRA*** Greeff, 1869

Fig. 104D

Hydroid: see family characters.
Remarks: often classified near the Hydridae, based on assumptions and convenience more than facts. Phylogenetic position uncertain; here tentatively incorporated into the Moerisiida.
Recent reference: Thiel (1988); Petersen (1990).

Protohydra caulleryi Dawydoff, 1930
Protohydra leuckarti Greeff, 1869

Suborder SPHAEROCORYNIDA Petersen, 1990

Hydroid: hydrorhiza either stolonal or mat-like, forming a basal plate; numerous long capitate tentacles arranged in 3-6 irregular aboral whorls around middle part of hydranth column, or in 1 or 5-6 close alternate oral whorls surrounding hypostome; gonophores borne on middle part of body, or on basal part of hydrocaulus, or on hydrorhiza.
Medusa: manubrium flask-shaped, quadrate or cruciform in cross-section; "gonads" interradial, adradial or circular; 2-4 perradial marginal capitate tentacles.
Recent references: Petersen (1990); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. hydrorhiza as a chitinised stolonal plate, tentacles in 5-6 whorls around hypostome . . . . Hydrocorynidae
– hydrorhiza as a creeping stolon; tentacles in 3-5 whorls in the middle part of hydranth column . . . . Sphaerocorynidae

KEY TO MEDUSAE

1. umbrella rounded . . . . Hydrocorynidae
– Umbrella conical or dome-shaped 2
2. marginal tentacles terminating in a hollow ellipsoid cnidocyst knob; umbrella with apical chamber . . . . Sphaerocorynidae
– normal capitate marginal tentacles with or without abaxial side branches; no apical chamber . . . . Zancleopsidae

Family HYDROCORYNIDAE Rees, 1957

Hydroid: colony issued from a chitinised hydrorhizal stolonal plate; hydranths columnar, extensile, with thickened, ridged mesogleal lamella; oral tentacles hollow, capitate, in 1 or 5 to 6 close-set whorls around a conical hypostome; fixed gonophores or medusa buds in clusters on proximal part of hydranth body or as eumedusoids, borne single on pedicel from hydrorhiza.
Medusa: umbrella evenly rounded; with or without gastric peduncle; 4 marginal tentacles with scattered cnidocyst knobs and a small capitation; tentacular bulbs clasping, with ocelli; manubrium broadly flask-shaped or tubular, quadratic or cruciform; oral part of manubrium prismatic, ending in a cruciform mouth with or without cnidocyst clusters; "gonads" interradial, without longitudinal groove, surrounding nearly the whole manubrium.

KEY TO HYDROIDS

1. with free medusae; hydranth with oral tentacles in 5-6 close set whorls. . . . . *Hydrocoryne*
– with eumedusoids; hydranth with oral tentacles in 1 whorl. . . . . *Samuraia*

Genus ***HYDROCORYNE*** Stechow, 1907
Fig. 107A-B

Hydroid: hydranth long, naked, spindle-shaped, with numerous (30-70) long hollow tentacles in 5 to 6 close-set whorls around long hypostome; gonophores on short-branched blastostyles on lower part of hydranth.
Medusa: see characters of the family.

Hydrocoryne bodegensis Rees, Hand & Mills, 1976
Hydrocoryne miurensis Stechow, 1907 [syn. *Sarsia resplendens* Bigelow, 1909]

Genus ***SAMURAIA*** Mangin, 1991
Fig. 107C-D

Hydroid: hydranth long, columnar, issued from a hard, encrusting, cup-shaped base; normally 1-3 hydranths per colony, highly extensile with a single row of 13-22 capitate tentacles; gonophores as single eumedusoids, borne on pedicel from hydrorhiza (or from base of hydranth body under laboratory conditions), either retained or liberated.
Medusa: liberated eumedusoids with "gonads" on manubrium, no mouth, tentacles and sense organs.

Samuraia tabularasa Mangin, 1991

Family SPHAEROCORYNIDAE Prévot, 1959

Hydroid: colony stolonal or erect; hydrorhiza creeping; hydrocaulus long, unbranched or slightly branched, with a terminal hydranth; perisarc thin, reaching hydranth base; hydranth vasiform with bulbous base, and proboscis; no oral tentacles but numerous solid, single or trifid capitate tentacles in 3-5 whorls around broadest part of column; gonophores as free medusae or as eumedusoids.
Medusa: umbrella bell-shaped, ovoid; apical mesoglea thick, apical projection conical or dome-shaped, apical chamber broad; manubrium with quadrate base, either flask-shaped, or cruciform; mouth simple, round or cruciform; in non mature specimens "gonads" interradial, apparently divided in adradial masses by longitudinal median grooves, "gonads" confluent in perradii in adult specimens; 4 hollow, marginal tentacles with either adaxial or spirally-arranged cnidocyst clusters and terminating in an ellipsoid capitation; marginal bulbs large, clasping exumbrella, with an adaxial expansion; abaxial ocelli.
Recent references: Wedler & Larson (1986); Calder (1988a); Petersen (1990); Bouillon & Boero (2000).

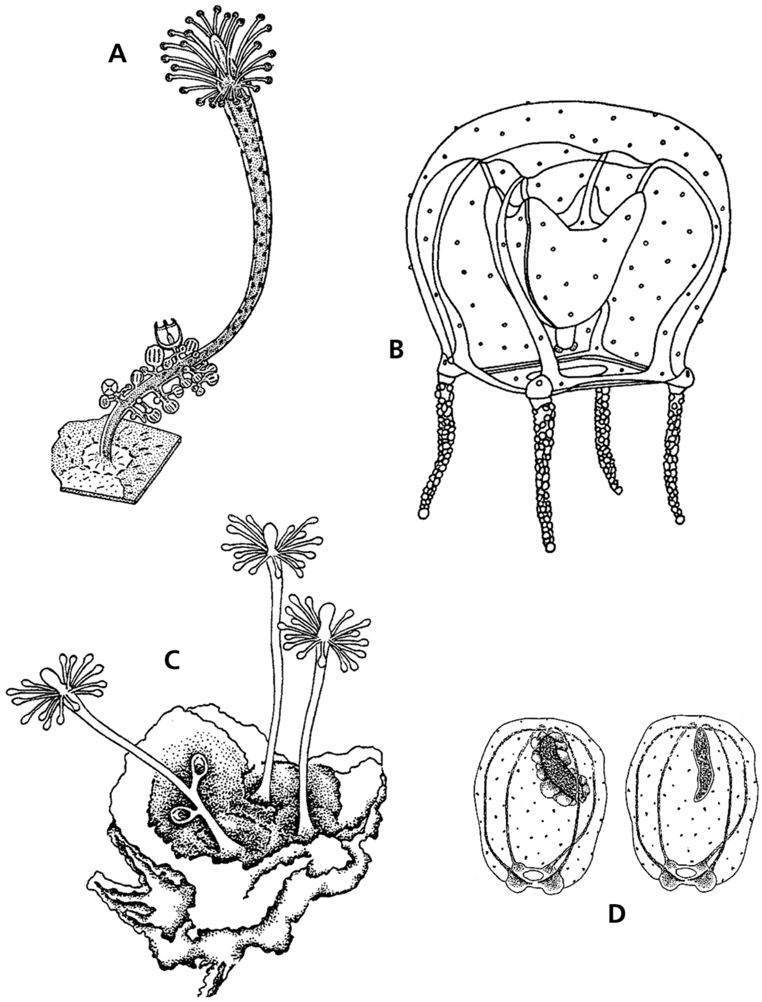


FIG. 107. Anthomedusae, Hydrocorynidae. A, *Hydrocoryne miurensis*, polyp. B, *Hydrocoryne bodegensis*, adult medusa. C-D, *Samuraia tabularasa*: C, polyp; D, free eumedusoids (A after Uchida & Nagao, 1967; B after Rees *et al*., 1976; C-D after Mangin, 1991: p. 445, fig. 2; p. 446, fig. 4).

FIG. 107. *Anthomedusae, Hydrocorynidae. A,* Hydrocoryne miurensis*, polype. B,* Hydrocoryne bodegensis*, méduse adulte. C-D,* Samuraia tabularasa : *C, polype ; D, eumédusoïdes libres (A d'après Uchida & Nagao, 1967 ; B d'après Rees et al., 1976 ; C-D d'après Mangin, 1991 : p. 445, fig. 2 ; p. 446, fig. 4).*

KEY TO HYDROIDS

1. free medusae; simple capitate tentacles only. . . . . *Sphaerocoryne*
– eumedusoids; both simple and trifid capitate tentacles. . . . . *Heterocoryne*

Genus ***HETEROCORYNE*** Wedler & Larson, 1986

Fig. 108C-E

Hydroid: colony stolonal; hydrocaulus unbranched; hydranth vasiform, with one whorl of simple long capitate tentacles and one whorl of long trifid capitate tentacles closely-set around broad basal part; gonophores single, on short pedicel, among upper whorl of simple capitate tentacles, reduced to eumedusoids.
Recent reference: Petersen (1990).

Heterocoryne caribbensis Wedler & Larson, 1986

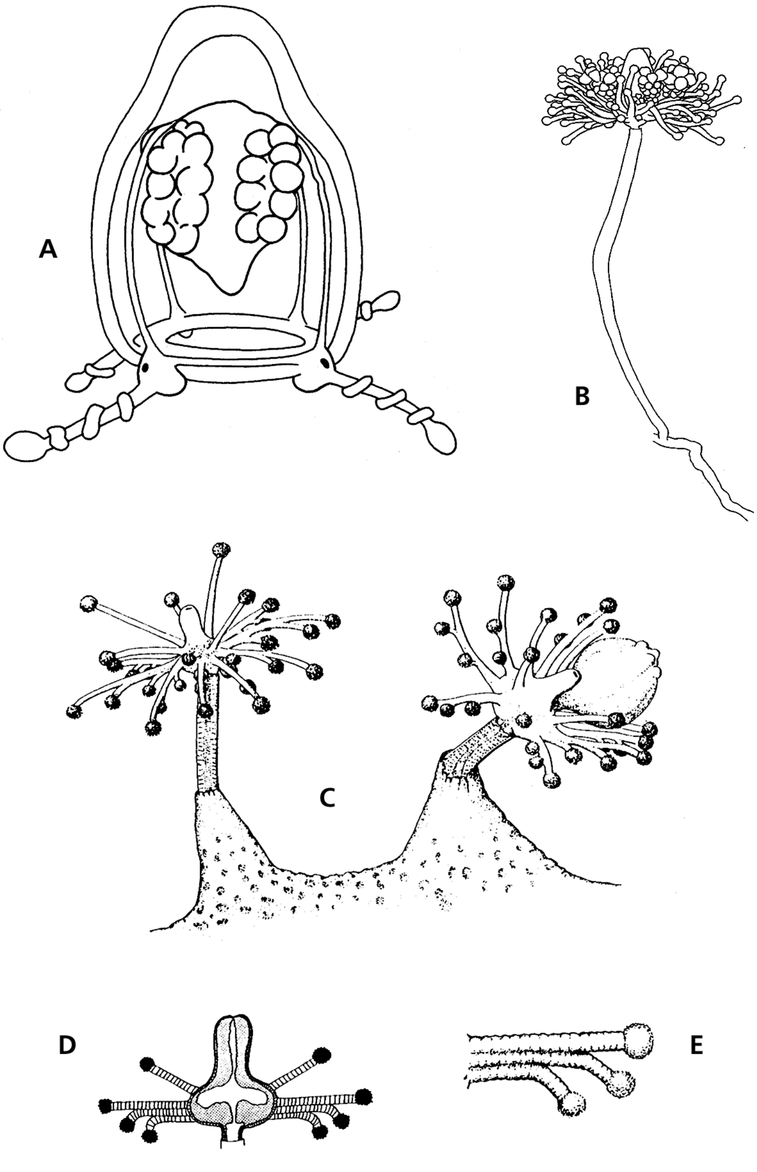


FIG. 108. Anthomedusae, Sphaerocorynidae. A-B, *Sphaerocoryne bedoti*: A, female medusa; B, hydranth with medusa buds. C-E, *Heterocoryne caribbensis*: C, hydranths embedded in sponge, the right one with an eumedusoid bud; D, sagittal section of a hydranth; E, aboral group of tentacles (A after Petersen, 1990; B after Hirohito, 1988; C-E after Wedler & Larson, 1986).

FIG. 108. *Anthomedusae, Sphaerocorynidae. A-B,* Sphaerocoryne bedoti : *A, méduse femelle ; B, hydranthe aves bourgeons médusaires. C-E,* Heterocoryne caribbensis : *C, hydranthes vivant dans une éponge, le spécimen de droite avec un bourgeon d'eumédusoïde ; D, coupe sagittale d'un hydranthe ; E, groupe de tentacules aboraux (A d'après Petersen, 1990 ; B d'après Hirohito, 1988 ; C-E d'après Wedler & Larson, 1986).*

Genus ***SPHAEROCORYNE*** Pictet, 1893

Fig. 108A-B

Synonym: *Linvillea* Mayer, 1910.

Hydroid: colony stolonal; hydrocaulus long, simple or slightly branched; hydranth vasiform, with numerous simple solid capitate tentacles in 3-5 whorls around broadest part; gonophores on short branching blastostyles above or among tentacles.

Medusa: see family characters.

Recent references: Petersen (1990); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Calder *et al.* (2003).

Linvillea arcuata (Haeckel, 1879) [doubtful status]
Sphaerocoryne agassizii (McCrady, 1859)
Sphaerocoryne bedoti Pictet, 1893
Sphaerocoryne peterseni Bouillon, 1984a

Family ZANCLEOPSIDAE Bouillon, 1978

Hydroid: unknown.

Medusa: umbrella conical or dome-shaped, no apical chamber; 2-4 capitate marginal tentacles, with or without lateral capitate branches; marginal bulbs clasping umbrella margin, with adaxial hemispherical projection armed with cnidocysts; manubrium broadly flask-shaped, with quadratic or cruciform base; mouth square or circular, with or without faint lips; "gonads" either surrounding manubrium, or in 4 interradial masses, with deep interradial grooves which may divide them into 8 adradial patches; with or without ocelli either on marginal bulbs, or on proximal part of tentacles.

Recent references: Bouillon (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. without ocelli; “gonads” circular in adults . . . . *Dicnida*
– with ocelli; “gonads” interradial . . . . *Zancleopsis*

Genus ***DICNIDA*** Bouillon, 1978

Fig. 109A

Hydroid: unknown.
Medusa: umbrella dome-shaped, apical projection present; 2 opposite capitate tentacles, with or without adaxial capitate ramification; 4 tentacular bulbs with hemispherical adaxial expansion covered with cnidocysts; manubrium with quadrate base, flask-shaped, cruciform in cross-section, short cylindrical oral part, mouth circular; immature “gonads” interradial, surrounding manubrium when ripe; without ocelli.

Dicnida rigida Bouillon, 1978c

Genus ***ZANCLEOPSIS*** Hartlaub, 1907

Fig. 109B-D

Synonym: *Cnidotiara* Uchida, 1927
Hydroid: unknown.
Medusa: 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 4 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.

Zancleopsis dichotoma (Mayer, 1900a)
Zancleopsis elegans Bouillon, 1978c
Zancleopsis gotoi (Uchida, 1927a) [as *Cnidotiara*]
Zancleopsis symmetrica Bouillon, 1985b
Zancleopsis tentaculata Kramp, 1928

Suborder TUBULARIIDA Fleming, 1828

Hydroid: hydranth with solid or parenchymatic oral tentacles in one whorl around hypostome or spreading down over hydranth body; with solid or parenchymatic aboral tentacles in one or three whorls or absent; free medusae or sporosacs.
Medusa: manubrium generally cylindrical, 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.
Recent references: Hirohito (1988); Petersen (1990).

KEY TO HYDROIDS

1. solitary 2
– colonial 9

2. pelagic . . . . Margelopsidae
– not pelagic 3

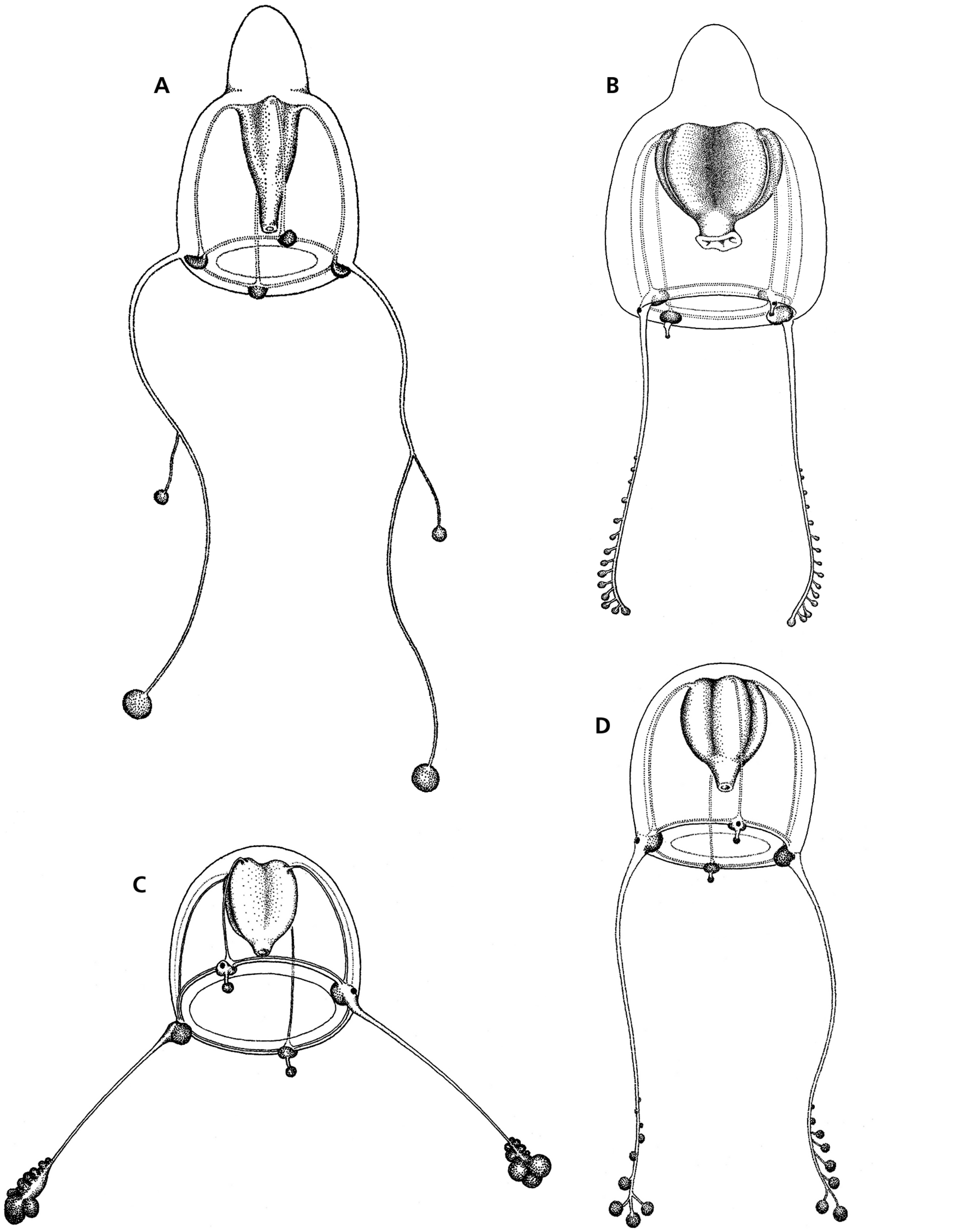


FIG. 109. Anthomedusae, Zancleopsidae. A, *Dicnida rigida*, adult medusa. B, *Zancleopsis tentaculata*, adult medusa. C-D, *Zancleopsis elegans*, adult medusae: C, specimen with contracted tentacles; D, specimen with extended tentacles (all after Bouillon, 1978c).

FIG. 109. *Anthomedusae, Zancleopsidae. A,* Dicnida rigida*, méduse adulte. B,* Zancleopsis tentaculata*, méduse adulte. C-D,* Zancleopsis elegans*, méduses adultes : C, spécimen ayant les tentacules contractés ; D, spécimen avec des tentacules en extension (d'après Bouillon, 1978c).*

3. hydrocaulus with parenchymatic endoderm often with peripheral canals. 4
– hydrocaulus without these characters 5

4. hydranth 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; perisarc usually feebly developed, restricted to base of hydrocaulus . . . . Corymorphidae
– hydranth with capitate, moniliform, filiform or pseudofiliform oral tentacles, in one to several close-set whorls; one whorl of long pseudofiliform or filiform aboral tentacles; perisarc well developed reaching hydranth base, forming a neck region . . . . Tubulariidae

5. tentacles capitate or not, disposed in distinct whorls 6
– numerous scattered capitate tentacles. . . . . Candelabriidae

6. one whorl of reduced tentacles, capitate or not, located in the oral or median part of the hydranth . . . . Boreohydridae
– hydrants with several tentacle whorls 7

7. hydrocaulus thin, with conspicuous inflated gelatinous periderm; oral whorl of capitate tentacles and 2 aboral whorls of moniliform tentacles . . . . Tricyclusidae
– hydrocaulus not surrounded by an inflated gelatinous periderm 8

8. one or two whorls of oral capitate tentacles, and a distal aboral whorl of large fleshy filiform tentacles . . . . Acaulidae
– oral whorl of short moniliform, capitate or filiform tentacles; moniliform or filiform aboral tentacles in 1 or 3 close-set whorls, or dispersed; often with aboral endodermal statocyst-like structure and adhesive mucus organ. . . . . Euphysidae

9. colony polymorphic . . . . Paracorynidae
– colony monomorphic 10

10. colony erect, arborescent, supported by chitinous reticular skeleton . . . . Solanderiidae
– colony different 11

11. colony pinnate (feather-like) . . . . Pennariidae
– colony not pinnate. 12

12. one whorl of oral capitate tentacles and usually below it more capitate tentacles in whorls or scattered; there may be filiform tentacles below capitate ones; hypostome with or without distinct button of gland cells around mouth . . . . Corynidae
– only one oral whorl of capitate tentacles, sometimes one aboral whorl of filiform sensory tentacles; with glandular cells forming a preoral cavity around the mouth . . . . Cladonematidae

KEY TO MEDUSAE

1. reduced medusae, with 4 rudimentary bulbs . . . . Pennariidae
– medusae not reduced, exceptionally without tentacles 2

2. marginal tentacles simple; with 1 - 4 marginal tentacles 3
– Marginal tentacles branched; usually with more than 4 radial canals . . . . Cladonematidae

3. marginal tentacular bulbs with ocelli . . . . Corynidae
– marginal tentacular bulbs without ocelli. 4

4. exumbrella without cnidocyst tracks 5
– exumbrella with cnidocyst tracks . . . . Tubulariidae

5. marginal tentacles in four groups . . . . Margelopsidae
– marginal tentacles solitary 6

6. with 1- 4 marginal tentacles, unequally developed or of the same length but all of same structure; without apical projection . . . . Euphysidae
– with up to four marginal tentacles of different size and structure; umbrella dome-shaped or with pointed apex . . . . Corymorphidae

Family ACAULIDAE Fraser, 1924

Hydroid: hydranth solitary, pear-shaped, with 1 or 2 whorls of oral capitate tentacles, and with a distal aboral whorl of large fleshy filiform tentacles, which may be absent or replaced by capitate tentacles; attached to substrate by a reduced hydrocaulus (= "root" or "peduncle"), by means of a gelatinous fixation tube, or by anchoring filaments, or by a mucous secretion; gonophores as fixed sporosacs in the lower or middle part of the hydranth, asexual reproduction by transverse fission in some species.
Recent references: Petersen (1990); Thomas *et al.* (1995); Schuchert (2001a).

KEY TO HYDROIDS

1. hydranth with filiform tentacles. . . . . *Acaulis*
– hydranth without filiform tentacles 2

2. hydranth very slender, elongated; with long thin only slightly capitate aboral tentacles . . *Cryptohydra*
– hydranth pear-shaped; aboral tentacles capitate . . . . *Acauloides*

Genus ***ACAULIS*** Stimpson, 1854

Fig. 110A

Synonym: *Blastothela* Verrill, 1878.
Hydroid: attached to substrate by modified hydrocaulus, secreting a gelatinous sheath or forming anchoring filaments; hydranth extensile, pear-shaped; oral capitate tentacles numerous, solid, with chordal endoderm; one whorl of aboral tentacles, long, stout filiform, with parenchymatic endoderm; gonophores fixed, carried singly or in clusters on short pedicels.
Recent references: Petersen (1990); Thomas *et al.* (1995); Schuchert (2001a).

Acaulis primarius Stimpson, 1854
Acaulis rosea (Verrill, 1878)

Genus ***ACAULOIDES*** Bouillon, 1965

Fig. 110B

Hydroid: hydrocaulus attached to substrate by a modified basal part, secreting a gelatinous sheath or forming anchoring filaments or by an adhesive basal disc; hydranth pear-shaped, one oral whorl of capitate tentacles and scattered aboral capitate tentacles of irregular length, all with chordal endoderm; gonophores in axils of scattered tentacles, asexual reproduction through transverse fission.
Recent references: Thiel (1988); Petersen (1990); Thomas *et al.* (1995).

Acauloides ammisatum Bouillon, 1965
Acauloides ilonae (Brinckmann-Voss, 1966)

Genus ***CRYPTOHYDRA*** Thomas, Edwards and Higgins, 1995

Fig. 110C

Hydroid: hydranth small from 150 µm up to 1.0 mm solitary, slender; hypostome elongated, flexile capable of sharp bending in region of oral tentacles; 2 separate alternate pairs of 2 short oral tentacles, or one whorl of three oral tentacles; 2, occasionally more, whorls of 3 to 4 long aboral tentacles each; all tentacles slightly capitate and solid; no perisarc;

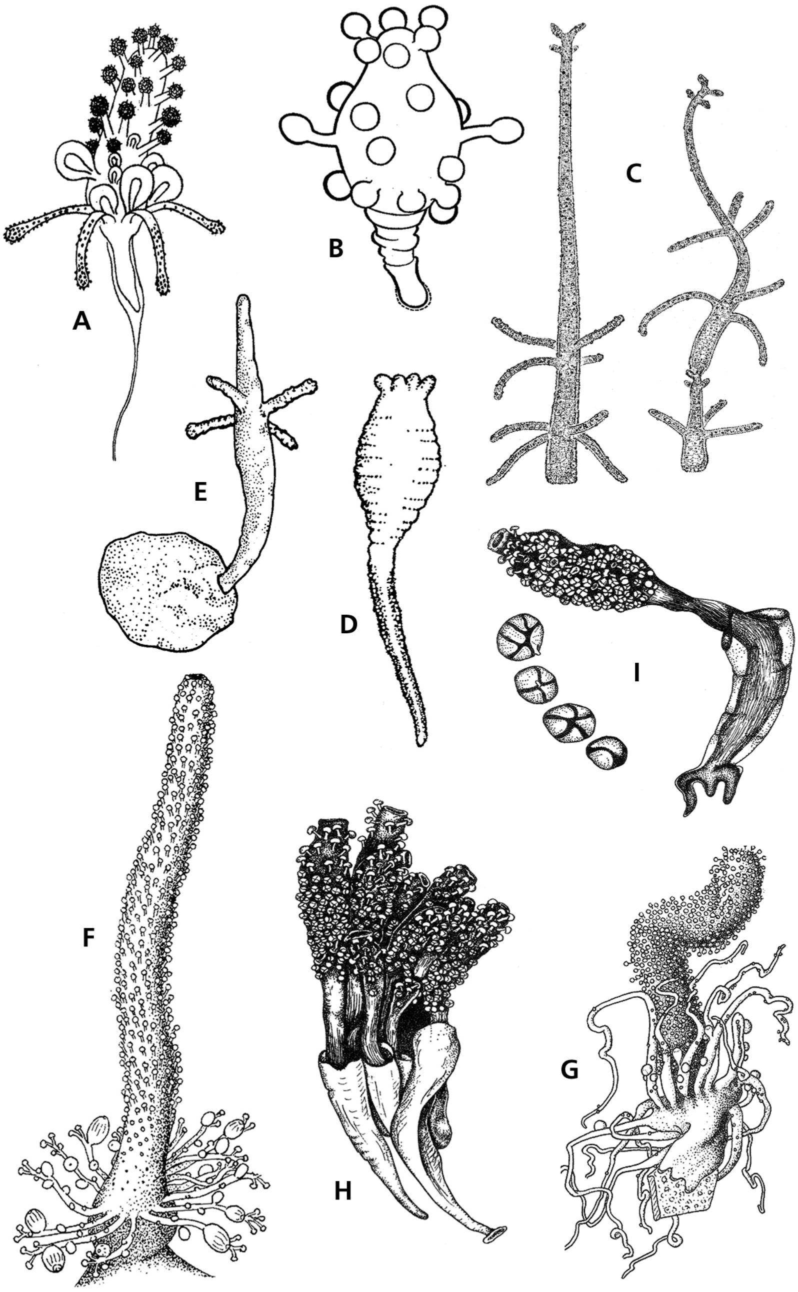


FIG. 110. Anthomedusae. A-C, Acaulidae: A, *Acaulis primarius*, hydranth; B, *Acauloides ammisatum*, hydranth; C, *Cryptohydra thieli*, extended hydranth (left), individual undergoing transverse fission (right). D-E, Boreohydridae: D, *Boreohydra simplex*, hydranth; E, *Psammohydra nanna*, hydranth. F-G, Candelabridae, *Candelabrum*: F, *Candelabrum capensis*, complete individual extended; G, *Candelabrum tentaculatum*, individual attached to a polyzoan. H-I, *Fabulosus kurilensis*: H, conglomerate of hydranths with interlacing perisarcal pedicels; I, isolated hydranth and detail of fixed sporosacs. (A after Hyman, 1940; B after Bouillon, 1971; C after Thomas *et al*., 1995; D after Westblad, 1937; E after Clausen & Salvini-Plauwen, 1986; F-G after Millard, 1975; H-I after Stepanjants *et al*., 1989).

FIG. 110. *Anthomedusae. A-C, Acaulidae : A,* Acaulis primarius*, hydranthe ; B,* Acauloides ammisatum*, hydranthe ; C,* Cryptohydra thieli*, hydranthe en extension (à gauche), individu présentant des divisions transversales (à droite). D-E, Boreohydridae : D,* Boreohydra simplex*, hydranthe ; E,* Psammohydra nanna*, hydranthe. F-G, Candelabridae,* Candelabrum *: F,* Candelabrum capensis*, spécimen complétement étendu ; G,* Candelabrum tentaculatum*, spécimen attaché à un bryozoaire. H-I,* Fabulosus kurilensis *: H, conglomérat d'hydranthes ayant leur pédicelles perisarcaux entrelacés ; I, hydranthe isolaté et détail des sporosacs fixés (A d'après Hyman, 1940 ; B d'après Bouillon, 1971 ; C d'après Thomas* et al.*, 1995 ; D d'après Westblad, 1937 ; E d'après Clausen & Salvini-Plauwen, 1986 ; F-G d'après Millard, 1975 ; H-I d'après Stepanjants* et al.*, 1989).*

glandular adhesive ectodermal basal disc surrounded by slightly overhanging vacuolated ectodermal cells; asexual reproduction by transverse fission; sexual reproduction unknown.

Cryptohydra thieli Thomas, Edwards & Higgins, 1995

Family BOREOHYDRIDAE Westblad, 1947

Hydroid: hydranths solitary, small, with one whorl of reduced tentacles, capitate or not, located in the oral or median part of column; perisarc reduced or absent; gonophores as fixed sporosacs.

Key to hydroids

1. hydranth with oral capitate tentacles and cnidocyst warts; hypostome normal . . . . *Boreohydra*
– hydranth with capitate tentacles in the middle of the body; hypostome extensible . . . . . . *Psammohydra*

Genus ***BOREOHYDRA*** Westblad, 1937

Fig. 110D

Hydroid: hydrocaulus covered by a sheath of agglutinated detritus which may bear rhizoids; hydranth club-shaped, with one oral whorl of 3 to 4 short capitate tentacles and numerous cnidocyst warts; gonophores as fixed sporosacs, resembling cryptomedusoids, which may be developing asexual polyp buds seated singly on lower part of hydranth; eggs occurring singly in ectoderm at border between hydranth and hydrocaulus; asexual reproduction through transverse fission.
Recent references: Thiel (1988); Petersen (1990); Schuchert (2001a).

Boreohydra simplex Westblad, 1937

Genus ***PSAMMOHYDRA*** Schulz, 1950

Fig. 110E

Hydroid: solitary mesopsammic hydranths with 3 to 5 non capitate tentacles in one circlet in the middle of the body; adhesive elements around extensile mouth used during caterpillar-like movements; sexual reproduction unknown, asexual reproduction by fission.
Remarks: *Psammohydra* has been seldom observed, it is the smallest known hydroid, measuring 250 to 400 μ; sometimes considered as *incertae sedis*, it is here included in the Boreohydridae because of its cnidome.
Recent references: Thiel (1988); Petersen (1990).

Psammohydra nana Schulz, 1950

Family CANDELABRIDAE Blainville, 1830

Hydroid: solitary or forming pseudo-colonies; hydrocaulus short, stout, with tubular or root-like adhesive processes, with or without perisarc; hydranth elongated, cylindrical, with thickened mesoglea and endodermal villi; numerous scattered, hollow capitate tentacles, simple or compound; gonophores fixed, developing directly on hydranth or on coryniform blastostyles from aboral part of hydranth, under body tentacles.
Recent references: Petersen (1990); Segonzac & Vervoort (1995); Schuchert (1996); Schuchert (2001a).

KEY TO HYDROIDS

1. capitate tentacles simple 2
– capitate tentacles compound . . . . *Monocoryne*
2. sporosacs borne on coryniform blastostyles; hydranth always solitary . . . . *Candelabrum*
– sporosacs borne singly on hydranth body; conglomerate hydranths forming pseudo-colonies . . . . *Fabulosus*

Genus ***CANDELABRUM*** Blainville, 1830

Fig. 110F-G

Synonym: *Myriothela* Sars, 1850.
Hydroid: hydranth solitary, long, cylindrical with numerous densely packed, simple capitate tentacles; hydrocaulus plate- or tuber-like, with adhesive processes that end in discs covered by firm, lamellar perisarc; gonophores as fixed sporosacs borne on coryniform blastostyles developed from aboral part of hydranth; fertilised eggs borne on special tentacle-like claspers situated among blastostyles.
Recent references: Petersen (1990); Segonzac & Vervoort (1995); Schuchert (1996), Watson (1997); Schuchert (2001a).

Candelabrum australe (Briggs, 1928)
Candelabrum austrogeorgiae (Jäderholm, 1904a)
Candelabrum capensis (Manton, 1940)
Candelabrum cocksii (Vigurs, 1849)
Candelabrum fritchmanii Hewitt & Goddard, 2001
Candelabrum giganteum (Bonnevie, 1898b)
Candelabrum harrisonii (Briggs, 1928)
Candelabrum meridianum (Briggs, 1939)
Candelabrum minutum (Bonnevie, 1898b)
Candelabrum mitra (Bonnevie, 1898b)
Candelabrum penola (Manton, 1940)
Candelabrum phrygium (Fabricius, 1780)
Candelabrum serpentarii Segonzac & Vervoort, 1995
Candelabrum tentaculatum Millard, 1966
Candelabrum verrucosum (Bonnevie, 1898b)

Genus ***FABULOSUS*** Stepanjants, 1990

Fig. 110 H-I

Hydroid: solitary, often forming a conglomerate or pseudo-colony of about 20 hydranths, loosely linked by their tangled basal perisarcal anchoring system, hydrocaulus partly covered with a basal perisarcal sheath forming an anchoring stolon; hydranth with numerous densely packed, single, capitate tentacles, scattered all over body; gonophores numerous (up to 200), only female known, as fixed sporosacs, borne singly, scattered between tentacles along the proximal two-thirds of hydranth.
Recent reference: Stepanjants *et al.* (1990).

Fabulosus kurilensis Stepanjants, Sheiko & Napara, 1990

Genus ***MONOCORYNE*** Broch, 1909

Fig. 111 A-B

Hydroid: solitary or colonial; when colonial, polyps loosely aggregated through fusion of basal processes into a plate, hydrocaulus with root-like adhesive processes, covered by thin, soft perisarc; hydranth stout, with scattered compound capitate tentacles (tentacles attached to one another in groups at their base); gonophores as fixed sporosacs borne singly on aboral half of hydranth.
Recent references: Petersen (1990), Stepanjants *et al.* (2003).

Monocoryne gigantea (Bonnevie, 1898a) [syn. *M. bracteata* (Fraser, 1941)]
Monocoryne minor Millard, 1966
Monocoryne sp. Stepanjants, Sheiko & Napara 2003

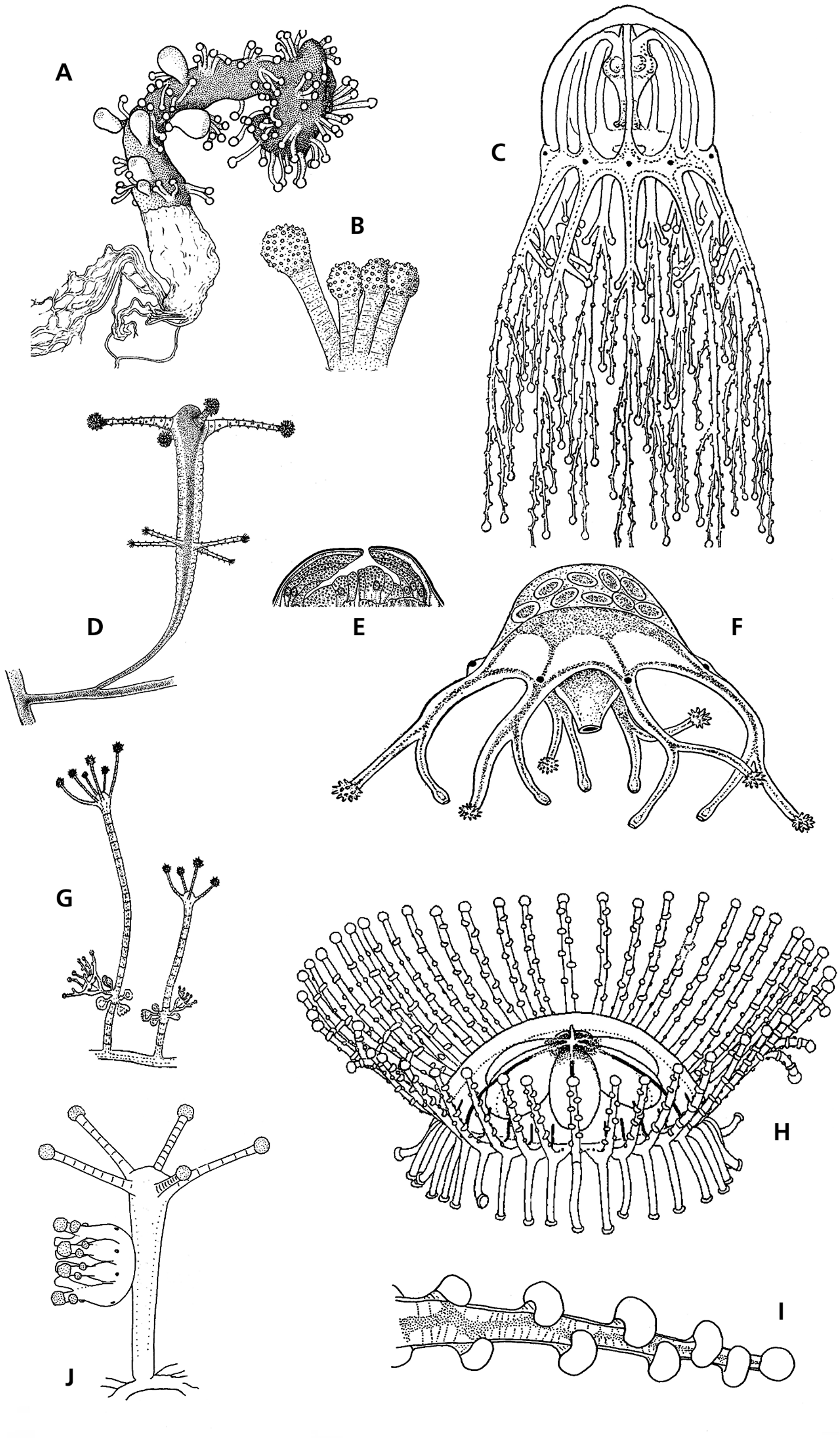


FIG. 111. Anthomedusae. A-B, Candelabridae, *Monocoryne minor*: A, complete individual; B, typical group of four tentacles. C-E, Cladonematidae, *Cladonema radiatum* : C, fully grown medusa; D, hydroid; E, schema of hypostome showing the ectodermal oral cavity. F-G, *Eleutheria dichotoma*: F, mature medusa with planulae inside brooding pouch; G, part of colony with hydranths developing medusa buds. H-J, *Staurocladia wellingtoni*: H, adult medusa; I, aboral view of a tentacle; J, polyp with a medusa bud (A-B after Millard, 1975; C after Russell, 1953; D after Leloup, 1952; E after Bouillon, 1971; F after Hincks, 1868; G after Hincks, 1861a; H-J after Schuchert, 1996).

FIG. 111. *Anthomedusae. A-B, Candelabridae,* Monocoryne minor *: A, hydranthe ; B, groupe typique de quatre tentacules. C-E, Cladonematidae,* Cladonema radiatum *: C, méduse adulte ; D, hydroïde ; E, schéma de l'hypostome montrant la cavité ectodermique orale. F-G,* Eleutheria dichotoma *: F, méduse mature avec des planulas dans la poche incubatrice ; G, portion d'une colonie dont les hydranthes développent des bourgeons médusaires. H-J,* Staurocladia wellingtoni *: H, méduse adulte ; I, vue aborale d'un tentacule ; J, polype développant un bourgeon médusaire (A-B d'après Millard, 1975 ; C d'après Russell, 1953 ; D d'après Leloup, 1952 ; E d'après Bouillon, 1971 ; F d'après Hincks, 1868 ; G d'après Hincks, 1861a ; H-J d'après Schuchert, 1996).*

Family CLADONEMATIDAE Gegenbaur, 1857

Hydroid: colony stolonal or erect, with creeping stolons; stem unbranched or sparingly branched; hydranth spindle-shaped, one whorl of 4-5 solid oral capitate tentacles, with or without aboral whorl of sensory filiform tentacles; mouth with oral ectodermal gland cells forming a preoral chamber; medusa buds not enclosed in perisarcal film, carried singly or in clusters at base of hydranth, distal to aboral tentacles, when these are present.

Medusa: able to walk and/or swim; with or without a thickened continuous or broken ring of cnidocysts around umbrellar margin, with or without apical chamber above manubrium; manubrium cylindrical, with or without per-radial pouches; mouth either with short lips, armed or not with cnidocyst clusters, or with ramified oral tentacles; with variable number of radial canals, some branched, some simple, final number of canals entering circular canal usually corresponding to, or exceptionally exceeding, the number of marginal tentacles; marginal tentacles hollow, with some capitate branches and some adhesive branches; "gonads" either completely surrounding manubrium, on subumbrella, or in special brooding pouches; with abaxial ocelli.

Remarks: The Cladonematidae are often separated in two families: the Cladonematidae and the Eleutheriidae (Russell 1953).

Recent references: Wedler & Larson (1986); Calder (1988a); Migotto (1996); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schierwater & Ender (2000).

KEY TO HYDROIDS

1. medusa buds in clusters or on short blastostyles at hydranth base; no aboral tentacles .... *Eleutheria*
– medusa buds borne singly on hydranth body, immediately above aboral tentacles, or in same position when those are absent .... *Cladonema* and *Staurocladia*

KEY TO MEDUSAE

1. mouth with branched oral tentacles; with apical chamber .... *Dendronema*
– mouth with simple or armed lips; without apical chamber 2

2. bell high; tentacles branching more than once.. *Cladonema*
– bell flat; tentacles branching only once 3

3. one cnidocyst knob on upper tentacular branches .... *Eleutheria*
– more than one cnidocyst knob on upper tentacular branches.......................... *Staurocladia*

Genus ***CLADONEMA*** Dujardin, 1843

Figs 28, 29, 30, 35D, 111C-E

Hydroid: see family characters; with mostly stolonal colony; hydrocaulus occasionally branching, medusa buds borne singly on hydranth body.

Medusa: creeping and swimming; manubrium cylindrical, with perradial pouches; mouth with short lips armed with 4 to 6 cnidocyst clusters; no apical chamber above manubrium; variable number of radial canals, some branched, some simple, final number of canals entering circular canal usually of same number as marginal tentacles; "gonads" completely surrounding manubrium; variable number of hollow branching marginal tentacles, each with 1 to 6 branches ending in an organ of adhesion and 1 to 10 branches with clusters of cnidocysts; with ocelli.

Recent references: Petersen (1990); Wedler & Larson (1986); Calder (1988a); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schierwater & Ender (2000).

Cladonema californicum Hyman, 1947
Cladonema myersi W.J. Rees, 1949
Cladonema pacificum Naumov, 1955
Cladonema radiatum Dujardin, 1843 [syn. *C. mayeri* Perkins, 1906, *C. novaezelandiae* Ralph, 1953, and *C. perkinsi* Mayer, 1904]
Cladonema uchidai Hirai, 1958

Genus *DENDRONEMA* Haeckel, 1879

Hydroid: unknown.
Medusa: oral tentacles branched; apical chamber above manubrium.

Dendronema stylodendron Haeckel, 1879 [doubtful status]

Genus *ELEUTHERIA* Quatrefages, 1842

Fig. 111F-G

Hydroid: see family characters, but with oral tentacles only and medusa buds borne in clusters or on short blastostyles at base of hydranth.
Medusa: umbrellar margin with a thickened cnidocyst ring; brood pouch above manubrium; manubrium simple; mouth, simple circular; "gonads" reduced, hermaphroditic; tentacles bifurcated, lower branch with adhesive disk, upper branch with only one terminal cnidocyst cluster; asexual reproduction by budding from circular canal either from subumbrellar side (*E. claparedei*) or from exumbrellar side (*E. dichotoma*); with ocelli.

Eleutheria claparedei Hartlaub, 1889
Eleutheria dichotoma Quatrefages, 1842

Genus *STAUROCLADIA* Hartlaub, 1917

Figs 13A, 111H-J

Hydroid: see family characters, hydrocaulus unbranched; hydranths with an oral whorl of capitate tentacles, with or without aboral filiform tentacles; medusa buds borne single on hydranth body.
Medusa: 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 cnidocyst knobs; with up to 60 marginal tentacles, dichotomous, upper branch with several cnidocyst clusters, lower with adhesive organ; often asexual reproduction by medusa budding or by fission; with ocelli.
Recent reference: Hirano *et al.* (2000).

Staurocladia acuminata (Edmonson, 1930)
Staurocladia alternata (Edmonson, 1930)
Staurocladia bilateralis (Edmonson, 1930)
Staurocladia charcoti (Bedot, 1908)
Staurocladia haswelli (Briggs, 1920)
Staurocladia hodgsoni (Browne, 1910)
Staurocladia kerguelensis (Gilchrist, 1918)
Staurocladia oahuensis (Edmonson, 1930)
Staurocladia portmanni Brinckmann, 1964a
Staurocladia schizogena Bouillon, 1978a
Staurocladia ulvae Bouillon, 1978a
Staurocladia vallentini (Browne, 1902) [syn. *S. capensis* (Gilchrist, 1918)]
Staurocladia wellingtoni Schuchert, 1996

Family CORYMORPHIDAE Allman, 1872

Hydroid: solitary, 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; either with one whorl of moniliform or capitate oral tentacles or several whorls of filiform oral tentacles; one to 3 whorls of moniliform or filiform aboral tentacles; gonophores as free medusae or fixed sporosacs.

Medusa: dome shaped or with pointed apex; 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; mouth, simple circular; 1- 4 capitate or moniliform marginal tentacles, of 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*).

Recent references: Calder (1988a); Petersen (1990); Pagès *et al.* (1992); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2001a).

KEY TO HYDROIDS

1. hydranth bilaterally symmetrical, with two sets of filiform tentacles; fixed sporosacs .... *Branchiocerianthus*
– hydranth radially symmetrical.. 2

2. hydranth with filiform tentacles only 3
– hydranth with all tentacles not filiform; medusae when present, without apical process 5

3. filiform tentacles in two sets... 4
– filiform tentacles scattered over entire hydranth .... *Hataia*

4. hydranth with canals radiating between aboral tentacles and blastostyles .... *Fukaurahydra*
– hydranth without canals radiating between aboral tentacles and blastostyles; medusa, when present, with pointed apical process and one moniliform tentacle .... *Corymorpha*

5. - hydranth with two rows of moniliform or pseudomoniliform tentacles; fixed sporosacs .... *Gymnogonos*
– hydranth with different tentacular armature; free medusae 6

6. hydranth with numerous oral capitate tentacles in irregular whorls; aboral tentacles filiform; medusae with 3 rudimentary tentacles and one long tentacle differing in size and structure........... *Euphysora*
– hydranth with moniliform oral tentacles; filiform aboral tentacles; medusae with one tentacle ending in an oval or cylindrical swelling armed with cnidocysts .... *Vannuccia*

KEY TO MEDUSAE

1. with one fully developed marginal tentacle.. 2
– usually with 3 short or rudimentary marginal tentacles and one long, fully developed marginal tentacle of different 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*
– exumbrella with uniform surface 3

3. bell margin slightly oblique to vertical axis of the umbrella, no apical process; principal marginal entacle short and thick, ending in long and large, oval to cylindrical ectodermal swelling containing numerous cnidocysts.. *Vannuccia*
– bell margin at right angle to vertical axis of the umbrella, fully developed marginal tentacles different. 4

4. "gonads" on manubrium and on 4 sausage-like interradial manubrial pouches.............. *Gotoea*
– "gonads" simple; manubrium without interradial pouches...................................... 5

5. fully developed marginal tentacle slender, long, moniliform; pointed apical process .... *Corymorpha*
– fully developed marginal tentacle ending in a single cnidocyst capitation or in clusters of cnidocyst capitations; no pointed apical process 6

6. fully developed marginal tentacle with a terminal cnidocyst knob; with one tentacular and three non tentacular bulbs . . . . *Paragotoea*
– fully developed marginal tentacle with terminal ramifications ending in numerous cnidocyst clusters; with only one marginal bulb bearing the tentacle . . . . *Yakovia*

Genus ***BRANCHIOCERIANTHUS*** Mark, 1898

Fig. 112A

Hydroid: very large, over 2 m, in some species; hydrocaulus long, with parenchymatic endoderm, with longitudinal canals, rooted by anchoring filaments; perisarc rudimentary; hydranth bilaterally symmetrical and excentrically seated on hydrocaulus; several whorls of filiform oral tentacles and one whorl of filiform aboral tentacles; thin diaphragm dividing gastric cavity into oral and aboral chambers; oral chamber with unbranched radial canals between blastostyles and aboral tentacles; gonophores as fixed sporosacs on blastostyles immediately above aboral tentacles.
Recent references: Brattström (1956); Petersen (1990).

Branchiocerianthus imperator (Allman, 1885)
Branchiocerianthus italicus Stechow, 1921c
Branchiocerianthus mirabilis Stechow, 1921c
Branchiocerianthus norvegicus Brattström, 1957
Branchiocerianthus reniformis Broch, 1918
Branchiocerianthus urceolus Mark, 1898

Genus ***CORYMORPHA*** M. Sars, 1835

Figs 26O, 112B-C

Synonyms: *Amalthaea* Schmidt, 1852; *Monocaulus* Allman, 1864.
Hydroid: hydrocaulus with thin perisarc, parenchymatic endoderm with longitudinal peripheral canals; lower part with short papillae or/and long anchoring didermic filaments; hydranth vasiform with one or several closely set whorls of oral filiform tentacles, and one whorl of aboral filiform tentacles; parenchymatic diaphragm; free medusae or fixed gonophores.
Medusa: dome-shaped or with pointed apical process, usually with apical canal; one long moniliform tentacle and 3 non tentacular rudimentary bulbs.
Remarks: Svoboda and Stepanjants (2001) distinguished *Corymorpha* from *Monocaulus* on the following features: "(1) unbranched (*Monocaulus*) versus branched (*Corymorpha*) blastostyles and (2) sedentary cryptomedusoids (*Monocaulus*) versus eumedusoids or liberated medusae (*Corymorpha*)". The blastostyles can be branched or unbranched in the same species (e.g., *Corymorpha glacialis* (see Schuchert (2001a)), and medusa reduction is not in itself a valid generic character. Consequently the genus *Monocaulus* is here considered as congeneric with *Corymorpha.*
Recent references: Schuchert (2001a); Svoboda & Stepanjants (2001).

Corymorpha abyssalis Broch, 1909
Corymorpha antarctica Pfeffer, 1889 [insufficiently described juvenile; perhaps in *Gymnogonos*]
Corymorpha appelloefi Bonnevie, 1901
Corymorpha carnea (Clark, 1876)
Corymorpha cingulata (Vanhöffen, 1910) [insufficiently described; perhaps in *Gymnogonos*]
Corymorpha glacialis M. Sars, 1859
Corymorpha groenlandica (Allman, 1876a)
Corymorpha intermedia Schuchert, 1996
Corymorpha iyoensis Yamada, 1958
Corymorpha januarii (Steenstrup, 1854)
Corymorpha microrhiza (Hickson & Gravely, 1907)
Corymorpha nana Alder, 1857
Corymorpha nutans M. Sars, 1835
Corymorpha palma Torrey, 1902
Corymorpha parvula (Hickson & Gravely, 1907)
Corymorpha sagamina Hirohito, 1988
Corymorpha sarsi (Steenstrup, 1854)
Corymorpha tentaculata Hartlaub, 1917 [syn. *Euphysa tentaculata* Linko, 1905]
Corymorpha uvifera (O. Schmidt, 1852)
Corymorpha vardoensis (Loman, 1889)

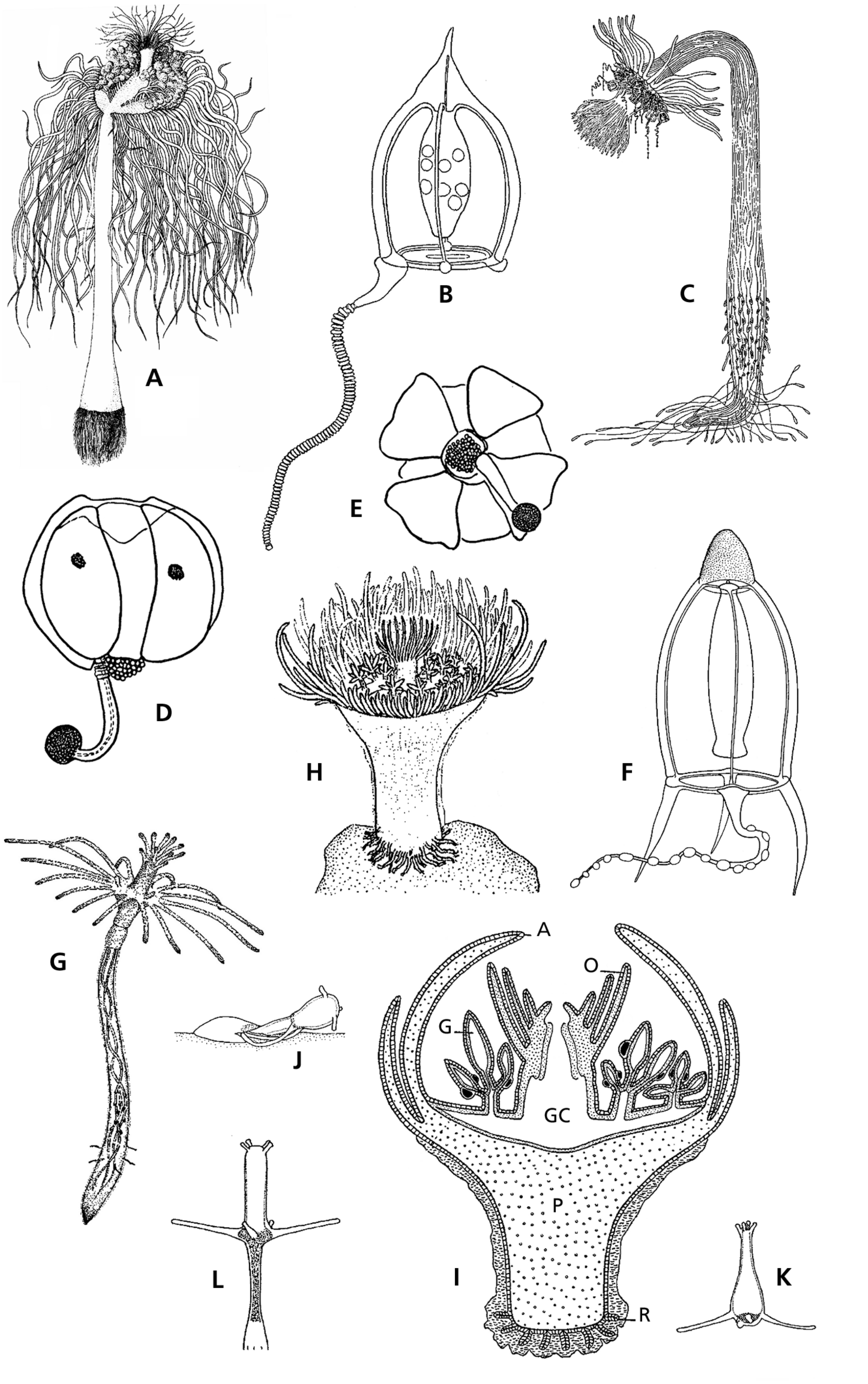


FIG. 112. Anthomedusae. A, Corymorphidae, *Branchiocerianthus imperator*, hydroid. B-C, *Corymorpha nutans*: B, mature medusa; C, hydroid. D-E, *Eugotoea petalina*, mature medusa: D, lateral view; E, oral view. F-G, *Euphysora bigelowi*: F, adult medusa; G, hydroid. H-L, *Fukaurahydra anthoformis*: H, mature male hydranth; I, diagrammatic figure of a female hydranth in longitudinal section; J, actinula creeping from cyst; K, free actinula; L, young polyp (A after Millard, 1975; B after Kramp, 1959b; C after Allman, 1872; D-E after Margulis, 1989; F after Petersen, 1990; G after Sassaman & Rees, 1978; H-I after Yamada *et al*., 1977; J-L afterYamada & Kubota, 1991: p. 160, fig. 2 A, B, C). A = aboral tentacle; G = gonophore; GC = gastric cavity; O = oral tentacle; P = parenchymatic endoderm; R = root process.

FIG. 112. *Anthomedusae. A, Corymorphidae,* Branchiocerianthus imperator, *hydroïde. B-C,* Corymorpha nutans : *B, méduse mature ; C, hydroïde. D-E,* Eugotoea petalina, *méduses matures : D, vue latérale ; E, vue orale. F-G,* Euphysora bigelowi : *F, méduse adulte ; G, hydroïde. H-L,* Fukaurahydra anthoformis : *H, hydranthe mature mâle ; I, figure diagrammatique d'un hydranthe femelle en coupe longitudinale ; J, larve actinula sortant de son cyste ; K, actinula libre ; L, jeune polype (A d'après Millard, 1975 ; B d'après Kramp, 1959b ; C d'après Allman, 1872 ; D-E d'après Margulis, 1989 ; F d'après Petersen, 1990 ; G d'après Sassaman & Rees, 1978 ; H-I d'après Yamada* et al., *1977 ; J-L d'après Yamada & Kubota, 1991 : p. 160, fig. 2 A, B, C). A = tentacule aboral ; G = gonophore ; GC = cavité gastrique ; O = tentacule oral ; P = endoderme parenchymatique ; R = processus radiculaire.*

Genus **EUGOTOEA** Margulis 1989

Fig. 112D-E

Hydroid: unknown.
Medusa: exumbrella divided into 4 prominent leaf-shaped facets separated by 4 longitudinal, large, deep grooves; no marginal bulbs; one marginal tentacle with a terminal cnidocyst knob; “gonads” surrounding manubrium.

Eugotoea armata Margulis, 1997
Eugotoea petalina Margulis, 1989

Genus **EUPHYSORA** Maas, 1905

Fig. 112F-G

Hydroid: known for *E. bigelowi*; hydrocaulus with thin perisarc, with cavity filled by parenchymatic endoderm with a limited number of simple peripheral endodermal canals, with anchoring rootlets; hydranth vasiform, with 35 oral tentacles set in irregular rows on hypostome, more or less distinctly capitate, with scattered cnidocyst batteries; 15-20 aboral elongated non contractile filiform tentacles; a parenchymatic diaphragm separates the hypostome from the polyp body; medusa buds in clusters on slightly branched inflated pedicels arising above aboral tentacles.
Medusa: usually with 3 short or rudimentary tentacles and one long principal tentacle that differs from others not only in size, but also in structure.
Recent reference: Huang (1999).

Euphysora abaxialis Kramp, 1962
Euphysora annulata Kramp, 1928
Euphysora apiciloculifera Xu and Huang, 2003
Euphysora bigelowi Maas, 1905
Euphysora brunnescentis Huang Jiaqui, 1999
Euphysora crassocanalis Xu and Huang, 2003
Euphysora furcata Kramp, 1948
Euphysora gemmifera Bouillon, 1978c
Euphysora gigantea Kramp, 1957
Euphysora gracilis (Brooks, 1882)
Euphysora interogona Xu and Huang, 2003
Euphysora macrobulbus Xu and Huang, 2003
Euphysora normani (Browne, 1916)
Euphysora pseudoabaxialis Bouillon, 1978c
Euphysora russelli Hamond, 1974
Euphysora solidonema Huang Jiaqui, 1999
Euphysora taiwanensis Xu and Huang, 2003
Euphysora valdiviae Vanhöffen, 1911
Euphysora verrucosa Bouillon, 1978c [syn. *E. knides* Huang, 1999]

Genus **FUKAURAHYDRA** Yamada, Konno & Kubota, 1977

Fig. 112H-L

Hydroid: hydrocaulus short, tapering from hydranth, completely filled by parenchymatic endoderm; base flat, circular, surrounded by stout, root-like processes; hydranth broad, vasiform; about 3 whorls of filiform oral tentacles and 2 close-set whorls of aboral filiform tentacles; gastric cavity confined to hypostome and radial canals branched between blastostyles and aboral tentacles; thin diaphragm delimiting radiating canals between aboral tentacles and blastostyles; fixed sporosacs borne on dichotomously branched blastostyles between oral and aboral tentacles.
Recent reference: Yamada & Kubota (1991).

Fukaurahydra anthoformis Yamada, Konno & Kubota, 1977

Genus *GOTOEA* Uchida, 1927

Fig. 113A-B

Hydroid: unknown.
Medusa: 4 radial canals, one bulb bearing a well developed, hollow tentacle, ending in a cnidocyst knob; 3 marginal bulbs without tentacles, clasping exumbrella; manubrium with interradial, sausage-like gastric pouches; mouth simple, without lips; “gonads” encircling manubrium, extending along gastric pouches; no ocelli.

Gotoea similis Kramp, 1959b
Gotoea typica Uchida, 1927a

Genus *GYMNOGONOS* Bonnevie, 1898

Fig. 113C-D

Hydroid: hydrocaulus stout, covered with thin mucous perisarc secreted just under aboral tentacles, endoderm parenchymatic, with peripheral longitudinal canals in aboral third; short papillae in whorls immediately under hydranth, sparsely scattered below and in groups with short rooting filaments around aboral end of hydrocaulus; papillae and rooting filaments with endodermal statocysts; hydranth broad, not clearly demarcated from hydrocaulus, one to three whorls of moniliform or pseudofiliform oral tentacles and one whorl of longer moniliform or pseudofiliform aboral tentacles; endodermal diaphragm absent; gonophores as fixed sporosacs carried on short pedicels over aboral tentacles.
Recent references: Schuchert (2001a), Stepanjants & Svoboda (2001).

Gymnogonos ameriensis (Stepanjants, 1979) [as *Corymorpha*]
Gymnogonos crassicornis Bonnevie, 1898b
Gymnogonos obvolutus (Kramp, 1933a)

Genus *HATAIA* Hirai and Yamada, 1965

Fig. 113E-G

Hydroid: hydrocaulus not developed; pedal disc present; no perisarc; hydranth claviform or sub-spherical, with 11-21 filiform tentacles with swollen tip, scattered over almost all body; tentacles not of equal length, upper and lower ones shorter than middle ones; gonophores as fixed sporosacs among tentacles; fertilised eggs develop inside female gonophore; egg able of encystment; asexual reproduction by buds produced from the tentaculate part of hydranth.
Recent reference: Yamada & Kubota (1991).

Hataia parva Hirai & Yamada, 1965

Genus *PARAGOTOEA* Kramp, 1942

(*sensu* Kramp 1961, not Ralph 1959)
Fig. 113H

Hydroid: unknown.
Medusa: no exumbrellar cnidocyst tracks; 4 radial canals, no gastric pouches; mouth circular; 1 well developed tentacle terminating in large cnidocyst knob, 3 large marginal bulbs without tentacles but with cnidocyst spurs; proximal part of tentacle hollow, distal part solid; simple gonad, annular in mature specimens; no ocelli.
Recent references: Pagès & Bouillon (1997); Brinckmann-Voss & Arai (1998).

Paragotoea bathybia Kramp, 1942
Paragotoea elegans Margulis, 1989

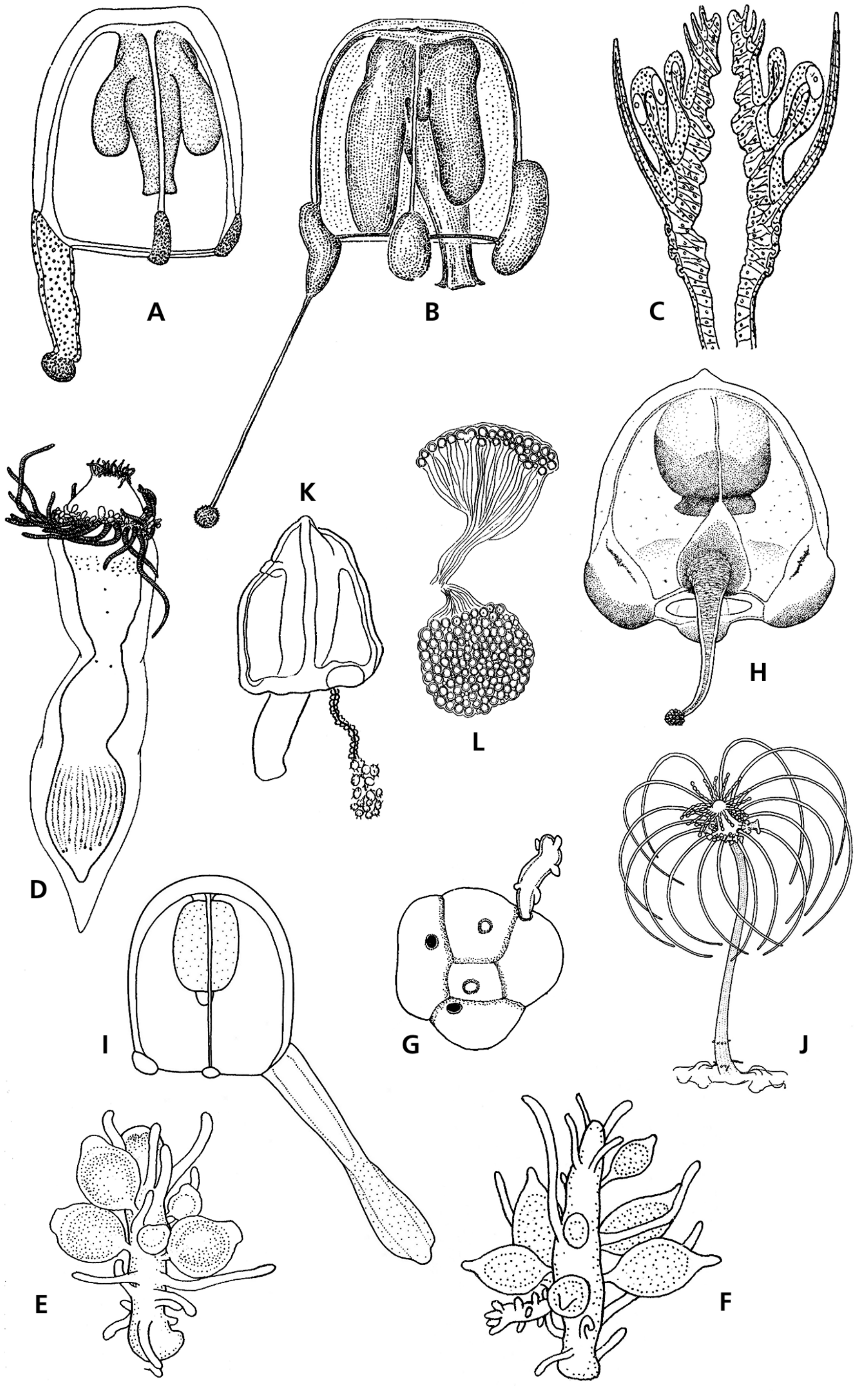


FIG. 113. Anthomedusae. A-B, Corymorphidae, *Gotoea*: A, *Gotoea typica*, adult medusa; B, *Gotoea similis,* adult medusa. C-D, *Gymnogonos*: C, *Gymnogonos crassicornis*, longitudinal section through a hydranth showing the position of the gonophores; D, *Gymnogonos obvolutus*, hydranth showing the mucoid periderm. E-G, *Hataia parva*: E, hydranth with female gonophores; F, hydranth with male gonophores and a new polyp bud; G, primary polyp just hatching from a mass of cysts. H, *Paragotoea bathybia*, adult medusa. I-J, *Vannuccia forbesii*: I, mature medusa; J, hydroid. K-L, *Yakovia polinae*: K, mature medusa; L, lateral & aboral view of a cnidocyst cluster (A-B after Kramp, 1968; C after Kramp, 1949; D after Petersen, 1990; E-F after Hirai & Yamada, 1965; G after Yamada & Kubota, 1991: p. 163, fig. 5 C; H after Pagès & Bouillon, 1997; I-J after Schuchert, 1996; K-L after Margulis, 1989).

FIG. 113. *Anthomedusae. A-B, Corymorphidae,* Gotoea : *A,* Gotoea typica*, méduse adulte ; B,* Gotoea similis*, méduse adulte. C-D,* Gymnogonos : *C,* Gymnogonos crassicornis*, section longitudinale au travers d'un hydranthe montrant la position des gonophores ; D,* Gymnogonos obvolutus*, hydranthe montrant le périderme mucoïde. E-G,* Hataia parva : *E, hydranthe avec des gonophores femelles ; F, hydranthe avec des gonophores et un nouveau bourgeon polypoïdal ; G, polype primaire venant d'éclore d'une masse de cystes. H,* Paragotoea bathybia*, méduse adulte. I-J,* Vannuccia forbesii : *I, méduse mature ; J, hydroïde. K-L,* Yakovia polinae : *K, méduse mature ; L, vue latérale et aborale d'un amas de cnidocystes (A-B d'après Kramp, 1968 ; C d'après Kramp, 1949 ; D d'après Petersen, 1990 ; E-F d'après Hirai & Yamada, 1965 ; G d'après Yamada & Kubota, 1991 : p. 163, fig. 5 C ; H d'après Pagès & Bouillon, 1997 ; I-J d'après Schuchert, 1996 ; K-L d'après Margulis, 1989).*

Genus *VANNUCCIA* Brinckmann-Voss, 1967

Fig. 113I-J

Synonym: *Altairina* Vargas-Hernandez & Ochoa-Figueroa, 1991.
Hydroid: hydrocaulus long, cylindrical, slightly enlarged at its two extremities, aboral third with papillae and, more aborally, numerous rooting anchoring filaments; filled with parenchymatic endodermal cells presenting numerous peripheral longitudinal canals; surrounded by a flexible perisarc extending slightly below hydranth; hydranth vasiform, 12-14 oral moniliform tentacles with 4-6 cnidocyst clusters, 16 to 20 long aboral filiform tentacles with a more or less developed terminal swelling; parenchymatic diaphragm; medusa buds naked, in clusters on short blastostyles above aboral whorl of tentacles; asexual reproduction by transverse constriction of the basal part of the hydrocaulus.
Medusa: bell margin usually slightly asymmetrical, with or without apical process; no exumbrellar cnidocyst tracks; marginal bulbs small, simple; 1 swollen marginal tentacle, hollow for half its length and ending in long, large, oval to cylindrical swelling armed with cnidocysts.

Vannuccia cargoi (Vargas-Hernandez & Ochoa-Figueroa, 1991)
Vannuccia forbesi (Mayer, 1894)

Genus *YAKOVIA* Margulis, 1989

Fig. 113K-L

Hydroid: unknown.
Medusa: 4 radial canals, 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; "gonads" encircling central part of manubrium.

Yakovia polinae Margulis, 1989

Family CORYNIDAE Johnston, 1836

Hydroid: branched or unbranched, monomorphic colonies rising from a creeping stolon or encrusted base; hydranths with an oral whorl of capitate tentacles and often more capitate tentacles below, in whorls or scattered; sometimes filiform tentacles (specialised sense organs) below capitate ones; gonophores usually on polyps, either as sessile sporosacs, eumedusoids or free medusae. Cnidome, where known: stenoteles with or without isorhizas or mastigophores.
Medusa: umbrella bell-shaped; with or without apical chamber; no cnidocyst tracks; manubrium tubular; mouth simple, circular; 4 radial canals and circular canal; with four tentacular bulbs with gastrodermal chamber and 2-4 hollow equally developed marginal tentacles; "gonads" encircling manubrium completely, in one or more rings; mostly with abaxial ocelli. Cnidome where known: as in hydroids but additionally with desmonemes.
Recent references: Wedler & Larson (1986); Calder (1988a); Brinckmann-Voss (1989); Petersen (1990); Kubota & Takashima (1992); Pagès *et al.* (1992); Migotto (1996); Schuchert (1996, 2001a; b); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. conspicuous button of ectodermal gland cells around mouth 2
– no distinct button of ectodermal gland cells around mouth 3

2. gonophores as free medusae; polyps often associated with sponges . . . . *Dipurena*
– sexual cells developing in the hydranth endodermal layer; polyps as members of meiofauna . . . . *Nannocoryne*

3. hydranth with an oral whorl of capitate tentacles and with or without capitate tentacles either scattered or in at least three whorls below oral one, with or without filiform tentacles 4
– hydranth with one oral and one basal whorl of capitate tentacles, with or without a median whorl . 5

4. gonophores develop either in the upper axil of the lower capitate tentacles or amongst the lower whorl . . . . *Coryne*
– gonophores develop below capitate tentacles and over filiform tentacles . . . . *Sarsia*

5. basal tentacles slightly more numerous than oral ones; gonophores as free medusae developing below basal tentacles . . . . *Dicyclocoryne*
– hydranth with or without one whorl of capitate tentacles between oral and basal ones, number of tentacles of basal whorl twice or more than in oral whorl; gonophores as sporosac developing above basal whorl of tentacles. . . . . *Bicorona*

KEY TO MEDUSAE*

1. marginal bulbs with adaxial cnidocyst pads 2
– marginal bulbs without adaxial cnidocyst pads. 3

2. with 2 - 4 equal marginal tentacles with abaxial peduncled cnidocyst knobs and bifurcating distally in two terminal cnidocyst knobs . . . . *Cladosarsia*
– with 2 - 4? marginal tentacles with a single terminal cnidocyst knob. . . . . *Paulinum*

3. "gonads" divided in two or more rings (except *Dipurena gemmifera*). . . . . *Dipurena*
– "gonads" not interrupted, undivided 4

4. adult medusae with manubrium extending beyond umbrella margin, with a thin proximal part . . . . *Sarsia*
– adult medusae with manubrium not extending beyond umbrella margin, without thin proximal part . . . . *Coryne*

**Dicyclocoryne*: medusae known only as newly liberated medusae, without ocelli.

Genus ***BICORONA*** Millard, 1966

Fig. 114A-C

Hydroid: forming large, branching colonies; hydranth vasiform, all tentacles capitate, with one oral whorl of four tentacles and one basal whorl of seven or more tentacles; with or without one whorl of four tentacles between distal and proximal whorl; gonophores as fixed sporosacs developing above aboral whorl of tentacles. Cnidocysts: stenoteles only.
Recent references: Schuchert (1996; 2001b).

Bicorona elegans Millard, 1966
Bicorona tricycla (Schuchert, 1996) [as *Coryne*]

Genus *CLADOSARSIA* Bouillon, 1978

Fig. 114D

Hydroid: unknown.
Medusa: marginal bulbs with large adaxial cnidocyst pads; 4 similar perradial tentacles with abaxial peduncled cnidocyst knobs, bifurcating at their end, each branch with terminal cnidocyst knob; "gonads" surrounding completely manubrium or only its oral half; ocelli.
Recent reference: Schuchert (2001b).

Cladosarsia capitata Bouillon, 1978c
Cladosarsia minima Bouillon, 1978a

Genus *CORYNE* Gaertner, 1774

Figs 5A, 12, 14A, 45, 46, 114E-F

Synonyms: *Syncoryna* Ehrenberg, 1834; *Staurocoryne* Rotch, 1872; *Actigia* Stechow, 1921.
Hydroid: colony stolonal or erect, branching; hydranth with an oral whorl of capitate tentacles and with or without capitate tentacles either scattered or in at least three whorls below oral one, with or without filiform tentacles; hypostome without distinct button of ectodermal mucous gland cells; gonophores as free medusae or fixed sporosacs developing singly or in couples, on short pedicels either in the upper axil of the lower capitate tentacles or amongst the lower whorl.
Medusae: adult medusae with manubrium not extending beyond umbrella margin and without thin proximal part; marginal bulbs without adaxial cnidocyst pads; "gonads" undivided.
Recent references: Brinckmann-Voss (1989; 2000); Petersen (1990); Kubota & Takashima (1992); Pagès *et al.* (1992); Schuchert (1996); Brinckmann-Voss & Arai (1998); Schuchert (2001a; b); Calder *et al.* (2003).

Coryne angulata (Mayer, 1900b) [doubtful status]
Coryne barentsi Linko, 1905 [doubtful status]
Coryne brachiata Nutting, 1901a
Coryne brachygaster (Grönberg, 1898) [doubtful status]
Coryne brevicornis Bonnevie, 1898a [doubtful status]
Coryne brevis Stechow, 1923b [doubtful status]
Coryne caespes Allman, 1871
Coryne clavata (Graeffe, 1884) [doubtful status]
Coryne cliffordi (Brinckmann-Voss, 1989)
Coryne codonoformis Haeckel, 1879 [perhaps a syn. of *C. prolifera*]
Coryne conferta Allman, 1876 [doubtful status]
Coryne conica (Haeckel, 1880) [doubtful status]
Coryne corrugata Fraser, 1925 [doubtful status]
Coryne crassa Fraser, 1914a
Coryne cylindrica (Kirkpatrick, 1890a) [doubtful status]
Coryne dubia Ritchie, 1907a [doubtful status]
Coryne epizoica Stechow, 1921c [doubtful status]
Coryne eximia Allman, 1859 [syn. *C. tenella* Farquhar, 1895]
Coryne ferox Wright, 1867 [doubtful status]
Coryne filiformis (W.J. Rees, 1936)
Coryne fucicola (de Filippi, 1866)
Coryne graeffei Jickeli, 1883 [doubtful status]
Coryne gracilis (Browne, 1902) [doubtful status, perhaps a syn. of *C. eximia*]
Coryne heroni Pennycuik, 1959 [doubtful status]
Coryne hincksii Bonnevie, 1898b
Coryne inabai (Uchida, 1933)
Coryne japonica (Nagao, 1962)
Coryne longicornis Bonnevie, 1898b [doubtful status]
Coryne minima (Von Lendenfeld, 1885a) [doubtful status]
Coryne muscoides (Linnaeus, 1761) [syn. *C. vaginata* Hincks, 1861]
Coryne nipponica (Uchida, 1927a)
Coryne nutans Allman, 1869 [doubtful status]
Coryne occidentalis (Fewkes, 1889) [doubtful status]
Coryne pintneri Schneider, 1898
Coryne producta (Wright, 1858)
Coryne prolifera(Forbes, 1848)
Coryne pusilla Gaertner, 1774 [syn. *C. fructicosa* Hincks, 1861]
Coryne radiata (Von Lendenfeld, 1884a) [doubtful status]
Coryne repens Fraser, 1938a [doubtful status]
Coryne rosaria L. Agassiz, 1862a [doubtful status]
Coryne sagamiensis Hirohito, 1988
Coryne sargassicola Calder, 1988a [doubtful status]
Coryne uchidai Stechow, 1931
Coryne vanbenedeni Hincks, 1868 [doubtful status]
Coryne wortleyi (Rotch,1872) [doubtful status]

Genus ***DICYCLOCORYNE*** Annandale, 1915

Fig. 114G-I

Hydroid: colony more or less branched; with one oral whorl of four capitate tentacles and one aboral whorl of 6 capitate tentacles; gonophores as free medusae borne on hydranths under aboral tentacles.
Medusa: only newly liberated 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 cnidocyst knob; no ocelli.
Recent references: Petersen (1990); Bouillon & Boero (2000), Schuchert (2001b).

Dicyclocoryne filamentata (Annandale, 1907)

Genus ***DIPURENA*** McCrady, 1859

Figs 13C, 26B, 114J-N

Hydroid: colony stolonal, creeping, rarely with branching stems; hydranth with one oral whorl of capitate tentacles and, in most species, with aboral capitate tentacles either scattered or in more or less distinct whorls, sometimes with a whorl of filiform tentacles beneath capitate ones; hypostome with a conspicuous button of high ectodermal gland cells; gonophores giving rise to free medusae usually in clusters, on short pedicels or blastostyle.
Medusa: 4 similar perradial tentacles; marginal bulbs without adaxial cnidocyst pads; with or without linear swellings on radial canals; "gonads" divided in two or more rings around manubrium (except *D. gemmifera*); endoderm of sexual parts digestive, endoderm of non sexual parts chordal; manubrium usually extending well beyond umbrellar margin; with ocelli.
Recent references: Petersen (1990); Pagès *et al.* (1992); Schuchert (1996; 2001b).

Dipurena baukalion Pagès, Gili & Bouillon, 1992
Dipurena bicircella J.T. Rees, 1977
Dipurena brownei (Bigelow, 1909) [probably a syn. of *D. ophiogaster*]
Dipurena dolichogaster Haeckel, 1864 [doubtful status]
Dipurena gemmifera (Forbes, 1848) [as *Sarsia*] [syn. *D. fertilis* Metschnikoff, 1871 and *Sarsia siphonophora* (Haeckel, 1879)]
Dipurena halterata (Forbes, 1846)
Dipurena pyramis (Haeckel, 1879) [doubtful status]
Dipurena reesi Vannucci, 1956
Dipurena simulans Bouillon, 1965
Dipurena spongicola Anger, 1972
Dipurena strangulata McCrady, 1859

Genus ***NANNOCORYNE*** Bouillon & Grohmann, 1994

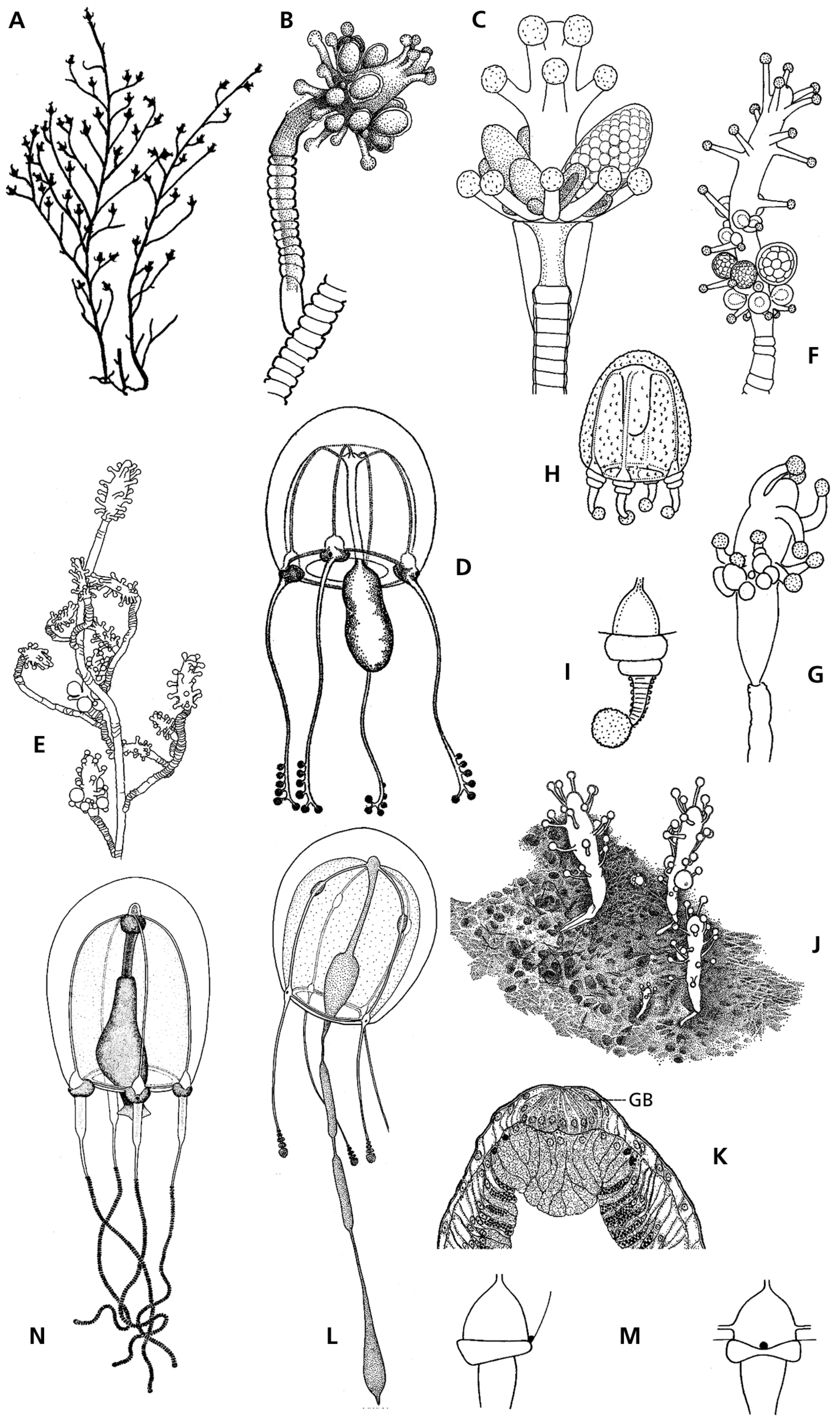
Fig. 115A

Hydroid: meiofaunal, stolonal, minute (500μ; hydrocaulus unbranched, short; hydranth caliciform to club-shaped with one whorl of oral capitate tentacles and one whorl of aboral filiform tentacles; ectodermal spherulous gland cells in a button around mouth; gonozooids similar to gastrozooids, sexual cells developing in the endodermal layer.
Recent reference: Schuchert (2001b).

Nannocoryne mammylia Bouillon & Grohmann, 1994

FIG. 114. Anthomedusae. A-C, Corynidae, *Bicorona*: A, *Bicorona elegans*, general view of a colony; B, mature hydranth bearing gonophores; C, *Bicorona tricycla*, mature hydranth. D, *Cladosarsia capitata*, adult medusa. E-F, *Coryne pusilla*: E, colony; F, hydranth with female gonophores. G-I, *Dicyclocoryne filamenata*: G, hydranth with medusa buds; H, new released medusa; I tentacle and bulb. J-N, *Dipurena*: J-M, *Dipurena halterata*: J, hydroid colony; K, longitudinal section of hypostome showing the glandular mucous button characteristic of the genus; L, adult medusa; M, marginal tentacular bulbs, lateral and frontal view; N, *Dipurena baukalion*, mature medusa (A-B after Millard, 1975; C after Schuchert, 1996: D after Bouillon, 1978c; E after Hirohito, 1988; F after Schuchert, 2001b; G-I after Annandale, 1915; J after Bouillon, 1971; K after Bouillon, 1968: p. 102, fig. 5; L & N after Pagès *et al*., 1992; M after Petersen, 1990). GB = glandular button.

***FIG.** 114. Anthomedusae. A-C, Corynidae,* Bicorona : *A,* Bicorona elegans*, vue générale d'une colonie ; B, hydranthe mature développant des gonophores ; C,* Bicorona tricycla*, hydranthe mature. D,* Cladosarsia capitata*, méduse adulte. E-F,* Coryne pusilla : *E, colonie ; F, hydranthe développant des gonophores femellles. G-I,* Dicyclocoryne filamenata : *G, hydranthe avec bourgeons medusaires ; H, jeune méduse venant de se libérer ; I, tentacule et bulbe. J-N,* Dipurena : *J-M,* Dipurena halterata : *J, colonie d'hydroïdes ; K, section longitudinale de l'hypostome montrant le bouton de cellules glandulaires ectodermiques muqueux caractéristique du genre ; L, méduse adulte; M, bulbes tentaculaires marginaux, vues latérale et frontale ; N,* Dipurena baukalion*, méduse mature (A-B d'après Millard, 1975 ; C d'après Schuchert, 1996 ; D d'après Bouillon, 1978c ; E d'après Hirohito, 1988 ; F d'après Schuchert, 2001b ; G-I d'après Annandale, 1915 ; J d'après Bouillon, 1971 ; K d'après Bouillon, 1968 : p. 102, fig. 5 ; L & N d'après Pagès* et al.*, 1992 ; M d'après Petersen, 1990). GB = bouton glandulaire.*
Dipurena ophiogaster *Haeckel, 1879 [possible syn.* Euphysa problematica *Schuchert, 1996]*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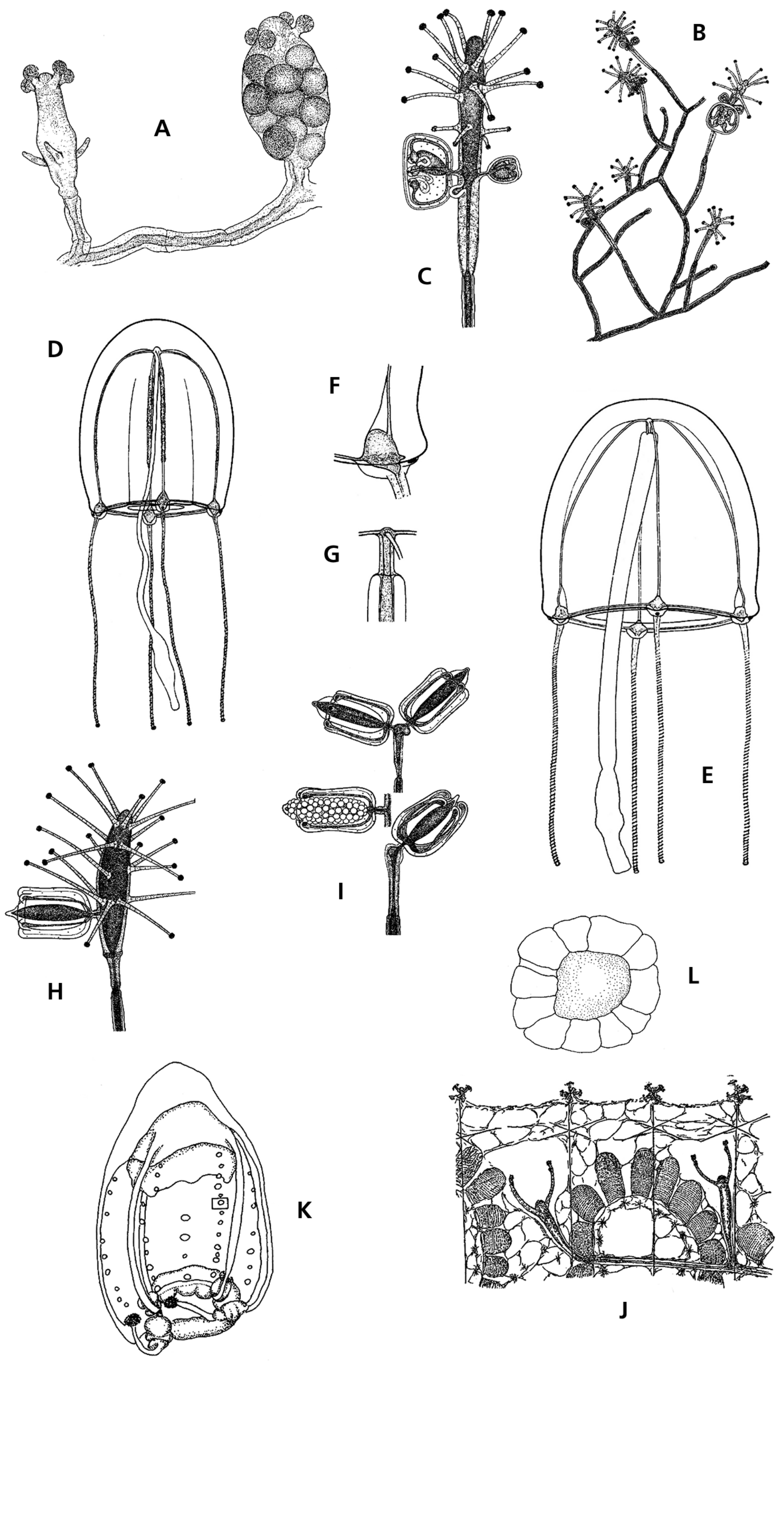


FIG. 115. Anthomedusae. A, Corynidae, *Nannocoryne mammylia*, part of colony with gonozooid. B-I, *Sarsia*: B-G, *Sarsia tubulosa*: B, hydroid colony; C, hydranth with medusa buds; D, subadult medusa; E, mature medusae; F, tentacle bulb; G, basal part of manubrium; H-I, *Sarsia lovenii*: H, hydranth with male ripe fixed eumedusoid; I, regressing hydranths with male and female eumedusoids. J, *Bibrachium euplectellae*, colony living in a hexactinelid sponge. K-L, *Paulinum lineatum*: K, medusa; L, detail of the inclusions in mesoglea, see square in figure (A after Bouillon & Grohmann, 1994; B-I after Edwards 1978; J after Schulze, 1880; K-L after Brinckmann-Voss & Arai, 1998).

FIG. 115. *Anthomedusae. A, Corynidae,* Nannocoryne mammylia, *fragment de colonie avec un hydranthe et un gonozoïde. B-I,* Sarsia : *B-G,* Sarsia tubulosa : *B, colonie d'hydroïde ; C, hydranthe avec des bourgeons médusaires ; D, méduse subadulte ; E, méduse mature ; F, bulbe tentaculaire ; G, partie basale du manubrium ; H-I,* Sarsia lovenii : *H, hydranthe avec des eumedusoïdes mâle mûrs ; I, hydranthes régressés avec des eumedusoïdes mâle et femelle. J,* Bibrachium euplectellae, *colonie vivant dans une éponge hexactinelides. K-L,* Paulinum lineatum : *K, méduse ; L, détail des inclusions dans la mésoglée, voir rectangle dans la figure (A d'après Bouillon & Grohmann, 1994 ; B-I d'après Edwards 1978 ; J d'après Schulze, 1880 ; K-L d'après Brinckmann-Voss & Arai, 1998).*

Genus ***SARSIA*** Lesson, 1843

Figs 25A-I, 26A, 35B, 115B-I, 162E

Synonym: *Stauridosarsia* Mayer, 1910.

Hydroid: hydranth with one oral whorl of capitate tentacles and with or without lower capitate tentacles, with or without filiform tentacles; tentacles usually longer and thinner than in other Corynidae; gonophores as free medusae or fixed sporosacs developing below capitate tentacles or over filiform ones; cnidome with or without isorhizae cnidocysts.

Medusa: manubrium extending beyond umbrella margin, divided in a thin, long, serpentine proximal part and a swollen distal one; "gonad" forming a cylinder around thin serpentine part of manubrium living distal part free.

Recent references: Brinckmann-Voss (1989; 2000); Petersen (1990); Kubota & Takashima (1992); Pagés *et al.* (1992); Schuchert (1996; 2001a; b); Brinckmann-Voss & Arai (1998).

Sarsia apicula (Murbach & Shearer, 1902)
Sarsia bella Brinckmann-Voss, 2000
Sarsia coccometra Bigelow, 1909 [probably a species of *Sphaerocoryne*]
Sarsia densa (Hartlaub, 1897) [probably Sarsia *tubulosa* (M. Sars, 1835)]
Sarsia erythrops Romanes, 1876a [doubtful status]
Sarsia fructescens (Allman, 1871) [doubtful status]
Sarsia hargitti (Mayer, 1910) [doubtful status]
Sarsia lovenii (M. Sars, 1846)
Sarsia marii Schierwater & Ender, 2000 [doubtful status]
Sarsia nana Stechow, 1923c [doubtful status]
Sarsia ocellata Busch, 1851[as *Dicodonium*] [doubtful status]
Sarsia occulta Edwards, 1978
Sarsia pattersoni Haddon, 1886 [doubtful status, could be a syn. of *Sarsia tubulosa*]
Sarsia piriforma Edwards, 1983
Sarsia polyocellata Uchida, 1927a [doubtful status]
Sarsia princeps (Haeckel, 1879)
Sarsia pulchella Forbes, 1848 [doubtful status]
Sarsia striata Edwards, 1983
Sarsia tubulosa (M. Sars, 1835)
Sarsia turricula McCrady, 1859a [doubtful status]
Sarsia viridis Brinckmann-Voss, 1980

Corynidae *incertae sedis*:

Genus ***BIBRACHIUM*** Stechow, 1919

Fig. 115J

Hydroid: living in sponges of the genus *Euplectella*; hydranth with two opposite capitate tentacles each with an adoral cluster of cnidocysts just below capitation; reproduction unknown.

Bibrachium euplectellae (Schulze, 1880)

Genus ***DICODONIUM*** Haeckel, 1879

Hydroid: unknown.

Medusa: 2 well-developed tentacles; with or without perradial rudimentary tentacles; without meridional lines of cnidocysts on exumbrella; with or without ocelli.

Remarks: several species of *Dicodonium* have been described, generally observed only once. Petersen (1990) suggested that they should all be considered as nomina dubia with the exception of *D. floridanum* Mayer, 1910 which is probably valid but does not belong to the Corynidae.

Dicodonium adriaticum Graeffe, 1884 [probably a young pandeid]
Dicodonium cornutum Haeckel, 1879 [doubtful status]
Dicodonium dissonema Haeckel, 1879 [doubtful status]
Dicodonium floridanum Mayer, 1910 [probably a corymorphid]
Dicodonium jeffersoni (Mayer, 1900) [probably a species of *Coryne*]

Genus ***PAULINUM*** Brinckmann-Voss & Arai, 1997

Fig. 115K-L

Hydroid: unknown.
Medusa: umbrella cone-shaped; manubrium wide, with conical extension of base into mesoglea, not tubular at mouth end; 4 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.
Recent reference: Schuchert (2001b).

Paulinum punctatum (Vanhöffen, 1911) [as *Dicodonium*]
Paulinum lineatum Brinckmann-Voss & Arai, 1998 [doubtful status]

Genus ***SARSIELLA*** Hartlaub, 1907

(no figure available)

Hydroid: unknown
Medusa: 2 opposite marginal tentacles; with ocelli.
Remarks: obsolete genus, due to insufficient description.

Sarsiella dinema Hartlaub, 1907 [doubtful status]

Family EUPHYSIDAE Haeckel, 1879

Hydroid: solitary, hydrocaulus without parenchymatic endoderm and peripheral canals, naked or surrounded by a reduced perisarc often of more or less gelatinous consistency; hydranth without parenchymatic diaphragm, with an oral whorl of short moniliform, capitate or filiform tentacles; aboral tentacles moniliform or filiform, in one or three close-set whorls, or dispersed; hydranth often with an aboral irregular whorl of 4-16 short papillae, each with an endodermal statocyst-like structure or with an adhesive mucus organ; gonophores as free medusae or fixed sporosacs developing above aboral whorl of tentacles.
Medusa: umbrella generally evenly rounded; no exumbrellar cnidocyst tracks; manubrium stoutly cylindrical, not extending beyond umbrella margin; mouth simple, circular; 1-4 marginal tentacles, either unequally developed or of similar length, all of same structure; "gonads" encircling almost all length of manubrium.
Remarks: Petersen (1990) recognised only two genera with medusae within the family Corymorphidae: *Corymorpha* and *Euphysa*. *Euphysa* medusae were defined by him as follows: "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:" Petersen's definition, however, appears not well founded: *Euphysa flammea*, *Euphysa japonica*, *Euphysomma brevia*, for instance, have four tentacles that are not unequally developed. Petersen (1990) considered the following genera as identical with *Euphysa*: *Hypolytus; Heteractis*; *Meiorhopalon*; *Euphysomma*. *Euphysomma* is here considered as valid.
Recent references: Petersen (1990); Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. mesopsammic, with tentacles more or less filiform; hydrocaulus with 4 short papillae with endodermal statocyst, covered by leaf-like ectodermal lappet . . . . . . *Siphonohydra*
– hydranth with two types of tentacles 2
1. mesopsammic, with capitate oral tentacles and aboral filiform tentacles; posterior part of hydranth with a glandular static fold and an aboral adhesive button . . . . . . *Pinushydra*

– oral tentacles capitate, aboral tentacles moniliform; hydrocaulus with an irregular whorl of glandular papillae below aboral whorl of tentacle, each with an endodermal statocyst-like structures .... *Euphysa*

KEY TO MEDUSAE

1. with 1- 4 marginal tentacles, either unequally developed or of similar length, usually moniliform or modified moniliform.......... *Euphysa*
– 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
– marginal tentacles very short, each dividing in 3-5 short capitate branches .... *Cnidocodon*

3. base of manubrium quadrate, "gonads" circular along all length of manubrium; marginal tentacles with numerous adaxial (8-11) or abaxial (6-9) transverse cnidocyst clasps and 1 small terminal cluster .... *Euphysilla*
– base of manubrium circular; "gonads" circular, leaving aboral part of manubrium free; manubrium with short rounded apical chamber; marginal tentacles with 2 to 4 abaxial shortly peduncled cnidocyst knobs and a terminal cluster.......... *Euphysomma*

Genus ***CNIDOCODON*** Bouillon, 1978

Fig. 116A

Hydroid: unknown.
Medusa: umbrella dome-shaped; scattered cnidocysts on exumbrella; 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" around manubrium, leaving only most oral part free.

Cnidocodon leopoldi Bouillon, 1978c [syn. *C. xiamenensis* Zhang & Wu, 1981]

Genus ***EUPHYSILLA*** Kramp, 1955

Fig. 116B

Hydroid: unknown.
Medusa: umbrella evenly rounded; manubrium with quadratic base; mouth circular; 4 equally developed tentacles with adaxial or abaxial clasps and a terminal cnidocyst cluster; no gastric peduncle; mature "gonads" circular, surrounding all manubrium; no ocelli.

Euphysilla peterseni Allwein, 1967
Euphysilla pyramidata Kramp, 1955

Genus ***EUPHYSA*** Forbes, 1848

Fig. 116C-G

Synonyms: *Hypolytus* Murbach, 1899; *Meiorhopalon* Salvini-Plawen, 1987.
Hydroid: hydrocaulus about twice as long as hydranth, embedded in a soft, sticky perisarc, covered by mud and detritus; with an irregular whorl of glandular papillae, each with an endodermal statocyst-like structure below aboral whorl of tentacles; hydranth almost cylindrical, with rounded hypostome, with 3-10 oral capitate tentacles and up to 20 aboral

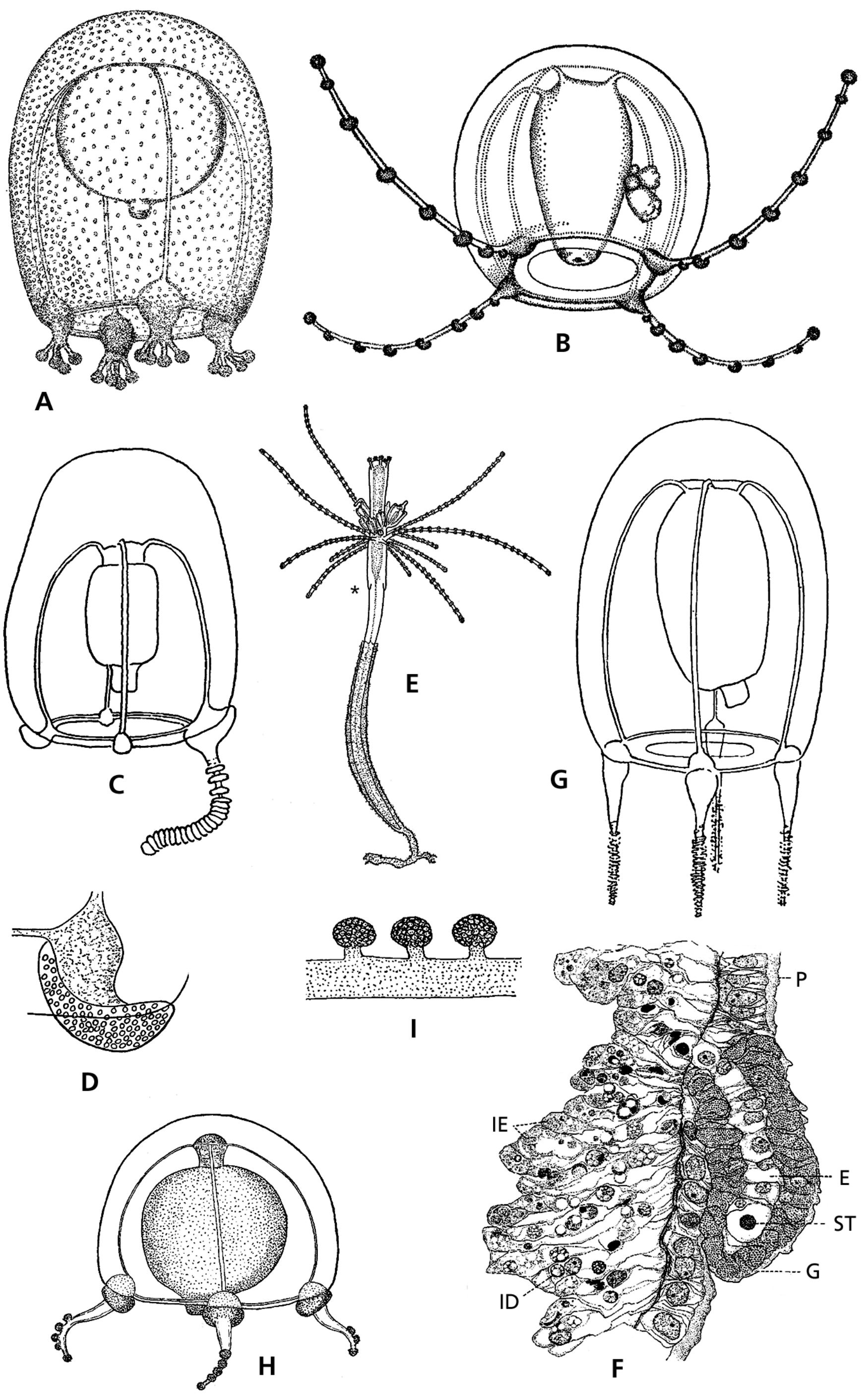


FIG. 116. Anthomedusae, Euphysidae. A, *Cnidocodon leopoldi*, adult medusa. B, *Euphysilla pyramidata*, adult medusa with medusa buds on manubrium. C-F, *Euphysa aurata*: C, mature medusa; D, view of a non tentacular marginal bulb; E, hydroid (asterisk, see figure F); F, longitudinal histological section of the basal papilla and statocyst of a hydranth (see asterisk figure E). G, *Euphysa flammea*: fully grown medusa. H-I, *Euphysomma brevia*: H, adult medusa; I, portion of tentacle with cnidocyst knobs (A-B after Bouillon, 1978c; C, G-H after Kramp, 1959b; D after Russell, 1953; E after Rees, 1938; F after Bouillon & Grohman, 1990; I after Allwein, 1967). E = endoderm; G = ectodermal granulations; ID = digestive inclusions; IE = excretory inclusions; P = periderm; ST = statocyst.

FIG. 116. *Anthomedusae, Euphysidae. A,* Cnidocodon leopoldi*, méduse adulte. B,* Euphysilla pyramidata*, méduse adulte présentant des bourgeons médusaires manubriaux. C-F,* Euphysa aurata *: C, méduse mature ; D, vue d'un bulbe non tentaculaire ; E, hydroïde (astérisque, voir figure F) ; F, section histologique longitudinale de la papille basale et du statocyste d'un hydranthe (voir astérisque figure E). G,* Euphysa flammea*, méduse adulte. H-I,* Euphysomma brevia *: H, méduse adulte ; I, portion d'un tentacule avec des boutons de cnidocystes (A-B d'après Bouillon, 1978c ; C, G-H d'après Kramp, 1959b ; D d'après Russell, 1953 ; E d'après Rees, 1938 ; F d'après Bouillon & Grohman, 1990 ; I d'après Allwein, 1967). E = endoderme ; G = granulations ectodermiques ; ID = inclusions digestives ; IE = inclusions excretrices ; P = périderme ; ST = statocyste.*

moniliform tentacles; asexual reproduction by constriction of distal end of hydrocaulus and budding of new hydranths with reversed polarity on lower part of mother hydranth; medusa buds singly or in clusters just above aboral tentacles.
Medusa: umbrella evenly rounded; 1-4 marginal tentacles often unequally developed but all of the same structure, tentacles usually moniliform.
Recent references: Brinckmann-Voss & Arai (1998).

Euphysa arenicola (Salvini-Plawen, 1987)
Euphysa aurata Forbes, 1848 [syn. *Corymorpha annulicornis* M. Sars, 1859]
Euphysa australis von Lendenfeld, 1885a [doubtful status]
Euphysa flammea (Linko, 1905) [as *Coryne*]
Euphysa japonica (Maas, 1909)
Euphysa monotentaculata Zamponi, 1983
Euphysa peregrina (Murbach, 1899)
Euphysa problematica Schuchert, 1996 [perhaps a syn. of *Dipurena ophiogaster*]
Euphysa ruthae Norenburg & Morse, 1983
Euphysa tentaculata Linko, 1905
Euphysa tetrabrachia Bigelow, 1904
Euphysa vervoorti Brinckmann-Voss & Arai, 1998
Euphysa sp. – Uchida, 1927a

Genus ***EUPHYSOMMA*** Kramp, 1962

Fig. 116 H-I

Hydroid: unknown.
Medusa: manubrium broad, surrounded by ring-like gonad leaving aboral part free; with short apical chamber; mouth rim simple, studded with cnidocysts; 4 short, hollow, identical, tentacles provided with abaxial shortly peduncled cnidocyst knobs and a terminal cnidocyst cluster; no ocelli.

Euphysomma brevia (Uchida, 1947a) [as *Sarsia*]

Genus ***PINUSHYDRA*** Bouillon & Grohmann, 1990

Fig. 117A-B

Hydroid: mesopsammic, with elongated, almost cylindrical centipede-like body; 9 to 12 scattered oral capitate oar-shaped tentacles and 8 to 18 scattered aboral filiform tentacles; posterior part of hydranth with glandular static fold and adhesive button; gonophores as 6 to 15 styloid sporosacs, scattered among aboral tentacles.

Pinushydra chiquitita Bouillon & Grohmann, 1990

Genus ***SIPHONOHYDRA*** Salvini-Plawen, 1966

Fig. 117C

Hydroid: mesopsammic; hydranth club-shaped with oral whorl of 4 short tentacles alternating with an aboral whorl of 4 longer tentacles with parenchymatic endoderm, tentacles more or less filiform; buds above aboral tentacles; upper end of hydrocaulus with four short papillae with endodermal statocyst, covered by leaf-like ectodermal lappet; gonophores unknown.
Recent references: Clausen & Salvini-Plawen (1986); Salvini-Plawen (1987); Thiel (1988); Petersen (1990).

Siphonohydra adriatica Salvini-Plawen, 1966

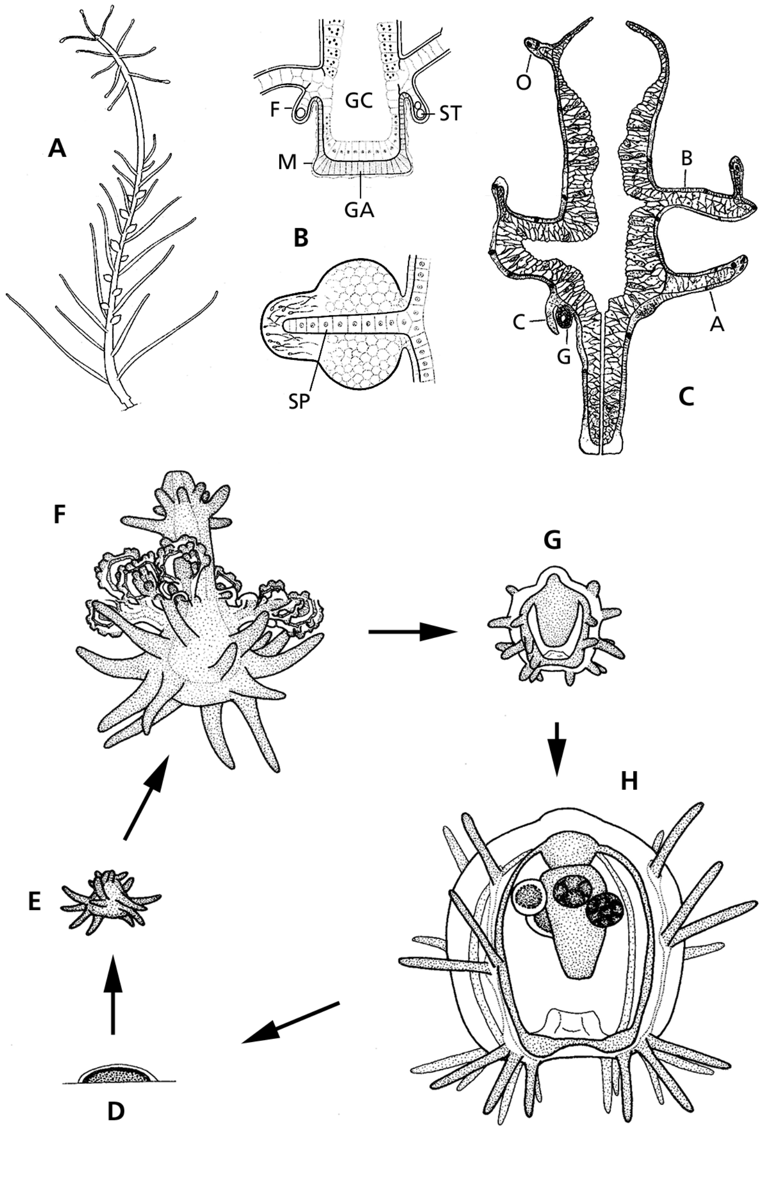


FIG. 117. Anthomedusae, Euphysidae (end). A-B, *Pinushydra chiquitita*: A, extended polyp; B, diagram of the basal part of a polyp showing the structure of the adhesive anchoring organ and the statocystic fold (above), diagram of a male gonophore (below). C, *Siphonohydra adriatica*, diagram of a longitudinal section trough a hydranth, radial (left), interradial (right). D-H, Margelopsidae, *Climacocodon ikarii*, life cycle: D, cyst; E, primary hydroid; F, well-developed hydroid with many medusa buds; G, newly liberated medusa; H, mature female medusa (A-B after Bouillon & Grohman, 1990; C after Salvini-Plawen, 1966; D-H after Kubota, 1993). A = aboral tentacle; B = bud; C = process covering the gonophore; F = static fold with statocyst; G = gonophore; GA= glandular adhesive organ; GC = gastric cavity; M = mucous periderm; O = oral tentacle; SP = spadix; ST = statocyst.

***FIG. 117.** Anthomedusae, Euphysidae (fin). A-B,* Pinushydra chiquitita : *A, polype en extension ; B, diagramme de la région basale d'un polype montrant la structure de l'organe d'ancrage adhésif et le repli statocytaire (au-dessus), diagramme d'un gonophore mâle (au dessous). C,* Siphonohydra adriatica*, diagramme d'une section longitudinale au travers d'un hydranthe, coupe radiale (à gauche), coupe interradiale (à droite). D-H, Margelopsidae,* Climacocodon ikarii*, cycle : D, cyste ; E, hydroïde primaire ; F, hydroïde développé présentant de nombreux bourgeons médusaires ; G, méduse venant de se libérer ; H, méduse femelle mature (A-B d'après Bouillon & Grohman, 1990 ; C d'après Salvini-Plawen, 1966 ; D-H d'après Kubota, 1993). A = tentacule aboral ; B = bourgeon ; C = processus couvrant le gonophore ; F = replis statocytaire ; G = gonophore ; GA= organe adhésif glandulaire ; GC = cavité gastrique ; M = périderme muqueux ; O = tentacule oral ; SP = spadix ; ST = statocyste.*

Family MARGELOPSIDAE Uchida, 1927

Hydroid: pelagic, solitary; hydrocaulus absent or reduced to a button-like process; hydranth vasiform, with one or several whorls of solid, filiform oral tentacles; with either 2 or 3 close-set, alternating whorls of aboral tentacles, or with numerous scattered aboral tentacles; medusa buds on short blastostyles.

Medusa: mouth simple, circular; "gonads" surrounding manubrium; 4 radial canals; tentacles solid, generally moniliform, in marginal clusters, or at different levels on exumbrella; no ocelli; eggs may develop into actinulae on manubrium or into encysted resting stages.

Recent references: Petersen (1990); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY FOR MEDUSAE

1. tentacle pairs at several levels on exumbrella . . . . *Climacocodon*
– umbrella with 4 perradial tentacle clusters. 2

2. tentacles all alike . . . . *Margelopsis*
– tentacles of different size in a special arrangement; only juvenile medusae known. . . . . *Pelagohydra*

Genus ***CLIMACOCODON*** Uchida, 1924

Fig. 117D-H

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

Climacocodon ikarii Uchida, 1924

Genus ***MARGELOPSIS*** Hartlaub, 1897

Fig. 118A-C

Hydroid: hydrocaulus short, button-like, vestigial; hydranth vasiform; no parenchymatic endodermal specializations; one whorl of oral tentacles, moniliform-like; 2 or 3 close-set, alternating whorls of aboral tentacles with cnidocysts arranged as on oral tentacles.
Medusa: four perradial rounded tentacular bulbs on bell margin, each with two to six stiff solid tentacles irregularly distributed; with actinulae on manubrium.

Margelopsis australis Browne, 1910
Margelopsis gibbesi (McCrady, 1859a)
Margelopsis haeckeli Hartlaub, 1897
Margelopsis hartlaubi Browne, 1903

Genus ***PELAGOHYDRA*** Dendy, 1902

Fig. 118D-F

Hydroid: hydranth pelagic, freely floating, no hydrocaulus, up to 35 mm long; divided into larger oval part (float) and smaller, tubular, oral part (proboscis); float with up to 150 scattered, tapering tentacles; oral part with up to 80 tentacles scattered over the distal three-quarters of its length, adnate to proboscis wall; some very short, differently coloured tentacles along mouth rim; all tentacles with slight terminal capitation; float with complicated internal anatomy consisting in an intricate structure of mesogleal lamellae and endodermal chambers which open in the gastric cavity of the proboscis; gonophores on branched blastostyles dispersed among aboral tentacles, up to 300 per animal; each blastostyle may bear up to 5 gonophores which develop into free medusae.
Medusa: only known as medusa buds; bell-shaped to quadrangular, mesoglea rather thick; exumbrella with many scattered cnidocysts; 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.

Pelagohydra mirabilis Dendy, 1902

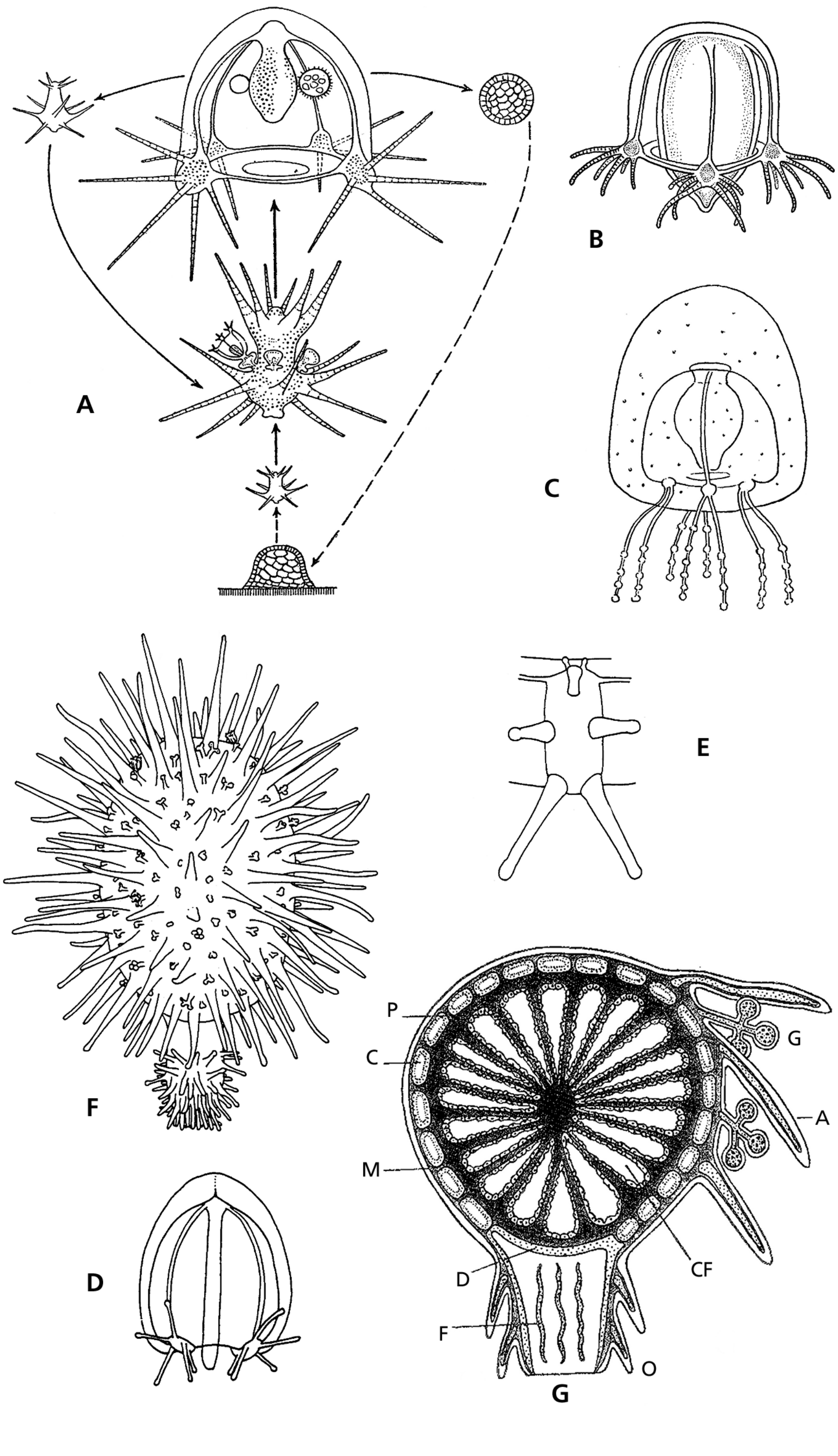


FIG. 118. Anthomedusae, Margelopsidae (end). A, *Margelopsis haeckeli*, life cycle, small summer egg developing directly into actinulae (left), large autumnal egg passing through a winter resting stage (cyst) before giving the hydranth (right). B, *Margelopsis gibbesi*, mature medusa. C, *Margelopsis hartlaubi*, adult medusa. D-G, *Pelagohydra mirabilis*: D, young medusa; E, oral view of tentacle bulb of a young medusa, the adaxial side faces upwards; F, floating polyp stage with medusa buds (mouth downwards); G, hypothetical schema of the floating organ (mouth downwards) (A after Werner, 1953; B-C after Kramp, 1959b; D-F after Schuchert, 1996; G after Rees & Ralph, 1970). A = aboral tentacle; C = endodermal canal; CF = floating cavity; D = diaphragm; F = hypostomial fold; G = gonophore with medusa buds; M = mesoglea; O = oral tentacle; P = parenchyma.

FIG. 118. *Anthomedusae, Margelopsidae (fin). A,* Margelopsis haeckeli, *cycle, petit œuf d'été se développant directement en actinule (à gauche), large œuf d'automne passant l'hiver sous forme de stade de résistance (cyste) avant de donner un hydranthe (à droite). B,* Margelopsis gibbesi, *méduse mature. C,* Margelopsis hartlaubi, *méduse adulte. D-F,* Pelagohydra mirabilis *: D, jeune méduse ; E, vue orale d'un bulbe tentaculaire d'une jeune méduse, la face adaxiale vers le haut ; F, stade polype flottant développant des bourgeons médusaires (la bouche vers le bas) ; G, schéma hypothétique d'un organe de flottaison (la bouche vers le bas) (A d'après Werner, 1953 ; B-C d'après Kramp, 1959b ; D-F d'après Schuchert, 1996 ; G d'après Rees & Ralph, 1970). A = tentacule aboral ; C = canal endodermique ; CF = cavité de flottaison ; D = diaphragme ; F = pli hypostomial ; G = gonophore avec bourgeons médusaires ; M = mésoglée ; O = tentacule oral ; P = parenchyme.*

Family PARACORYNIDAE Picard, 1957

Hydroid: colony flat, circular, polymorphic; basal plate divided in upper layer of broad endodermal cavities and basal layer of large, parenchymatic endoderm cells continuous with those in dactylozooids, crossed by mesogleal lamellae, all enveloped in layer of ectoderm, lacking perisarc; gastrozooid short, stout, with 1 to 4 whorls of solid capitate tentacles; gonozooids short, lacking tentacles and mouth; dactylozooids around edge of colony, long, finger-shaped, filled with parenchymatic endoderm; gonophores cryptomedusoid; eggs developed into actinulae inside gonophore, or into encysted resting stage.
Recent reference: Petersen (1990).

Genus *PARACORYNE* Picard, 1957

Figs 42, 43

See family characters.

Paracoryne huvei Picard, 1957

Family PENNARIIDAE McCrady, 1859

Hydroid: colony large, pinnate, arising from a network of creeping stolons; 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 colony, 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; a whorl of 4-6 oral capitate tentacles, up to 18 capitate tentacles scattered or in more or less regular whorls on hydranth body, aboral whorl of up to 16 semifiliform to slightly capitate aboral tentacles; 3-5 eumedusoids arising on short stalks just above aboral tentacles; sexes separated per colony; eumedusoids free or not.

Medusa: reduced to short-living eumedusoids; manubrium not extending beyond umbrella margin; mouth simple, circular or absent; 4 radial canals; "gonads" completely surrounding manubrium; 4 permanently rudimentary tentacles, usually reduced to mere bulbs, with or without ocelli.

Remarks: many of the reduced medusa species described in this family could be eumedusoids belonging to several Tubulariida or Zancleida families; only the few species with known cycle can be referred to the Pennariidae.

Recent references: Wedler & Larson (1986); Calder (1988a); Migotto (1996); Schuchert (1996); Bouillon & Barnett (1999); Bouillon & Boero (2000).

Genus *PENNARIA* Goldfuss, 1820

Figs 5B, 14B, 56B, 119A-C

Eumedusoid and hydroid with characters of the family.
Recent references: Calder *et al.* (2003); Schuchert (2003).

Pennaria adamsia von Lendenfeld, 1885a
Pennaria armata Vanhöffen, 1911 [doubtful status]
Pennaria disticha Goldfuss, 1820 [syn. *P. tiarella* (Ayres, 1852) and *Corydendrium splendidum* Boone, 1938]
Pennaria grandis Kramp, 1928
Pennaria pauper Kramp, 1959b
Pennaria rosea von Lendenfeld, 1885a
Pennaria vitrea Agassiz & Mayer, 1899 [doubtful status]
Pennaria wilsoni Bale, 1913

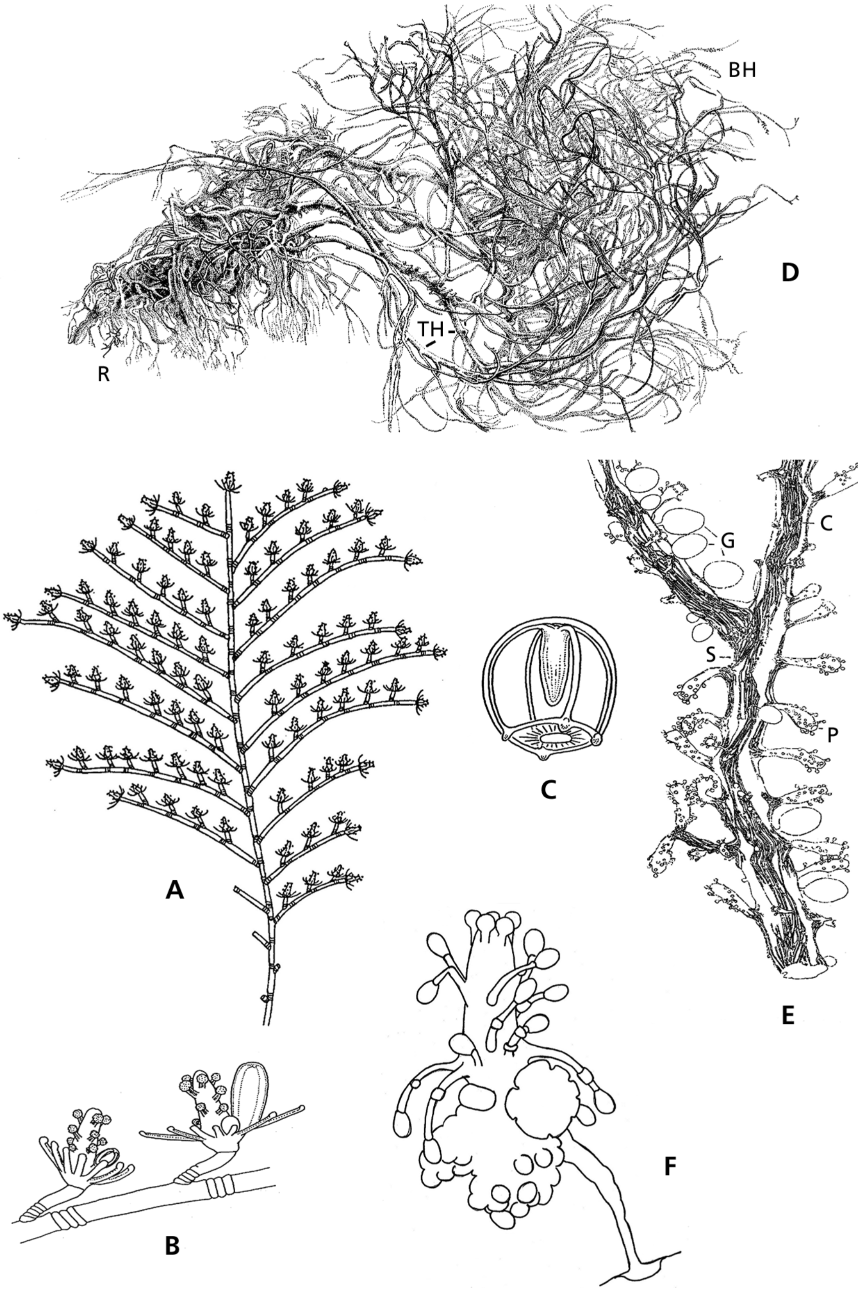


FIG. 119. Anthomedusae. A-C, Pennariidae, *Pennaria disticha*: A, branch of a colony; B, part of hydrocladium; C, eumedusoid (atypical, as they are always very elongate and not rounded). D-E, Solanderiidae, *Solanderia*: D, *Solanderia ericopsis*, colony; E, *Solanderia minima*, detail of a branch. F,Tricyclusidae, *Tricyclusa singularis*, hydranth (A-B after Schuchert, 1996; C after Kramp, 1959b; D-F Bouillon, original). BH = branches; C = coenosarc; G = gonophores; P = polyps; R = roots; S = stem; TH = hydrocaulus.

FIG. 119. *Anthomedusae. A-C, Pennariidae,* Pennaria disticha : *A, branche d'une colonie ; B, portion d'hydroclade ; C, eumedusoïde. D-E, Solanderiidae,* Solanderia : *D,* Solanderia ericopsis, colonie ; *E,* Solanderia minima*, détail d'une branche. F, Tricyclusidae,* Tricyclusa singularis*, hydranthe (A-B d'après Schuchert, 1996 ; C d'après Kramp, 1959b ; D-F d'après Bouillon, original). BH = branches ; C = coenosarc ; G = gonophores ; P = polypes ; R = racines ; S = branche ; TH = hydrocaule.*

Family SOLANDERIIDAE Marshall, 1873

Hydroid: colony large, branching, with chitinous internal anastomosing skeleton formed by coalescence and modification of adjacent hydrocauline tubes; coenosarc covering entire colony and penetrating skeletal interstices; hydranths over whole colony surface, uniform in structure, cylindrical, with a single circlet of capitate tentacles around mouth and numerous similar tentacles scattered over body; gonophores, where known, cryptomedusoid or eumedusoid, arising directly from coenosarc.

Recent references: Bouillon & Cornelius (1988); Bouillon *et al.* (1992); Schuchert (1996).

Genus *SOLANDERIA* Duchassaing & Michelin, 1846

Fig. 119D-E

Synonym: *Chitina* Carter, 1873.
See family characters.
Recent references: Schuchert (2003).

Solanderia dendritica (Fraser, 1938a)
Solanderia ericopsis (Carter, 1873)
Solanderia fusca (Gray, 1868)
Solanderia gracilis Duchassaing & Michelin, 1846
Solanderia misakinensis (Inaba, 1892)
Solanderia procumbens (Carter, 1873)
Solanderia secunda (Inaba, 1892) [syn. *S. minima* (Hickson, 1903)]

Family TRICYCLUSIDAE Kramp, 1949

Hydroid: hydrocaulus thin, as long as hydranth, ending in small pedal disc; perisarc covering hydrocaulus inflated, gelatinous; hydranth pear-shaped; one whorl of six oral capitate tentacles and two widely spaced whorls each of 8-14 stout, solid aboral, imperfectly moniliform tentacles; hydroid buds produced from lower part of hydranth.; actinuloid larvae arising from under aboral tentacles; gonophores as fixed sporosacs, only male observed.

Recent reference: Petersen (1990).

Genus *TRICYCLUSA* Stechow, 1919

Fig. 119F

See family characters.

Tricyclusa singularis (Schulze, 1876)

Family TUBULARIIDAE Fleming, 1828

Hydroid: solitary or colonial; hydrocaulus divided into distal neck region covered by thin perisarc, and proximal stem which may be either short and thick with tuber-like aboral processes, or long, cylindrical or cone-shaped with basal disc or with stolons covered by thicker perisarc; neck perisarc secreted from a groove on the hydranth proper; hydranth vasiform, tentacles in two sets, oral ones filiform or pseudofiliform in one to several close-set whorls, exceptionally capitate, or moniliform, (oral tentacles often slightly capitate or capitate in juveniles); aboral ones in one whorl, long pseudofiliform or filiform, sitting on a more or less developed parenchymatic cushion; gonophores as free medusae or fixed sporosacs; often actinula larvae.

Medusae: usually with exumbrellar cnidocyst tracks; 4 radial canals; mouth usually circular; “gonads” encircling manubrium completely; 1-4 marginal tentacles; no ocelli (Fig. 7A).

Recent references: Wedler & Larson (1986); Calder (1988a); Petersen (1990); Migotto (1996); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2001a).

KEY TO HYDROIDS

1. hydrocaulus lumen open, without parenchyme and peripheral endodermal canals but with longitudinal endodermal ridges 2
– hydrocaulus filled with parenchyme and with longitudinal peripheral endodermal canals 3

2. oral tentacles in one whorl; two, rarely up to five longitudinal endodermic ridges; medusa radially symmetrical with 2 or 4 groups of tentacles . . . . . *Ectopleura*
– oral tentacles in two whorls; up to 8 or more longitudinal endodermic ridges; medusae asymmetrical with one group of marginal tentacles . . . . . *Hybocodon*

3. one longitudinal endodermic peripheral canals larger than the others 4
– all endodermic peripheral canals of equal size 5

4. hydrocaulus widening from base to distal end; blastostyles unbranched or pinnate . . . . . *Tubularia*
– hydrocaulus tubular; blastostyles dichotomously branched . . . . . *Ralpharia*

5. endodermal canals radially arranged, ribbon like; hydranth with short neck region; hydrocaulus widening from base to distal end; with basal disc . . . . . *Bouillonia*
– endodermal canals not ribbon-like; with long cylindrical neck region; hydrocaulus widening toward basal end; with rootlets and swollen storage tubers . . . . . *Zyzzyzus*

KEY TO MEDUSAE

1. no tentacular marginal bulbs 2
– tentacular marginal bulbs . . . . . *Rhabdoon*

2. umbrella normal, symmetrical 3
– umbrella asymmetrical, bell margin obliquely set to the vertical axis . . . . . *Hybocodon*

3. longitudinal exumbrellar cnidocyst tracks or rows . . . . . *Ectopleura*
– exumbrellar cnidocysts scattered singly or in clumps . . . . . *Plotocnide*

Genus ***BOUILLONIA*** Petersen, 1990

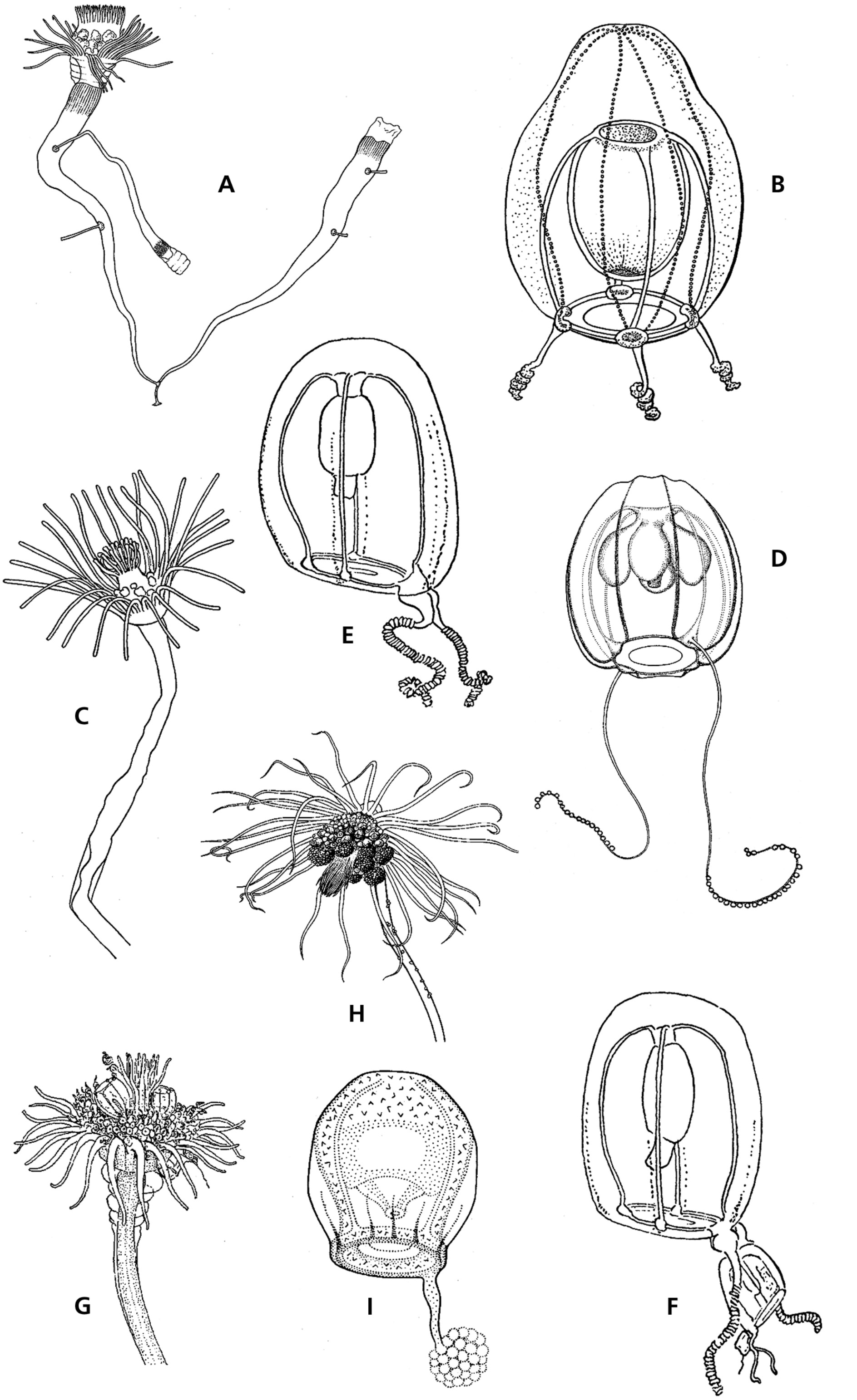
Fig. 120A

Hydroid: solitary; hydrocaulus curved, widening considerably from thin base attached by small, circular basal disc; centre of hydrocaulus filled by parenchymatic endoderm penetrated by numerous equally-sized longitudinal endodermal canals of oblong cross-section, radially arranged, filmy perisarc covering short neck region secreted from groove around base of hydranth just under aboral tentacle whorl; hydranth with rounded base, hypostome wide, cylindrical with wide mouth; several closely set whorls of short oral filiform tentacles and one whorl of longer aboral pseudofiliform tentacles; gonophores as fixed sporosacs on dichotomously branched blastostyles.

Bouillonia cornucopia (Bonnevie, 1898b)

FIG. 120. Anthomedusae, Tubulariidae. A, *Bouillona cornucopiae*, three hydranths, the largest one with cryptomedusoid sporosacs. B-D, *Ectopleura*: B-C, *Ectopleura dumortieri*: B, mature medusa; C, hydranth; D, *Ectopleura sacculifera*, adult medusa. E-G, *Hybocodon prolifer*: E, mature medusa without medusa buds; F, mature medusa with medusa buds on marginal tentacular bulb; G, hydranth. H, *Rhalpharia sanctisebastiani*, hydranth with eumedusoids. I, *Rhabdoon singulare*, mature medusa (A & H after Petersen, 1990; B after Mayer, 1910; C & G after Russell, 1953; D after Bouillon, 1978c; E-F after Kramp, 1959b; I after Vannucci & Soares, 1966a).

FIG. 120. *Anthomedusae, Tubulariidae. A,* Bouillona cornucopiae, *trois hydranthes, le plus large avec des sporosacs cryptomédusoides. B-D, Ectopleura : B-C,* Ectopleura dumortieri : *B, méduse mature ; C, hydranthe ; D,* Ectopleura sacculifera, *méduse adulte. E-G,* Hybocodon prolifer *: E, méduse mature sans bourgeons médusaires ; F, méduse mature avec des bourgeons médusaires sur le bulbe tentaculaire marginal ; G, hydranthe. H,* Rhalpharia sanctisebastiani, *hydranthe développant des eumedusoïdes. I,* Rhabdoon singulare, *méduse mature (A & H d'après Petersen, 1990 ; B d'après Mayer, 1910 ; C & G d'après Russell, 1953 ; D d'après Bouillon, 1978c ; E-F d'après Kramp, 1959b ; I d'après Vannucci & Soares, 1966a).*


A
B
E
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F

Genus *ECTOPLEURA* L. Agassiz, 1862
Figs 7A, 120B-D

Hydroid: solitary or colonial; hydrocaulus high, simple, with open lumen, without parenchymatic endoderm and longitudinal endodermal canals, but weakly divided by two, rarely up to five, internal longitudinal endodermic ridges; perisarc thin, covering piriform neck region, originating from collar on neck region and does not cover whole neck;hydranth vasiform with filiform (except in *E. wrighti* where they are moniliform to capitate) oral tentacles in one whorl and a whorl of long, filiform, aboral tentacles; gonophores right above aboral tentacles, producing free medusae, eumedusoid or fixed sporosacs.
Medusa: umbrella symmetrical, rounded, or piriform; 8 longitudinal exumbrellar cnidocyst rows, issuing in pairs from tentacular bulbs; manubrium short, at most reaching bell margin; 2 opposite or 4 equally developed, simple perradial marginal tentacles, moniliform or with abaxial cnidocyst clusters; 4 radial canals.
Remarks: Many hydroid-based nominal species of *Ectopleura* have recently been described, the medusae being known either as just liberated juveniles or as medusa buds; some medusae with unknown cycle, and described long ago, could correspond to some of those hydroids. In groups with species based on either polyps or medusae only, rearing experiments are necessary to elucidate life cycles before assigning new specific names.
Recent references: Schuchert (2001a, 2003); Calder *et al.* (2003).

Ectopleura americana Petersen, 1990
Ectopleura bethae (Warren, 1908)
Ectopleura crocea (L. Agassiz, 1862a) [syn. *E. ralphi* (Bale, 1884); *Tubularia cristata* McCrady, 1859 may be a senior synonym]
Ectopleura dumortieri (Van Beneden, 1844)
Ectopleura exxonia (Watson, 1978)
Ectopleura grandis Fraser, 1944
Ectopleura indica Petersen, 1990
Ectopleura integra (Fraser, 1938a) comb. nov. [as *Tubularia*]
Ectopleura japonica (Hirohito, 1988)
Ectopleura larynx (Ellis & Solander, 1786) [syn. *Tubularia bellis* Allman, 1863]
Ectopleura latitaeniata Xu & Zhang, 1978
Ectopleura marina (Torrey, 1902)
Ectopleura mayeri Petersen, 1990
Ectopleura media Fraser, 1948
Ectopleura minerva Mayer, 1900a
Ectopleura multicirrata Schuchert, 1996
Ectopleura obypa Migotto & Marques, 1999
Ectopleura pacifica Thornely, 1900 [perhaps a syn. of *E. viridis*]
Ectopleura prolifica Hargitt, 1908
Ectopleura radiata (Uchida, 1937)
Ectopleura sacculifera Kramp, 1957
Ectopleura venusta (Yamada, 1950)
Ectopleura viridis (Pictet, 1893)
Ectopleura wrighti Petersen, 1979
Ectopleura xiamenensis Zhang & Lin, 1984

Genus *HYBOCODON* L. Agassiz, 1862
Figs 26R, 120E-G

Hydroid: solitary, with high stems; hydrocaulus tubular, with open lumen, without parenchyma and longitudinal peripheral canals but weakly divided by eight or more longitudinal endodermic ridge; perisarc originating just below hydranth and much inflated around whole neck region; secreted from groove between hydranth and neck; oral tentacles filiform to pseudofiliform in two closely set whorls, aboral tentacles in one whorl, filiform to pseudofiliform; blastostyles dichotomously branched.
Medusa: bilaterally symmetrical, with umbrella margin at oblique angle to vertical axis; no 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; 3 remaining perradial bulbs rudimentary.
Recent references: Schuchert (1996).

Hybocodon atentaculatus Uchida, 1947b
Hybocodon cryptus Watson, 1984 [short lived eumedusoids]
Hybocodon octopleurus Kao, Li, Chang & Li, 1958
Hybocodon pendulus (L. Agassiz, 1862a)
Hybocodon prolifer L. Agassiz, 1862a
Hybocodon unicus (Browne, 1902)

Genus *RALPHARIA* Watson, 1980

Fig. 120H

Synonym: *Serehyba* Da Silveira & Migotto, 1984. *Propachycordyle* M. E. Thiel, 1931 may also be a synonym.
Hydroid: solitary or colonial; hydrocaulus cylindrical, filled with parenchymatic endoderm with 10-20 peripheral longitudinal endodermal canals, one larger than the others; hydrorhiza long, branched or unbranched, buried in octocoral; filmy perisarc around neck region secreted from groove between hydranth base and neck; hydranth with 2 or more whorls of filiform oral tentacles and one whorl of long aboral filiform tentacles; reproduction by free or fixed eumedusoids or fixed gonophores, carried on dichotomously branched blastostyles with or without terminal cluster of nematophores.
Recent reference: Watson (1999).

Ralpharia coccinea Watson, 1984
Ralpharia gorgoniae Petersen, 1990
Ralpharia magnifica Watson, 1980
Ralpharia neira Petersen, 1990
Ralpharia parasitica (Korotneff, 1887) [*Propachycordyle canalifera* M. E. Thiel, 1931 may be the eumedusoid]
Ralpharia sanctisebastiani (Da Silveira & Migotto, 1984)

Genus *RHABDOON* Keferstein and Ehlers, 1861

Fig. 120I

Synonym: *Rhysomedusa* Vannucci & Soares Moreira, 1966.
Hydroid: unknown.
Medusa: single marginal tentacle, hollow, ending in large, complex knob of cnidocyst clusters; no 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.

Rhabdoon singulare Keferstein & Ehlers, 1861 [syn. *R. pomponina* Vannucci & Soares Moreira, 1966a]

Genus *TUBULARIA* Linnaeus, 1758

Figs 5C, 121A-D

Hydroid: solitary; hydrocaulus long, tubular, widening from base to distal end, inner lumen filled with parenchymatic endoderm, penetrated by 8 or more longitudinal endodermal peripheral canals, one wider than the others; circular or lobed basal disc, and supporting tubes developed from lower part of stem; thin perisarc around neck secreted from groove between hydranth base and neck; hydranth vasiform, with two or more whorls of oral filiform and one whorl of filiform aboral tentacles; bases of aboral tentacles continued as ridges over hydranth base; blastostyle with unbranched main stem, with or without thin side branches; gonophores reduced to eumedusoid or to sessile cryptomedusoid, with or without distal processes, in which the origin from a biradially symmetrical medusa, can be usually traced.
Recent references: Petersen (1990); Schuchert (2001a).

Tubularia acadiae Petersen, 1990
Tubularia amoyensis (Hargitt, 1927)
Tubularia asymmetrica Bonnevie, 1898b
Tubularia aurea Fraser, 1936a
Tubularia borealis Clark, 1876b [probably a syn. of *T. regalis*]
Tubularia ceratogyne Pérez, 1920
Tubularia chilensis (Hartlaub, 1905)
Tubularia crassa Fraser, 1941
Tubularia cristata McCrady, 1859a [probably a syn. of *Ectopleura crocea*]
Tubularia harrimani Nutting, 1901a
Tubularia indivisa Linnaeus, 1758 [syn. *T. couthouyi* L. Agassiz, 1862a and *T. simplex* Alder, 1862a]
Tubularia multitentaculata Fraser, 1938a
Tubularia regalis Boeck, 1860
Tubularia spectabilis (L. Agassiz, 1862a)
Tubularia tenella (L. Agassiz, 1862a)

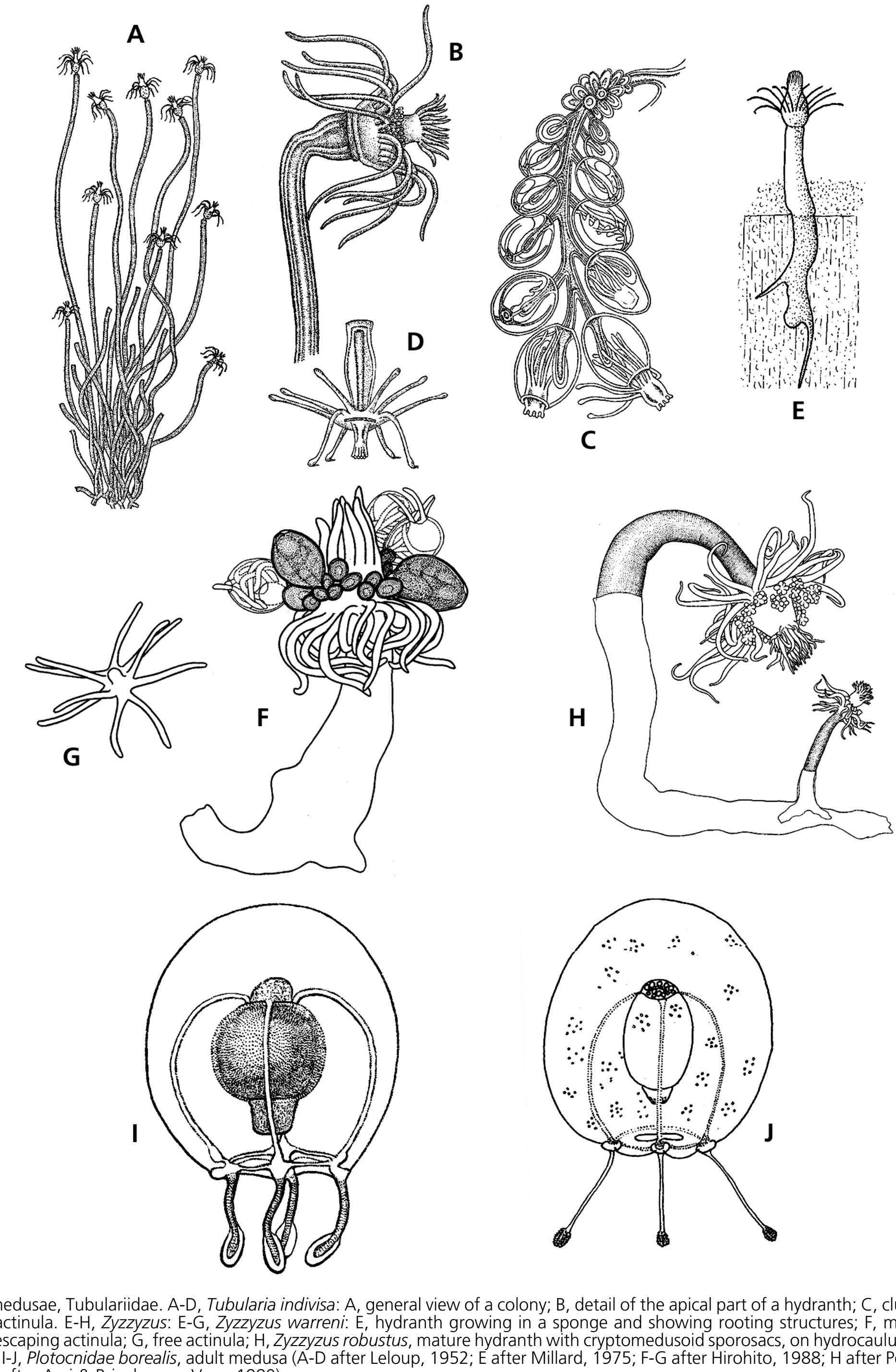


FIG. 121. Anthomedusae, Tubulariidae. A-D, *Tubularia indivisa*: A, general view of a colony; B, detail of the apical part of a hydranth; C, cluster of gonophores; D, just liberated actinula. E-H, *Zyzzyzus*: E-G, *Zyzzyzus warreni*: E, hydranth growing in a sponge and showing rooting structures; F, mature hydranth with gonophores and escaping actinula; G, free actinula; H, *Zyzzyzus robustus*, mature hydranth with cryptomedusoid sporosacs, on hydrocaulus of which a younger polyp has settled. I-J, *Plotocnidae borealis*, adult medusa (A-D after Leloup, 1952; E after Millard, 1975; F-G after Hirohito, 1988; H after Petersen, 1990; I after Naumov, 1969; J after Arai & Brinckmann-Voss, 1980).

FIG. 121. *Anthomedusae, Tubulariidae. A-D,* Tubularia indivisa : *A, vue générale d'une colonie ; B, détail de la partie apicale d'un hydranthe ; C, grappe de gonophores; D, actinule venant de se libérer. E-H,* Zyzzyzus : *E-G,* Zyzzyzus warreni *: E, hydranthe se développant dans une éponge et montrant le système de racines fixatrices ; F, hydranthe pourvus de gonophores matures dont s'échappent des actinules ; G, actinules libre ; H,* Zyzzyzus robustus*, hydranthe mature dévelopant des sporosacs cryptomédusoïdes et sur l'hydrocaule duquel un jeune polype vient de se fixer. I-J,* Plotocnidae borealis*, méduses adultes (A-D d'après Leloup, 1952 ; E d'après Millard, 1975 ; F-G d'après Hirohito, 1988 ; H d'après Petersen, 1990 ; I d'après Naumov, 1969 ; J d'après Arai & Brinckmann-Voss, 1980).*

Genus ***ZYZZYZUS*** Stechow, 1921

Fig. 121E-H

Hydroid: solitary; hydrocaulus stout, widening towards basal end, with centre filled by parenchymatic endoderm penetrated by peripheral endodermal longitudinal canals of equal size; hydrorhiza forming rootlets and swollen storage tubers; with long cylindrical neck region covered by thin closely fitting perisarc originating in groove immediately under hydranth; hydranth with one or more close-set whorls of filiform oral tentacles and one whorl of longer, filiform to pseudofiliform aboral tentacles with laterally flattened bases which are not continued as ridges over hydranth base; gonophore as reduced symmetrical cryptomedusoids, carried single or on dichotomously branched blastostyles.
Recent references: Petersen (1990).

Zyzzyzus calderi Petersen, 1990
Zyzzyzus floridanus Petersen, 1990
Zyzzyzus robustus Petersen, 1990
Zyzzyzus spongicolus (Von Lendenfeld, 1885a)
Zyzzyzus warreni Calder, 1988a [syn. *Tubularia solitaria* Warren, 1906, non Rapp, 1829]

Tubulariidae *incertae sedis:*

Genus ***PLOTOCNIDE*** Wagner, 1885

Fig. 121I-J

Hydroid: unknown.
Medusa: exumbrellar cnidocysts scattered singly or in clumps; with a dome-shaped apical chamber lined with vacuolated endodermal cells.
Remarks: the systematic position of the single, rare, arctic species of this genus is doubtful. Mayer (1910) described a short gastric peduncle (see also Hartlaub 1907) and considered it as a *Protiara*. For Uchida (1933; 1969) it could be conspecific with *Coryne* (= *Sarsia*) *inabai* Uchida, 1933, an opinion shared by Kramp (1942) and by Arai & Brinckmann-Voss (1980a). Kramp considered it as phylogenetically related to *Eucodonium*, including both in the Tubulariidae *s.l.* (Kramp, 1959a; 1961a; 1968), followed by Arai & Brinckmann-Voss (1980a) and Bouillon (1985a; 1995a). For Naumov (1960, 1969) *Plotocnide* is congeneric with *Eucodonium,* but this decision is unsound since the cnidome of *Eucodonium* comprises euryteles and desmonemes allowing assignment to a distinct family of Filifera, the Eucodoniidae (see Schuchert, 1996). The cnidome of *Plotocnide* contains desmonemes and stenoteles (Hand & Kan 1961) justifying assignment to the Capitata Tubulariidae. We concur with Petersen (1990) who, awaiting the discovery of the hydroid stage, considered *Plotocnide* as a Tubulariidae *incertae sedis*. 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 status]

Suborder ZANCLEIDA Russell, 1953

Hydroid: colony floating or fixed; 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, oral tentacles capitate or moniliform, aboral tentacles in whorls or scattered, either capitate, moniliform, ramified capitate, reduced or without tentacles; free medusae, eumedusoids or sporosacs.

Medusa: manubrium flask-shaped, with quadrate or octagonal base and cylindrical mouth tube; "gonads" usually interradial; exumbrellar cnidocyst pouches or tracks; 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.

Recent references: Petersen (1990); Boero *et al.* (1995); Bouillon (1999); Bouillon & Barnett (1999); Boero *et al.* (2000).

KEY TO HYDROIDS

1. floating hydroids . . . . Porpitidae
– colony fixed by hydrorhizae 2

2. hydrorhiza embedded in calcareous coenosteum 3
– hydrorhiza without calcareous skeleton 4

3. colony polymorphic, embedded in a massive coenosteum . . . . Milleporidae
– colony monomorphic, partly or totally embedded in a flabellate thin coenosteum . . . . Pseudosolanderiidae (see also 5)

4. hydrorhiza incrusting, forming a crust-like stolonal plate 6
– hydrorhiza different 5

5. hydrorhiza forming upright, branched structures consisting of a central axis of folded, lamellar perisarc with spongy centre, coverd by coenosarc supported by perisarcal ridges and spines . . . . *Pseudosolanderia* (see also 3a)
– hydrorhiza formed by creeping stolon tubes covered by perisarc 7

6. colony polymorphic . . . . Teissieridae
– colony monomorphic . . . . Rosalindidae

7. cnidocysts on hydranth body wall arranged in conspicuous rounded patches; . . . . . . Cladocorynidae
– cnidocysts not in patches on hydranth body wall 8

8. hydranth with moniliform aboral tentacles . . . . Asyncorynidae
– hydrants without moniliform tentacles . . . . Zancleidae

KEY TO MEDUSAE

1. marginal tentacles without cnidophores . . . . Porpitidae
– marginal tentacles usually with cnidophores 2

2. medusae with 2 exumbrellar cnidocyst pouches on non-tentaculate perradial bulbs; pouches with macrobasic euryteles . . . . Cladocorynidae
– medusae with 0 or 4 exumbrellar cnidocyst pouches with stenoteles 3

3. medusae with ocelli . . . . Teissieridae
– medusae without ocelli . . . . Zancleidae

Family ASYNCORYNIDAE Kramp, 1949

Hydroid: hydrocaulus short, rising from creeping stolons; perisarc of both hydrocaulus and hydrorhiza lamellar, complex, made up of numerous distinct inflated layers, with intracoenosarcal perisarcal tubular connections; stolonal coenosarc locally divided by several longitudinal endodermal canals; hydranth club-shaped, with one oral whorl of 4 to 6 solid capitate tentacles and numerous solid moniliform aboral tentacles scattered over body; medusa buds on lower third of hydranth.

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

Recent references: Petersen (1990); Boero *et al.* (1995); Migotto (1996).

Genus *ASYNCORYNE* Warren, 1908

Fig. 122A-B

See family characters. *Pteronema* Haeckel, 1879 may be a synonym.

Asyncoryne philippina (Hargitt 1924) [*Pteronema darwini* Haeckel, 1879 may be a synonym]
Asyncoryne ryniensis Warren, 1908

Family CLADOCORYNIDAE Allman, 1872

Hydroid: stem simple or slightly branched, rising from a creeping stolon; hydranth club-shaped, oral tentacles moniliform or capitate, in one whorl, aboral tentacles moniliform or branched capitate, scattered or in several whorls; cnidocysts on body wall arranged in conspicuous rounded patches or scattered around the base of oral and aboral tentacles; gonophores carried singly or on short, branched pedicels, on lower or middle part of hydranth; with free medusae or fixed cryptomedusoid sporosacs.

Medusa: 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.

Recent references: Wedler & Larson (1986); Bouillon *et al.* (1987); Petersen (1990); Boero *et al.* (1995); Migotto (1996); Schuchert (1996).

KEY TO HYDROIDS

1. hydranth with moniliform oral tentacles; gonophores as free medusae .... *Pteroclava*
– hydranths with capitate oral tentacles; gonophores as fixed sporosacs .... *Cladocoryne*

Genus *CLADOCORYNE* Rotch, 1871

Figs 5H, 13B, 15B, 122C-D

Hydroid: hydrocaulus long, unbranched or sparingly branched, covered by perisarc, arising from a creeping hydrorhiza; hydranth club-shaped, with oral whorl of 4-6 short capitate tentacles, one to four whorls of branched-capitate aboral tentacles; one or two patches of macrobasic eurytele cnidocysts on hydranth body; gonophores as cryptomedusoids fixed sporosacs or as medusa buds, on short pedicels between or over aboral tentacles.

Recent references: Bouillon *et al.* (1987); Calder *et al.* (2003); Schuchert (2003).

Cladocoryne floccosa Rotch, 1871 [syn. *C. pelagica* Allman, 1874a]
Cladocoryne haddoni Kirkpatrick, 1890a
Cladocoryne littoralis (Mammen, 1963)
Cladocoryne simplex Perrier, 1886
Cladocoryne travancorensis (Mammen, 1963)

Genus *PTEROCLAVA* Weill, 1931

Fig. 122E-F

Hydroid: colony growing on alcyonaceans, with perisarc-covered hydrorhiza embedded in host tissues; hydrocaulus short, covered by finely striated perisarc; hydranth with oral whorl of 6 moniliform tentacles, up to 30 quasi moniliform tentacles scattered on an elongated body; one to 4 rounded patches of large cnidocysts on lower part of hypostome, under oral tentacles; gonophores as medusae borne singly or in groups in the mid region of hydranth.

Medusa: 4 radial canals; 2 big perradial tentaculate bulbs clasping exumbrellar margin, without cnidocyst pouches and 2 small non-tentaculate perradial bulbs with cnidocyst pouches containing macrobasic euryteles; tentacles with about 100 abaxial cnidophores; manubrium conical, slightly extruding from velar opening; "gonads" interradial over two thirds of manubrium, leaving oral region free.
Recent references: Boero *et al.* (1995).

Pteroclava crassa (Pictet 1893) [only medusa buds known]
Pteroclava krempfi (Billard, 1919a)

Family MILLEPORIDAE Fleming, 1828

Hydroid: colony forming massive, calcareous exoskeleton (= coenosteum) of varied shape; coenosteum with an internal complex network of coenosarcal tubes and covered externally by a thin ectodermal layer, coenosteal surface perforated by pores; margins of pores not protruding from surface of coenosteum; large gastropores surrounded by smaller dactylopores, forming indistinct cyclosystems; no gastrostyles and dactylostyles; polyps polymorphic; gastrozooids relatively short and stout, with an oral whorl of 4 to 7 short capitate tentacles, arising from gastropores; dactylozooids long, slender, mouthless, with scattered capitate tentacles, arising from dactylopores; cnidome with macrobasic mastigophores; gonophores arising from coenosarc within ampullae's embedded in the coenosteum.
Medusa: free swimming eumedusoids with exumbrellar cnidocyst patches, narrow velum, radial and circular canals, "gonads" occupying the place of an indistinct manubrium and without tentacles and sense organs.
Recent references: Calder (1988a); Petersen (1990); Lewis (1991); Razak & Hoeksema (2003).

Genus ***MILLEPORA*** Linnaeus, 1758

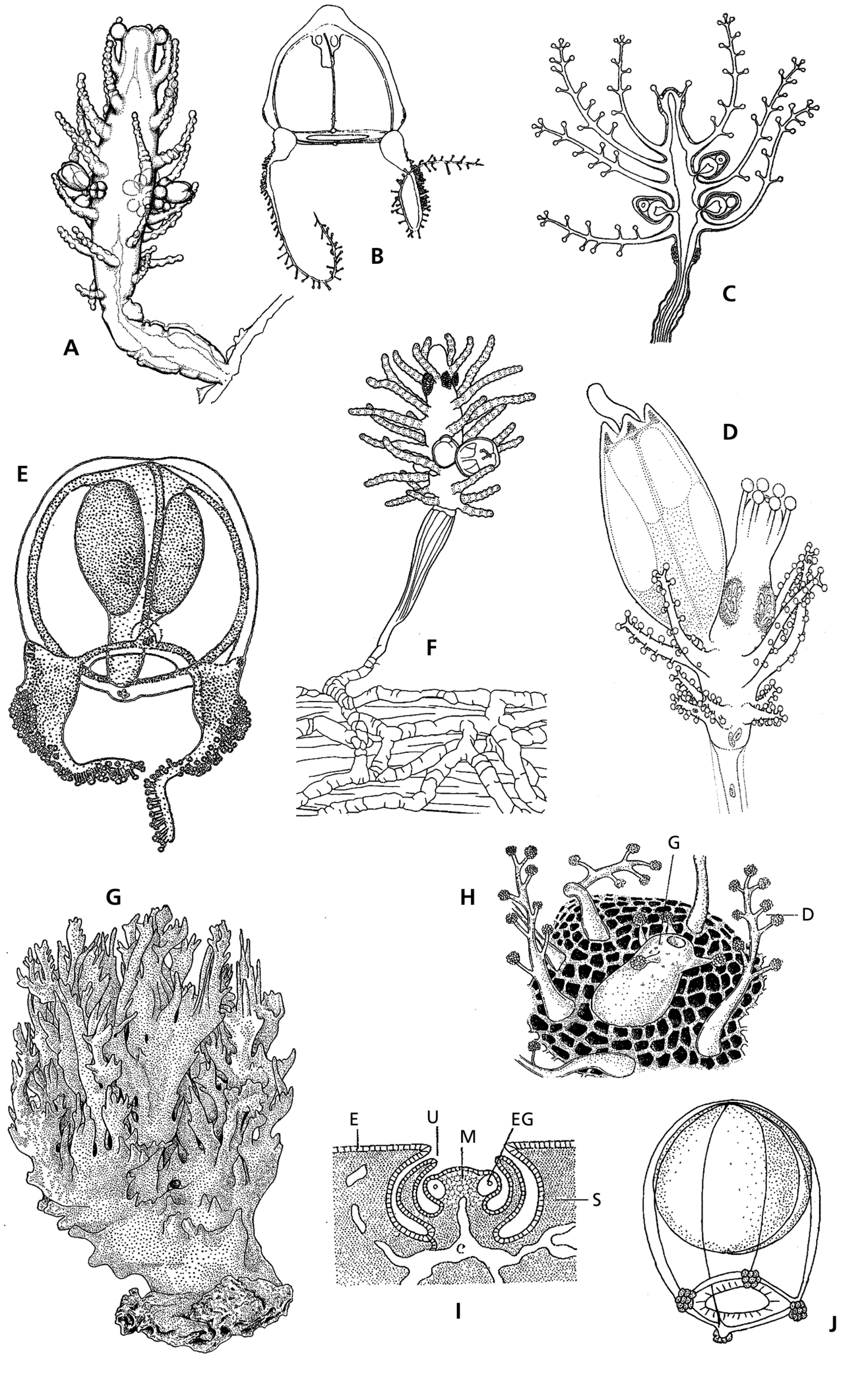
Fig. 122G-J

See family characters.

Millepora alcicornis Linnaeus, 1758
Millepora aspera Linnaeus, 1767
Millepora boschmai De Weerdt & Glynn, 1991
Millepora brasiliensis Verrill, 1868
Millepora complanata Lamarck, 1816
Millepora dichotoma (Forskål, 1775)
Millepora exaesa (Forskål, 1775) [syn. *M. tuberosa* Boschma, 1966b]
Millepora foveolata Crossland, 1952
Millepora intricata Milne-Edwards & Haime, 1860 [syn. *M. murrayi* Quelch, 1884b and *M. xishaensis* Zou, 1978]
Millepora latifolia Boschma, 1948
Millepora moniliformis Dana, 1848
Millepora nitida Verrill, 1868
Millepora nodulosa Nemenzo, 1984 [probably a syn. of *M. intricata*]
Millepora platyphylla Hemprich & Ehrenberg [in Ehrenberg], 1834
Millepora squarrosa Lamarck, 1816
Millepora striata Duchassaing & Michelotti, 1864
Millepora tenella (Ortmann, 1892) [syn. *M. tenera* Boschma, 1949 and *M. cruzi* Nemenzo, 1975]

FIG. 122. Anthomedusae. A-B, Asyncorynidae, *Asyncoryne ryniensis*: A, hydranth with medusa buds; B, mature medusa. C-D, Cladocorynidae, *Cladocoryne*: C, *Cladocoryne floccosa,* hydranth with gonophores; D, *Cladocoryne haddoni*, mature hydranth with cryptomedusoid gonophore releasing a planula. E-F, *Pteroclava krempfi*: E, adult medusa; F, hydranth with medusa buds. G-J, Milleporidae, *Millepora*: G-I, *Millepora* sp.: G, general view of a colony; H, detail of a cyclosystem; I, schematic section through an ampulla containing a developing eumedusoid; J, *Millepora complanata*, eumedusoid (A, C, G-I after Bouillon, 1995a: p. 302, fig. 92 B; p. 310, fig. 95 A, p. 312, fig. 96; B after Migotto, 1996; D after Bouillon *et al*., 1987; E after Boero *et al*., 1995; F after Hirohito, 1988; J after Lewis, 1991: p. 167, fig. 3 b). D = dactylozooid; G =gastrozooid; E = ectoderm; EG = egg; M = manubrium; S= skeleton; U = subumbrella.

FIG. 122. *Anthomedusae. A-B, Asyncorynidae.* Asyncoryne ryniensis : *A, hydranthe pourvu de bourgeons médusaires ; B, méduse mature. C-D, Cladocorynidae,* Cladocoryne : *C,* Cladocoryne floccosa*, hydranthe avec gonophores ; D,* Cladocoryne haddoni*, hydranthe mature pourvus d'un gonophore cryptomedusoïde relâchant une planula. E-F,* Pteroclava krempfi *: E, méduse adulte ; F, hydranthe pourvus de bourgeons médusaires. G-J, Milleporidae,* Millepora : *G-I,* Millepora *sp : G, vue générale d'une colonie ; H, détail d'un cyclosystème ; I, section schématique au travers d'une ampoule sexuée contenant un eumédusoïde en développement ; J,* Millepora complanata*, eumédusoïde (A, C, G-I d'après Bouillon, 1995a : p. 302, fig. 92 B ; p. 310, fig. 95 A, p. 312, fig. 96 ; B d'après Migotto, 1996 ; D d'après Bouillon* et al.*, 1987 ; E d'après Boero* et al.*, 1995 ; F d'après Hirohito, 1988; J after Lewis, 1991 : p. 167, fig. 3 b). D = dactylozoïde ; G =gastérozoïde ; E = ectoderme ; EG = œuf ; M = manubrium ; S= squelette ; U = sous-ombrelle.*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Family PORPITIDAE Goldfuss, 1818

Hydroid: colony floating, with a chitinous internal skeleton, covered by mantle, and forming a floating chamber; central, large, gastrozooid; gastro-gonozooids and dactylozooids.

Medusa: 4 or 8 of exumbrellar stenotele cnidocyst tracks issued from marginal bulbs; 4 or 8 radial canals and a circular canal; manubrium short, conical; with quadrate or octagonal base; mouth circular; "gonads" perradial or irregularly arranged perradially and interradially; 2 opposite, perradial, capitate marginal tentacles; with or without 2 additional smaller capitate tentacles adaxial to the first; tentacles with macrobasic euryteles; zooxanthellae generally present.

Recent references: Calder (1988a); Petersen (1990); Pagès *et al.* (1992); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. disc-shaped floating colony without sail . . . . *Porpita*
– oval to elliptical-shaped floating colony; with a median sail . . . . *Velella*

KEY TO MEDUSAE

1. 4 radial canals; manubrium with quadrate base; 4 capitate tentacles . . . . *Velella*
– 8 radial canals; manubrium octagonal; 2 capitate tentacles . . . . *Porpita*

Genus ***PORPITA*** Lamarck, 1801

Fig. 123A-B

Synonym: *Porpema* Haeckel, 1888.

Hydroid: colony floating, 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; internal chitinous float consisting of a series of concentric chambers; a disks-shaped reservoir of cnidocysts 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.

Medusa: 8 radial canals; manubrium conical, with octagonal base; 2 opposite marginal capitate tentacles, 6 non tentaculate bulbs; "gonads" 8, perradial; short exumbrellar cnidocyst tracks above each bulb.

Porpita prunella (Haeckel, 1888)
Porpita porpita (Linnaeus, 1758) (syn. *P. pacifica* Lesson, 1826 and *P. linneana* Lesson, 1843]

Genus ***VELELLA*** Lamarck, 1801

Fig. 123C-D

Hydroid: colony floating; float flattened, oval, elliptical, with a triangular sail; up to 40 mm long and 20 mm wide, higher in the centre than at the edges; two mirror images of the animal (left and right sailing); float and sail 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

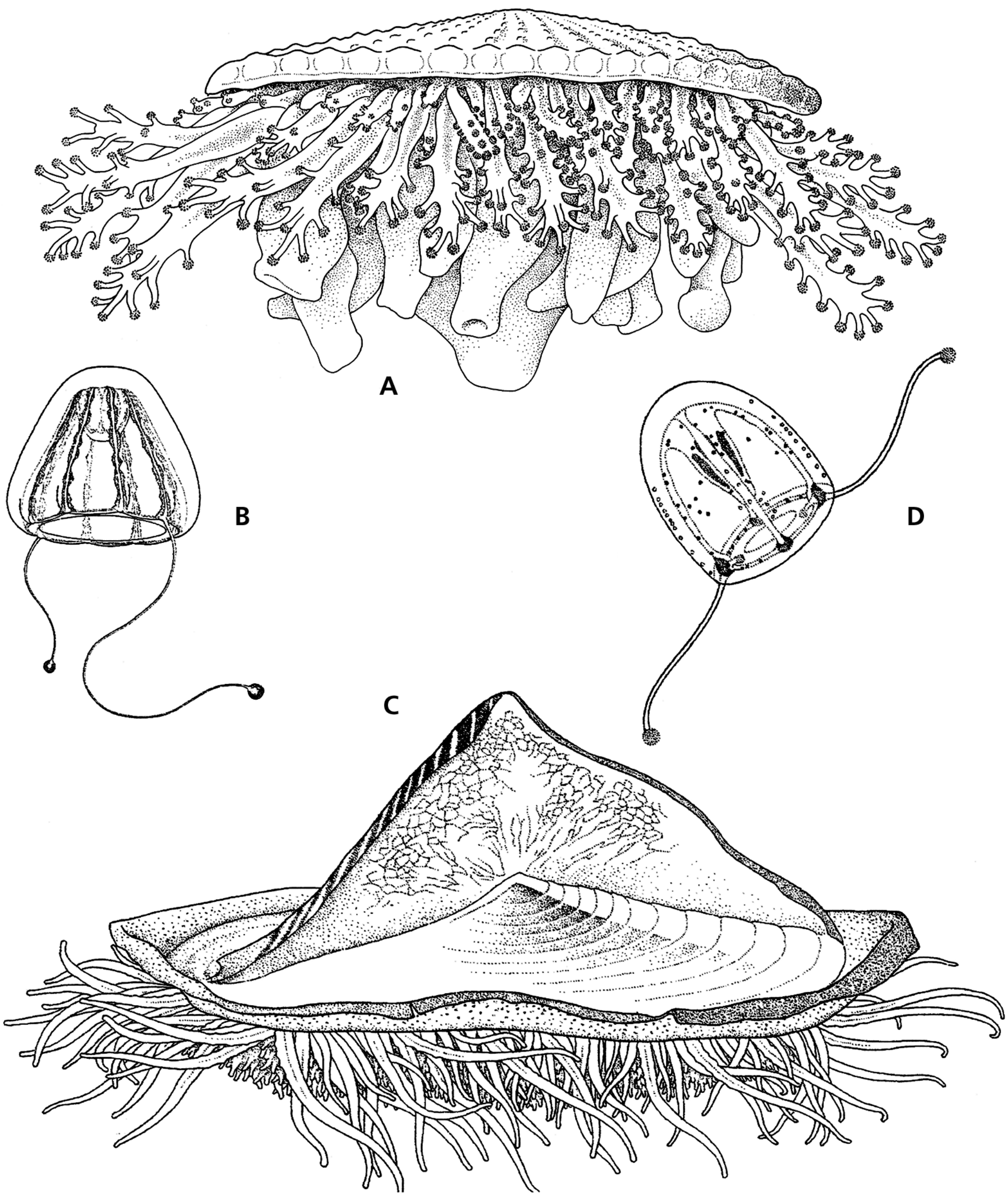


FIG. 123. Anthomedusae, Porpitidae. A-B, *Porpita porpita*: A, polyp; B, medusa. C-D, *Velella velella*: C, polyp; D, medusa (A & C after Pagès *et al*., 1992; B after Bouillon, 1984d; D after Brinckmann-Voss, 1964).

FIG. 123. *Anthomedusae, Porpitidae. A-B,* Porpita porpita *: A, polype ; B, méduse. C-D,* Velella velella *: C, polype ; D, méduse (A & C d'après* Pagès et al.*, 1992 ; B d'après Bouillon, 1984d ; D d'après Brinckmann-Voss, 1964).*

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; colour: 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 1966).

Medusa: 4 exumbrellar cnidocyst rows, 4 radial canals; 2 pairs of opposite, perradial tentacles, a short adaxial one and a long abaxial one, each with a large terminal cnidocyst cluster; 2 perradial marginal bulbs without tentacles; manubrium conical with quadrate base; mouth tubular; "gonads" irregularly arranged perradially and interradially.

Velella velella (Linnaeus, 1758) [syn. *V. lata* Chamisso & Eysenhardt, 1821]

Family ROSALINDIDAE Bouillon, 1985

Hydroid: colonial; stolonal plate crust-like, consisting of a thin perisarcal sheet covered by coenosarc and an external peridermal film; coenosarc supported by perisarcal spines and trabeculae forming a more or less thick framework of meshes; hydranth plump sausage-shaped, with 30-50 scattered capitate tentacles, almost sessile; cnidome comprising subspherical stenoteles and macrobasic mastigophores; fixed gonophores or free medusae? with two tentacles apparently provided with cnidophores, known in one species (*Rosalinda naumovi*), carried singly or on short pedicels among proximal tentacles.

Genus ***ROSALINDA*** Totton, 1949

Fig. 124 F-I

See family characters.

Rosalinda incrustans (Kramp, 1947b)
Rosalinda marlina Watson, 1978
Rosalinda naumovi Antsulevich & Stepanjants, 1985
Rosalinda williami Totton, 1949

Family PSEUDOSOLANDERIIDAE Bouillon & Gravier-Bonnet, fam. nov.

Hydroid: colony with erect, branched, flabellate hydrorhiza; axial skeleton either exclusively chitinous, or chitinous and partly or quite totally calcified; chitinous skeleton consisting of a central axis of folded, lamellar perisarc with spongy centre and developing superficial ridges and spines the all covered but not invested by coenosarc, coenosarc consisting of inner ectodermal layer underlying endodermal tubes running in the longitudinal depressions of the axis and an outer ectoderm which secretes a thin filmy periderm; hydranth short, plump with an oral group of 3 to 5 tentacles mainly consisting of a spherical capitation of large stenoteles, and 20-30 scattered, longer aboral tentacles with smaller capitations of small stenoteles; macrobasic euryteles only in the coenosarc of the colony; gonophores as spherical eumedusoids.

Recent references: Bouillon & Gravier-Bonnet (1987); Hirohito (1988).

Genus ***PSEUDOSOLANDERIA*** Bouillon & Gravier-Bonnet, 1987

Fig. 124A-E

See family characters.

Pseudosolanderia picardi Bouillon & Gravier-Bonnet, 1987
Pseudosolanderia sagamina (Hirohito, 1988)

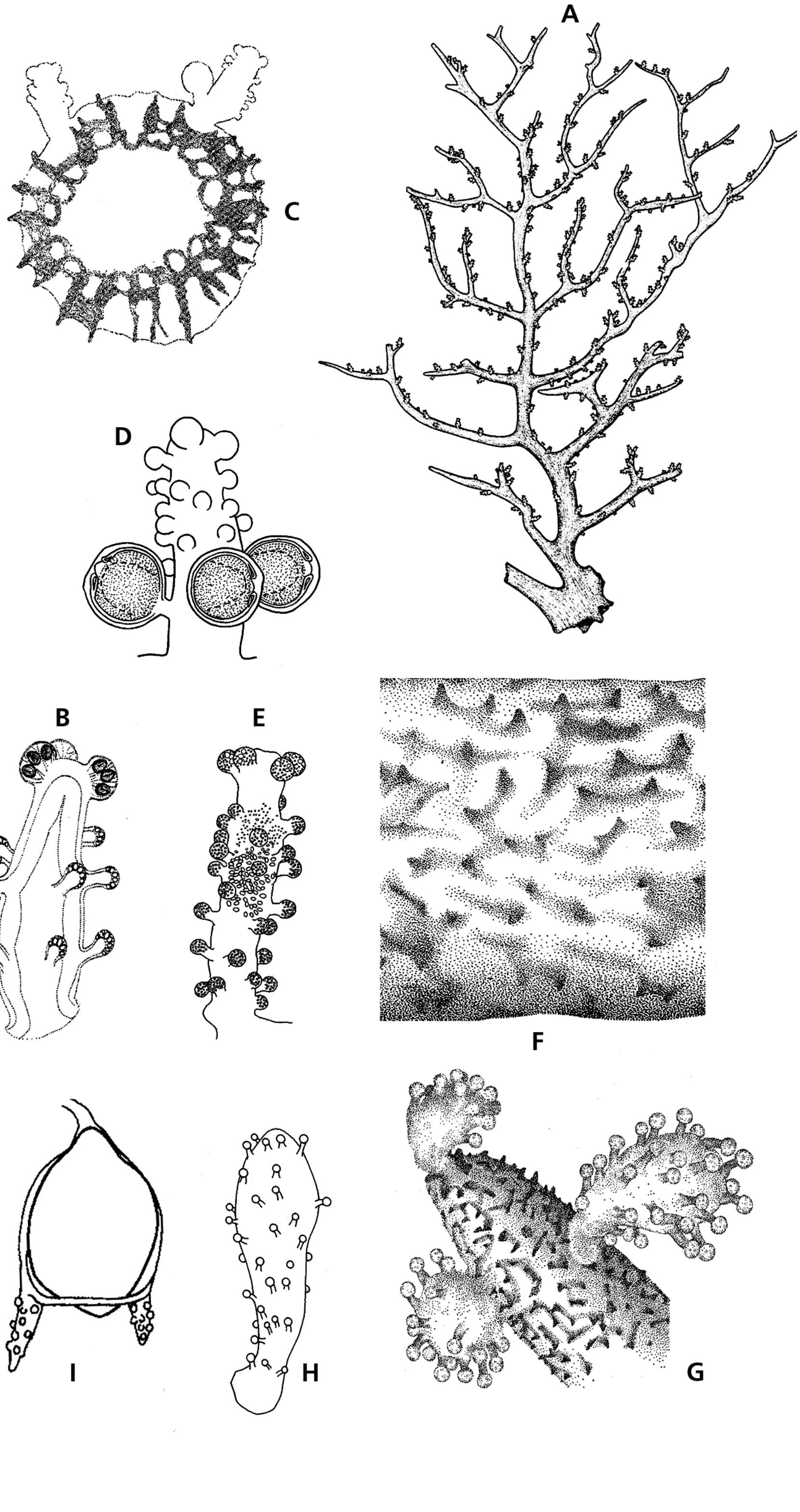


FIG. 124. Anthomedusae, Pseudosolanderiidae. A-B, *Pseudosolanderia picardi*: A, general view of a colony; B, hydranth. C-E, *Pseudosolanderia sagamina*: C, cross section of a branch and hydranths; D, hydranth with gonophores; E, hydranth. F-I, Rosalindidae, *Rosalinda*: F-H, *Rosalinda incrustans*: F, semi-diagrammatic drawing of a part of coenosarc and spines; G, detail of a portion of colony on a spine of *Anamathia rissoana* showing three hydranths; H, detail of a hydranth. I, *Rosalinda naumovi*, developing medusa bud (A-B after Bouillon & Gravier-Bonner, 1987; C-E after Hirohito, 1988; F-G after Vervoort 1966; H after Petersen, 1990; I after Antsulevich & Stepanjants, 1985).

FIG. 124. *Anthomedusae, Pseudosolanderiidae. A-B,* Pseudosolanderia picardi *: A, vue générale d'une colonie ; B, détail d'un hydranthe. C-E,* Pseudosolanderia sagamina *: C, section transversale d'une branche et de deux hydranthes ; D, hydranthe avec gonophores. E, hydranthe. F-I, Rosalindidae,* Rosalinda *: F-H,* Rosalinda incrustans *: F, dessin semi-schématique d'une partie de coenosarc couvert d'épines ; G, détail d'une portion de colonie sur une épine d'*Anamathia rissoana *montrant trois hydranthes ; H, détail d'un hydranthe. I,* Rosalinda naumovi*, bourgeon médusaire prêt à se détacher (A-B d'après Bouillon & Gravier-Bonner, 1987 ; C-E d'après Hirohito, 1988 ; F-G d'après Vervoort 1966 ; H d'après Petersen, 1990 ; I d'après Antsulevich & Stepanjants, 1985).*

Family TEISSIERIDAE Bouillon, 1974

Hydroid: colony polymorphic; basal hydrorhizal encrusting plate provided with spines penetrating the overlaying coenosarc; gastro-gonozooids broad, sausage-shaped, with numerous scattered capitate tentacles, with or without a clear whorl of oral tentacles; with 1 or 2 types of dactylozooids; gonophores as free medusae, medusa buds carried single or in small groups among the tentacles of gastro-gonozooids.

Medusa: with or without apical projection; 4 radial canals; 4 perradial exumbrellar cnidocyst pouches on base of radial canals, containing stenoteles; 2 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.

Recent reference: Petersen (1990).

Genus ***TEISSIERA*** Bouillon, 1974

Figs 1, 15A, 125A-B

See family characters.

Teissiera australe Bouillon, 1978c
Teissiera macrocystae Xu, Huang & Chen Xu, 1991 [doubtful status]
Teissiera medusifera Bouillon, 1978c
Teissiera milleporoides Bouillon, 1974
Teissiera polypofera Xu, Huang & Chen Xu, 1991 [doubtful status]

Family ZANCLEIDAE Russell, 1953

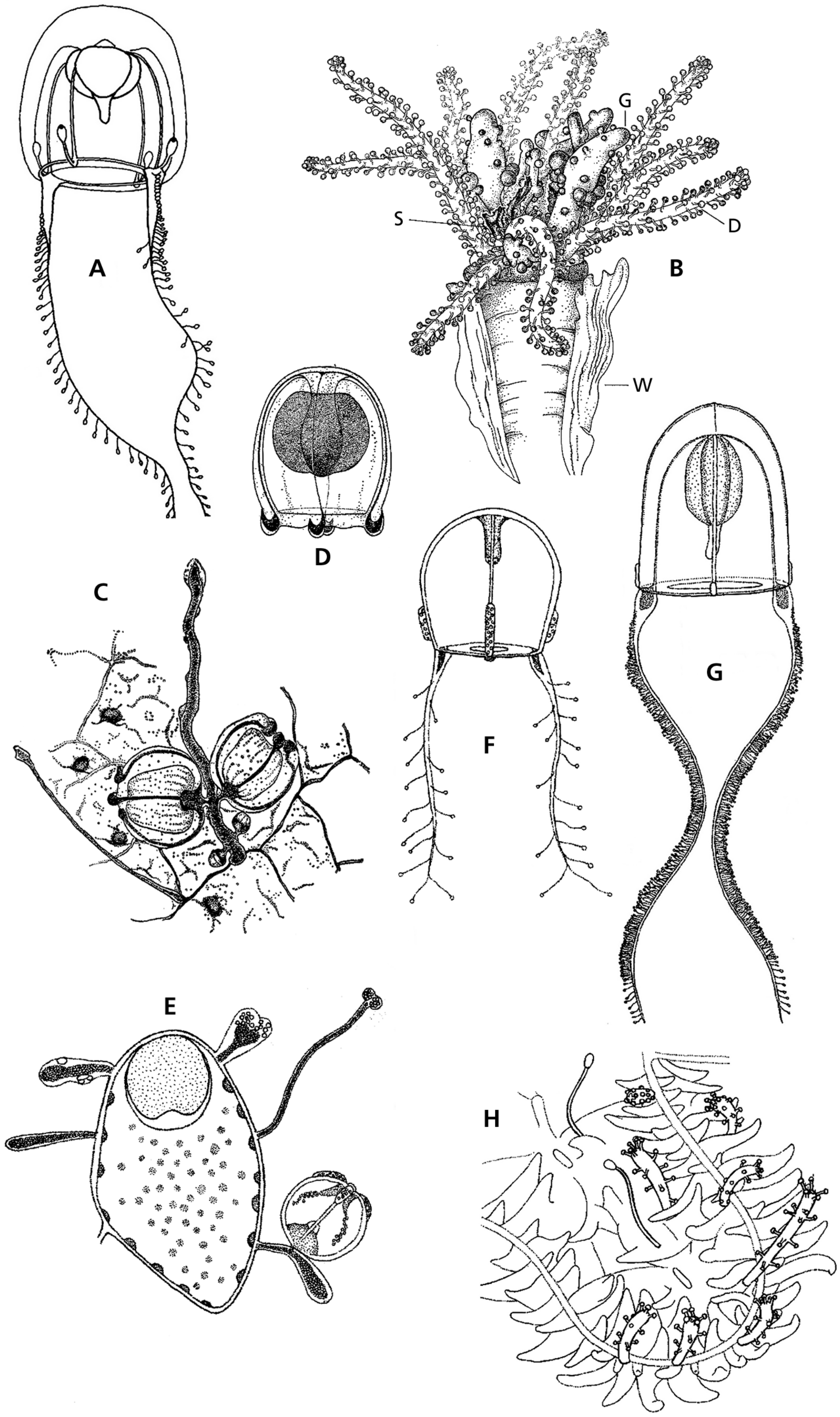
Hydroid: colonial; hydrorhiza creeping, stolonal; perisarc enveloping hydrocaulus and hydrorhiza not lamellar, as a simple tube; hydrocaulus unbranched; polyps monomorphic or polymorphic; gastrozooid either with oral and aboral capitate tentacles, or with reduced capitate tentacles, or without tentacles; gonozooid and dactylozooid, when present, varied in expression.

Medusa: umbrella bell-shaped; 4 perradial exumbrellar cnidocyst pouches, either oval, clavate, elongate or linear, usually containing stenoteles; mouth simple, circular, without oral tentacles (except in *Oonautes*, of uncertain family affinity; see Capitata *incertae sedis*); 4 radial canals (exceptionally bifurcated in *Ctenaria*, of uncertain family affinity; see Capitata *incertae sedis*); marginal tentacles 0, 2 or 4, hollow, each with numerous abaxial cnidophores, with macrobasic euryteles; "gonads" usually interradial, rarely in a single mass around manubrium; without ocelli.

Recent references: Wedler & Larson (1986); Calder (1988a); Petersen (1990); Gravili *et al.* (1996); Schuchert (1996); Bouillon (1999); Bouillon & Barnett (1999); Boero *et al.* (2000); Bouillon & Boero (2000).

FIG. 125. Anthomedusae. A-B, Teissieridae: A, *Teissiera australe*, mature medusa; B, *Teissiera milleporoides*, colony living on the operculum of the worm *Spirobranchus tetraceros*. C-F, Zancleidae, *Halocoryne*: C-D, *Halocoryne epizoica*: C, general view of a part of colony living on a bryozoan host showing two polyps, one with medusa buds; D, newly released eumedusoid; E-F, *Halocoryne pirainoid*: E, hydroid colony on bryozoan host showing various polyps, one with a medusa bud; F, newly released medusa. G-H, *Zanclea, Zanclea gilii*: G, mature medusa; H, general view of a colony living on coral (A after Bouillon, 1978c; B after Bouillon, 1974; C-D after Bouillon, 1995a; E-H after Boero *et al.*, 2000). D = dactylozooid; G = gastrozooid; S = spine; W = worm host.

FIG. 125. *Anthomedusae. A-B, Teissieridae : A,* Teissiera australe*, méduse mature ; B,* Teissiera milleporoides*, colonie vivant sur l'opercule d'un polychète* Spirobranchus tetraceros*. C-F, Zancleidae,* Halocoryne *: C-D,* Halocoryne epizoica *: C, vue générale d'une partie de colonie vivant sur un bryozoaire et montrant deux polypes dont l'un présente des bourgeons médusaires ; D, eumédusoïde venant de se libérer ; E-F,* Halocoryne pirainoid *: E, colonie hydroïdes vivant sur un bryozoaire et montrant divers polypes dont un avec un bourgeon médusaire ; F, méduse venant de se libérer. G-H,* Zanclea, Zanclea gilii *: G, méduse mature ; H, vue générale d'une colonie vivant sur un madréporaire (A d'après Bouillon, 1978c ; B d'après Bouillon, 1974 ; C-D d'après Bouillon, 1995a ; E-H d'après Boero* et al.*, 2000). D = dactylozoïde ; G = gastérozoïde ; S = épine ; W = polychète.*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H

KEY TO HYDROIDS

1. gastrozooid reduced, without tentacles .... *Halocoryne*
– gastrozooid with tentacles 2
2. gastrozooid usually with reduced number of tentacles .... *Zanclella*
– gastrozooids with numerous tentacles .... *Zanclea*

KEY TO MEDUSAE

1. umbrella laterally compressed in tentacular plane .... *Zanclella**
– umbrella not laterally compressed .... *Zanclea* and *Halocoryne**

*Most of the various Zancleidae medusae are not identifiable without knowing the polyp cnidome and the life cycle.

Genus ***HALOCORYNE*** Hadzi, 1917

Fig. 125C-F

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.
Medusa: 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.
Recent reference: Piraino *et al.* (1992).

Halocoryne epizoica Hadzi, 1917
Halocoryne frasca Boero, Bouillon & Gravili, 2000
Halocoryne orientalis (Browne, 1916) [as *Halocoryne*]
Halocoryne pirainoid Boero, Bouillon & Gravili, 2000

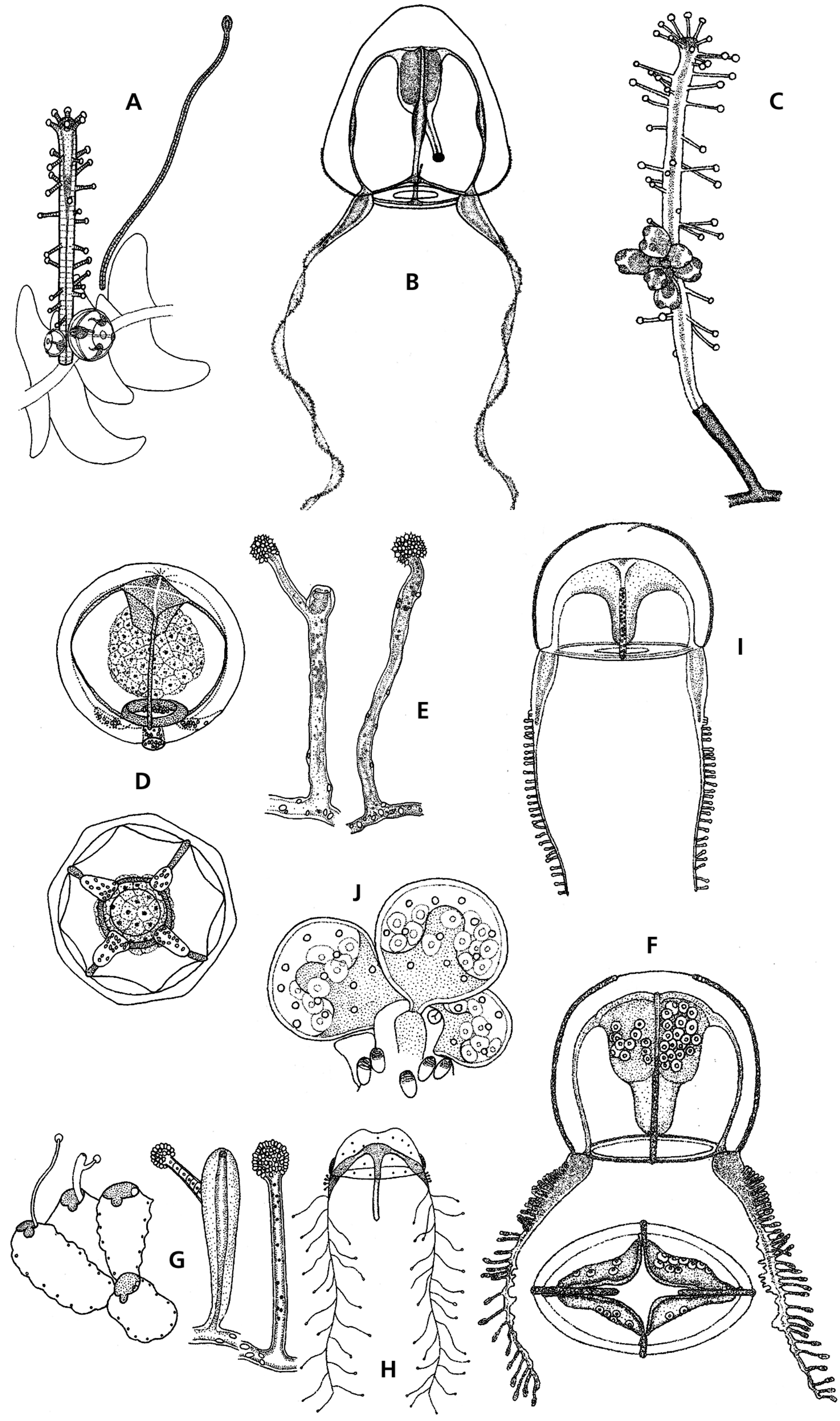
Genus ***ZANCLEA*** Gegenbaur, 1857

Figs 24A, 125G-H, 126A-C

Hydroid: colonial, stolonal with creeping hydrorhiza; hydrocaulus unbranched; often associated with bryozoans, bivalves and corals; polyps monomorphic or polymorphic; polymorphic colony with gastrozooids, dactylozooids, gonozooids; 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.

FIG. 126. Anthomedusae, Zancleidae (end). A-C, *Zanclea*: A, *Zanclea gilii*, detail of a colony living on coral and showing a gastro-gonozooid and a dactylozooid; B, *Zanclea sessilis*, mature medusa; C, *Zanclea giancarloi*, hydranth with medusa buds. D-J, *Zanclella*: D-E, *Zanclella bryozoophila*: D, eumedusoid, lateral view (above), oral view (below); E, gastrozooid (left), dactylozooid (right). F-I, *Zanclella glomboides*: F, side view and above view of a mature medusa showing the compressed umbrella; G, hydroid colony on bryozoan host (left), gastrozooid and dactylozooid (rigth); H, newly released medusa; I, lateral view of a young immature medusa compressed in the plane of the two tentacular bulbs. J, *Zanclella diabolica*, medusa buds on hydrorhiza (all after Boero, Bouillon & Gravili, 2000).

FIG. 126. *Anthomedusae, Zancleidae (fin). A-C,* Zanclea : *A,* Zanclea gilii*, détail d'une colonie vivant sur un madréporaire et montrant un gastro-gonozoïde et un dactylozoïde ; B,* Zanclea sessilis*, méduse mature ; C,* Zanclea giancarloi*, hydranthe développant des bourgeons médusaires. D-J,* Zanclella : *D-E,* Zanclella bryozoophila *: D, eumedusoïde, vue latérale (au dessus), vue orale (au-dessous) ; E, gastérozoïde (à gauche), dactylozoïde (à droite) ; F-I,* Zanclella glomboides *: F, vues latérale et apicale d'une méduse adulte montrant la compression de l'ombrelle ; G, colonie d'hydroïdes vivant sur un bryozoaire (à gauche), un gastérozoïde et un dactylozoïde (à droite) ; H, jeune méduse venant de se libérer ; I, vue latérale d'une jeune méduse immature comprimée dans le plan des deux bulbes tentaculaires. J,* Zanclella diabolica*, bourgeons médusaires sur l'hydrorhize (d'après Boero, Bouillon & Gravili, 2000).*


A
B
C
D
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J
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G
H

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

Zanclea alba (Meyen, 1834)
Zanclea bomala Boero, Bouillon & Gravili, 2000
Zanclea costata Gegenbaur, 1857
Zanclea divergens Boero, Bouillon & Gravili, 2000
Zanclea dubia Kramp, 1959a
Zanclea indica Mammen, 1963
Zanclea fanella Boero, Bouillon & Gravili, 2000
Zanclea giancarloi Boero, Bouillon & Gravili, 2000
Zanclea gilii Boero, Bouillon & Gravili, 2000
Zanclea hirohitoi Boero, Bouillon & Gravili, 2000
Zanclea medusapolypata Boero, Bouillon & Gravili, 2000
Zanclea polymorpha Schuchert, 1996
Zanclea retractilis Boero, Bouillon & Gravili, 2000
Zanclea sessilis (Gosse, 1853)
Zanclea spp. – Boero, Bouillon & Gravili, 2000

Genus ***ZANCLELLA*** Boero & Hewitt, 1992

Fig. 126D-J

Hydroid: colony living in association with bryozoans; polymorphic, gastrozooids usually with reduced number of tentacles, and dactylozooids.
Medusa: eumedusoid, bearing exumbrellar cnidocyst chambers; with no tentacular bulbs, no mouth or tentacles; with "gonads" in a single mass encircling manubrium; or medusa with 2 tentacles with stiff cnidophores; with umbrella laterally compressed in the tentacular plane; 4 radial canals and circular canal when adult; exumbrellar cnidocyst chambers; "gonads" interradial on manubrium; medusae with only two radial canals and without circular canal at liberation.

Zanclella bryozoophila Boero & Hewitt, 1992
Zanclella diabolica Boero, Bouillon & Gravili, 2000
Zanclella glomboides Boero, Bouillon & Gravili, 2000

Capitata *incertae sedis:*

Genus ***CTENARIA*** Haeckel, 1879

Fig. 127A

Hydroid: unknown.
Medusa: apical cavity above manubrium; 4 bifurcated radial canals; 2 feathered marginal tentacles and simple unbranched oral tentacles; 8 adradial, meridional lines of cnidocysts on exumbrella and a cnidocyst track above base of each marginal tentacle.

Ctenaria ctenophora Haeckel, 1879 [doubtful status]

Genus ***OONAUTES*** Damas, 1936

Fig. 127B

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

Oonautes hanseni Damas, 1936 [doubtful status]

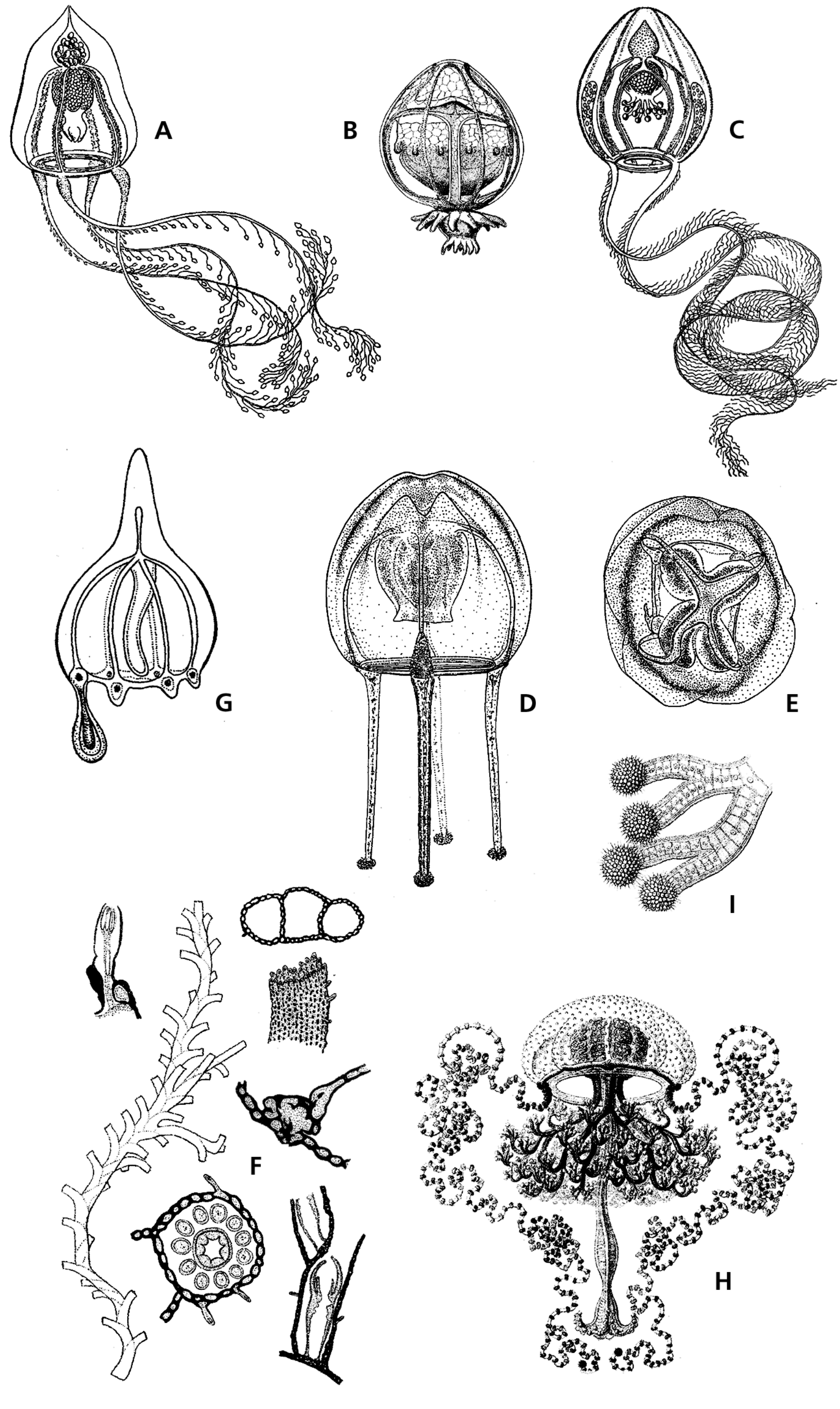


FIG. 127. Anthomedusae, Capitata incertae sedis. A, *Ctenaria ctenophora*, medusa. B, *Oonautes hanseni*, medusa. C, *Pteronema darwini*, medusa. D-E, *Tetraralphia hypothetica*: D, reconstructed diagram of a medusa; E, medusa viewed from apex to show the quadrate manubrium and the four stomach pouches. Anthomedusae incertae sedis. F, *Clathrozoella drygalskii*, showing the general view of a colony, the hydranth in a ''false hydrotheca'', a nematotheca and nematophore and the structure of the skeleton. G, *Mitrocampa conica*, medusa. H-I, *Thamnostylus dinema*: H, medusa; I, detail of an oral tentacle (A & C after Kramp, 1968; B after Kramp, 1959b; D-E after Ralph, 1959: p. 173, figs A, D; F after Vanhöffen, 1910; G after Mayer,1910; H-I after Haeckel, 1881).

FIG. 127. *Anthomedusae,* Capitata incertae sedis. *A,* Ctenaria ctenophora*, méduse. B,* Oonautes hanseni*, méduse. C,* Pteronema darwini*, méduse. D-E,* Tetraralphia hypothetica : *D, diagramme de la reconstruction d'une méduse ; E, méduse vue de l'apex montrant le manubrium quadratique et les quatre poches stomacales. Anthomedusae incertae sedis. F,* Clathrozoella drygalskii*, vue générale d'une colonie, un hydranthe dans une ''fausse hydrothèque'', une nématothèque, un nématophore et la structure du squelette. G,* Mitrocampa conica*, méduse. H-I,* Thamnostylus dinema : *H, méduse ; I, détail d'un tentacule oral (A & C d'après Kramp, 1968 ; B d'après Kramp, 1959b ; D-E d'après Ralph, 1959 : p. 173, figs A, D ; F, d'après Vanhöffen, 1910 ; G, d'après Mayer, 1910 ; H-I d'après Haeckel, 1881).*

Genus ***PTERONEMA*** Haeckel, 1879

Fig. 127C

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

Pteronema darwini Haeckel, 1879 [probably a syn. of *Asyncoryne philippina*]

Genus ***TETRARALPHIA*** Pagès & Bouillon, 1997

Fig. 127D-E

Hydroid: unknown.
Medusa: 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; four manubrial pouches and simple circular mouth, no ocelli.

Tetraralphia hypothetica Pagès & Bouillon, 1997

Anthomedusae *Incertae sedis*:

Genus ***MICROCAMPANA*** Fewkes, 1889

Fig. 127G

Hydroid: unknown.
Medusa: with apical canal; 6 radial canals; 6 radially placed marginal tentacles, 5 of which rudimentary and one well developed, club-shaped; manubrium conical to spindle-shaped, as long as bell cavity.

Microcampana conica Fewkes, 1889

Genus ***PROPACHYCORDYLE*** Thiel, 1931

(no figure available)

Hydroid: unknown.
Medusa: umbrella bell-shaped; manubrium short, spherical; “gonads” in ectoderm; 4 radial canals; ring canal and velum present; no tentacles, tentacular bulbs and ocelli.

Propachycordyle canalifera Thiel, 1931 [probably eumedusoid of *Ralpharia parasitica*]

Genus ***THAMNOSTYLUS*** Haeckel, 1879

Fig. 127H-I

Hydroid: unknown.
Medusa: 2 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; 4 large, perradial, oral tentacles, several times dichotomously branched, with capitate ends, issued far away from mouth opening, just under gonads; 4 radial canals; ring canal conspicuous; abaxial ocelli on tentacular bulbs and on small non tentacular perradial bulbs. Doubtful genus.
Remarks: not found again since Haeckel's description.

Thamnostylus dinema Haeckel, 1879 [doubtful status]

Subclass LAINGIOMEDUSAE Bouillon, 1978

Hydroid: unknown.
Medusa: umbrella almost hemispherical, margin lobed, divided by peronial grooves or similar structures; 4 radial canals; no typical circular canal but a solid core of endodermal cells around umbrella margin; tentacles solid, inserted on 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 4 masses on the manubrium or as epidermal lining of interradial pockets of the manubrium; marginal sense organs apparently missing; cnidome: macrobasic mastigophores or macrobasic euryteles. Sexual reproduction unknown.
Remarks: The presence of marginal tentacular bulbs, and the formation of a medusary nodule in two of the four medusae presently included in this subclass, *Kantiella enigmatica* and *Laingia jaumotti*, suggest affinity with the Hydroidomedusa. The lobed margin and the endodermal marginal core, however, suggest affinity with the Narcomedusae. The Laingiomedusae, thus, present a mosaic of characters of Narcomedusae and Hydroidomedusa, but more information about their life cycle are needed to allow a decision about their phylogenetic position.
Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

Family LAINGIIDAE Bouillon, 1978

Hydroid: unknown.
Medusa: umbrella lobed, divided by peronial grooves or similar structures; four radial canals; no typical circular canal but a solid core of endodermal cells around umbrellar margin; tentacles solid, inserted on the exumbrellar surface above bell margin; alternating with tentacles there may be narrow exumbrellar cnidocyst 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; no sense organs; cnidome: macrobasic mastigophores or macrobasic euryteles.

KEY

1. no exumbrellar cnidocyst bands 2
– exumbrellar cnidocyst bands; marginal tentacular bulbs largely separated from marginal circular strand . . . . *Kantiella*
2. interradial ciliated fields; marginal bulbs only somewhat displaced towards exumbrella . . . . *Fabienna*
– no interradial ciliated fields, marginal bulbs largely displaced towards exumbrella forming peronial-like structures. . . . . *Laingia*

Genus ***FABIENNA*** Schuchert, 1996

Fig. 128A-C

Hydroid: unknown.
Medusa: umbrellar margin slightly lobed; 4 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" interradial, on manubrium only.

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

Genus ***KANTIELLA*** Bouillon, 1978

Fig. 128D-F

Hydroid: unknown.
Medusa: with exumbrellar cnidocyst bands; "gonads" on walls of 4 manubrial interradial pouches; 4 short marginal tentacles with terminal cluster of cnidocysts, above peronia-like structures.

Kantiella enigmatica Bouillon, 1978a

Genus ***LAINGIA*** Bouillon, 1978

Fig. 128G

Hydroid: unknown.
Medusa: no 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.

Laingia jaumotti Bouillon, 1978d

Subclass LEPTOMEDUSAE Haeckel, 1866 (1879)

Hydroid: as "Thecata" hydroids; all parts of colony typically protected by a rigid chitinous perisarcal structure of definite shape: hydranth with hydrotheca, nematophore with nematotheca and gonophores with gonotheca. Rarely with naked hydranths.
Medusae: flatter than bell-shaped, typically with hemispherical or flattened umbrella; "gonads" confined to radial canals, exceptionally extending onto the proximal part of manubrium; marginal sense organs, when present, in form of ectodermal velar statocysts, rarely cordyli, occasionally adaxial ocelli; marginal tentacles peripheral and hollow (except in *Obelia*), 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.

Order CONICA Broch, 1910

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

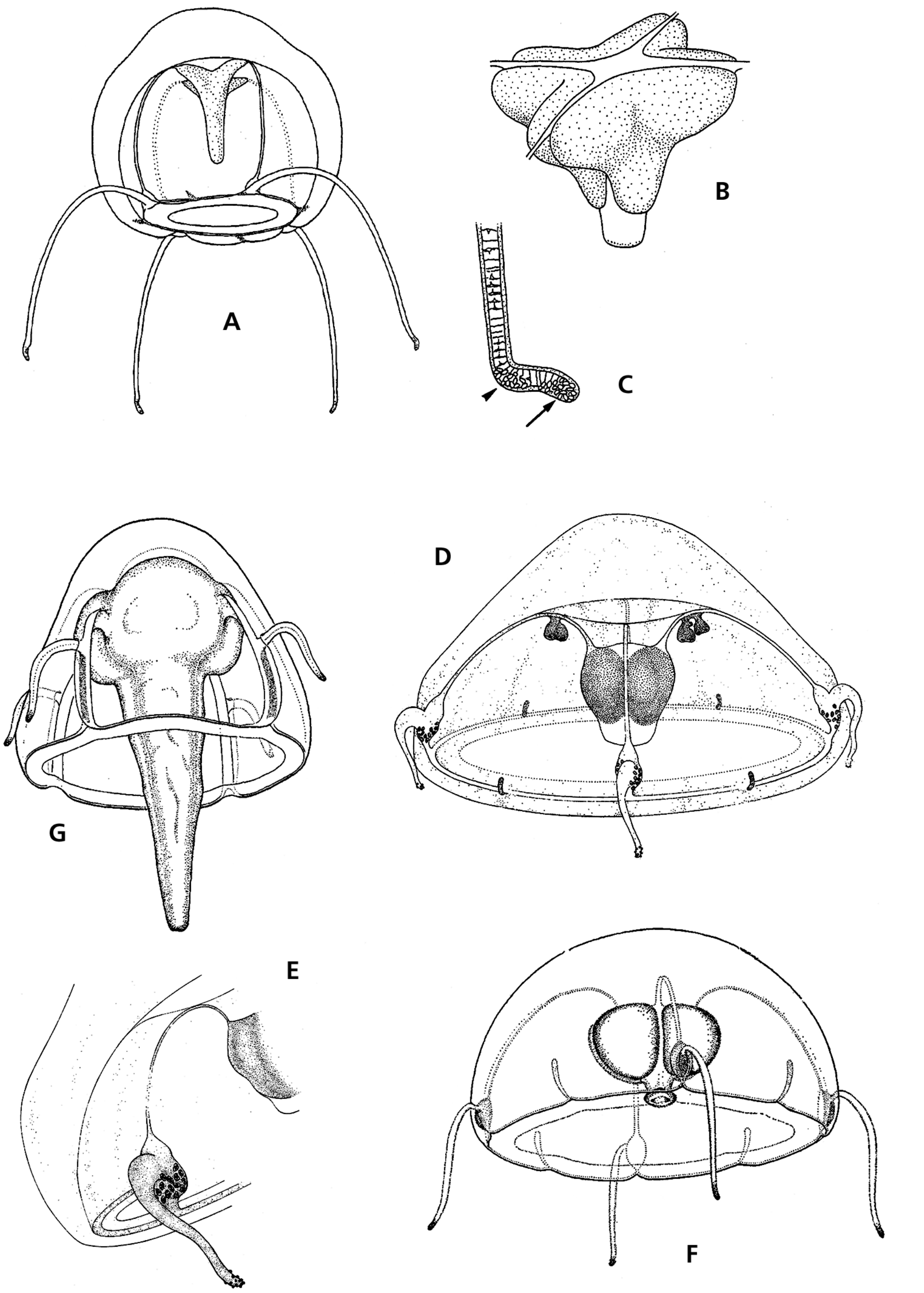


FIG. 128. Laingiomedusae, Laingiidae. A-C, *Fabienna sphaerica*: A, medusa; B, manubium with mature ''gonads''; C, tentacle tip showing the characteristic bending with adjacent and terminal clusters of cnidocysts (arrows). D-F, *Kantiella enigmatica*: D, adult medusa with medusa buds; E, mature medusa; F, detail of a tentacular bulb and tentacle. G, *Laingia jaumotti*, mature medusa (A-C after Schuchert, 1996; D-G after Bouillon, 1978 a & b).

FIG. 128. *Laingiomedusae, Laingiidae. A-C,* Fabienna sphaerica : *A, méduse ; B, manubrium avec des ''gonades''matures ; C, extrémité tentaculaire montrant la courbure caractéristique et les amas adjacent et terminal de cnidocystes (flèche). D-F,* Kantiella enigmatica : *D, méduse adulte développant des bourgeons médusaires ; E, détail d'un bulbe tentaculaire et d'un tentacule ; F, méduse mature. G,* Laingia jaumotti*, méduse mature (A-C d'après Schuchert, 1996 ; D-G d'après Bouillon, 1978 a & b).*

KEY TO HYDROIDS

1. colony arborescent, skeleton of complexly anastomosing chitinous stolons........... Clathrozoidae
– colony different.. 2
2. hydranth naked, without intertentacular membrane................................. Melicertidae
– hydranth typically with hydrotheca (when exceptionally naked, i.e. Eirenidae, with intertentacular membrane) 3
3. hydrotheca with operculum 4
– hydrotheca without operculum 10
4. hydrotheca generally bilaterally symmetrical; usually with marginal cusps....................... 5
– hydrotheca radially symmetrical; without true marginal teeth.................................. 6
5. hydrotheca generally pedicellate; usually with annular perisarcal diaphragm; hydranths with annular ectodermal fold .... Thyroscyphidae
– hydrotheca generally sessile, adnate; diaphragm in few pedicellate forms, others with eccentric hydropore; some species with abcauline gastric caecum and mantle (ectodermal lamella); no basal annular ectodermal fold .... Sertulariidae
6. operculum of two pleated membranes meeting like a gable roof .... Tiarannidae
– operculum of 4 or more valves sharply or not sharply demarcated from hydrothecal wall 7
7. hydrotheca adhering to substrate for almost its entire length .... Lineolariidae
– hydrotheca not adhering to substrate 8
8. hydrotheca sessile .... all the medusa families with pleated or segmented operculum and with "*Cuspidella*-like" colony: Campanulinidae in part; Cirrholoveniidae; Dipleurosomatidae; Laodiceidae .... Mitrocomidae; Tiaropsidae
– hydrothecae pedicellate = all the medusa families with pleated or segmented operculum with "Campanulinida-type" of hydroids 9
9. hydranth without intertentacular web........... Campanulinidae in part; Lovenellidae; Phialellidae
– with intertentacular web .... Aequoreidae; Blackfordiidae; Campanulinidae in part; Eirenidae;Lovenellidae; .... Malagazziidae; Sugiuridae
10. hydrotheca saucer- or basin-shaped, usually too small to contain contracted hydranth .. Haleciidae
– hydrotheca usually deep enough to contain contracted hydranth 11
11. hydrotheca always restricted to one side of stem or branches; nematophores present in regular arrangement, usually 3-5 per hydrotheca 12
– hydrotheca on two or more sides of stem or branches; nematophores if present seldom regularly arranged 15
12. paired lateral nematothecae fused to hydrothecae............................... Aglaopheniidae
– paired lateral nematothecae present or absent, when present not fused to hydrothecae........... 13
13. paired lateral nematothecae absent; median nematothecae usually reduced and seldom two-chambered .... Kirchenpaueriidae
– paired lateral nematothecae present; nematothecae usually two-chambered 14
14. hydrocladia arising from erect stem; no cauline hydrotheca; hydrocauli when polysiphonic giving rise to hydrocladia from a single axial tube .... Plumulariidae
– hydrocladia arising from erect main stem or directly independently from hydrorhiza; stem or branches either with cauline hydrothecae or fascicled and giving rise to hydrocladia or pinnae from any of its component tubes.. Halopterididae
15. hydrotheca with a definite floor, always sessile and bilaterally symmetrical, no nematothecae........ .... Syntheciidae
– hydrotheca with no definite floor, with or without diaphragm, sessile or peduncled ; bilaterally or radially symmetrical; nematothecae present or absent.. 16
16. colony usually stolonal; hydrothecae pedicellate; either with an annular perisarcal thickening and membranous diaphragm or thick diaphragm an no annular thickening; gonothecae single, swimming gonophores, eumedusoids or free medusae .... Hebellidae

– colony usually erect; hydrotheca with or without pedicel, with or without diaphragm; without annular perisarcal thickening; gonophores as fixed sporosacs, gonothecae aggregated, exceptionally single or in pairs . . . . Lafœidae

KEY TO MEDUSA

1. with only one manubrium 2
– with up to 6 manubria; without centripetal canals . . . . Sugiuridae*

2. without statocysts or cordyli 3
– with statocysts or cordyli 5

3. gastric peduncle large, broad; many filiform, solid tentaculiform structures without marginal bulbs, not connected to circular canal . . . . Orchistomatidae
– no gastric peduncle 4

4. base of manubrium attached over its whole surface; radial canals simple or bifurcated . . Melicertidae
– base of manubrium narrow; radial canals either branched or, if simple, irregularly arranged . . . . Dipleurosomatidae

5. cordyli or cordyli-like structures 6
– statocysts 9

6. manubrium with 4 perradial lobes connected to subumbrella; "gonads" on manubrium, extending on perradial lobes; cordyli-like structures. . . . . Tiarannidae
– manubrium without perradial lobes 7

7. with cordyli 8
– with cordyli-like structures; "gonads" elongated forming linear sacs on radial canals, separated from manubrium; with or without open statocysts . . . . Teclaiidae

8. 4 or 8 simple radial canals . . . . Laodiceidae
– 4 or more branched radial canals . . . . Hebellidae

9. closed statocysts 11
– open statocysts. . . . . 10 see also 7a

10. open statocysts associated with ocelli . . . . Tiaropsidae
– open statocysts without ocelli. . . . . Mitrocomidae

11. closed statocysts, adaxial ocelli . . . . Barcinidae
– closed statocysts, without ocelli 12

12. distinct gastric peduncle; 8 or many statocysts . . . . Eirenidae
– no distinct gastric peduncle. 13

13. manubrium very broad; many (more than 16) radial canals; tentacle bulbs with excretory pores on excretory papillae or not . . . . Aequoreidae
– manubrium narrow; normally 4-8 radial canals 14

14. tentacle bulbs with excretory pores, 4-8 radial canals (exceptionally 12) . . . . Malagazziidae
– tentacle bulbs without excretory pores 15

15. tentacle bulbs with lateral cirri . . . . Lovenellidae
– tentacle bulbs without lateral cirri 16

16. exumbrella with marginal cirri . . . . Cirrholoveniidae
– exumbrella without marginal cirri 17

17. "gonads" divided in two lateral parts separated by a median groove 18
– "gonads" completely surrounding radial canals1 9

18. 8 marginal statocysts; no marginal tentaculae; 4 radial canals . . . . Phialellidae
– numerous statocysts; marginal tentaculae; 8 radial canals . . . . Octocannoidae

19. endodermal core of tentacles extending into bell mesoglea. . . . . Blackfordiidae
– no endodermal tentacular expansions . . . . Campanulariidae (see under Proboscoida)

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

Family AEQUOREIDAE Eschscholtz, 1829

Hydroid: of "campanulinid" type; colony stolonal or erect, when erect only sparingly and sympodially branched; hydrotheca delicate, tubular, elongated, radially symmetrical, operculum as a continuation of hydrothecal wall, formed by several triangular convergent folds continuing downwards nearly to base of hydrotheca and not delimited by crease-line; in older colonies operculum generally lost, hydrotheca reduced to a perisarcal collar, acquiring a haleciid shape; hydranth contractile, with basal intertentacular web, tentacles amphicoronate, moniliform-like when completely extended; gonothecae pedicellate, very large, cylindrical, giving rise to one rarely to two medusae.
Medusa: manubrium very wide, circular; usually no gastric peduncle; many simple or branched radial canals; "gonads" on radial canals, separated from manubrium; marginal tentacles hollow; usually with excretory pores or papillae; no marginal or lateral cirri; statocysts closed; no ocelli.
Remarks: without knowledge of life cycle, the hydroids of *Aequorea* are inadequate for species description (see Cornelius 1995); some hydroid-based nominal species of *Aequorea* have nevertheless been described; their medusae, however, might have been described since a long time and they could be junior synonyms: *Aequorea africana* Millard, 1966; *Aequorea phillipensis* Watson, 1998.
Recent references: Pagès *et al.* (1992); Watson (1998); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO MEDUSAE

1. radial canals branched or bifurcated. . . . . *Zygocanna*
– radial canals simple 2
2. manubrium with circular rows of papillae in same number as radial canals. . . . . *Gangliostoma*
– manubrium without circular papillae 3
3. subumbrella with radial rows of gelatinous papillae . . . . *Rhacostoma*
– subumbrella without radial rows of gelatinous papillae. . . . . *Aequorea*

Genus ***AEQUOREA*** Péron & Lesueur, 1810
Figs 25E, 129A-F

Hydroid: see family characters.
Medusa: numerous simple radial canals; subumbrella without rows of gelatinous papillae.

Aequorea africana Millard, 1966 [doubtful status]
Aequorea albida L. Agassiz, 1862a
Aequorea australis Uchida, 1947a
Aequorea coerulescens (Brandt, 1838)
Aequorea conica Browne, 1905a
Aequorea floridana (L. Agassiz, 1862a)
Aequorea forskalea Péron & Lesueur, 1810b
Aequorea globosa Eschscholtz, 1829
Aequorea krampi Bouillon, 1984b
Aequorea macrodactyla (Brandt, 1835)
Aequorea minima Bouillon, 1985a
Aequorea papillata Huang & Xu, 1994
Aequorea parva Browne, 1905a
Aequorea pensilis (Eschscholtz, 1829)
Aequorea phillipensis Watson, 1998 [doubtful status]
Aequorea sp. Menon, 1945
Aequorea tenuis (L. Agassiz, 1862a)
Aequorea victoria (Murbach & Shearer, 1902)
Aequorea vitrina Gosse, 1853
See also *Orchistomella graeffei* and *O. tentaculata*, p. 355.

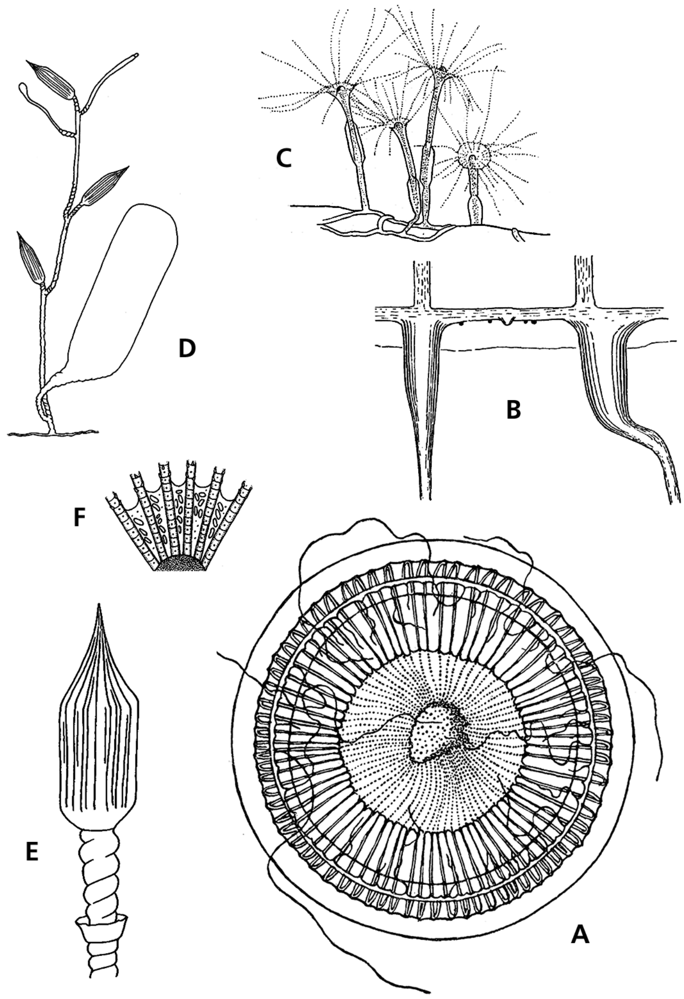


FIG. 129. Leptomedusae, Aequoreidae. A-F, *Aequorea*: A-B, *Aequorea forskalea*: A, adult medusa; B, portion of umbrella margin; C-F, *Aequorea* spp., hydroid: C, portion of a colony; D, branch of a colony; E, hydrotheca; F, basal web between tentacles of hydranth (A-B after Kramp, 1959b; C after Russell, 1953; D after Hincks, 1868; E after Cornelius, 1995; F after Rees, 1938).

***FIG. 129.** Leptomedusae, Aequoreidae. A-F,* Aequorea : *A-B,* Aequorea forskalea : *A, méduse adulte ; B, portion du bord exombrellaire ; C-F,* Aequorea *spp. Hydroïde : C, portion d'une colonie ; D, branche d'une colonie ; E, hydrothèque ; F, membrane intertentaculaire d'un hydranthe (A-B d'après Kramp, 1959b ; C d'après Russell, 1953 ; D d'après Hincks, 1868 ; E d'après Cornelius, 1995 ; F d'après Rees, 1938).*

Genus ***GANGLIOSTOMA*** Xu, 1983

Fig. 130A-B

Hydroid: unknown.
Medusa: manubrium very broad, with a basal circular row of as many papillae as radial canals; no subumbrellar gelatinous papillae.

Gangliostoma guangdongensis Xu, 1983

Genus ***RHACOSTOMA*** L. Agassiz, 1850

Fig. 130C-D

Hydroid: unknown.
Medusa: radial canals numerous, simple; subumbrella with radial rows of gelatinous papillae.

Rhacostoma atlanticum L. Agassiz, 1850

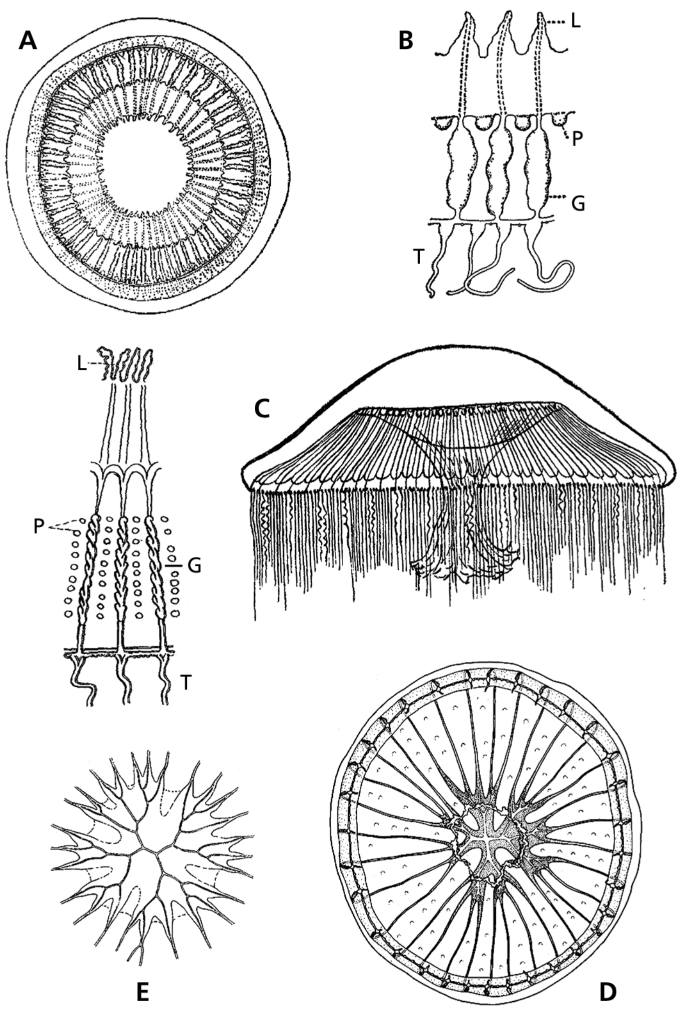


FIG. 130. Leptomedusae, Aequoreidae. A-B, *Gangliostoma guangdongensis*: A, oral view of an adult medusa; B, detail of a part of the umbrella. C-D, *Rhacostoma atlanticum*: C, lateral view of an adult medusa; D, detail of a part of the umbrella. E-F, *Zygocanna vagans*: E, oral view of an adult medusa; F, aboral view of the manubrium (A-B after Xu, 1983; C-D after Kramp, 1933b; E after Pagès *et al*, 1992; F after Bigelow, 1919). G = ''gonad''; L = lip; P= papilla; T = tentacle.

FIG. 130. *Leptomedusae, Aequoreidae. A-B,* Gangliostoma guangdongensis : *A, vue orale d'une méduse adulte ; B, détail d'un fragment de l'exombrelle. C-D,* Rhacostoma atlantica : *C, vue latérale d'une méduse adulte ; D, détail d'une partie de l'exombrelle. E-F,* Zygocanna vagans : *E, vue orale d'une méduse adulte ; F, vue aborale du manubrium (A-B d'après Xu, 1983 ; C-D d'après Kramp, 1933b ; E d'après Pagès* et al*, 1992 ; F d'après Bigelow, 1919). G = ''gonade'' ; L = lèvre ; P= papille ; T = tentacule.*

Genus ***ZYGOCANNA*** Haeckel, 1879

Fig. 130E-F

Hydroid: unknown.
Medusa: radial canals numerous, branched or bifurcated; exumbrella sometimes with radial rows of gelatinous papillae.

Zygocanna buitendijki Stiasny, 1928
Zygocanna diploconus (Haeckel, 1879)
Zygocanna pleuronota (Péron & Lesueur, 1810a)
Zygocanna purpurea (Péron & Lesueur, 1810a)
Zygocanna vagans Bigelow, 1912

Family AGLAOPHENIIDAE L. Agassiz, 1862

Hydroid: colony upright, mono- or polysiphonic, branched or unbranched, arising from creeping hydrorhiza or from anchoring filaments; hydrocladia alternate or opposite in one plane, or arranged spirally; hydrothecae uniseriate, usually completely adnate, with or without marginal cusps, with or without intrathecal septum, absent from hydrocaulus except in basalmost segment; nematophores with nematothecae, not as naked sarcostyles; nematothecae at least partially fused to hydrothecae, one-chambered (monothalamic) and immovable; hydrotheca typically flanked with one pair of lateral nematothecae, and with an unpaired median inferior nematotheca that may be doubled or have two terminal apertures; sometimes also a pair of superior nematothecae; gonothecae lacking nematothecae, unprotected, or surrounded by curved branches in phylactocarp, or nearly completely enclosed within corbulae both richly armed in cnidocysts; fixed sporosacs or swimming gonophores.

Recent references: Svoboda & Cornelius (1991); Cornelius (1995); Migotto (1996); Calder (1997); Calder & Vervoort (1998); Ansín Agís *et al.* (2001); Watson (2000); Schuchert (2001a; 2003).

KEY TO HYDROIDS

1. gonotheca unprotected . . . . *Gymnangium*
– gonotheca protected in corbula or in phylactocarp 2

2. gonotheca protected in corbula replacing hydrocladia with secondary ribs 3
– no true corbula, gonotheca solitary and protected by branched or unbranched phylactocarps 5

3. corbula with ribs developing on both sides of modified hydrocladium (phylactogonium) 4
– corbula with ribs developing only on one side of phylactogonium (hemicorbula) . . . . *Monoserius*

4. corbula ribs comprising nematothecae and hydrothecae . . . . *Lytocarpia*
– corbula comprising only nematothecae . . . . *Aglaophenia*

5. phylactocarps formed by a modified hydrocladium, single or aggregated into pseudo-corbulae . . . .
. . . . *Macrorhynchia*
– phylactocarps arising as appendages of an unmodified hydrocladium 6

6. - phylactocarp terminating in a nematophorous spike . . . . *Cladocarpoides*
– phylactocarps without nematophorous spike 7

7. hydrocladia arranged in a spiral around stem. . . . . *Streptocaulus*
– hydrocladia arranged in two longitudinal rows. . . . . *Cladocarpus*

Genus ***AGLAOPHENIA*** Lamouroux, 1812

Figs 9N-U, 10G, 131A-G

Synonym: *Pentandra* von Lendenfeld, 1884.

Hydroid: colony erect, hydrocaulus branched or unbranched, monosiphonic or polysiphonic, arising from creeping hydrorhiza or anchoring filaments; hydrocladia unbranched, pinnately arranged, arising from alternate apophyses; hydrothecae only on hydrocladia, typically more or less cone to sac-shaped, margin usually deeply toothed; intrathecal septum variably developed; each hydrotheca flanked typically by a pair of lateral nematothecae and a partly to wholly adnate, median inferior nematotheca sometimes a pair of median superior nematothecae; gonothecae aggregated, enclosed within a corbula formed by modified hydrocladia bearing alternately inserted secondary ribs with nematothecae and lacking basal hydrothecae, corbula ribs fused or not; as fixed sporosacs, or released swimming gonophores.

Remarks: Von Lendenfeld (1885a) created *Pentandra* to accommodate *P. balei* and *P. parvula*, with 5 nematothecae surrounding the hydrothecae: one median inferior, two lateral and a pair of superior, the last pair having been treated by many authors as a supplementary pair of lateral nematothecae. Bedot (1921a) listed a series of genera and species showing deviations in numbers to the typically three hydrothecal nematothecae and stated that there was no need to create new genera for such variations. We agree with his conclusions and consider *Pentandra* as congeneric with *Aglaophenia*.

Recent references: Svoboda & Cornelius (1991); Ramil & Vervoort (1992a); Calder (1997); Schuchert (2001a; 2003); Calder *et al.* (2003); Vervoort & Watson (2003).

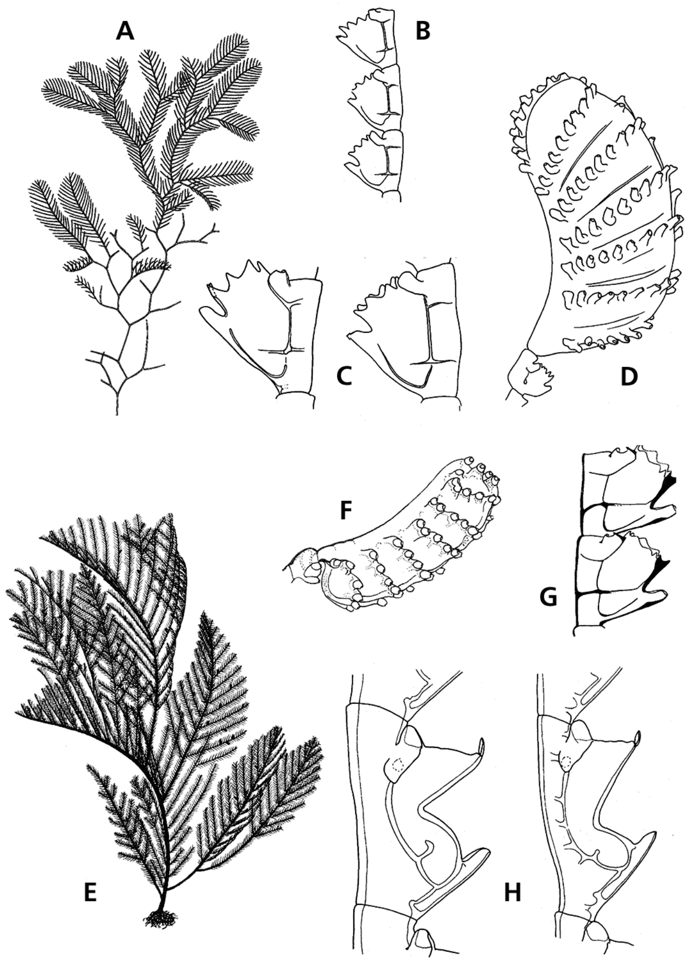


FIG.131. Leptomedusae, Aglaopheniidae. A-G, *Aglaophenia*: A-D, *Aglaophenia pluma*: A, general view of a colony; B, detail of a hydrocladium; C, two hydrothecae and associated nematothecae; D, corbula; E-F, *Aglaophenia cupressina*: E, general view of a stem; F, corbula; *G, Aglaophenia laticarinata*, part of hydrocladium. H, *Cladocarpoides yucatanicus*, hydrothecae (A after Bedot, 1919; B, C right, D after Cornelius, 1995 ; C left, E-G after Millard, 1975; H after Bogle, 1984).

FIG.131. *Leptomedusae, Aglaopheniidae. A-G,* Aglaophenia : *A-D,* Aglaophenia pluma : *A, vue générale d'une colonie ; B, détail d'un hydroclade ; C, deux hydrothèques et leurs nématothèques associées ; D, corbule ; E-F,* Aglaophenia cupressina : *E, vue générale d'une branche ; F, corbule ; G,* Aglaophenia laticarinata*, partie d'un hydroclade. H,* Cladocarpoides yucatanicus*, hydrothèque (A d'après Bedot, 1919 ; B, C à droite, D d'après Cornelius, 1995 ; C à gauche, E-G d'après Millard, 1975 ; H d'après Bogle, 1984).*

Aglaophenia acacia Allman, 1883
Aglaophenia acanthocarpa Allman, 1876a
Aglaophenia allmani Nutting, 1900
Aglaophenia amoyensis Hargitt, 1927
Aglaophenia aperta Nutting, 1900
Aglaophenia bakeri Bale, 1919
Aglaophenia bicornuta Nutting, 1900
Aglaophenia billardi Bale, 1914a
Aglaophenia bilobidentata Stechow, 1907
Aglaophenia carinifera Bale, 1914b
Aglaophenia ctenata (Totton, 1930)
Aglaophenia coarctata Allman, 1883
Aglaophenia constricta Allman, 1877
Aglaophenia contorta Nutting, 1900
Aglaophenia cristifrons Nutting, 1900
Aglaophenia cupressina Lamouroux, 1816
Aglaophenia curvidens Fraser, 1937a
Aglaophenia dannevigi Bale, 1914a
Aglaophenia decumbens Bale, 1914a
Aglaophenia dentata Billard, 1913
Aglaophenia diegensis Torrey, 1904
Aglaophenia difficilis Vervoort & Watson, 2003
Aglaophenia digitulus Vervoort & Watson, 2003
Aglaophenia dispar Fraser, 1948
Aglaophenia divaricata (Busk, 1852)
Aglaophenia diversidentata Fraser, 1948
Aglaophenia dubia Nutting, 1900
Aglaophenia elongata Meneghini, 1845
Aglaophenia epizoica Fraser, 1948
Aglaophenia filicula Allman, 1883
Aglaophenia fluxa Fraser, 1948
Aglaophenia galatheae Kramp, 1956
Aglaophenia gracillima Fewkes, 1881
Aglaophenia harpago Von Schenck, 1965
Aglaophenia holubi Leloup, 1934a
Aglaophenia howensis Briggs, 1918

Aglaophenia hystris Vervoort & Watson, 2003
Aglaophenia inconspicua Torrey, 1902
Aglaophenia inconstans Fraser, 1914b
Aglaophenia insignis Fewkes, 1881
Aglaophenia integriseptata Fraser, 1948
Aglaophenia kirchenpaueri (Heller, 1868)
Aglaophenia latecarinata Allman, 1877
Aglaophenia lateseptata Fraser, 1948
Aglaophenia latirostris Nutting, 1900
Aglaophenia laxa Allman, 1876a
Aglaophenia longicarpa Fraser, 1938c
Aglaophenia lophocarpa Allman, 1877
Aglaophenia meganema Fraser, 1937a
Aglaophenia octocarpa Nutting, 1900
Aglaophenia octodonta (Heller, 1868)
Aglaophenia parvula Bale, 1882
Aglaophenia phyllocarpa Bale, 1888
Aglaophenia picardi Svoboda, 1979
Aglaophenia pinguis Fraser, 1938c
Aglaophenia pluma (Linnaeus, 1758)
Aglaophenia plumosa Bale, 1882
Aglaophenia postdentata Billard, 1913
Aglaophenia praecisa Fraser, 1938a
Aglaophenia prominens Fraser, 1938b
Aglaophenia propinqua Fraser, 1938c
Aglaophenia rhynchocarpa Allman, 1877
Aglaophenia rigida Allman, 1877
Aglaophenia septata Ritchie, 1909a
Aglaophenia sibogae Billard, 1913
Aglaophenia struthionides (Murray, 1860)
Aglaophenia subspiralis Vervoort & Watson, 2003
Aglaophenia suensonii Jäderholm, 1896
Aglaophenia tasmanica Bale, 1914a
Aglaophenia trifida L. Agassiz, 1862a
Aglaophenia triplex Fraser, 1948
Aglaophenia tubiformis Marktanner-Turneretscher, 1890
Aglaophenia tubulifera (Hincks, 1861)
Aglaophenia venusta Fraser, 1948
Aglaophenia whiteleggei Bale, 1888

Genus ***CLADOCARPOIDES*** Bogle, 1984

Fig. 131H

Synonym: *Carpocladus* Vervoort & Watson, 2003.
Hydroid: colony formed by a cluster of unbranched monosiphonic hydrocauli arising from a mass of hydrorhizal fibers; alternate hydrocladia only along distal half of hydrocauli and a longitudinal row of fused nematothecae along one side of basal half; hydrocladia on alternate cauline apophyses, each bearing usually three nematothecae, one hydrotheca per hydrocladial internode; hydrotheca adnate, with an adcauline intrathecal septum, hydrothecal rim sinuous, with one large mesial tooth flanked by two lower ones, three hydrothecal nematothecae, one mesial and two lateral ones, supra-calycine; fixed sporosacs protected by open corbula-like structure arising from proximal internode of unmodified primary hydrocladia and consisting of a long central rachis supporting alternate and dichotomously branched, pinnate phylactocarps each bearing a hydrotheca on basal branch and terminating by a nematophorous spike.
Remarks: The structural differences described by Vervoort and Watson (2003) to distinguish *Cladocarpoides* from *Carpocladus,* as, for instance, the strongly sclerotised condition of the dagger shaped internode and the forked appendage in the first genus, do not justify, in our opinion, generic distinction.
Recent references: Bogle (1984); Calder (1997); Vervoort & Watson (2003).

Cladocarpoides yucatanicus Bogle, 1984
Cladocarpoides fertilis (Vervoort & Watson, 2003)

Genus ***CLADOCARPUS*** Allman, 1874

Figs 5L, 9M, 132A-D

Synonyms: *Aglaophenopsis* Fewkes, 1881; *Nematocarpus* Broch, 1918; *Wanglaophenia* Vervoort and Watson, 2003
Hydroid: colony erect, monosiphonic or polysiphonic, hydrocaulus branched or unbranched, bearing alternate usually unbranched hydrocladia; hydrocladia internodes with numerous septa; hydrotheca deep, often S-shaped, with or without intrathecal septa, usually with a median abcauline tooth, with or without lateral teeth; nematotheca usually with more than

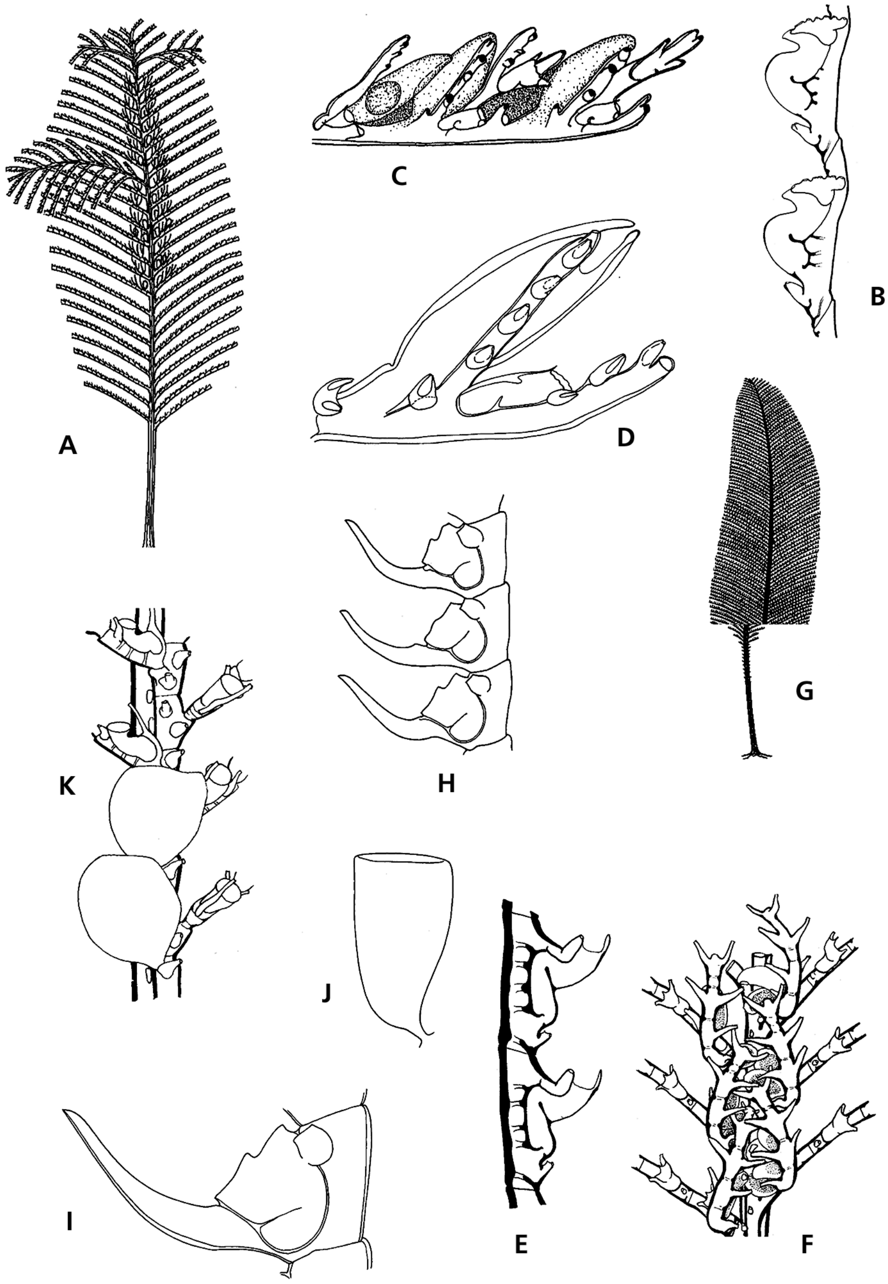


FIG. 132. Leptomedusae, Aglaopheniidae. A-D, *Cladocarpus*: A, *Cladocarpus formosus*, general view of a colony; B-C, *Cladocarpus valdiviae*: B, hydrocladium; C, anterior view a a stem showing phylactocarps; D, *Cladocarpus millardae*, hydrocladium. E-I, *Gymnangium*: E-H, *Gynamgium montagui*: E, general view of a colony; F, detail of a hydrocladium; G, hydrotheca and associated nematothecae; H, gonotheca. I, *Gymnangium gracicaule*, anterior view a stem showing gonothecae and origins of hydrocladia (A after Allman, 1874; B-D & I after Millard, 1975; E-H after Cornelius, 1995).

***FIG. 132.** Leptomedusae, Aglaopheniidae. A-D,* Cladocarpus : *A,* Cladocarpus formosus*, vue générale d'une colonie ; B-C,* Cladocarpus valdiviae : *B, hydroclade ; C, vue antérieure d'une branche montrant les phylactocarpes ; D,* Cladocarpus millardae*, hydroclade. E-I,* Gymnangium : *E-H,* Gynamgium montagui : *E, vue générale d'une colonie ; F, détail d'un hydroclade ; G, hydrothèque et nématothèques associés ; H, gonothèque. I,* Gymnangium gracicaule, *vue antérieure d'une branche montrant les gonothèques et les origines des hydroclades (A d'après Allman, 1874 ; B-D & I d'après Millard, 1975 ; E-H d'après Cornelius, 1995).*

one aperture, median inferior nematotheca short, usually below hydrotheca, never reaching thecal margin, sometimes a superior nematotheca; gonothecae not contiguous, usually protected by loose phylactocarps with either unbranched or dichotomously branched axis (= rachis, homologous with a hydrocaulus of other Aglaopheniidae); axis made of a regular succession of segments each with 2-3 nematothecae and bearing an alternate apophysis supporting a nematophorous branch, usually without hydrothecae, phylactocarp structures resembling stag antlers.

Remarks: The phylactocarps of the various species of the genus *Cladocarpus* as defined above may be different in structure. Ramil and Vervoort (1992b) distinguished two types of phylactocarps in the genus *Cladocarpus* s.l., one where the rachis (axis) of the phylactocarps is homologous with the hydrocaulus (*Cladocarpus* sensu stricto), the other, where the rachis is similar to the hydrocladia (genus *Streptocaulus*). As remarked by Schuchert (2001a), however, some species of *Cladocarpus* have the proximal part of the phylactocarps of one type and the distal one of the other type (*Cladocarpus bonneviae*) and in some species of *Cladocarpus* the phylactocarps are not referable to one of the described types (*C. integer*). Schuchert (2001a) considered therefore that the genus needs a comprehensive phylogenetic analysis to recognise monophyletic taxa with sufficient reliability and that the types of phylactocarps have to be defined more precisely. Consequently he advised to continue to use the genus diagnosis of *Cladocarpus* as defined by Bouillon (1985), reprised with some modification above.

The diagnosis of the genus *Wanglaophenia* Vervoort and Watson (2003) agrees with the above given definition, therefore the genus is considered as congeneric with *Cladocarpus*.

Recent references: Bouillon (1985); Schuchert (2001a); Schuchert (2003); Vervoort & Watson (2003).

Cladocarpus alatus Jarvis, 1922
Cladocarpus anonymus Ramil & Vervoort, 1992a
Cladocarpus (Gray, 1843) [doubtful status]
Cladocarpus bathyzonatus Ritchie, 1911
Cladocarpus bicuspis (G.O. Sars, 1874)
Cladocarpus bocki Jäderholm, 1919
Cladocarpus bonneviae Jäderholm, 1909 [syn. *Aglaophenia compressa* (Bonnevie, 1899) non Fewkes, 1881]
Cladocarpus boucheti Ramil & Vervoort, 1992a
Cladocarpus campanulatus Ritchie, 1912
Cladocarpus carinatus Nutting, 1900
Cladocarpus cartieri Bedot, 1921a
Cladocarpus compressus Fewkes, 1881
Cladocarpus cornutus Verrill, 1879
Cladocarpus crenatus (Fewkes, 1881)
Cladocarpus crepidatus Millard, 1975
Cladocarpus delicatus Bogle, 1990
Cladocarpus diana Broch, 1918
Cladocarpus distans (Nutting, 1900)
Cladocarpus distomus Clarke, 1907
Cladocarpus dofleini (Stechow, 1911)
Cladocarpus dolichotheca Allman, 1877
Cladocarpus elongatus Bedot, 1921b
Cladocarpus flexilis Verrill, 1885
Cladocarpus flexuosus Nutting, 1900
Cladocarpus formosus Allman, 1874b
Cladocarpus gracilis Fraser, 1948
Cladocarpus grandis Nutting,1900
Cladocarpus hirsutus (Fewkes, 1881)
Cladocarpus indicus Rees & Vervoort, 1987
Cladocarpus inflatus Vervoort, 1966
Cladocarpus integer (G.O. Sars, 1874)
Cladocarpus keiensis Schuchert, 2003
Cladocarpus leloupi Millard, 1962
Cladocarpus lignosus (Kirchenpauer, 1872)
Cladocarpus longipinna Fraser, 1945
Cladocarpus longicarpa (Vervoort & Watson, 2003)
Cladocarpus millardae Vervoort, 1966
Cladocarpus moderatus Fraser, 1948
Cladocarpus multiseptatus (Bale, 1915)
Cladocarpus natalensis Millard, 1977
Cladocarpus obliquus Nutting, 1900
Cladocarpus paradiseus Allman, 1877
Cladocarpus paraformosus Schuchert, 2000
Cladocarpus paraventricosus Ramil & Vervoort, 1992a
Cladocarpus paries Millard, 1975
Cladocarpus pectiniferus Allman, 1883
Cladocarpus pegmatis Millard, 1980
Cladocarpus pinguis Fraser, 1948
Cladocarpus pourtalesi Verrill, 1879
Cladocarpus ramuliferus (Allman, 1874b)
Cladocarpus rostriformis (Vervoort & Watson, 2003)
Cladocarpus septatus Nutting, 1900
Cladocarpus sewelli Rees & Vervoort, 1987
Cladocarpus sibogae Billard, 1911a
Cladocarpus sigma (Allman, 1877)
Cladocarpus sinuosus Vervoort, 1966
Cladocarpus stechowi Ramil & Vervoort, 1992a
Cladocarpus tenuis Clarke, 1879
Cladocarpus tortus Fraser, 1938a
Cladocarpus unicornis Millard, 1975
Cladocarpus vaga (Briggs, 1918)
Cladocarpus valdiviae Stechow, 1923a
Cladocarpus vancouverensis Fraser, 1914a
Cladocarpus ventricosus Allman, 1877
Cladocarpus verrilli (Nutting, 1900)

Genus ***GYMNANGIUM*** Hincks, 1874

Fig. 132E-I

Synonyms: *Haliaria* Stechow, 1921; *Halicetta* Stechow, 1921.

Hydroid: colony erect, often stout, monosiphonic or polysiphonic, arising from a creeping hydrorhiza or from anchoring filaments; hydrocladia unbranched, alternate or opposite, giving off from opposite sides of hydrocaulus; hydrothecae only on hydrocladia, typically more or less cone-shaped, intrathecal septum present or absent, margin with or without cusps; each hydrotheca with a pair of lateral nematothecae and a single adnate median inferior nematotheca, conspicuously longer than hydrotheca and having more than one opening; gonotheca solitary, usually borne on hydrocladia, not protected by phylactocarps or corbulae; fixed sporosacs, one species with swimming gonophores (*G. ferlusi*).

Recent references: Cornelius (1995); Calder (1997); Schuchert (2003); Vervoort & Watson (2003).

Gymnangium africanum (Millard, 1958)
Gymnangium allmani (Marktanner-Turneretscher, 1890)
Gymnangium arcuatum (Lamouroux, 1816)
Gymnangium aureum (Watson, 1973)
Gymnangium birostratum (Bale, 1914a)
Gymnangium elegans (Lamarck, 1816)
Gymnangium eximium (Allman, 1874a)
Gymnangium expansum (Jäderholm, 1903)
Gymnangium explorationis Vervoort & Watson, 2003
Gymnangium exsertum (Millard, 1962)
Gymnangium ferlusi (Billard, 1901)
Gymnangium furcatum (Bale, 1884)
Gymnangium gracilicaule (Jäderholm, 1903)
Gymnangium haswelli (Bale, 1884)
Gymnangium hians (Busk, 1852)
Gymnangium humilis (Bale, 1884)
Gymnangium indivisa (Fraser, 1936b)
Gymnangium intermedium (Billard, 1913)
Gymnangium ishikawai (Stechow, 1907)
Gymnangium japonica Watson & Vervoort, 2001
Gymnangium longicaudum (Nutting, 1900)
Gymnangium longicorne (Busk, 1852)
Gymnangium longirostre (Kirchenpauer, 1872)
Gymnangium magnirostre (Nutting, 1927)
Gymnangium mammillatus (Fraser, 1943)
Gymnangium montagui (Billard, 1912)
Gymnangium pennatulum (Ellis & Solander, 1786)
Gymnangium prolifera (Bale, 1882)
Gymnangium regalis (Totton, 1930)
Gymnangium richardi (Bedot, 1921b)
Gymnangium setosum (Armstrong, 1879)
Gymnangium sibogae (Billard, 1918) [doubtful status]
Gymnangium sinosum (Fraser, 1925)
Gymnangium speciosum (Allman, 1877)
Gymnangium superbum (Bale, 1882)
Gymnangium tenuirostre (Nutting, 1927)
Gymnangium thetidis (Ritchie, 1911)
Gymnangium tubuliferum (Bale, 1914b)
Gymnangium twista (Rho & Park, 1984)
Gymnangium undulatum Watson, 2000
Gymnangium urceoliferum (Lamarck, 1816)
Gymnangium vegae (Jäderholm, 1903)

Genus ***LYTOCARPIA*** Kirchenpauer, 1872

Fig. 133A-G

Synonyms: *Acanthocladium* Allman, 1883; *Thecocarpus* Nutting, 1900.

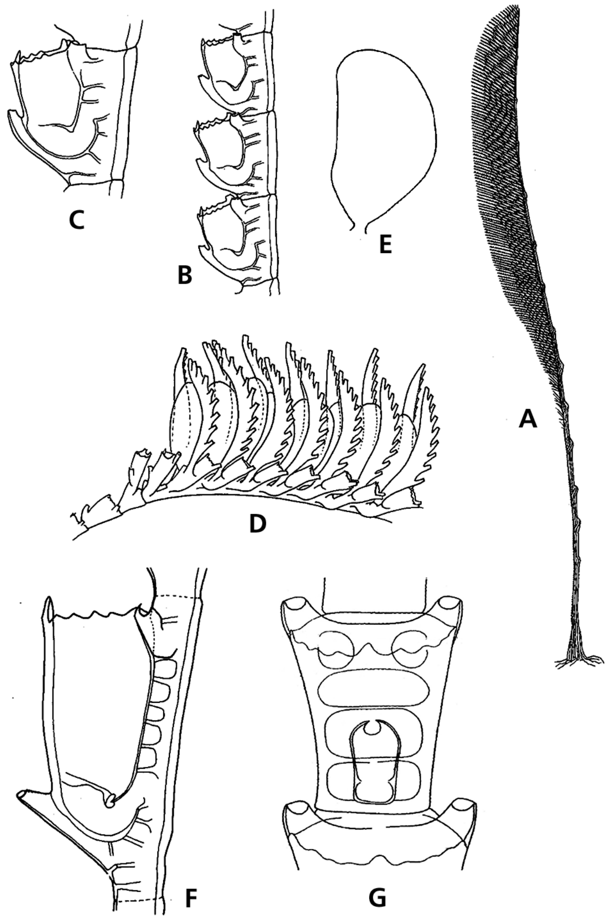
Hydroid: colony erect, branched or unbranched, bearing alternate unbranched pinnate hydrocladia; hydrotheca sac-shaped to deep, usually with intrathecal septum; generally with teeth or lobed margin; mesial outer tooth of hydrothecal rim usually prominent; median inferior nematotheca fairly short, not reaching hydrothecal margin, sometimes a superior dissymmetrical nematotheca (i.e. *Lytocarpia peramata*); corbulae formed by modified hydrocladia bearing secondary unfused ribs bearing a row of approximately 12 nematothecae, some, in at least one sex, bearing one hydrotheca; fixed sporosacs.

Recent references: Calder (1997); Schuchert (2001a, 2003); Vervoort & Watson (2003).

Lytocarpia alata Vervoort & Watson, 2003
Lytocarpia angulosa (Lamarck, 1816)
Lytocarpia armata (Bale, 1914b)
Lytocarpia bathyalis Ryland & Gibbons, 1991
Lytocarpia benedicti (Nutting, 1900)
Lytocarpia bispinosa (Allman, 1877)
Lytocarpia brevirostris (Busk, 1852)
Lytocarpia calycifera (Bale, 1914b)
Lytocarpia canepa (Blanco & Bellusci de Miralles, 1971a)
Lytocarpia chiltoni (Bale, 1924)
Lytocarpia crucialis (Lamouroux, 1816)
Lytocarpia delicatula (Busk, 1852)
Lytocarpia distans (Allman, 1877)
Lytocarpia epizoica Vervoort & Watson, 2003
Lytocarpia flexuosus (Lamouroux, 1816)
Lytocarpia formosa (Busk, 1851)

FIG. 133. Leptomedusae, Aglaopheniidae. A-G, *Lytocarpia myriophyllum*: A, general view of a colony; B, hydrocladium; C, hydrotheca and associated nematothecae; D, corbula; E, gonotheca removed from within corbula; F-G, lateral and fontal views of a hydrocladial internodes with hydrotheca and nematothecae (A-E after Cornelius, 1995; F after Ramil & Vervoort, 1992a; G after Vervoort, 1972).

FIG. 133. *Leptomedusae, Aglaopheniidae. A-G,* Lytocarpia myriophyllum *: A, vue générale d'une colonie ; B, hydroclade ; C, hydrothèque et nématothèques associés ; D, corbule ; E, gonothèque isolée de sa corbule ; F-G, vues latérale et frontale d'internodes hydrocladiaux avec hydrothèques et nématothèques (A-E d'après Cornelius, 1995 ; F d'après Ramil & Vervoort, 1992a ; G d'après Vervoort, 1972).*



Lytocarpia furcata Vervoort, 1941
Lytocarpia incisa (Coughtrey, 1875)
Lytocarpia lepida Watson & Vervoort, 2001
Lytocarpia megalocarpa (Bale, 1914a)
Lytocarpia myriophyllum (Linnaeus, 1758)
Lytocarpia nicpenni Ryland & Gibbons, 1991
Lytocarpia niger (Nutting, 1905)
Lytocarpia normani (Nutting, 1900)
Lytocarpia orientalis (Billard, 1908) [syn. *Gymnangium unjinense* Watson, 2000]
Lytocarpia perarmata (Billard, 1908) n. comb.
Lytocarpia phyteuma (Kirchenpauer, 1876)
Lytocarpia rigida Vervoort & Watson, 2003 [generic position doubtful]
Lytocarpia similis Vervoort & Watson, 2003 [generic position doubtful]
Lytocarpia spiralis (Totton, 1930)
Lytocarpia striata Vervoort & Watson, 2003
Lytocarpia subdichotoma (Ralph, 1961)
Lytocarpia tenuissima (Bale, 1914b)
Lytocarpia tridentata (Versluys, 1899)
Lytocarpia vitiensis Ryland & Gibbons, 1991
Lytocarpia vulgaris Vervoort & Watson, 2003

Genus ***MACRORHYNCHIA*** Kirchenpauer, 1872

Figs 9L, 56D, 134A-D

Synonyms: *Lytocarpus* Allman, 1883; *Nematophorus* Clarke, 1879.

Hydroid: colony erect, hydrocauli branched or unbranched, polysiphonic, often stout, arising from creeping hydrorhiza or anchoring filaments; hydrocladia unbranched, pinnately arranged, arising alternately from apophyses on axial tube of hydrocaulus and branches; hydrothecae only on hydrocladia, more or less cone to sac-shaped; hydrothecal margin dentate; abcauline or adcauline intrathecal septum present; cauline internodes with triangular nematotheca; each hydrotheca with a pair of lateral nematothecae and a single partly adnate median inferior nematotheca; gonothecae on unbranched phylactocarps formed by modified hydrocladia, occurring single or aggregated in pseudocorbula; fixed sporosacs, one species with swimming gonophores (*M. philippina*).

Recent references: Calder (1997); Calder *et al.* (2003); Schuchert (2003).

Macrorhynchia allmani (Nutting, 1900) [syn. *Aglaophenia mercatoris* Leloup, 1937]
Macrorhynchia ambigua Watson, 2000
Macrorhynchia balei (Nutting, 1905)
Macrorhynchia clarkei (Nutting, 1900)
Macrorhynchia filamentosa (Lamarck, 1816)
Macrorhynchia gravelyi Mammen, 1967
Macrorhynchia meteor El Beshbeeshy, 1995

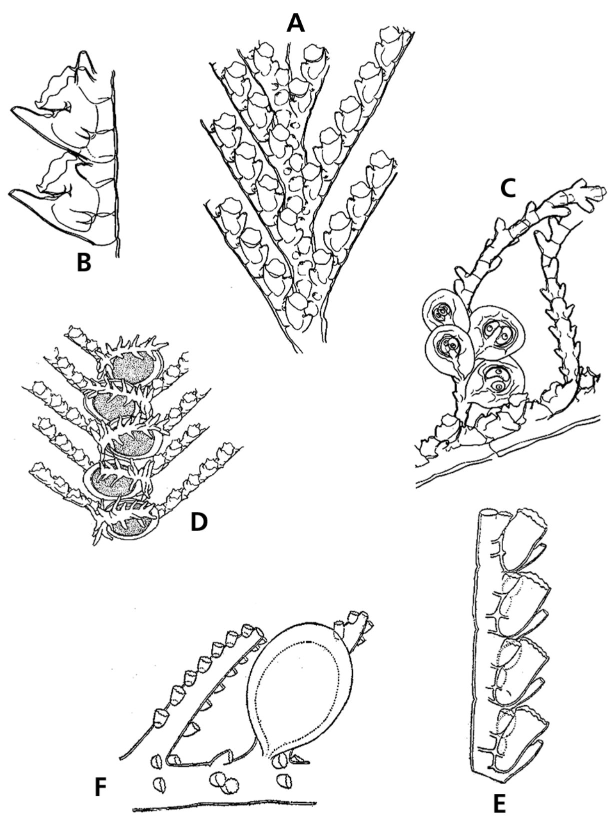


FIG. 134. Leptomedusae, Aglaopheniidae. A-D, *Macrorhynchia*: A-C, *Macrorhynchia philippina*: A, part of colony with origins of hydrocladia; B, part of hydrocladia in lateral view; C, phylactocarps bearing female gonophores; D, *Macrorhynchia phoenicea*, part of stem with phylactocarps bearing gonophores. E-F, *Monoserius pennarius*: E, part of hydrocladia; F, phylactocarp and gonotheca (A-D after Hirohito, 1995; E-F after Mammen, 1967).

***FIG. 134.** Leptomedusae, Aglaopheniidae. A-D,* Macrorhynchia : *A-C,* Macrorhynchia philippina : *A, partie de colonie montrant l'origine des hydroclades ; B, fragment d'hydroclade en vue latérale ; C, phylactocarpes portant des gonophores femelles ; D,* Macrorhynchia phoenicea*, partie d'une branche avec des phylactocarpes portant des gonophores. E-F,* Monoserius pennarius *: E, partie d'hydroclade ; F, phylactocarpe et gonothèque (A-D d'après Hirohito, 1995 ; E-F d'après Mammen, 1967).*

Macrorhynchia mulderi (Bartlett, 1907)
Macrorhynchia multiplicatopinnata (Kirchenpauer, 1876)
Macrorhynchia nuttingi Hargitt, 1927
Macrorhynchia philippina (Kirchenpauer, 1872)
Macrorhynchia phoenicea (Busk, 1852)
Macrorhynchia protectus (Antsulevich, 1991)
Macrorhynchia quadriarmata Watson, 2000
Macrorhynchia racemifera (Allman, 1883)
Macrorhynchia ramosa (Fewkes, 1881)
Macrorhynchia sibogae (Billard, 1913)
Macrorhynchia similis (Nutting, 1905)
Macrorhynchia singularis (Billard, 1913)

Genus ***MONOSERIUS*** Marktanner-Turneretscher, 1890

Fig. 134E-F

Synonym: *Hemicarpus* Billard, 1913.
Hydroid: colony erect, branched or unbranched, polysiphonic; hydrocladia pinnately arranged, divided in internodes bearing hydrothecae; hydrothecae with abcauline intrathecal septum and toothed margin; nematotheca monothalamic and unmovable, cauline nematophores absent, mesial inferior nematotheca adnate to hydrotheca. Gonothecae aggregated, protected by modified hydrocladium bearing ribs only on one side, so forming a hemicorbula; ribs with nematothecae and one hydrotheca.
Remarks: The genus *Monoserius* was created by Marktanner-Turneretscher (1890) for *Aglaophenia secunda* Kirchenpauer, 1872. Mammen (1965), however, considered *M. secundus*, *M. fasciculatus* and *M. pennarius* as conspecific with *Monoserius pennarius*. The validity of this genus needs confirmation by further observation.
Recent references: Calder (1997); Schuchert (2003).

Monoserius pennarius (Linnaeus, 1758) [syn. *M. banksii* (Gray, 1843) and *M. fasciculatus* (Thornely, 1904)]
Monoserius secundus (Kirchenpauer, 1872) [probably a syn. of *M. pennarius*]

Genus ***STREPTOCAULUS*** Allman, 1883

Fig. 135A-C

Hydroid: colony erect; hydrocauli branched or unbranched; hydrocladia pinnate in young colonies, gradually becoming spirally arranged by axis torsion with age; hydrothecae adnate, hydrothecal rim with weakly developed cusps; three hydrothecal nematothecae present; fixed sporosacs protected by phylactocarps with axis homologous to a hydrocladium; rachis axis unbranched or irregularly branched, divided in segments, each bearing one or several pairs of more or less opposite lateral nematothecae; rachis axis bearing one or more gonothecae; when axis and phylactocarps are long, the structure appears centipede-like.

Remarks: The genus *Streptocaulus* seems polyphyletic based on phylactocarp morphology (Calder, 1997).

Recent references: Ramil & Vervoort (1992a); Medel & Vervoort (1995); Calder (1997); Ramil *et al.* (1998).

Streptocaulus corneliusi (Ramil & Vervoort, 1992a)
Streptocaulus dollfusi (Billard, 1924a)
Streptocaulus gracilis Fraser, 1937a
Streptocaulus pectiniferus (Allman, 1883)
Streptocaulus pulcherrimus Allman, 1883
Streptocaulus sinuosus (Vervoort, 1966) [doubtful status]

Family BARCINIDAE Gili, Bouillon, Pagès, Palanques & Puig, 1999

Hydroid: unknown.
Medusa: marginal vesicles closed; ocelli adaxial; manubrium narrow, no peduncle; 4 simple radial canals; 4 marginal tentacles; tentacular bulbs large, globular; "gonads" linear, ribbon-like, surrounding radial canals.

Genus ***BARCINO*** Gili, Bouillon, Pagès, Palanques & Puig, 1997
Fig. 136A-B

See family characters.

Barcino foixensis Gili, Bouillon, Pagès, Palanques & Puig, 1999

Family BLACKFORDIIDAE Bouillon, 1984

Hydroid: colony reptant, rarely slightly ramified; hydrotheca with diaphragm; operculum of numerous triangular flaps meeting centrally and showing no clear demarcation from hydrothecal margin; hydranth with a whorl of 12-16 filiform tentacles, with membranous intertentacular web; gonothecae developing on stem or on hydranth stalk, one medusa in each gonophore.
Medusa: manubrium narrow, short; mouth with 4 long, fluted lips; numerous hollow tentacles; tentacle endodermal core extending inwards from bell margin into bell mesoglea; 4 radial canals; "gonads" completely surrounding radial canals; no permanent rudimentary tentacles; numerous closed statocysts.

Recent references: Mills & Sommer (1995); Bouillon (1999); Bouillon & Boero (2000); Mills & Rees (2000).

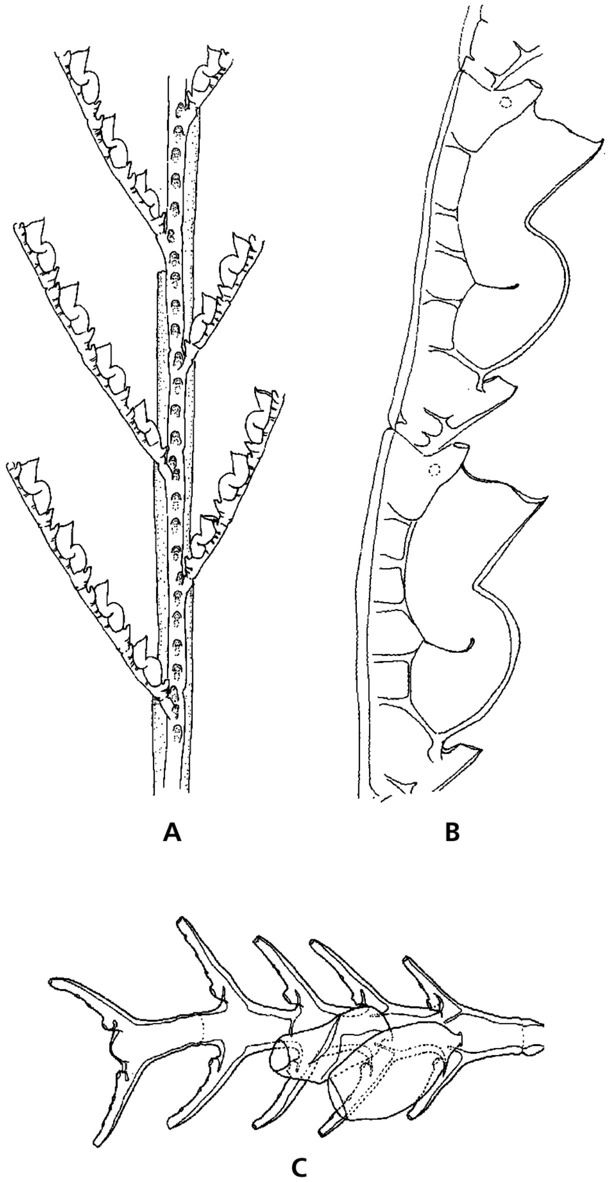


FIG. 135. Leptomedusae, Aglaopheniidae. A-C, *Streptocaulus*: A-B, *Steptocaulus dollfusi*: A, part of main axis with hydrocladia; B, two internodes with hydrothecae and nematothecae; C, *Streptocaulus corneliusi*, fertile phylactocarp, view from above (A-B after Medel & Vervoort, 1995; C after Ramil & Vervoort, 1992a).

FIG. 135. *Leptomedusae, Aglaopheniidae. A-C,* Streptocaulus : *A-B,* Steptocaulus dollfusi : *A, partie de l'axe principal avec des hydroclades ; B, deux internodes montrant des hydrothèques et des nématothèques ; C,* Streptocaulus corneliusi, *phylactocarpe fertile, vue du dessus (A-B d'après Medel & Vervoort, 1995 ; C d'après Ramil & Vervoort, 1992a).*

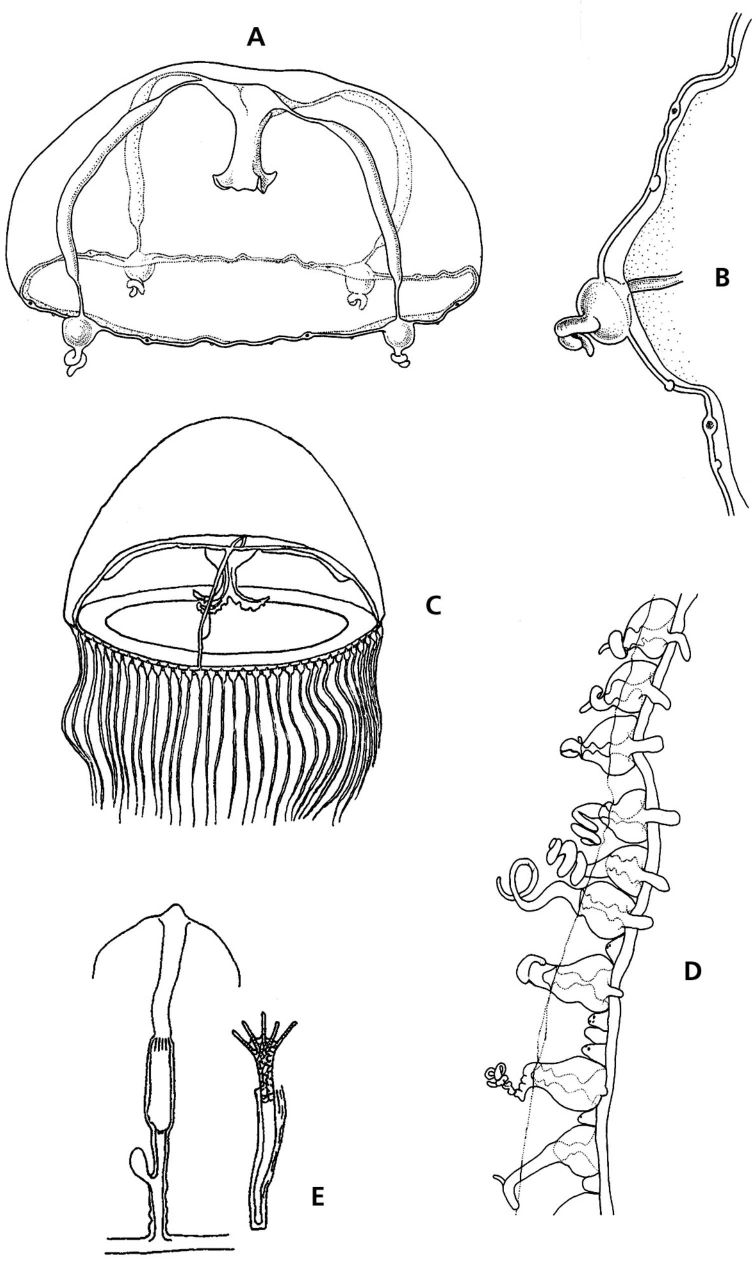


FIG. 136. Leptomedusae. A-B, Barcinidae, *Barcino foixensis*: A, adult medusa; B, portion of the umbrella margin. C-E, Blackfordiidae, *Blackfordia virginica*: C, adult medusa; D, portion of the umbrella margin; E, polyp (A-B after Gili *et al*., 1999; C after Kramp, 1959b; D after Moore, 1987; E after Valkanov, 1935).

FIG. 136. *Leptomedusae. A-B, Barcinidae,* Barcino foixensis : *A, méduse adulte ; B, portion du bord exombrellaire. C-E, Blackfordiidae,* Blackfordia virginica : *C, méduse adulte ; D, portion du bord exombrellaire ; E, polype (A-B d'après Gili* et al.*, 1999 ; C d'après Kramp, 1959b ; D d'après Moore, 1987 ; E d'après Valkanov, 1935).*

Genus ***BLACKFORDIA*** Mayer, 1910

Fig. 136C-E

See family characters.

Blackfordia manhattensis Mayer, 1910
Blackfordia polytentaculata Hsu & Chang, 1962
Blackfordia virginica Mayer, 1910

Family CAMPANULINIDAE Hincks, 1868

Hydroid: colony stolonal or erect; hydrocaulus branched or unbranched; hydrotheca usually campanulate or cylindrical, with or without pedicel, always covered by operculum of several triangular flaps, sharply demarcated from hydrotheca or not; with or without diaphragm; with or without nematophore; gonophores as fixed sporosacs or as free medusae.

Medusa: see remarks below.

Remarks: The Campanulinidae represent a polyphyletic taxon, traditionally comprising species having hydroids of a generalised "campanulinid type". The distinction between two types of operculum (pleated or segmented, formed by numerous flaps which may or not be delimited by a prominent crease-line at the base of the cusps) has not the taxonomic value that it was formerly given (see Lovenellidae).

Many "campanulinid" hydroids release medusae that are referable to unrelated medusa-based families. This is not the only case of inconsistency between hydroid and medusan morphology: Rees (1956), for instance, already showed that the hydroids (nearly 40 species) referred to the hydroid-based genus *Perigonimus* M. Sars 1846, which are as similar morphologically to each other as are the "campanulinid" hydroids, are referable to five medusa-based families: four of Anthomedusae and even one of Leptomedusae. Most of the described "campanulinid" hydroids, unfortunately, have unknown or poorly known life cycles and, consequently, cannot be confidently identified at a generic or family level. Due to the difficulty of assigning such operculate hydroids to family-group taxa, taxonomists have usually lumped them, for convenience, in the family Campanulinidae. Only the knowledge of the complete life cycles of those species will contribute to resolve this situation. Calder (1991), to avoid the practice of employing the Campanulinidae as a catch-all family, provisionally included the genera *Opercularella* and *Plicatotheca* (see remarks under *Opercularella*) in the Phialellidae and included into "Family *incertae sedis*" those genera that cannot be assigned with any degree of certainty to a family (for instance *Lafœina* and *Egmundella*). Calder (1991) proposed also a new definition of the family Campanulinidae covering more or less the Eirenidae Haeckel, 1879. He also argued that *Campanulina tenuis* Van Beneden, 1847, the misidentified type genus of Hincks Campanulinidae family (see *Campanulina*), could correspond to a hydroid with regressed hydrotheca, similar to those found in some aged eirenid hydroids and that, due to this similarity, the two families should be considered identical, with the name Campanulinidae having priority. We do not follow this proposal: *Campanulina tenuis* is a poorly described, non-operculate, species considered here as an *incertae sedis* (see *Campanulina*). This species can in any case be attributed to an existing genus of Eirenidae, a medusa-based family with a vast array of hydroid types. Finally, campanulinid regressed hydroids similar to those described for some Eirenidae exist in many other Leptomedusae families. It appear thus that, at present, it is not possible to obtain a complete and satisfactory classification of campanulinid hydroids and that, as stated by Cornelius (1995), the Campanulinidae paradox has still to be resolved, and little is to be gained from attempting a new family diagnosis or from retaining the old one.

In the diagnosis given above we keep in the Campanulinidae only the genera from which the gonosome is known as fixed sporosacs, the species with identifiable medusae being transferred to their medusae families in agreement with the law of priority. The campanulinid hydroids with fixed sporosacs can represent the results of multiple and independent medusa reduction within different Leptomedusae family groups and it is presently impossible to refer them safely to any family with free medusae and to establish their real phylogenetic relationships. It seems more reasonable to retain them under a common denomination until further research will allow more natural groupings, than to include them, without phylogenetic support, in any medusa-based family; molecular biology techniques will surely help to resolve these ambiguities. The campanulinid genera with unknown gonosome will be provisionally included here in the Campanulinidae *incertae sedis*. This appears more convenient than to refer them to "Family *incertae sedis*" as proposed by Calder (1991), since our proposal at least gives an idea of the general morphology of the hydroid stage.

Recent reference: Schuchert (2001a).

KEY TO CAMPANULINIDAE GIVING RISE TO DETERMINABLE MEDUSA STAGE
(SEE CORRESPONDING MEDUSA STAGE FAMILIES)

KEY TO CAMPANULINID HYDROIDS WITH FIXED SPOROSACS,
UNIDENTIFIABLE MEDUSA BUDS OR UNKNOWN GONOPHORES

1. operculum of 4 valves 2
– operculum of more than 4 valves 4

2. opercular valves sharply demarcated from hydrothecal wall . . . . . . *Tetrapoma*
– opercular valves not sharply demarcated from hydrothecal wall. 3

3. operculum of gonothecae membranous. . . . . . *Tripoma*
– operculum of gonothecae as two lateral plates . . . . . . *Stegella*

4. opercular valves seated in distinct embayments of thecal margin and sharply demarcated from it . . . . . . *Calycella*
– operculum of numerous segments, opercular valves not sharply demarcated 5

5. nematophores present 6
– nematophores absent. 8

6. hydrotheca sessile and tubular; nematothecae oval to tubular; gonophores producing fixed sporosacs or medusa buds . . . . . . *Lafœina*
– hydrotheca pedicellate; nematotheca not tubular 7

7. hydrotheca widest at distal end, tubular to top-shaped; gonophores where known with medusa buds . . . . . . *Egmundella*
– hydrotheca rounded, widest in the middle narrowing at base and distal end; gonophores unknown . . . . . . *Oplorhiza*

8. hydrotheca pedicellate. 9
– hydrotheca sessile, rising directly from stolon, long and tubular, gonophores unknown or containing unidentifiable medusa buds (when free adult medusae known, see medusae genera) . . . . . . *Cuspidella*

9. gonophores unknown or containing unidentifiable medusa buds (when free adult medusae known, see medusae genera) . . . . . . *Campanulina*
– gonophores as fixed sporosacs . . . . . . *Opercularella*

Genus ***CALYCELLA*** Allman, 1864

Figs 6A, 137A-C

Hydroid: colony stolonal; pedicel usually sharply twisted and short; hydrotheca tubular, deep, margin crenulated; operculum with a scalloped crease-line at base of opercular segments not quite meeting in the centre; hydranth without intertentacular web; nematophores absent; gonophore borne on hydrorhiza as fixed sporosacs, with acrocyst; no medusa stage recorded.

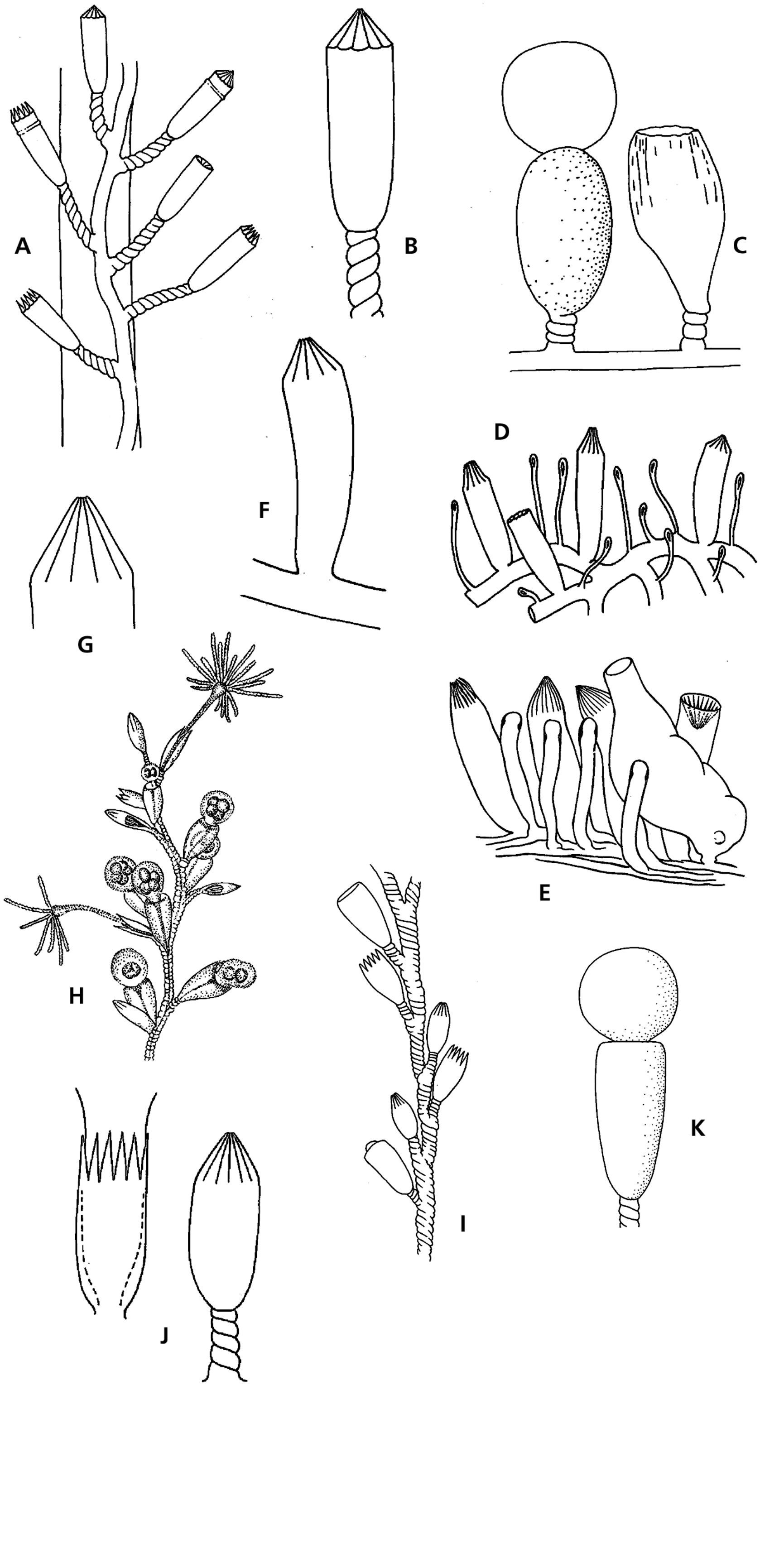


FIG. 137. Leptomedusae, Campanulinidae. A-C, *Calycella syringa*: A, part of colony, note subterminal annulus on some hydrotheca; B, hydrotheca; C, two gonothecae, the one on the left with an acrocyst. D, F-G, *Lafœina tenuis*: D, part of a colony; F, hydrotheca; G, detail of operculum. E, *Lafœina maxima*, detail of a colony with gonotheca. H-K, *Opercularella lacerta*: H, part of colony; I, detail a branch of colony; J, two hydrothecae; K, gonotheca with acrocyst (A-D, F-G, I-K after Cornelius, 1995; E after Naumov, 1969; H after Leloup, 1952).

FIG. 137. *Leptomedusae, Campanulinidae. A-C,* Calycella syringa : *A, partie d'une colonie, notez l'anneau subterminal sur certaines hydrothèques ; B, hydrothèque ; C, deux gonothèques, celle de gauche avec un acrocyste. D, F-G,* Lafœina tenuis : *D, fragment d'une colonie ; F, hydrothèque ; G, détail de l'opercule. E,* Lafœina maxima*, détail d'une colonie avec des gonothèques. H-K,* Opercularella lacerta : *H, partie d'une colonie ; I, détail d'une branche ; J, deux hydrothèques ; K, gonothèque avec acrocyste (A-D, F-G, I-K d'après Cornelius, 1995 ; E d'après Naumov, 1969 ; H d'après Leloup, 1952).*

Remarks: *Calycella gracilis* Hartlaub, 1897 has unknown gonophores and is here considered as *incertae sedis*, its description is not taken in consideration in the above diagnosis.
Recent references: Cornelius (1995); Hirohito (1995); Blanco *et al.* (2000); Schuchert (2001a).

Calycella gracilis Hartlaub, 1897 [doubtful status]
Calycella hispida (Nutting, 1896)
Calycella oligista Ritchie, 1910
Calycella syringa (Linnaeus, 1767)

Genus *LAFOEINA* G.O. Sars, 1874

Figs 9P, 137D, F-G

Synonym: *Keratosum* Hargitt, 1909.
Hydroid: colony stolonal, or irregularly branched, with polysiphonic stem; hydrotheca cylindrical, pedicel absent, operculum composed of numerous triangular segments without basal crease-line; hydranth without intertentacular web; nematotheca tubular, without operculum, aperture minute and sub-distal on one side; gonotheca similar to hydrotheca, same size or larger; gonophores, when known, as fixed sporosacs or giving rise to medusae buds with four tentacles and eight lateral cirri; adult medusa unknown.
Recent references: Calder (1991); Cornelius (1995); Hirohito (1995); Blanco *et al.* (2000); Schuchert (2001a); Calder *et al.* (2003).

Lafœina amirantensis (Millard & Bouillon, 1973)
Lafœina complexum (Hargitt, 1909)
Lafœina maxima Levinsen, 1893
Lafœina tenuis G.O. Sars, 1874

Genus *OPERCULARELLA* Hincks, 1868

Fig. 137H-K

Hydroid: colony stolonal or erect and sympodially branched; pedicel, with 5 or more twists, not well differentiated from hydrotheca; hydrotheca pedicellate, cigar-shaped or ovoid; opercular flaps gradually merging with hydrothecal walls, without distinct boundaries, opercular segments not quite meeting in the centre; degenerate diaphragm present; intertentacular web, when present, not well developed; gonophores as fixed sporosacs, female one usually with acrocyst for planula development, gonotheca on pedicel arising from main stem or on hydrorhiza.
Remarks: Rees (1939) revised the Campanulinidae and ascribed, for the sake of convenience, all campanulinid species with fixed sporosacs or with unknown gonophores to the genus *Opercularella*. Calder (1991) provisionally included the genera *Opercularella* and *Plicatotheca* in the Phialellidae, without any convincing taxonomic reason if not to remove both genera from the dubious scope of the Campanulinidae. Doing so, however, he transferred the problem from one family to another. Almost all specialists agree that medusa reduction is not a reliable phylogenetic taxonomic character to separate two genera, but in a large taxon like the Campanulinidae it is impossible, at the state of our present knowledge, to attribute the species with fixed sporosacs (for instance *Opercularella*) to the corresponding genera with free medusae. The genus *Opercularella* is accepted here in a more restricted sense than Rees' (1939), including only the forms with fixed gonophores, the "*Opercularella*-like hydroid" species with unknown gonophores or indeterminable medusa buds being referred to the genus *Campanulina incertae sedis*, pending further information on their cycles.
Recent references: Calder (1991); Cornelius (1995); Genzano (1995); Blanco *et al.* (2000); Schuchert (2001a); Calder *et al.* (2003).

Opercularella belgicae (Hartlaub, 1904)
Opercularella denticulata (Clarke, 1907)
Opercularella lacerata (Johnston, 1847)
Opercularella ramosa (Fraser, 1938a) [as *Campanulina*]

Genus ***STEGELLA*** Stechow, 1919

Fig. 138A-C

Hydroid: colony polysiphonic, rhizocaulomic, sparingly branched; hydrotheca more or less in verticils, peduncled, campanulate; operculum formed by 4 large triangular flaps not distinctly demarcated (? See Totton 1930, Fig. 10a) from hydrotheca; hydranth large, not completely retractable in hydrotheca; without intertentacular web; no nematothecae; gonophores as fixed sporosacs, gonothecae pedicellate, tubular, with a terminal slit-like opening between two parallel flattened and rounded terminal plates.
Recent reference: Blanco *et al.* (2000).

Stegella grandis Stechow, 1919b

Campanulinidae *incertae sedis* with gonophores unknown or with indeterminable medusa buds:

Genus ***CAMPANULINA*** auct.

Figs 6B, 138D-G

Hydroid: colony stolonal or erect; hydrotheca tubular, with a pointed pleated or segmented operculum which may or not be delimited basally by a crease line; no nematophores; usually with diaphragm; gonophores unknown or arising as indeterminable medusa buds.
Remarks: the original description of *Campanulina tenuis*, type species of *Campanulina*, was a brief preliminary account made by Van Beneden in 1847 of a non operculate, non fertile hydroid, not corresponding to the concept of an operculate Campanulinidae as understood by all further authors, Van Beneden (1867) included (see Rees 1939; Calder 1991). *Campanulina tenuis* has never been observed since its description and should be considered as an indeterminate species. The genus *Campanulina* has slowly been the dumping ground for species belonging to several other campanulinid genera; even at present the same hydroid species can be found described in literature under different generic names *Opercularella*, *Campanulina* and *Phialella* depending on authors, showing the great confusion existing within the campanulinid hydroids and the definition of their genera! Such confusion is partly linked to the difficulty to distinguish morphologically from each other the different hydroid species but, above all, to the absence of knowledge about their life cycle. The genus *Campanulina* is here conserved as a "collective group" for the "Campanulinid type" species with unknown or incompletely known cycle awaiting the discovery of their type of gonophoral contents or of the determinable medusae allowing their final attribution to a completely diagnosed genus.
Recent references: Schuchert (2001a, 2003); Calder *et al.* (2003).

Campanulina maduraensis Billard, 1940a
Campanulina panicula G.O. Sars, 1874
Campanulina paucilaminosa Billard, 1940a
Campanulina pumila (Clarke, 1875)
Campanulina rugosa Nutting, 1901a

Genus ***CUSPIDELLA*** Hincks, 1866

Fig. 138H-I

Hydroid: colony stolonal, hydrotheca tubular and usually sessile, lacking pedicel, in some species separated from stolon by basal constriction; operculum conical, several cups meeting centrally, with or without basal crease-line; hydranth very extensile, tentacles amphicoronate, with or without basal intertentacular web; gonophores, when known, as free medusae; gonotheca resembling hydrotheca but, usually, larger.
Remarks: medusae from different genera and families produce "*Cuspidella*-like" hydroid larval stages; when the life cycle is clarified, the species with this type of hydroids have been named in accordance to the law of priority, being usually

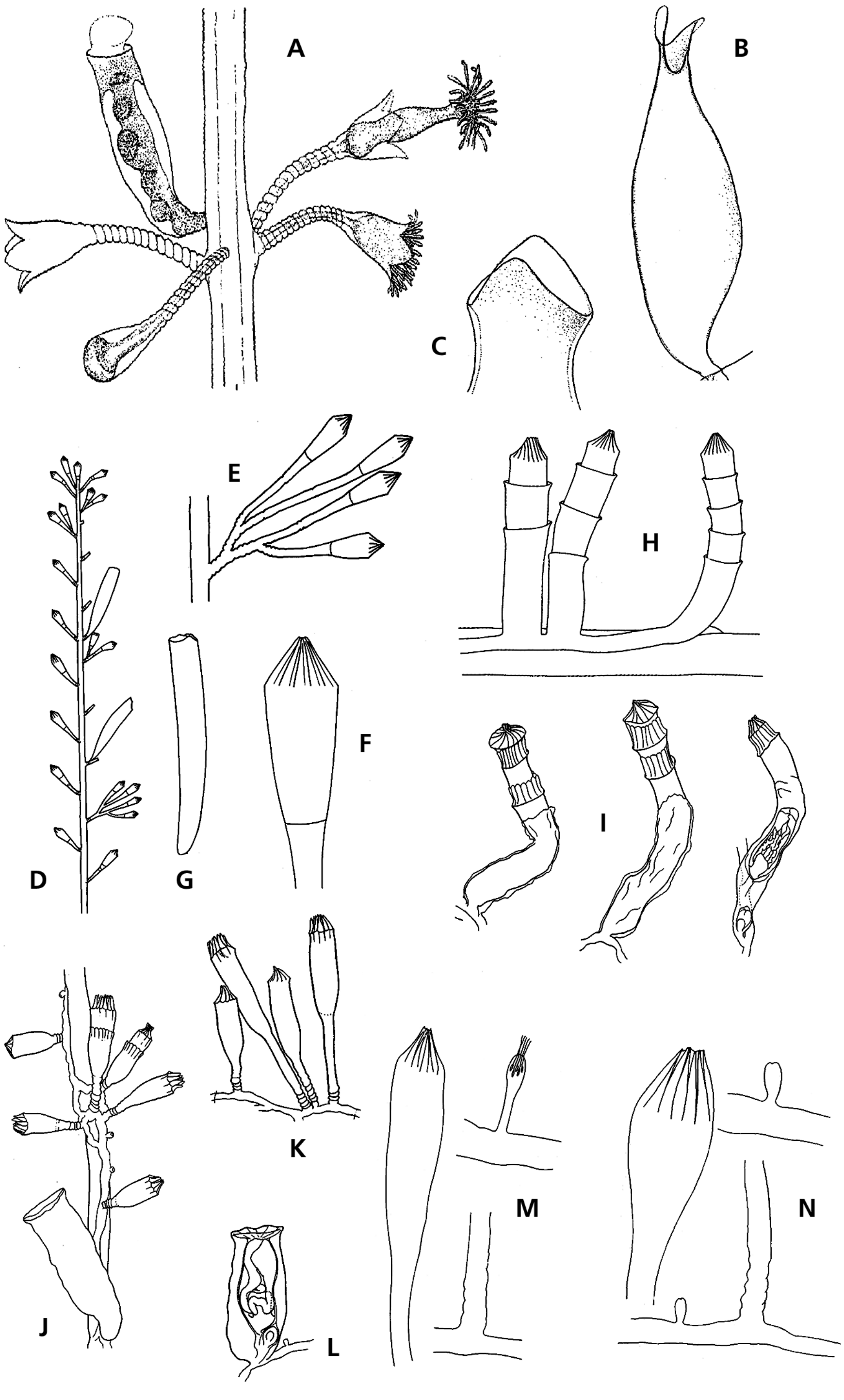


FIG.138. Leptomedusae, Campanulinidae. A-C, *Stegella lobata*: A, part of a colony; B, gonotheca; C, detail of apical part of the gonotheca. D-G, *Campanulina panicula*: D, portion of colony; E, group of hydrothecae; F,detail of hydrotheca; G, gonotheca. H-I, ''*Cuspidella*'': H, hydroid facies, hydrotheca without basal crease line; I, *Cuspidella gigantea*, hydrotheca with basal crease line and gonotheca with medusa buds. J-L, *Egmundella humilis*: J, part of colony with gonotheca; K, group of hydrothecae; L, gonotheca containing medusa buds. M, *Egmundella superba*, hydrotheca, basal part of pedicel and nematophore. N, *Egmundella valdiviae*, hydrotheca, basal part of pedicel and nematophores (A-C after Blanco *et al.*, 2000; D-H after Cornelius, 1995; I-L after Hirohito, 1995; M-N after Vervoort, 1966).

***FIG. 138.** Leptomedusae, Campanulinidae. A-C,* Stegella lobata *: A, partie d'une colonie ; B, gonothèque ; C, détail de la partie apicale de la gonothèque. D-G,* Campanulina panicula *: D, portion d'une colonie ; E, groupe d'hydrothèques ; F, détail d'une hydrothèque ; G, gonothèque. H-I, ''*Cuspidella*'' : H, faciès d'hydroïdes avec des hydrothèques sans dépressions du bord marginal ; I,* Cuspidella gigantea*, hydrothèques avec des dépressions du bord marginal limitant l'opercule, gonothèque avec des bourgeons médusaires. J-L,* Egmundella humilis *: J, fragment de colonie avec gonothèque ; K, groupe d'hydrothèques ; L, une gonothèque contenant des bourgeons médusaires. M,* Egmundella superba*, hydrothèque, partie basale du pédicelle et un nématophore. N,* Egmundella valdiviae*, hydrothèque, partie basale du pédicelle et nématophores (A-C d'après Blanco* et al.*, 2000 ; D-H d'après Cornelius, 1995 ; I-L d'après Hirohito, 1995 ; M-N d'après Vervoort, 1966).*

assigned to medusa-based taxa. *Cuspidella* hydroids with unknown cycle or with gonophores with unidentifiable medusa buds remain included here in *Cuspidella* as a collective group name awaiting further investigations.
Recent reference: Schuchert (2001a).

Cuspidella gigantea Stechow, 1923d
Cuspidella humilis (Alder, 1862b)
Cuspidella grandis Hincks, 1868 [probably a syn. of *Cosmetira pilosella*]
Cuspidella procumbens Kramp, 1911
Cuspidella urceolata Hirohito, 1995

Genus ***EGMUNDELLA*** Stechow, 1921

Fig. 138J-N

Hydroid: colony usually stolonal, infrequently erect and branched; hydrocaulus polysiphonic; hydrotheca pedicellate, deeply campanulate, turbinate, widest at distal end, thin perisarcal shelf present; operculum cone-shaped not distinctly demarcated from hydrotheca; diaphragm present or reduced; nematophores solitary or aggregated, bulbous through clavate or tubular, on hydrorhiza or on both hydrorhiza and hydrocaulus; gonophores giving rise to medusa buds, gonotheca borne on hydrorhiza, non pedicellate or shortly pedicellate, similar to hydrotheca.
Remarks: this genus is considered *incertae sedis* pending further knowledge about the nature of the adult medusae.
Recent references: Calder (1991); Hirohito (1995).

Egmundella fasciculata Fraser, 1940b
Egmundella gracilis Stechow, 1921a
Egmundella grimaldii Leloup, 1940a
Egmundella humilis Fraser, 1936b
Egmundella modesta Millard & Bouillon, 1975
Egmundella polynema Fraser, 1948
Egmundella sibogae Billard, 1940b
Egmundella superba Stechow, 1921a
Egmundella valdiviae Stechow, 1923b

Genus ***EUCUSPIDELLA*** Fraser, 1944

Fig. 139A

Hydroid: colony stolonal; hydrotheca tubular, tapering slightly at base into a slender pedicel without any definite line of demarcation; operculum conical, with several converging flaps meeting centrally, not demarcated from hydrotheca; gonophores unknown.
Remarks: created by Fraser (1944) for pedicellate *Cuspidella*-like hydroids, this genus has been provisionally retained by Vervoort (1972) for such species of Campanulinidae and Lovenellidae in which the gonophores are unknown and is thus here considered as *incertae sedis*.

Eucuspidella pedunculata (Allman, 1877)

Genus ***GALANTHULA*** Hartlaub, 1899

Insufficiently described genus.
Recent reference: Bouillon (1985a).

Genus ***OPLORHIZA*** Allman, 1877

Fig. 139B

Hydroid: colony stolonal; hydrotheca pedicellate, rounded, widest in the middle, narrowing at base and distal end, limit between hydrotheca and pedicel sharp; operculum with several converging flaps meeting centrally, not demarcated from

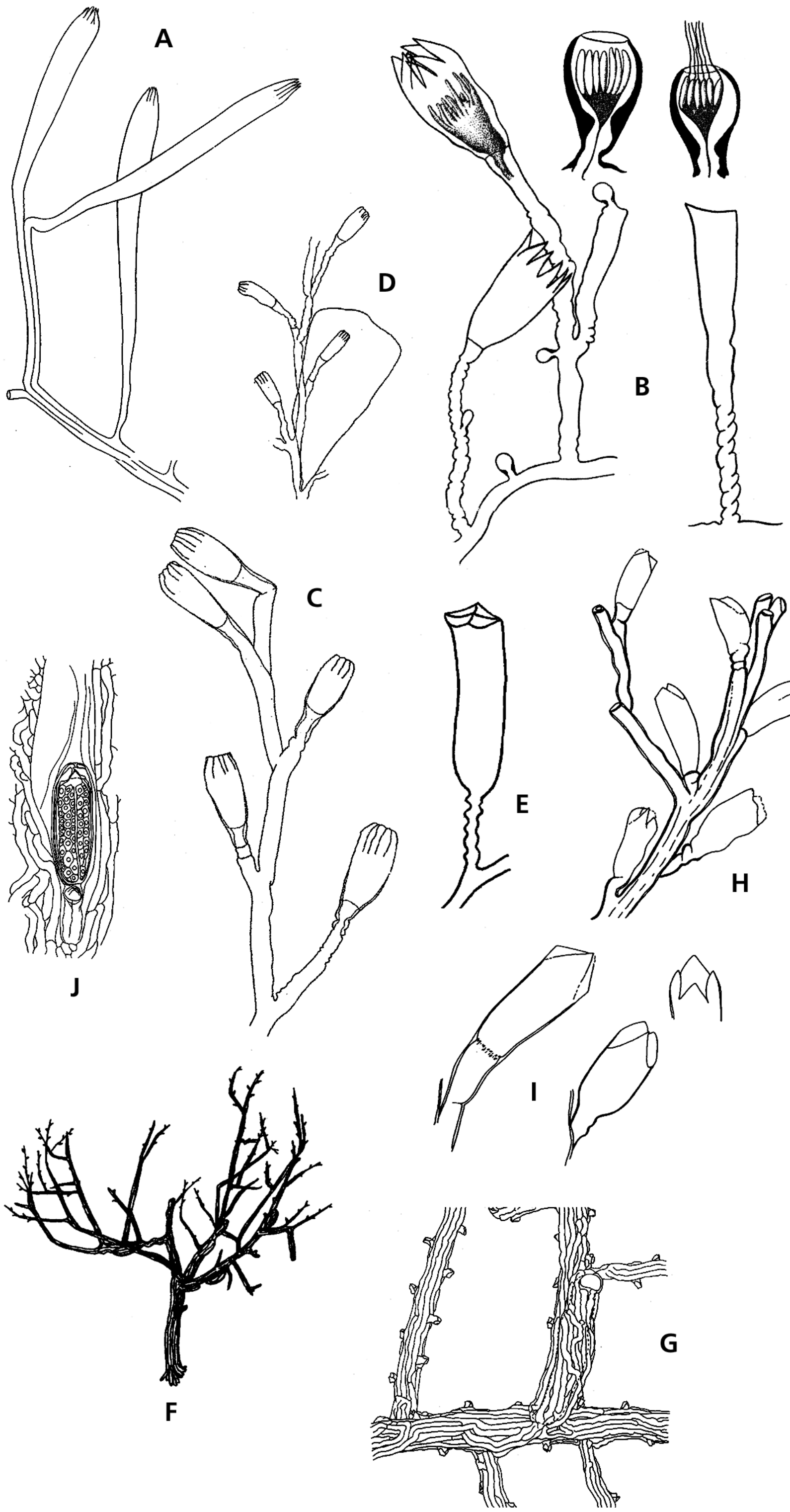


FIG.139. Leptomedusae, Campanulinidae. A, *Eucuspidella pedunculata*, fragment of a colony. B, *Oplorhiza diaphragmata*, fragment of a colony with hydrotheca and nematothecae (left), gonotheca (right), two nemathothecae (above). C-D, *Plicatotheca anitae*: C, part of branch; D, part of stem with gonotheca. E, *Tetrapoma quadridentatum*, hydrotheca. F-J, *Tripoma arboreum*: F, general view of a colony; G, part of a fascicled stem showing embedded hydrotheca; H, detail of a distal branch of a colony; I, hydrothecae; J, embedded female gonophore (A after Vervoort, 1972; B & E after Naumov, 1969; C-D after Gili *et al.*, 1989; F, H-I after Watson & Vervoort, 2000; G & J after Hirohito, 1995).

FIG. 139. *Leptomedusae, Campanulinidae. A,* Eucuspidella pedunculata*, fragment d'une colonie. B,* Oplorhiza diaphragmata*, fragment d'une colonie montrant une hydrothèque et des nématothèques (à gauche), gonothèque (à droite), deux nématothèques (au-dessus). C-D,* Plicatotheca anitae *: C, partie d'une branche ; D, part d'une branche avec une gonothèque. E,* Tetrapoma quadridentatum*, hydrothèque. F-J,* Tripoma arboreum *: F, vue générale d'une colonie ; G, partie d'une branche polysiphonique montrant une hydrothèque encastrée ; H, détail d'une branche distale d'une colonie ; I, hydrothèques ; J, gonophore femelle encastré (A d'après Vervoort, 1972 ; B & E d'après Naumov, 1969 ; C-D d'après Gili* et al.*, 1989 ; F, H-I d'après Watson & Vervoort, 2000 ; G & J d'après Hirohito, 1995).*

hydrotheca; diaphragm present or not; hydranth without intertentacular web; nematotheca oval or elongated, never tubular; with a short pedicel, without operculum, on hydrorhiza and hydrocaulus; gonophores unknown.
Remarks: close to *Egmundella*, the two being sometimes considered as identical; they differ mainly in the form and attachment of hydrothecae; here considered as *incertae sedis* awaiting further knowledge on its gonophores.

Oplorhiza diaphragmata Naumov, 1960
Oplorhiza gracilis (Stechow, 1921a)
Oplorhiza parvula Allman, 1877

Genus ***PLICATOTHECA*** Calder & Vervoort, 1986

Fig. 139C-D

Hydroid: hydrorhiza creeping, colony erect, with polysiphonic stem, sympodially branched; hydrotheca with diaphragm, on long and smooth pedicel, closed by a cone-shaped operculum consisting of folded, not demarcated continuation of hydrothecal wall, opercular facets rounded and converging distally, but not meeting in centre; gonophores unknown, empty gonothecae flattened, triangular, on short pedicel.
Recent references: Gili *et al.* (1989); Calder (1991).
Remarks: very close to *Opercularella*, with which it has been tentatively included in the Phialellidae by Calder (1991) (see *Opercularella* for discussion). Since gonophores are unknown, *Plicatotheca* is here considered as *incertae sedis*.

Plicatotheca anitae Calder & Vervoort, 1986

Genus ***TETRAPOMA*** Levinsen, 1892

Fig. 139E

Hydroid: colony stolonal; hydrotheca nearly tubular, operculate, 4 teeth on margin; operculum as a low pyramid of 4 triangular flaps sharply demarcated from hydrotheca; no diaphragm; gonophore and gonotheca unknown.
Remarks: this genus is here considered as *incertae sedis* pending further knowledge about life cycles.
Recent references: Hirohito (1995); Watson & Vervoort (2000).

Tetrapoma quadridentatum (Hincks, 1874)

Genus ***TRIPOMA*** Hirohito, 1995

Fig. 139F-J

Hydroid: colony erect; stem and branches fascicled, not divided distinctly in internodes; hydrotheca tubular, bending or not, embedded in rhizocaulus, pedicellate, without diaphragm; operculum composed by 4 distinct but delicate flaps not demarcated from margin; gonophore containing one eumedusoid (only a poorly preserved one known) with radial canals and ring canal; 4 hollow marginal tentacles; velum; position of “gonads” unclear, gonothecae cocoon-like, embedded in fascicular tubes, operculum terminal, membranous.
Remarks: here considered as *incertae sedis* awaiting further knowledge about the adult medusa stage.
Recent reference: Watson & Vervoort (2000).

Tripoma arboreum Hirohito, 1995

Family CIRRHOLOVENIIDAE Bouillon, 1984

Hydroid: colony stolonal, of "*Cuspidella*" type; hydrotheca sessile, tubular, closed by a pyramidal operculum formed by numerous flaps meeting centrally and not clearly demarcated from margin; no intertentacular web; gonotheca unknown.

Medusa: manubrium small; 4 simple radial canals; "gonads" on radial canals separated from manubrium; marginal tentacles hollow; with marginal cirri; 4 or more closed statocysts.

Genus ***CIRRHOLOVENIA*** Kramp, 1959

Fig. 140A-C

Hydroid: only known in *C. tetranema*.
Medusa: 4-40 marginal tentacles; 7-8 marginal cirri between successive marginal tentacles.

Cirrholovenia polynema Kramp, 1959a
Cirrholovenia tetranema Kramp, 1959a

Family CLATHROZOIDAE Stechow, 1921

Hydroid: colony arborescent, with a skeleton of complexly anastomosing chitinous tubes; hydrotheca tubular, wholly or largely embedded in skeleton; hydranth cylindrical, deeply retractile in hydrotheca; nematotheca tubular, scattered on surface of skeleton; gonophore as fixed sporosacs or free eumedusoids, gonotheca developed in anastomoses of stolons.

KEY TO HYDROIDS

1. hydrothecae spirally arranged on branchlets, completely embedded in skeleton; with a peridermal layer enclosing skeleton; gonophores as eumedusoids . . . . *Clathrozoon*
– hydrothecae arranged right and left alternately on branchlets, protruding markedly from skeleton; no peridermal layer enclosing skeleton; gonophores as fixed sporosacs. . . . . *Pseudoclathrozoon*

Genus ***CLATHROZOON*** Spencer, 1891

Fig. 140G-H

Hydroid: colony arborescent, growing in one plane; skeleton of chitinous stolons, complexly anastomosing; stem and main branches gradually flattened in the colonial plane with growth; hydrotheca arranged spirally on branchlets, connected with stolon basally and embedded in skeleton up to its opening; operculum funnel-shaped; hydranths cylindrical, deeply retractile into hydrothecae; numerous tubular nematothecae, each containing a nematophore, arising from thin peridermal layer which encloses skeleton; dactylozooids filiform and very thin; gonophore as liberable eumedusoid, no manubrium, with velum, radial canals, 8 short tentacles and "gonads" on radial canals; gonotheca sac-like, shallowly embedded in skeleton, with funnel-shaped operculum.
Recent reference: Hirohito (1995).

Clathrozoon wilsoni Spencer, 1891

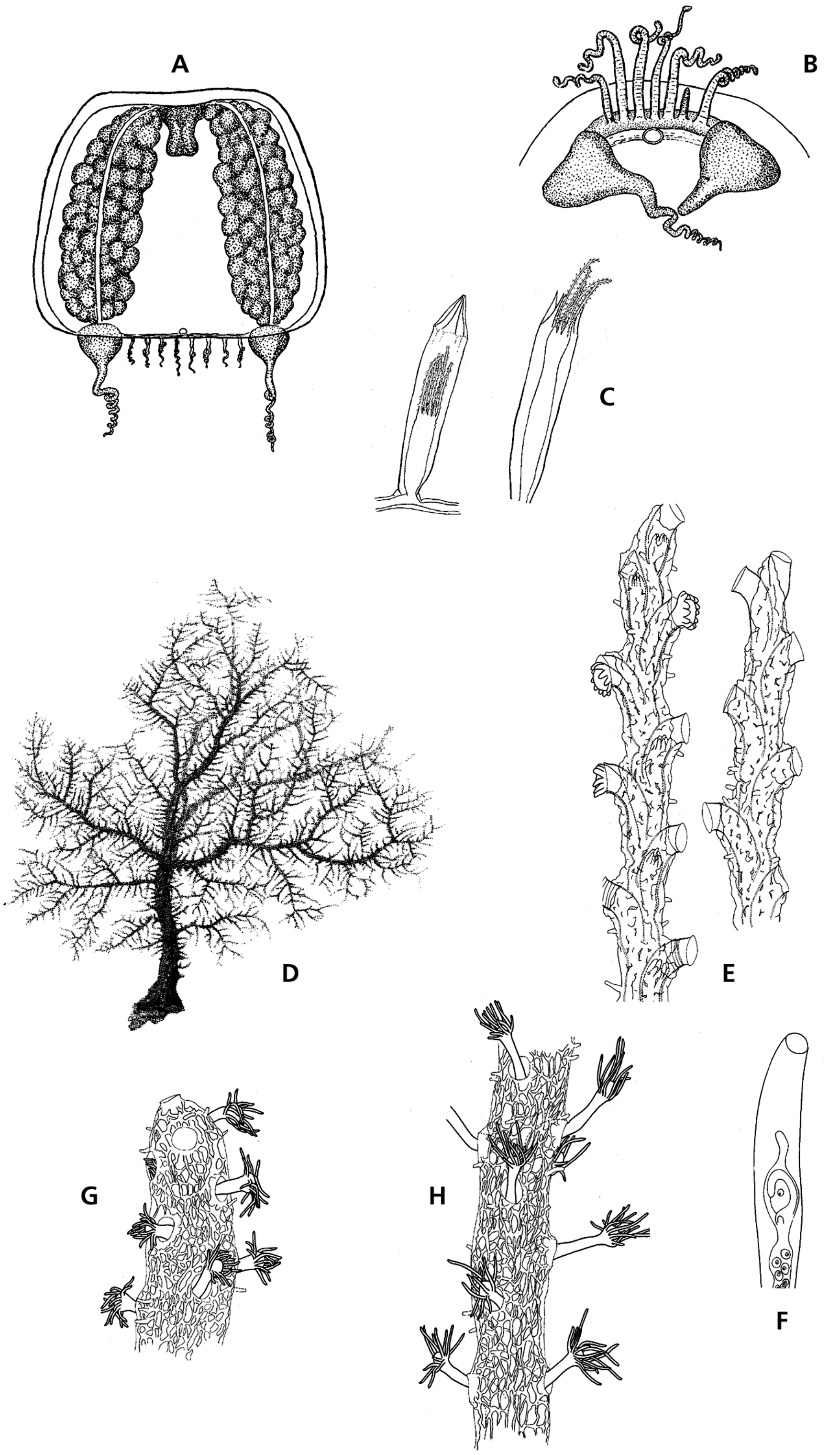


FIG. 140. Leptomedusae, Cirrholovenidae. A-C, *Cirrholovenia tetranema*: A, adult medusa; B, portion of umbrella margin; C, polyp. Clathrozonidae. D-F, *Pseudoclathrozoon cryptolaroides*: D, general view of a colony; E, branchlets of the colony; F, schematic figure of a gonotheca. G-H, *Clathrozoon wilsoni*, branches of a colony (A-B after Kramp, 1959a; C after Brinckmann-Voss, 1965b; D-H after Hirohito, 1967).

FIG. 140. *Leptomedusae, Cirrholovenidae. A-C,* Cirrholovenia tetranema : *A, méduse adulte ; B, portion du bord exombrellaire ; C, polype. Clathrozonidae. D-F,* Pseudoclathrozoon cryptolaroides : *D, vue générale d'une colonie ; E, branche d'une colonie ; F, figure schématique d'une gonothèque. G-H,* Clathrozoon wilsoni, *branches d'une colonie (A-B d'après Kramp, 1959a ; C d'après Brinckmann-Voss, 1965b ; D-H d'après Hirohito, 1967).*

Genus ***PSEUDOCLATHROZOON*** Hirohito, 1967

Fig. 140D-F

Hydroid: colony arborescent, growing in one plane, skeleton of chitinous stolons, complexly anastomosing; stem and main branches gradually flattened at right angles to colonial plane with growth; hydrothecae arising from a central tube, arranged right and left alternatively on branchlets, protruding markedly from skeleton and frequently multiple; hydrothecal margin everted, without operculum; hydranth cylindrical, deeply retractile in hydrotheca; numerous tubular nematothecae, each containing a nematophore arising directly from external stolon, no peridermal layer enclosing skeleton; gonophores as fixed sporosacs reduced to "gonads", gonothecae tubular embedded in stolons, without operculum.
Recent reference: Hirohito (1995).

Pseudoclathrozoon cryptolarioides Hirohito, 1967

Family DIPLEUROSOMATIDAE Russell, 1953

Hydroid: "*Cuspidella*"-like, only known from rearing in *Dipleurosoma typicum*.
Medusa: manubrium with narrow base; 3, 4 or more radial canals either branched or, if simple, irregularly arranged; "gonads" on radial canals separated from manubrium; marginal tentacles hollow or solid?; ocelli may be present.

KEY TO MEDUSAE

1. radial canals regularly arranged and branched, all branches reaching circular canal. 2
– 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*
– 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 lateral branches . . . . *Cannota*
– main canals as well as lateral branches repeatedly branched . . . . *Cuviera*

Genus ***CANNOTA*** Haeckel, 1879

(no figure available)

Hydroid: unknown.
Medusa: 4 radial canals, each giving rise to 2 simple unbranched side branches joining circular canal on either side of the main canal; 12 "gonads" on the four main canals and side branches.
Remarks: this species has never been found since its discovery.

Cannota dodecantha Haeckel, 1879

Genus ***CUVIERA*** Péron, 1807

Fig. 141A-B

Hydroid: unknown.
Medusa: 4 main radial canals, branching repeatedly, all branches joining circular canal; "gonads" on terminal branches of canals.

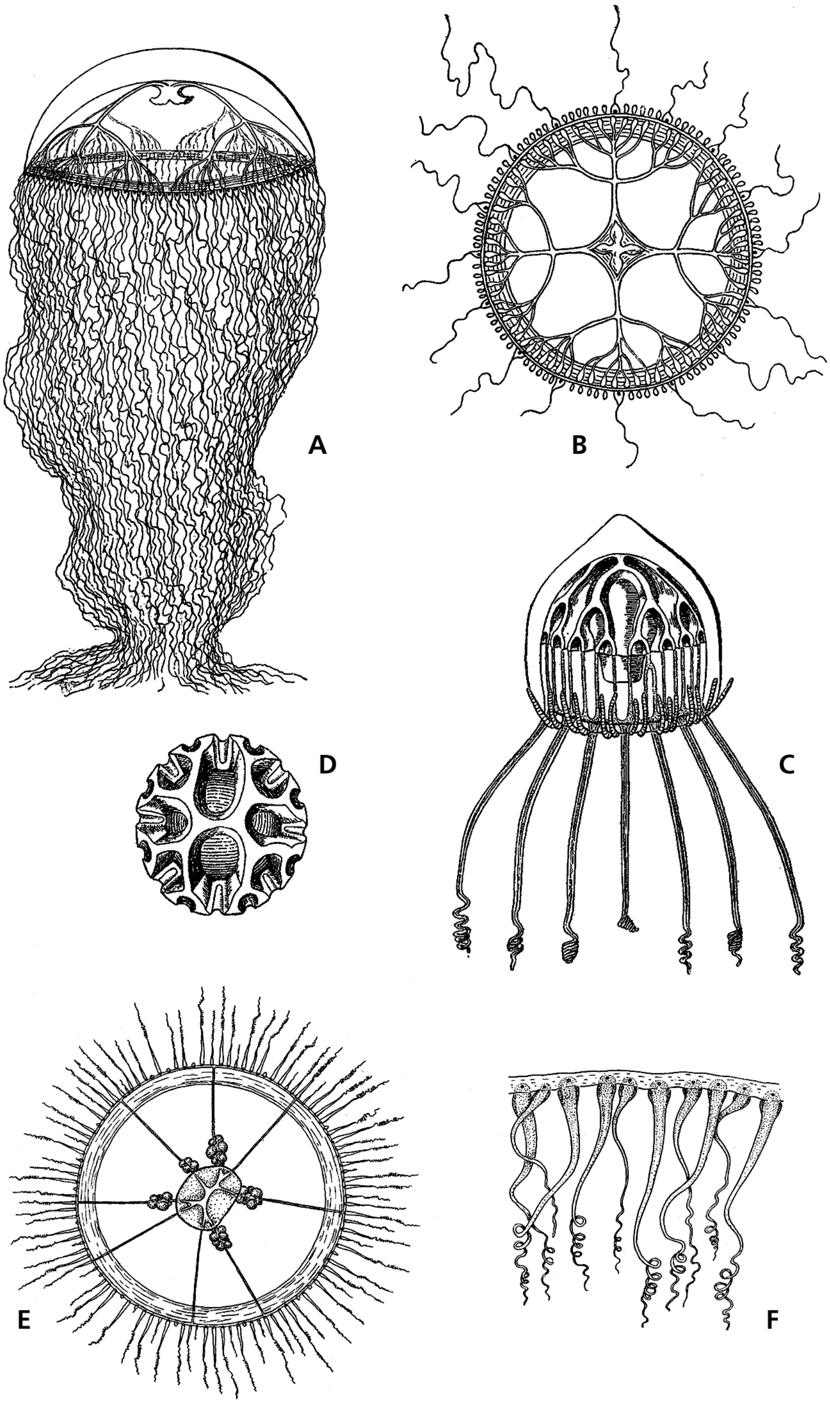


FIG.141. Leptomedusae, Dipleurosomatidae. A-B, *Cuviera*: A, *Cuviera carisochroma*, adult medusa; B, *Cuviera huxlei*, adult medusa. C-D, *Dichotomia cannoides*: C, adult medusa; D, schema showing the arrangement of the radial canals. E-F, *Dipleurosoma typicum*: E, adult medusa; F, portion of umbrella margin (A-D after Mayer, 1910; E after Kramp, 1933; F after Russell, 1953).

FIG. 141. *Leptomedusae, Dipleurosomatidae. A-B,* Cuviera : *A,* Cuviera carisochroma*, méduse adulte ; B,* Cuviera huxlei*, méduse adulte. C-D,* Dichotomia cannoides *: C, méduse adulte ; D, schéma montrant la disposition des canaux radiaires. E-F,* Dipleurosoma typicum : *E, méduse adulte ; F, portion du bord exombrellaire (A-D d'après Mayer, 1910 ; E d'après Kramp, 1933 ; F d'après Russell, 1953).*

Remarks: none of the two species has been found since its discovery.

Cuviera carisochroma Péron, 1807
Cuviera huxleyi (Haeckel, 1879)

Genus ***DICHOTOMIA*** Brooks, 1903

Fig. 141C-D

Hydroid: unknown.
Medusa: 4 main radial canals, bifurcating into two diverging branches, each giving rise to lateral branches, all reaching circular canal; "gonads" adjacent to manubrium, extending outwards along the canals and their branches.

Dichotomia cannoides Brooks, 1903

Genus ***DIPLEUROSOMA*** Boeck, 1866

Fig. 141E-F

Hydroid: see family characters.
Medusa: 5 or more main radial canals some or all branching irregularly; radial canals originate from manubrium or branching at short distance from manubrium and normally joining circular canal; tentacles numerous; ocelli adaxial; with or without club-shaped bodies.

Dipleurosoma collapsum (Mayer, 1900a)
Dipleurosoma gemmifera M. E. Thiel, 1938b
Dipleurosoma pacificum Agassiz & Mayer, 1902
Dipleurosoma typicum A. Boeck, 1866

Family EIRENIDAE Haeckel, 1879

Hydroid: colony of benthic species stolonal or erect ramified; bivalve-inhabiting species without perisarc, with pedal disc, usually solitary; planktonic species (*Eirene hexanemalis*) solitary, polyp budding totally into a single medusa; hydrotheca cylindrical in young colonies of erect forms, with diaphragm and folded pleated operculum formed by convergent flaps not demarcated from the hydrothecal rim (*Campanulina* type); in older colonies of this type, operculum generally lost and hydrotheca reduced to perisarcal collar, of haleciid type; hydrotheca usually reduced or absent in stolonal colonies, hydranth naked, borne directly on hydrorhiza or on short pedicels (*Campanopsis* type); hydranth of commensal species elongated, extensile, with filiform tentacles in a single amphicoronate whorl; intertentacular web present; gonophores on hydranths, hydrocaulus, or hydrorhiza, naked or more usually at least initially in a gonotheca, in form of medusae or medusoids with gonads on radial canals.
Medusa: 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.
Recent references: Calder (1991), Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Kubota (2000); Schuchert (2001a).

KEY TO HYDROIDS

The hydroids of the Eirenidae can be of "*Campanulina*", "*Campanopsis*" or "*Eugymnanthea*" type, but these types are not consistent with the corresponding medusae. The medusae are usually conspicuous and have been described, with different names from those of their corresponding hydroids, before their hydroid stages, medusa-based names having priority overy hydroid-based names.

KEY TO MEDUSAE

1. more than 8, typically indefinite number of statocysts 2
– usually 8 statocysts, rarely 12; without excretory papillae 6
2. without cirri; with or without excretory papillae 3
– cirri 4
3. "gonads" only on subumbrellar part of radial canals; without marginal warts . . . . *Eirene*
– "gonads" along entire length of radial canals; with marginal warts . . . . *Tima*
4. lateral cirri at base of some or all marginal tentacles 5
– marginal cirri; "gonads" only on subumbrellar part of radial canals . . . . *Phialopsis*
5. "gonads" restricted to subumbrellar parts of radial canals . . . . *Helgicirrha*
– "gonads" on entire length of radial canals . . . . *Irenium*
6. reduced medusae without marginal tentacles . . . . *Eugymnanthea*
– normal medusae, with marginal tentacles 7
7. without cirri 9
– with cirri 8
8. lateral cirri on marginal warts and usually also on marginal tentacles . . . . *Eutima*
– marginal cirri; with very long lips . . . . *Eutimalphes*
9. without cirri and marginal warts, "gonads" restricted to subumbrella . . . . *Eutonina*
– without cirri, with marginal warts, "gonads" along entire length of radial canals . . . . *Neotima*

Genus ***EIRENE*** Eschscholtz, 1829

Figs 25L, 40, 142A-F, 143A-B

Hydroid: *Campanopsis* or *Campanulina* type, see family characters.
Medusa: distinct gastric peduncle; no 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 to gastric peduncle; numerous statocysts.
Remarks: some *Eirene* species have been described only from the hydroid stage with medusa buds, the adult medusa stage being not known. They are here considered as species of doubtful status, eirenid hydroids alone being insufficient for generic or specific diagnosis.

Eirene brevigona Kramp, 1959a
Eirene brevistylis Huang & Xu, 1994
Eirene ceylonensis Browne, 1905a
Eirene elliceana (Agassiz & Mayer, 1902)
Eirene gibbosa (McCrady, 1859a)
Eirene hexanemalis (Goette, 1886)
Eirene kambara A. Agassiz & A.G. Mayer, 1899
Eirene lactea (Mayer, 1900a) [syn. *E. chiaochowensis* Kao, Li, Chang & Li, 1958]
Eirene lacteoides Kubota & Horita, 1992
Eirene menoni Kramp, 1953
Eirene mollis Torrey, 1909
Eirene palkensis Browne, 1905a
Eirene parvitentaculata Bouillon, 1984
Eirene proboscidea Bouillon & Barnett, 1999
Eirene pyramidalis (A. Agassiz, 1862)
Eirene quadrigatum (Haeckel, 1879) [doubtful status]
Eirene tenuis (Browne, 1905b)
Eirene troglodyta Watson, 1998 [doubtful status]
Eirene viridula (Péron & Lesueur, 1810)
Eirene sp. – Calder, 1991

Genus ***EUGYMNANTHEA*** Palombi, 1935

Fig. 143C-D

Hydroid: 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.

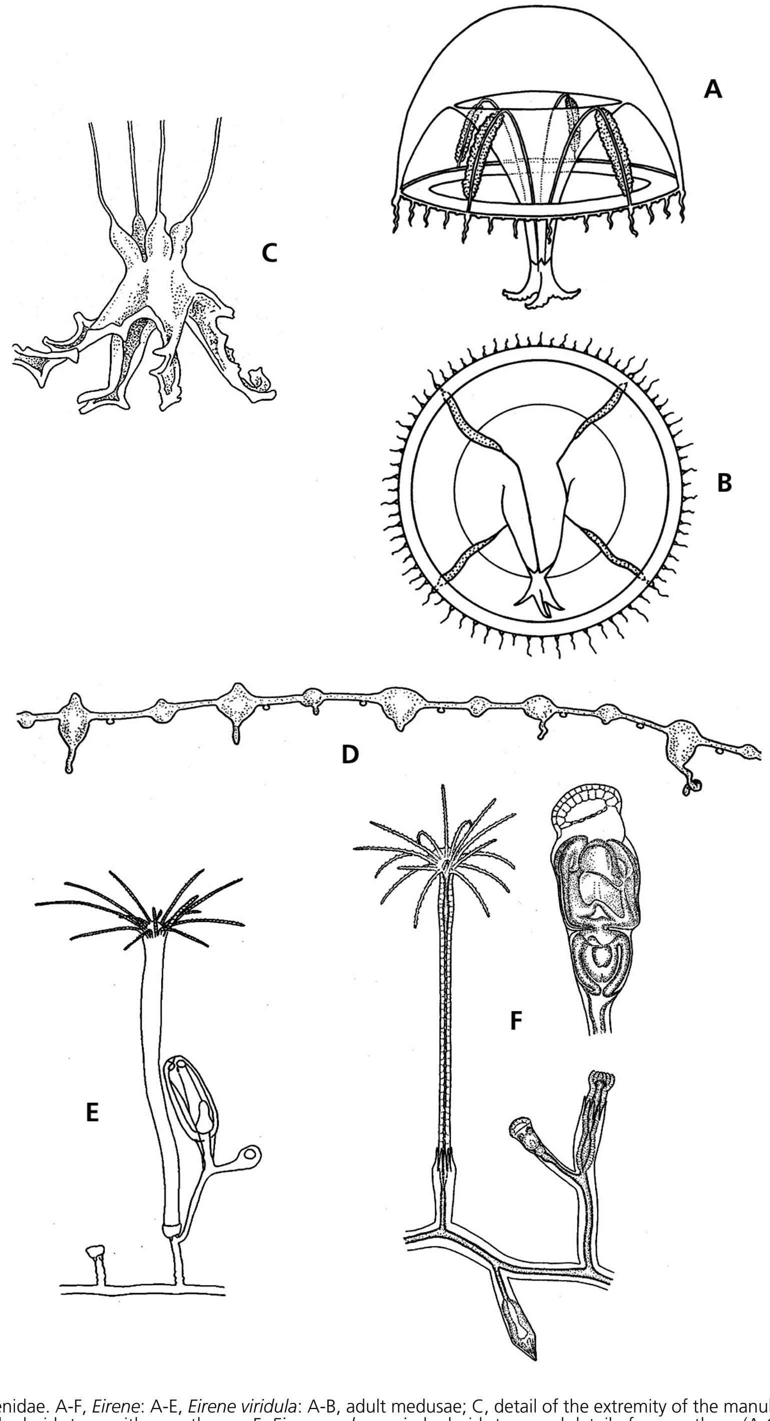


FIG. 142. Leptomedusae, Eirenidae. A-F, *Eirene*: A-E, *Eirene viridula*: A-B, adult medusae; C, detail of the extremity of the manubrium and four mouth-lips; D, detail of umbrella margin; E, hydroid stage with gonothecae; F, *Eirene ceylonensis*, hydroid stage and detail of a gonotheca (A-C after Kramp, 1959b; D after Russell, 1963; E after Günzl, 1984; F after Bouillon *et al.*, 1988).

FIG. 142. *Leptomedusae, Eirenidae. A-F,* Eirene : *A-E,* Eirene viridula : *A-B, méduses adultes ; C, détail de l'extrémité du manubrium et des quatres lèvres buccales ; D, détail du bord exombrellaire ; E, stade hydroïde avec des gonothèques ; F,* Eirene ceylonensis*, stade hydroïde et détail d'une gonothèque (A-C d'après Kramp, 1959b ; D d'après Russell, 1963 ; E d'après Günzl, 1984 ; F d'après Bouillon* et al.*, 1988).*

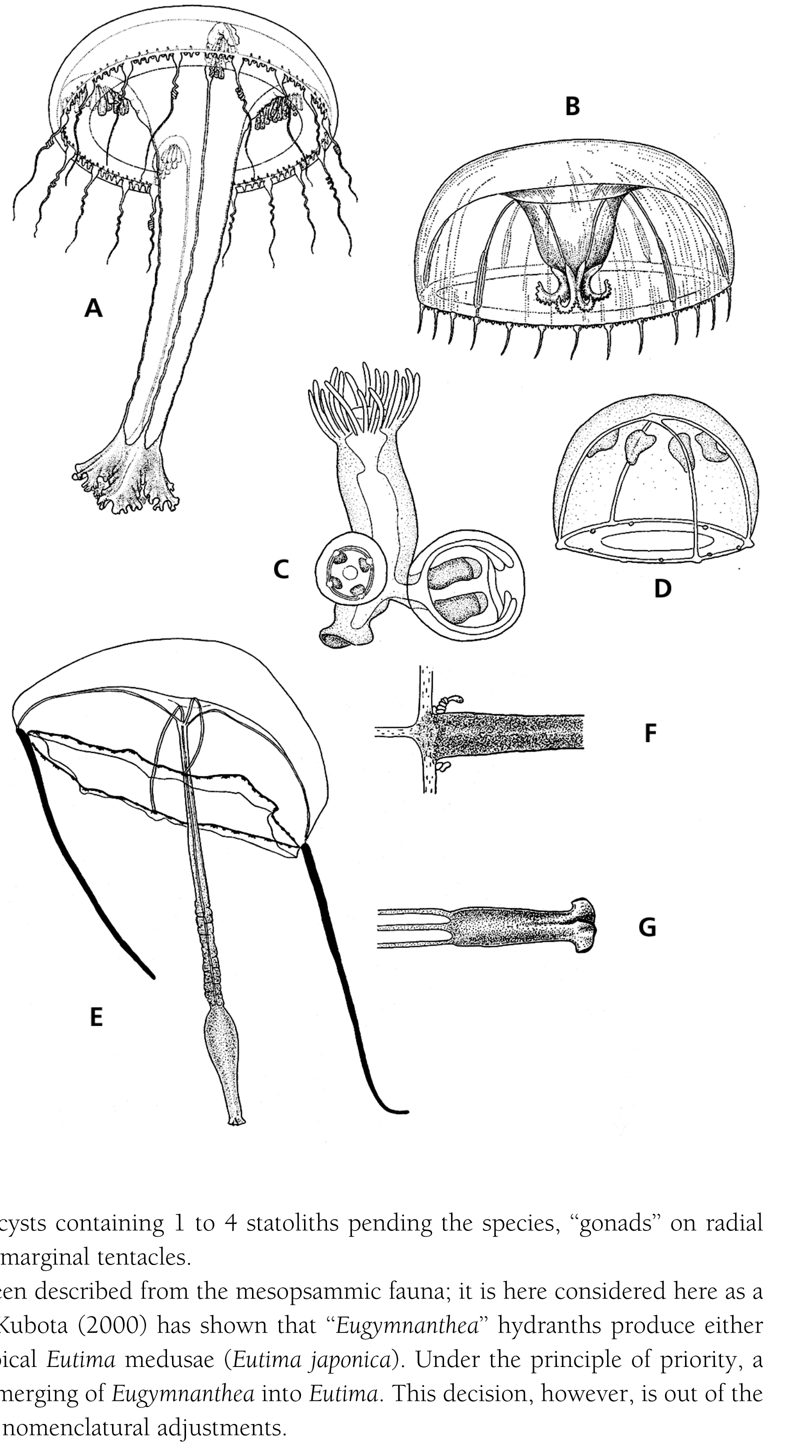


FIG.143. Leptomedusae, Eirenidae. A, *Eirene elliceana*, adult medusa with hydroid blastostyles on radial canals giving rise to medusa buds. B, *Eirene hexanemalis,* adult medusa. C-D, *Eugymnanthea inquilina*: C, polyp with gonophore; D, eumedusoid. E-G, *Eutima gracilis*: E, adult medusa; F, base of marginal tentacle with lateral cirri; G, manubrium and mouth (A after Bouillon, 1984b; B after Kramp, 1968; C-D after Morri, 1981; E-G after Russell, 1953).

FIG. 143. *Leptomedusae, Eirenidae. A,* Eirene elliceana*, méduse adulte avec des blastostyles polypodiaux sur leur canaux radiaires différenciant des bourgeons médusaires. B,* Eirene hexanemalis*, méduse adulte. C-D,* Eugymnanthea inquilina *: C, polype avec gonophore ; D, eumédusoïde. E-G,* Eutima gracilis *: E, méduse adulte ; F, base d'un tentacule marginal avec des cirres latéraux ; G, manubrium et bouche (A d'après Bouillon, 1984b ; B d'après Kramp, 1968 ; C-D d'après Morri, 1981 ; E-G d'après Russell, 1953).*

Medusa: eumedusoid, with 8 marginal statocysts containing 1 to 4 statoliths pending the species, "gonads" on radial canals; with or without manubrium; without marginal tentacles.

Remarks: *Eugymnanthea psammobionta* has been described from the mesopsammic fauna; it is here considered here as a species of doubtful status (see *Anthohydra*). Kubota (2000) has shown that "*Eugymnanthea*" hydranths produce either eumedusoids (*Eugymnanthea inquilina*) or typical *Eutima* medusae (*Eutima japonica*). Under the principle of priority, a revision of the two genera should lead to the merging of *Eugymnanthea* into *Eutima*. This decision, however, is out of the scope of the present work and requires some nomenclatural adjustments.

Eugymnanthea inquilina Palombi, 1935 [syn. *E. polimantii* (Cerruti, 1941)]

Eugymnanthea japonica Kubota, 1979

Eugymnanthea psammobionta (Salvini-Plawen & Chandrasekhara-Rao, 1973) [doubtful status]

Genus ***EUTIMA*** McCrady, 1859

Figs 27A, 143E-G, 144A-I

Hydroid: either single hydranths, or erect colony arising from creeping stolons, or epizootic naked polyps; in non epizootic forms, hydrocaulus with smooth perisarc, young colonies with cylindrical hydrotheca 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, operculum generally lost and hydrotheca reduced to a perisarcal collar of haleciid type; usually with intertentacular web.
Medusa: distinct gastric peduncle; lateral cirri (difficult to observe and often destroyed after fixation); marginal swellings or warts; mouth with simple lips; 4 simple radial canals; "gonads" on radial canals, either beneath subumbrella or on gastric peduncle or on both; with 8 (exceptionally 12) statocysts.

Eutima brownei (Torrey, 1909)
Eutima coerulea (L. Agassiz, 1862a)
Eutima commensalis Santhakumari, 1970
Eutima cuculata Brooks, 1883 [doubtful status]
Eutima curva Browne, 1905a
Eutima gegenbauri (Haeckel, 1864)
Eutima gentiana (Haeckel, 1879)
Eutima gracilis (Forbes & Goodsir, 1851)
Eutima hartlaubi Kramp, 1958
Eutima japonica Uchida, 1925 [syn. *E. cirrhifera* (Kakinuma, 1964) and *Eucheilota intermedia* Kubota, 1984]
Eutima levuka (Agassiz & Mayer, 1899)
Eutima longigonia Bouillon, 1984b
Eutima mira McCrady, 1859a [syn. *E. orientalis* (Browne, 1905a)]
Eutima modesta (Hartlaub, 1909b)
Eutima mucosa Bouillon, 1984b
Eutima neucaledonia Uchida, 1964b
Eutima ostrearum Mattox & Crowell, 1951
Eutima sapinhoa Narchi & Hebling, 1975
Eutima suzannae Allwein, 1967
Eutima variabilis McCrady, 1859a

Genus ***EUTONINA*** Hartlaub, 1897

Fig. 145A-D

Hydroid: of campanulinid erect type, hydrotheca very delicate, in young specimens cylindrical, with diaphragm and conical operculum formed by convergent sharp flaps not demarcated from hydrothecal rim; in old specimens the hydrotheca disintegrates, leaving just a crumpled membranous collar sheath; 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.
Medusa: with 8 statocysts; without cirri; without marginal warts; "gonads" restricted to subumbrella, not extending onto peduncle.
Recent reference: Schuchert (2001a).

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

Genus ***EUTIMALPHES*** Haeckel, 1879

Fig. 145E

Hydroid: unknown.
Medusa: broad gastric peduncle; mouth with complexly folded, large lips; 8 adradial statocysts; numerous marginal tentacles; with marginal cirri; with a few marginal warts.

Eutimalphes pretiosa Haeckel, 1879

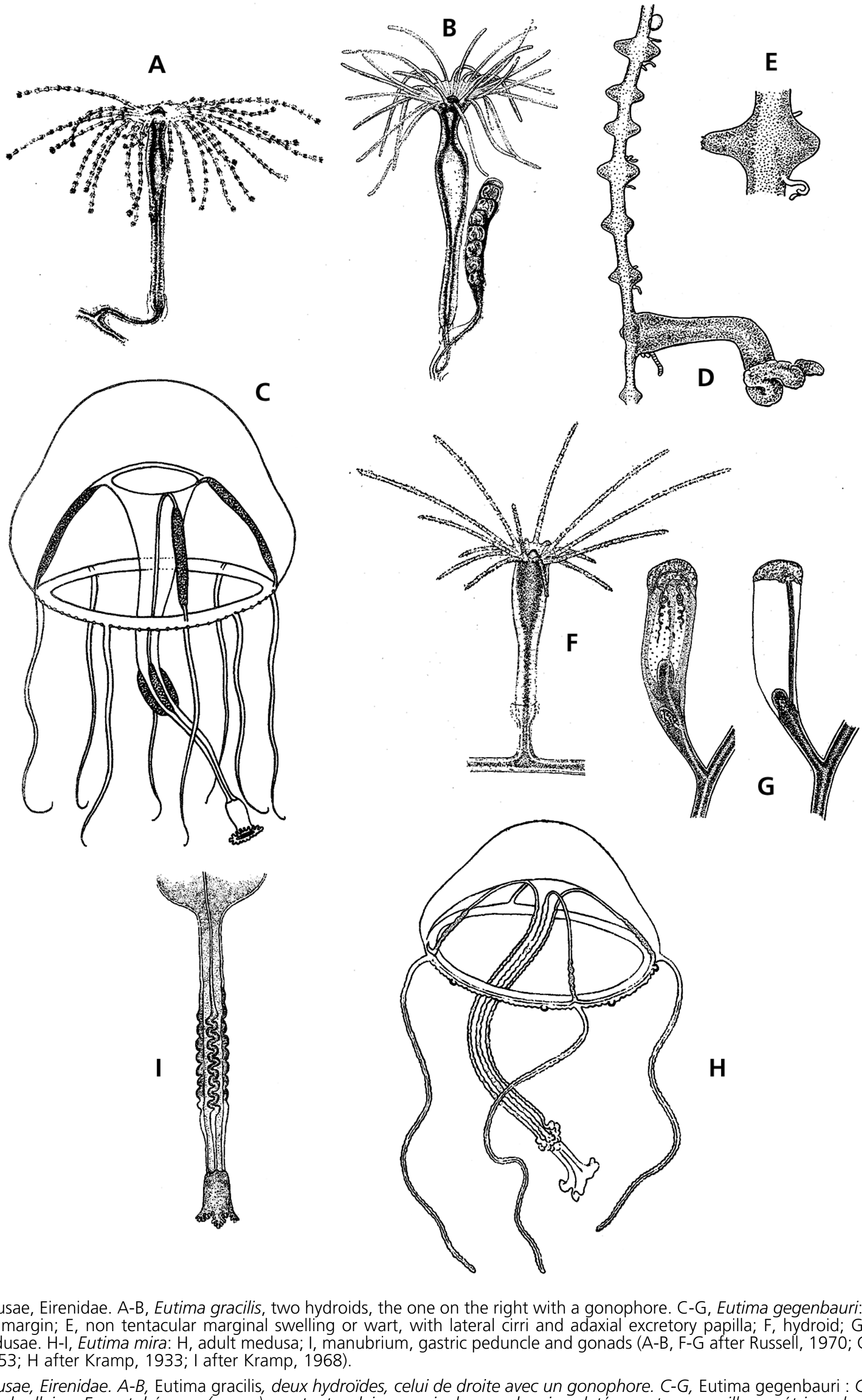


FIG. 144. Leptomedusae, Eirenidae. A-B, *Eutima gracilis*, two hydroids, the one on the right with a gonophore. C-G, *Eutima gegenbauri*: C, adult medusa; D, portion of umbrella margin; E, non tentacular marginal swelling or wart, with lateral cirri and adaxial excretory papilla; F, hydroid; G, gonangium before liberation of the medusae. H-I, *Eutima mira*: H, adult medusa; I, manubrium, gastric peduncle and gonads (A-B, F-G after Russell, 1970; C after Russell, 1963; D-E after Russell, 1953; H after Kramp, 1933; I after Kramp, 1968).

FIG. 144. *Leptomedusae, Eirenidae. A-B,* Eutima gracilis*, deux hydroïdes, celui de droite avec un gonophore. C-G,* Eutima gegenbauri *: C, méduse adulte ; D, portion du bord exombrellaire ; E, protubérance (verrue) non tentaculaire marginale avec des cirres latéraux et une papille excrétrice adaxiale ; F, hydroïde ; G, gonange avant la libération des méduses. H-I,* Eutima mira *: H, méduse adulte ; I, manubrium, pédoncule gastrique et ''gonades'' (A-B, F-G d'après Russell, 1970 ; C d'après Russell, 1963 ; D-E d'après Russell, 1953 ; H d'après Kramp, 1933 ; I d'après Kramp, 1968).*

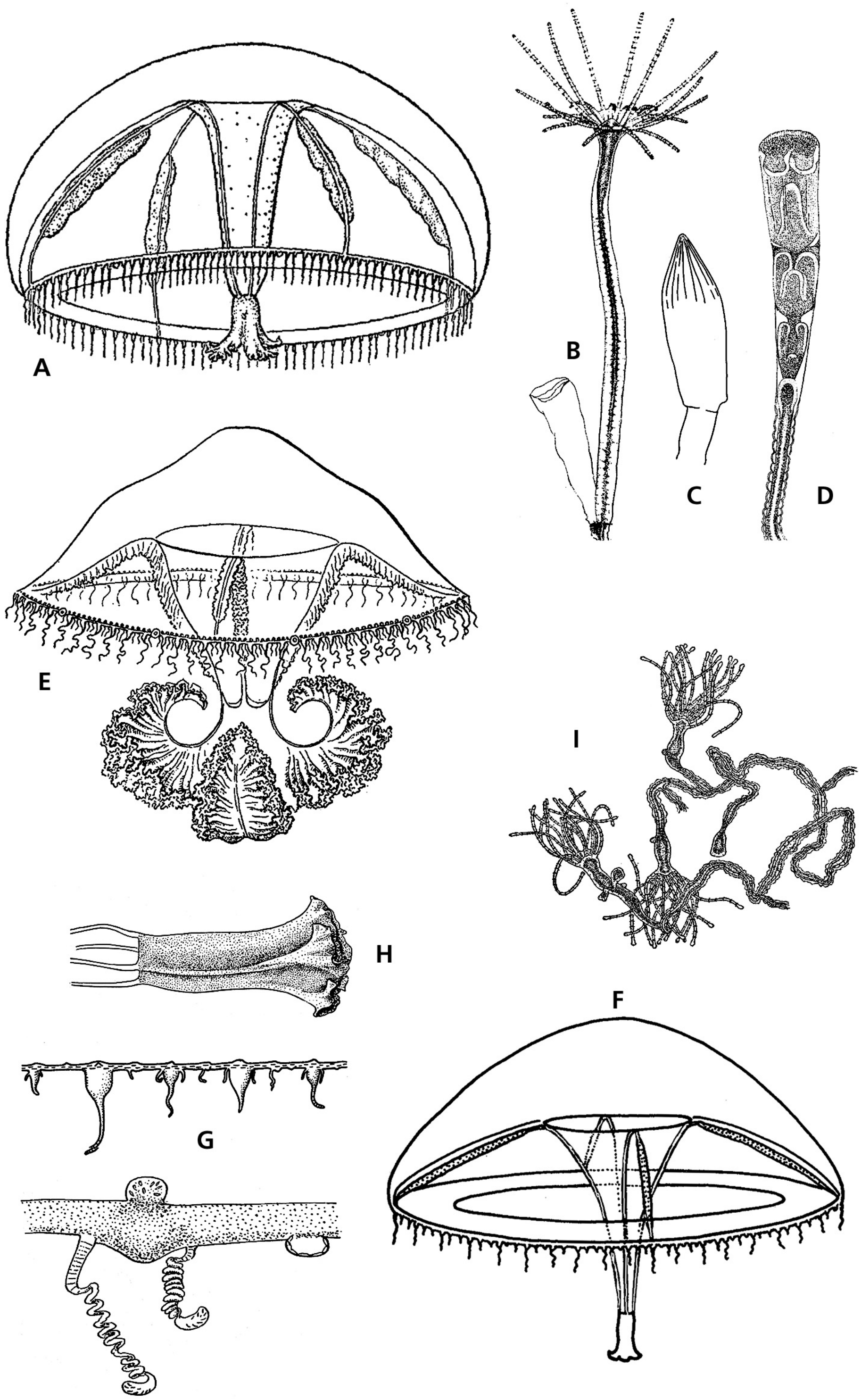


FIG. 145. Leptomedusae, Eirenidae. A-D, *Eutonina indicans*: A, adult medusa; B, hydroid with empty gonotheca; C, detail of hydrotheca before rupture of operculum; D, gonangium with medusa buds. E, *Eutimalphes pretosia*, adult medusa. F-I, *Helgicirrha schulzei*: F, adult medusa; G, portion of umbrella margin showing marginal tentacles of two sizes (above), detail of margin showing the lateral cirri, statocyst and excretory papillae (below); H, manubrium and mouth; I, hydroid colony (A after Kramp, 1959b; B & D after Werner, 1968b; C after Cornelius, 1995; E after Kramp, 1968; F after Russell,1963; G-H after Russell,1953; I after Bouillon, 1971).

FIG. 145. *Leptomedusae, Eirenidae. A-D,* Eutonina indicans : *A, méduse adulte ; B, un hydroïde et une gonothèque vide ; C, détail d'une hydrothèque avant la rupture de l'opercule ; D, gonange avec des bourgeons médusaires. E,* Eutimalphes pretosia, *méduse adulte. F-I,* Helgicirrha schulzei : *F, méduse adulte ; G, portion du bord exombrellaire montrant les tentacules marginaux de deux tailles différentes (au-dessus), détail du bord exombrellaire montrant les cirres latéraux, un statocyste et une papille excrétrice (au-dessous) ; H, détail du manubrium et de la bouche ; I, colonie d'hydroïdes (A d'après Kramp, 1959b ; B & D d'après Werner, 1968b ; C d'après Cornelius, 1995 ; E d'après Kramp, 1968 ; F d'après Russell, 1963 ; G-H d'après Russell, 1953 ; I d'après Bouillon, 1971).*

Genus *HELGICIRRHA* Hartlaub, 1909

Fig. 145F-I

Hydroid: campanopsid; colony with a net-like hydrorhiza giving rise to unbranched upright hydranths; hydrorhiza and base of hydranths enclosed in a thin and sticky perisarc; hydranth naked, club-shaped, with 26 to 30 amphicoronate filiform tentacles with a small intertentacular web; medusa buds borne in the middle of hydranth or sometimes even higher, single or up to three per hydranth.
Medusa: lateral cirri at the base of some or of all marginal tentacle bulbs; with excretory papillae.

Helgicirrha brevistyla Xu & Huang, 1983a
Helgicirrha cari (Haeckel, 1864)
Helgicirrha cornelii Bouillon, 1984b
Helgicirrha danduensis (Bigelow, 1904)
Helgicirrha gemmifera Bouillon, 1984
Helgicirrha irregularis Bouillon, Seghers & Boero, 1988
Helgicirrha malayensis (Stiasny, 1928)
Helgicirrha medusifera (Bigelow, 1909)
Helgicirrha schulzei Hartlaub, 1909c
Helgicirrha weaveri Allwein, 1967

Genus *IRENIUM* Haeckel, 1879

Fig. 146A

Hydroid: unknown.
Medusa: numerous statocysts; numerous marginal warts; marginal tentacles and warts with lateral cirri; mature “gonads” along entire radial canals.

Irenium alabiatum Zamponi, Suárez-Morales & Gasca, 1999 [incomplete specimens]
Irenium labiatum Zamponi, Suárez-Morales & Gasca, 1999
Irenium quadrigatum Haeckel, 1879
Irenium teuscheri (Haeckel, 1879)

Genus *NEOTIMA* Petersen, 1962

Fig. 146B-C

Hydroid: unknown.
Medusa: with 8 statocysts, without cirri; with marginal warts; “gonads” on entire length of radial canals.

Neotima lucullana (Delle Chiaje, 1822)
Neotima peterseni Bouillon, 1984b

Genus *PHIALOPSIS* Torrey, 1909

Fig. 146D

Hydroid: unknown.
Medusa: gastric peduncle short; with marginal cirri; without excretory pores; with “gonads” restricted to subumbrellar portion of radial canals; with numerous statocysts.

Phialopsis diegensis Torrey, 1909

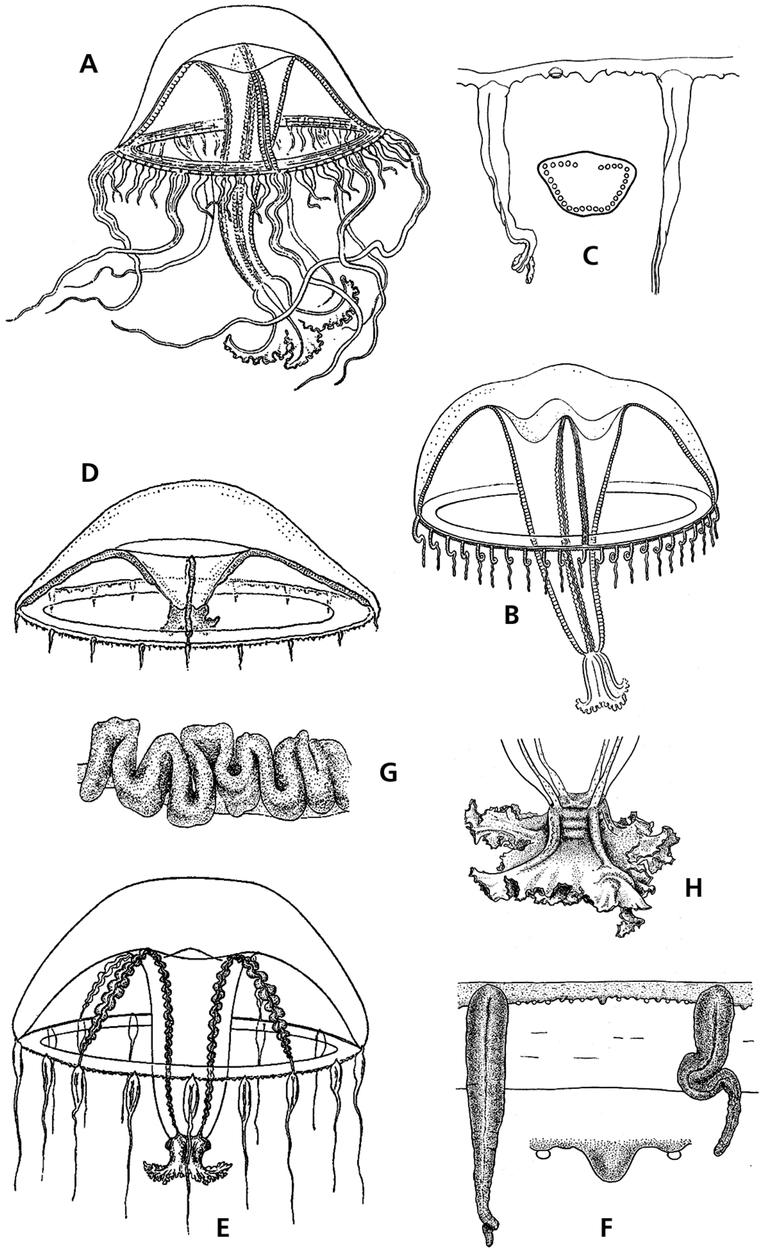


FIG. 146. Leptomedusae, Eirenidae. A, *Irenium teuscheri*, adult medusa. B-C, *Neotima lucullana*: B, adult medusa; C, part of umbrella margin and detail of statocyst. D, *Phialopsis diegensis*, adult medusa. E-H, *Tima bairdi*: E, adult medusa; F, portion of umbrella margin (above), marginal swelling or wart with statocysts (below); G, portion of male ''gonad''; H, manubrium and mouth (A-B, D-E after Kramp, 1959b; C after Petersen, 1962; F-H after Russell, 1953).

***FIG. 146.** Leptomedusae, Eirenidae. A,* Irenium teuscheri, *méduse adulte. B-C,* Neotima lucullana *: B, méduse adulte ; C, partie du bord exombrellaire et détail d'un statocyste. D,* Phialopsis diegensis, *méduse adulte. E-H,* Tima bairdi *: E, méduse adulte ; F, portion du bord exombrellaire (au-dessus), protubérance marginale ou verrue avec des statocystes (au-dessous) ; G, portion d'une ''gonade'' mâle ; H, détail du manubrium et de la bouche (A-B, D-E d'après Kramp, 1959b ; C d'après Petersen, 1962 ; F-H d'après Russell, 1953).*

Genus ***TIMA*** Eschscholtz, 1829

Fig. 146E-H

Hydroid: poorly known, probably of "*Campanulina*" type.

Medusa: with distinct gastric peduncle; without cirri; with marginal warts; "gonads" upon entire length of radial canals; with numerous statocysts.

Tima bairdii (Johnston, 1833)
Tima flavilabris Eschscholtz, 1829
Tima formosa L. Agassiz, 1862a
Tima saghalinensis Bigelow, 1913

Family HALECIIDAE Hincks,1868

Hydroid: colony stolonal or erect, arising from a creeping hydrorhiza; hydrotheca sessile or pedicellate, shallow; hydranth much larger than hydrotheca, often robust, with or without intertentacular web, hydrothecal rim usually even, strongly to scarcely flaring, hydrotheca lacking operculum; renovation common, regenerated hydrothecae arranged in tiers; diaphragm and a basal ring of large, often birefringent, desmocytes; endoderm of hydranths differentiated into proximal digestive part and distal non digestive pert, nematophores, nematothecae and nematodactyls present or absent; gonophores usually as fixed sporosacs, some species with acrocyst, medusa stage totally suppressed from life cycle, swimming gonophores in one genus (*Nemalecium*), gonothecae solitary or grouped into a glomulus, infrequently with naked gonophores.

Recent references: Calder (1991); Cornelius (1995); Migotto (1996); Calder & Vervoort (1998); Medel & Vervoort (2000); Watson (2000); Schuchert (2001a).

KEY TO HYDROIDS

1. nematophores present . . . . *Hydrodendron*
– nematophores absent. 2

2. colony with swimming gonophores and nematodactyls . . . . *Nemalecium*
– colony with fixed gonophores and without nematodactyls. . . . . *Halecium*

Genus ***HALECIUM*** Oken, 1815

Figs 5IK, S, 9F-G, 10D, 21, 57B, 147A-F

Synonyms: *Endothecium* Fraser, 1935, non Koker, 1922; *Baleum* Billard, 1929; *Plumalecium* Antsulevich, 1982; *Sagamihydra* Hirohito, 1995. Although published in a work placed on the Official Index, the name *Halecium* Oken, 1815 has been conserved by ICZN Opinion 1220.

Hydroid: colony usually erect, monosiphonic or polysiphonic, branched or unbranched, arising from a creeping hydrorhiza, stem and branches divided in internodes bearing apohyses near distal end; hydrothecae alternate, sessile or pedicellate, borne on apophyses when not pedicellate, shallow; rim commonly everted and regenerated; a ring of large desmocytes and a basal diaphragm; hydranth not retractable into hydrotheca, often with an annular bugle half way up the gastric column; intertentacular web present or not; nematophores and nematodactyls absent; gonophores as fixed sporosacs sometimes with acrocyst, gonothecae either solitary or aggregated to form a glomulus, usually sexually dimorphic, sometimes with gonophoral polyps or arising from within hydrothecae; typically sexually dimorphic.

Recent references: Calder (1991); Cornelius (1995); Hirohito (1995); Migotto (1996); Pagliara *et al.* (2000); Schuchert (2001a, 2003); Calder *et al.* (2003); Vervoort & Watson (2003).

Halecium amphibolum Watson, 1993
Halecium annulatum Torrey, 1902
Halecium antarcticum Vanhöffen, 1910
Halecium banyulense Motz-Kossowska, 1911
Halecium beanii (Johnston, 1838)
Halecium bermudense Congdon, 1907
Halecium birulai Spassky, 1929
Halecium brashnikowi Linko, 1911
Halecium bruniensis Watson, 1975
Halecium capillare (De Pourtalès, 1869)
Halecium conicum Stechow, 1919a
Halecium corrugatissimum Trebilcock, 1928
Halecium corrugatum Nutting, 1899
Halecium crinis Stechow, 1913a
Halecium curvicaule von Lorenz, 1886
Halecium cymiforme Allman, 1888
Halecium cymosum Fraser, 1935
Halecium delicatulum Coughtrey, 1876 [syn. *H. mediterraneaum* Weismann, 1883]
Halecium densum Calkins, 1899
Halecium dichotomum Allman, 1888
Halecium diminutivum Fraser, 1940b
Halecium dubium Fraser, 1941
Halecium dufresneae Millard, 1977b
Halecium dyssymetrum Billard, 1929a
Halecium exiguum Fraser, 1948
Halecium expansum Trebilcock, 1928
Halecium fasciculatum Fraser, 1938a
Halecium filicula Allman, 1877
Halecium flabellatum Fraser, 1935
Halecium flexum Fraser, 1948
Halecium fragile Hodgson, 1950
Halecium fraseri Ralph, 1958
Halecium fruticosum Fraser, 1943
Halecium galeatum Billard, 1937
Halecium groenlandicum Kramp, 1911
Halecium halecinum (Linnaeus, 1758)
Halecium humile Pictet, 1893
Halecium incertus Naumov & Stepanjants, 1962
Halecium inhacae Millard, 1958
Halecium insolens Fraser, 1938a
Halecium interpolatum Ritchie, 1907b
Halecium jaederholmi Vervoort, 1972
Halecium kofoidi Torrey, 1902
Halecium labiatum Billard, 1933
Halecium labrosum Alder, 1859 [syn. *H. undulatum* Billard, 1921]
Halecium laeve Kramp, 1932b
Halecium lankesteri (Bourne, 1890)
Halecium lenticulare Trebilcock, 1928
Halecium lightbourni Calder, 1991
Halecium linkoi Antsulevich, 1980
Halecium liouvillei Billard, 1934
Halecium lucium Antsulevich, 1979
Halecium luteum Watson, 1975
Halecium macrocephalum Allman, 1877
Halecium magellanicum Hartlaub, 1905 [doubtful status]

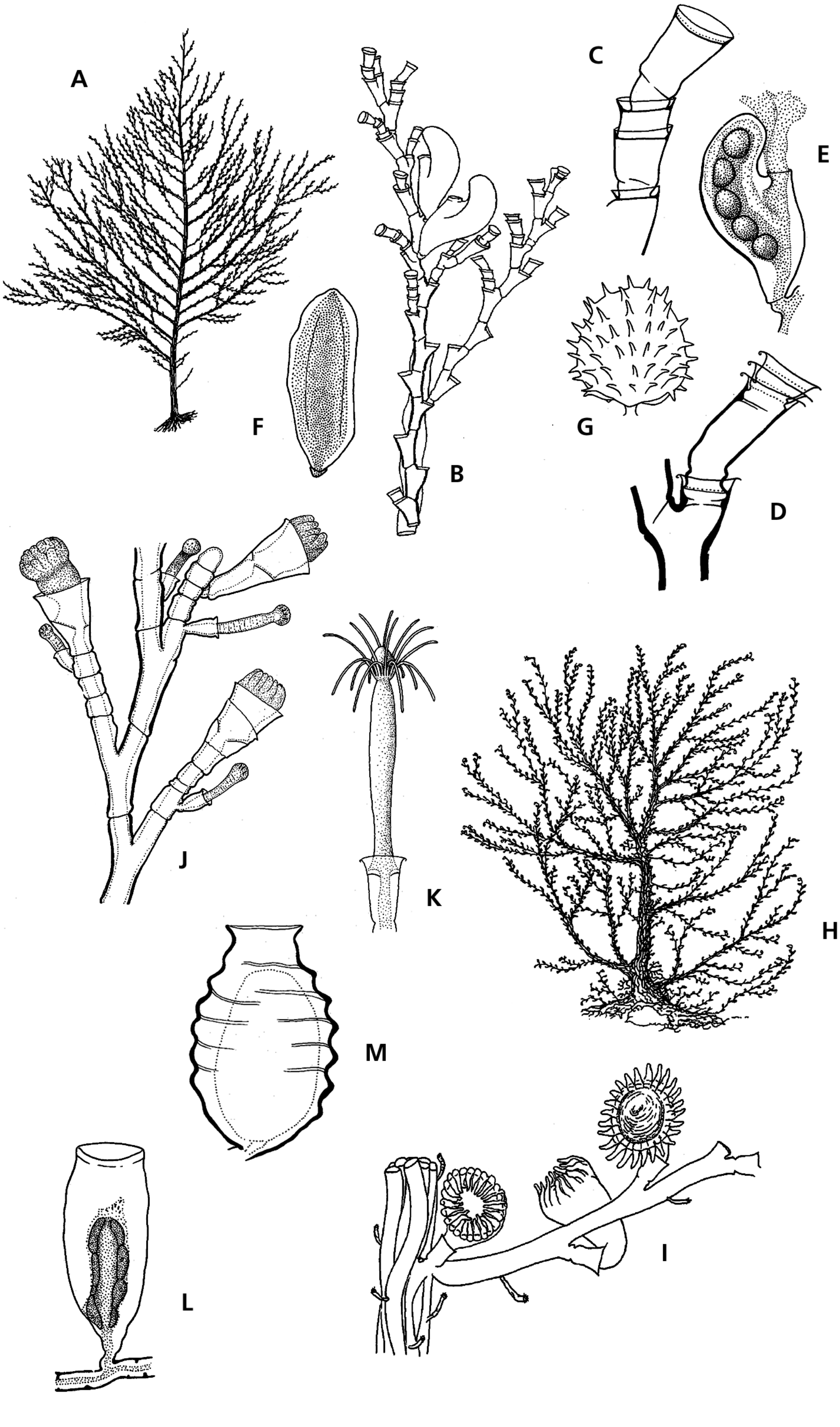


FIG. 147. Leptomedusae, Haleciidae. A-C, E-F, *Halecium beani*: A, general view of colony; B, stem with hydrothecae and female gonothecae; C, regenerated hydrothecae; E, female gonophore with hydranth emerging from the adcauline aperture; F, male gonophore. D, *Halecium delicatulum*, part of stem with regenerated hydrothecae. G, *Halecium muricatum*, gonothecae, male and female identical. H-I, *Hydrodendron gorgonoide*: H, general view of colony; I, detail of hydrothecae and nematothecae. J, *Hydrodendron gardineri*, part of erect colony showing hydrothecae, nematothecae and nematophores. K-L, *Hydrodendron mirabilis*: K, living hydranth; L, female gonotheca. M, *Hydrodendron sympodiformis,* gonotheca (A, G-I after Cornelius, 1995; B-F, J-M after Millard, 1975).

FIG. 147. *Leptomedusae, Haleciidae. A-C, E-F,* Halecium beani *: A, vue générale d'une colonie ; B, hydroclades avec des hydrothèques et des gonothèques femelles ; C, hydrothèques secondaires régénérées ; E, gonophore femelle avec un hydranthe émergeant de l'orifice apical adcaulinaire ; F, gonophore mâle. D,* Halecium delicatulum*, partie d'hydroclade avec des hydrothèques regénérées. G,* Halecium muricatum*, gonothèque (mâle et femelle identiques). H-I,* Hydrodendron gorgonoide *: H, vue générale d'une colonie ; I, détail d'hydrothèques et de nématothèques. J,* Hydrodendron gardineri*, partie d'une colonie érigée montrant les hydrothèques, nématothèques et les nématophores. K-L,* Hydrodendron mirabilis *: K, hydranthe* in vivo *; L, gonothèque femelle. M,* Hydrodendron sympodiformis*, gonothèque (A, G-I d'après Cornelius, 1995 ; B-F, J-M d'après Millard, 1975).*

Halecium marsupiale Bergh, 1887
Halecium minor Fraser, 1935
Halecium minutum Broch, 1903
Halecium mirandus Antsulevich & Regel, 1986
Halecium muricatum (Ellis & Solander, 1786)
Halecium nanum Alder, 1859
Halecium ochotense Linko, 1911
Halecium ornatum Nutting, 1901a
Halecium ovatum Totton, 1930
Halecium paucinodum (Fraser, 1947)
Halecium perexiguum Hirohito, 1995
Halecium petrosum Stechow, 1919a
Halecium plicatocarpum Vervoort & Watson, 2003
Halecium plumosum Hincks, 1868
Halecium profundum Calder & Vervoort, 1998
Halecium pusillum (M. Sars, 1857)
Halecium pygmaeum Fraser, 1911
Halecium pyriforme Hirohito, 1995
Halecium ralphae Watson & Vervoort, 2001
Halecium reduplicatum (Fraser, 1935)
Halecium reflexum Stechow, 1919a
Halecium regulare Fraser, 1938a
Halecium repens Jäderholm, 1907
Halecium reversum Nutting, 1901a
Halecium robustum Nutting, 1901a
Halecium schneideri Bonnevie, 1898b
Halecium scutum Clark, 1877
Halecium secundum Jäderholm, 1904a
Halecium sessile Norman, 1867
Halecium sibogae Billard, 1929a
Halecium singulare (Billard, 1929a)
Halecium spatulum Watson, 2000
Halecium speciosum Nutting, 1901a
Halecium telescopicum Allman, 1888
Halecium tenellum Hincks, 1861
Halecium tensum Fraser, 1941
Halecium textum Kramp, 1911
Halecium tortum Fraser, 1938a
Halecium vagans Fraser, 1938a
Halecium vasiforme Fraser, 1935
Halecium wilsoni Calkins, 1899

Genus ***HEMITHECA*** Hilgendorf, 1898

Doubtful, unrecognizable genus

Hemitheca intermedia Hilgendorf, 1898 [doubtful status]

Genus ***HYDRODENDRON*** Hincks, 1874

Figs 9Q, 147H-M

Synonyms: *Ophiodissa* Stechow, 1919; *Scoresbia* Watson, 1969.
Hydroid: colony stolonal or erect, monosiphonic or polysiphonic; hydrothecae short cylindrical, haleciid type, pedicellate or on internodal apophyses, in two alternate rows in erect colonies, basal part with or without desmocytes; hydranth with or without an intertentacular web; nematophore extensile, elongate, simple-ended or capitate, nematotheca, when present, simple, sometimes minute; gonophores as solitary fixed sporosacs, gonothecae simple or aggregated in a glomulus.
Recent references: Rees and Vervoort (1987); Vervoort (1987); Calder (1991); Cornelius (1995); Hirohito (1995); Schuchert (2003).

Hydrodendron arboreum (Allman, 1888)
Hydrodendron armatum (Stechow, 1924)
Hydrodendron australis (Bale, 1919)
Hydrodendron blackburni (Watson, 1973)
Hydrodendron carchesium (Fraser, 1914b)
Hydrodendron cornucopiae (Millard, 1955)
Hydrodendron corrugatum (Fraser, 1936a)
Hydrodendron daidalum (Watson, 1969)
Hydrodendron dichotomum (Allman, 1888)
Hydrodendron expansum (Fraser, 1948)
Hydrodendron gardineri (Jarvis, 1922)
Hydrodendron gorgonoide (G.O. Sars, 1874)
Hydrodendron gracilis (Fraser, 1914a)
Hydrodendron laxum (Fraser, 1938a)
Hydrodendron leloupi Hirohito, 1983
Hydrodendron mirabile (Hincks, 1866a)
Hydrodendron negligens (Fraser, 1938a)
Hydrodendron parasiticum (G.O. Sars, 1874)
Hydrodendron sibogae (Billard, 1929b)
Hydrodendron stechowi Hirohito, 1995
Hydrodendron sympodiformis Millard & Bouillon, 1974
Hydrodendron tottoni Rees & Vervoort, 1987
Hydrodendron violaceum Hirohito, 1995

Genus ***NEMALECIUM*** Bouillon, 1986

Fig. 148A-D

Hydroid: colony erect, monosiphonic or slightly polysiphonic; hydrocaulus branched or unbranched, arising from a creeping hydrorhiza; hydrothecae sessile or peduncled, shallow, often regenerated, with a ring of large desmocytes and a diaphragm basally, in two opposite alternate rows from hydrocaulus and hydrocladia; hydranth large, elongated, not retractable into hydrotheca, intertentacular web absent, gland cells at base of tentacles; a pair nematodactyls between tentacular whorl and curving over hypostome; cnidome: microbasic mastigophores and pseudostenoteles; gonotheca solitary, urn to cone-shaped; swimming gonophores.

Recent references: Calder (1991); Gravier-Bonnet & Migotto (2000).

Nemalecium lighti (Hargitt, 1924)

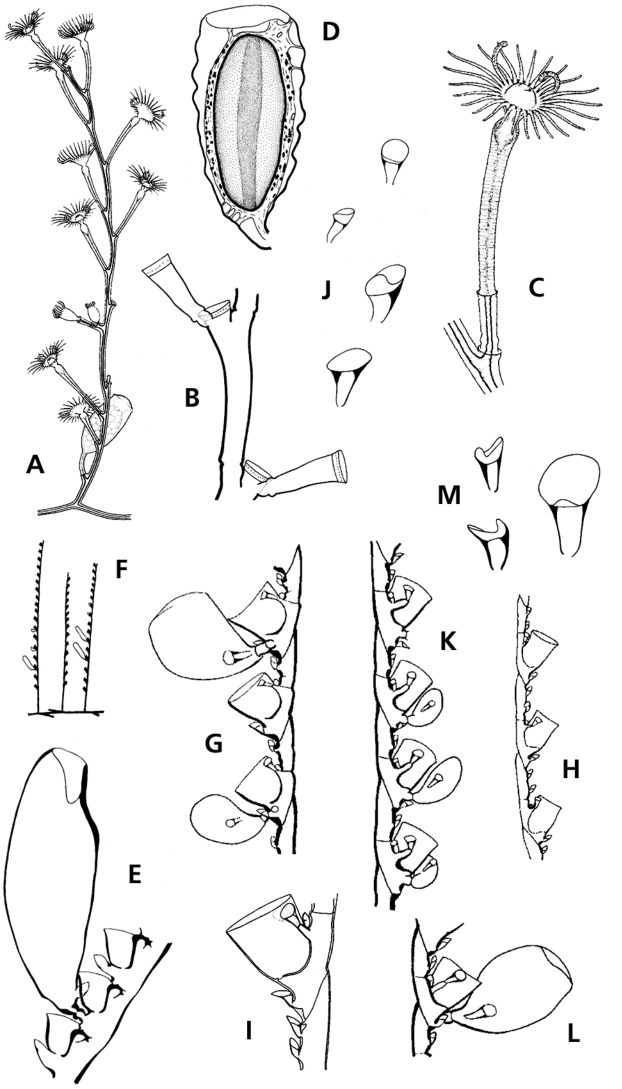


FIG. 148. Leptomedusae. A-D, Haleciidae (concluded), *Nemalecium lighti*: A, general view of a branch of a colony; B, part of hydrocaulus; C, hydranth with nematodactyls; D, male eumedusoid. E-M, Halopterididae: E, *Anarthrocladia parmata*, portion of hydrocladium with hydrothecae, nematothecae and gonotheca. F-M, *Antennella*: F, *Antennella silicosa*, part of fertile colony; G-J, *Antennella secundaria*: G, part of hydrocladia with a proximal male and a distal female gonotheca; H, non fertile hydrocladia; I, detail of part of stem with complete segmentation; J, lateral nematothecae; K-M, *Antennella quadriaurita*: K, portion of hydrocladium with hydrothecae, nematothecae and male gonothecae; L, fragment of hydrocladia with a hydrotheca, nematothecae and a female gonotheca; M, lateral nematothecae (A & C after Bouillon, 1987; B & D after Calder, 1991; E after Naumov, 1969; F & I after Schuchert, 1997; G-H, J-M after Millard, 1975).

***FIG. 148.** Leptomedusae. A-D, Haleciidae (fin),* Nemalecium lighti : *A, vue générale d'un hydrocaule montrant les hydrothèques et une gonothèque ; B, détail d'une partie d'hydrocaule ; C, hydranthe avec ses nematodactyles ; D, eumedusoïde mâle. E-M, Halopterididae : E,* Anarthrocladia parmata*, portion d'un hydroclade avec des hydrothèques, nématothèques et une gonothèque ; F-M,* Antennella : *F,* Antennella silicosa*, partie d'une colonie fertile ; G-J,* Antennella secundaria *: G, partie d'hydroclade avec une gonothèque mâle proximale et une gonothèque femelle distale ; H, hydroclade non fertile ; I, détail d'une partie d'un hydroclade avec segmentation complète ; J, nématothèques latérales ; K-M,* Antennella quadriaurita : *K, portion d'hydroclade montrant des hydrothèques, des nématothèques et des gonothèques mâles ; L, fragment d'une hydroclade portant une hydrothèque, des nématothèques et une gonothèque femelle ; M, nématothèque latérales (A & C d'après Bouillon, 1987 ; B & D d'après Calder, 1991 ; E d'après Naumov, 1969 ; F & I d'après Schuchert, 1997 ; G-H, J-M d'après Millard, 1975).*

Genus ***SAABA*** Stechow, 1922

Doubtful genus, containing two poorly and insufficiently described species.

Saaba arenosa (Bale, 1919) [doubtful status]
Saaba scandens Trebilcock, 1928 [doubtful status]

Family HALOPTERIDIDAE Millard, 1962

Hydroid: colony with either erect hydrocauli, or with hydrocladia arising directly from hydrorhiza; hydrocaulus, when present, branched or unbranched, monosiphonic or polysiphonic, arising from a creeping or root-like hydrorhiza, giving rise to alternate or opposite, or irregularly arranged, branched or unbranched, hydrocladia; when arising from polysiphonic hydrocauli and branches, hydrocladia given off from either a single axial tube or from superficial tubes; hydrothecae on hydrocladia typically large, with cusped or even rim; cauline hydrothecae typically present, well developed, less frequently atrophied, lacking on polysiphonic hydrocladia and branches, when component tubes give rise to hydrocladia; nematophores with nematothecae, not as naked sarcostyles; nematothecae typically well developed, varied in structure, one- or two-chambered, movable or immovable, not fused to hydrothecae (except in the lateral nematothecae of *Antennellopsis* which are partly fused); a minimum of three, one median inferior and a pair of lateral, adjacent to each hydrotheca; cnidome: usually microbasic mastigophores of several size classes, sometimes isorhizas, microbasic euryteles and pseudostenoteles; gonophores as fixed sporosacs contained in a simple gonotheca, usually solitary, arising from caulus or hydrocladia, neither aggregated or protected by phylactocarps, frequently sexually dimorphic, with at least the female normally bearing nematothecae.

Recent references: Cornelius (1995), Migotto (1996); Calder (1997); Schuchert (1997); Peña Cantero, Carrascosa & Vervoort (1999); Watson (2000); Ansín Agís *et al.* (2001); Schuchert (2001a).

KEY TO HYDROIDS

1. lateral nematothecae fused to hydrothecae . . . . *Antennellopsis*
– lateral nematothecae not fused to hydrothecae, either movable or fused to its pedicel 2

2. unbranched erect stems arising directly from creeping hydrorhiza . . . . *Antennella*
– erect structures branched, either as cormoids, branched hydrocladia or polysiphonic stems 3

3. stem polysiphonic, tubes all of equal importance and all giving rise to hydrocladia or cormoids . . . . *Corhiza*
– stem mono- or polysiphonic, main axial tube bearing hydrocladia 4

4. hydrothecae with more than one marginal tooth . . . . *Gattya*
– hydrothecae with even rim or with one marginal tooth 5

5. hydrocladia branched basally, arising successively on ahydrothecate basal segment of previous hydrocladium . . . . *Monostaechas*
– hydrocladia unbranched or, if branched, second order branches arising from side of hydrothecae bearing part of other hydrocladium 6

6. hydrocladia with large "mamelons" (atrophied hydrothecae) 7
– hydrocladia without "mamelons" 8

7. with unbranched hydrocladia . . . . *Pseudoplumaria*
– with hydrocladia branched in a regular fashion . . . . *Polyplumaria*

8. cauline and cladial hydrothecae differ in morphology and two widely separated pairs of immovable lateral nematothecae present . . . . *Astrolabia*
– not both condition as stated above found together 9

9. stem normally monosiphonic, cormoids pinnate . . . . *Halopteris*
– stem polysiphonic and with one main axial tube bearing hydrocladia 10

10. anterior side of cladial hydrothecae with a long tapering, segmented branch with nematothecae . . . . *Calvinia*
– cladial hydrothecae without segmented branch bearing nematothecae 11

11. hydrothecae with two pairs of lateral nematothecae 12
– hydrothecae with one pair of lateral nematothecae 13

12. median inferior nematothecae absent, lateral nematothecae widely separated, nematothecae immovable and fused to pedicel . . . . *Pentatheca*
– median inferior nematothecae present, movable. . . . . *Diplopteroides*

13. lateral nematothecae movable, not fused to their pedicels, hydrocladia branched, part of adcauline hydrothecal wall free. . . . . *Schizotricha*
– lateral nematothecae immovable, fixed to their pedicels, hydrothecae completely adnate 14

14. hydrocladia unbranched, lateral nematothecae scale-shaped . . . . *Anarthroclada*
– hydrocladia branched, lateral nematothecae one-chambered, cup shaped. . . . . *Nuditheca*

Genus ***ANARTHROCLADA*** Naumov, 1955

Fig. 148E

Hydroid: colony polysiphonic, stem pinnate, main axial tube bearing hydrothecae; hydrocladia in two close opposite rows, unbranched, often unsegmented, devoid of inner septa; hydrotheca completely adnate; lateral paired nematothecae immovable, fused to pedicel, outer wall elongated, flattened, in form of a scutum; gonophores as fixed sporosacs, gonotheca with nematothecae.
Recent reference: Schuchert (1997).

Anarthroclada parmata Naumov, 1955

Genus ***ANTENNELLA*** Allman, 1877

Fig. 148F-M

Hydroid: hydrocladia arising directly, independently, from a creeping hydrorhiza, normally unbranched, not polysiphonic; hydrotheca cup- to vase-shaped, rim even unthooted; nematotheca two-chambered, movable; lateral nematothecae flanking each hydrotheca and borne on prominent peduncles adhering to hydrothecal wall; colony often monoecious, gonophores as fixed sporosacs, gonotheca solitary, sexually dimorphic, borne on hydrocladia with basal nematothecae.
Recent references: Hirohito (1995); Calder (1997); Schuchert (1997); Calder *et al.* (2003).

Antennella allmani Armstrong, 1879
Antennella ansini Cantero & Garcia Carrascosa, 2002
Antennella avalonia Torrey, 1902
Antennella biarmata Nutting, 1927
Antennella campanuliformis (Mulder & Trebilcock, 1909)
Antennella compacta Fraser, 1938c
Antennella curvitheca Fraser, 1937a
Antennella kiwiana Schuchert, 1997
Antennella microscopica (Mulder & Trebilcock, 1909)
Antennella quadriaurita Ritchie, 1909b
Antennella recta Nutting, 1927
Antennella secundaria (Gmelin, 1791)
Antennella sibogae Billard, 1911a
Antennella siliquosa (Hincks, 1877)
Antennella tubulosa (Bale, 1894)
Antennella varians (Billard, 1911a)

Genus *ANTENNELLOPSIS* Jäderholm, 1896

Fig. 149A-C

Hydroid: hydrocladia simple, unbranched, either arising directly from hydrorhiza or from a polysiphonic stem formed by stolon-like tubes; lateral nematothecae completely fused to hydrothecae, median inferior nematotheca free from hydrotheca.

Remarks: sometimes considered as congeneric with either *Antennella* or *Corhiza,* Schuchert (1997) kept it as a separate genus due to the arrangement of nematothecae.

Recent references: Rho & Chang (1972); Rho & Park (1986); Park (1992); Hirohito (1995); Schuchert (1997).

Antennellopsis integerrima Jäderholm, 1896 [syn. *A. dofleini* Stechow, 1907]

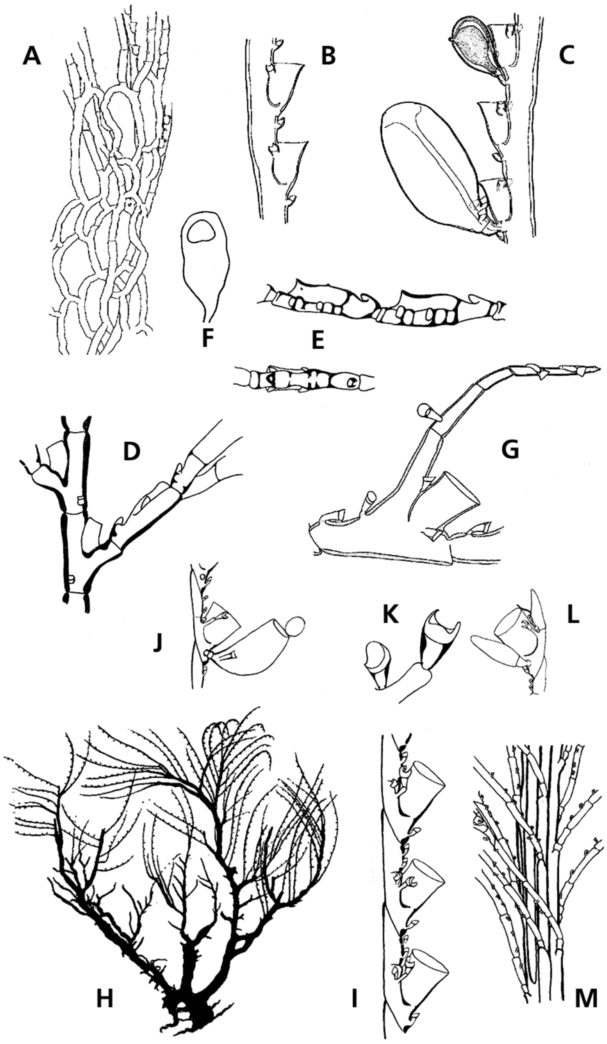


FIG. 149. Leptomedusae, Halopterididae. A-C, *Antennellopsis integerrima*: A, hydrorhiza; B, part of hydrocladium with hydrothecae; C, part of hydrocladium with a proximal female and a distal male gonotheca. D-F, *Astrolabia heterotheca*: D, two internodes of the stem; E, two segment of hydrocladium in various position; F, gonotheca. G, *Calvinia mirabilis*, hydrocladial segment with accessory structure. H-L, *Corhiza pannosa*: H, general view of a colony; I, portion of hydrocladium with hydrothecae and nematothecae; J, fragment of hydrocladium with female gonotheca; K, two lateral nematothecae in adcauline view; L, fragment of hydrocladium with male gonotheca. M, *Corhiza scotiae*, part of fascicled stem showing origin of hydrocladia (A-C after Hirohito, 1995; D-F after Naumov, 1969; G after Schuchert, 1997; H-M after Millard, 1975).

FIG. 149. *Leptomedusae, Halopterididae. A-C,* Antennellopsis integerrima *: A, hydrorhize ; B, partie d'un hydroclade montrant les hydrothèques ; C, partie d'un hydroclade avec une gonothèque femelle proximale et une gonothèque mâle distale. D-F,* Astrolabia heterotheca *: D, deux internodes de l'hydrocaule ; E, deux segments d'un hydroclade en différentes positions ; F, gonothèque. G,* Calvinia mirabilis*, segment hydrocladial avec structure accessoire. H-L,* Corhiza pannosa *: H, vue générale d'une colonie ; I, portion d'hydroclade avec hydrothèques et nématothèques ; J, fragment d'hydroclade avec une gonothèque femelle ; K, deux nématothèques latérales en vue adcaulinaire ; L, fragment d'hydroclade avec des gonothèques mâles. M,* Corhiza scotiae*, partie d'une branche polysiphonique montrant l'origine des hydroclades (A-C d'après Hirohito, 1995 ; D-F d'après Naumov, 1969 ; G d'après Schuchert, 1997 ; H-M d'après Millard, 1975).*

Genus *ASTROLABIA* Naumov, 1955

Fig. 149D-F

Synonym: *Tetranema* Fraser, 1937, not *Tetranema* Haeckel, 1879.
Hydroid: pinnate cormoids arising directly from hydrorhiza; hydrocaulus mono- or polysiphonic, if polysiphonic with main axial tube only bearing hydrothecae and hydrocladia; hydrocladia branched; hydrothecae deep, with smooth rim, completely adnate, cauline and cladial ones differing in morphology and size; hydrocladial ones with 2 pairs of lateral nematothecae, most proximal hydrotheca of hydrocladium can have one pair only; lateral nematothecae well separated, immovable, fused to pedicel; gonophores as fixed sporosacs, gonotheca solitary, pear-shaped, on hydrocladia.
Recent reference: Schuchert (1997).

Astrolabia furcata (Fraser, 1937b)
Astrolabia heterotheca Naumov, 1955

Genus *CALVINIA* Nutting, 1900

Fig. 149G

Hydroid: colony with erect, branched, polysiphonic stems; hydrocladia arising alternately from main axial tube on stem surface; main axial tube with cauline hydrothecae at base of each hydrocladium; hydrothecal rim smooth; a long, tapering segmented branch with nematothecae arising from anterior side of each cladial hydrotheca; gonophores as fixed sporosacs, gonothecae ovate, borne on the sides of proximal nematophorous branches, each with two basal nematothecae.
Recent reference: Schuchert (1997).

Calvinia mirabilis Nutting, 1900

Genus *CORHIZA* Millard, 1962

Fig. 149H-M

Hydroid: stem erect, polysiphonic, branched or unbranched, composed of intercommunicating tubes of equal diameter and importance, irregularly giving rise either to hydrocladia or to hydrocladia-bearing hydrocauli; these, if present, with cauline hydrothecae and pinnately arranged hydrocladia; hydrocladia unbranched, occasionally (as secondarily growth-form) arising independently from hydrorhiza; hydrotheca cup-shaped with smooth, though sometimes sinuous rim; nematothecae two-chambered and usually movable; gonophores as fixed sporosacs, gonothecae solitary; female ones with nematothecae; male and female gonothecae often on the same colony and sexually dimorphic.
Recent references: Schuchert (1997); Vervoort & Watson (2003).

Corhiza bellicosa Millard, 1962
Corhiza complexa (Nutting, 1905)
Corhiza fascicularis (Allman, 1883)
Corhiza pannosa Millard, 1962
Corhiza scotiae (Ritchie, 1907b)
Corhiza sociabilis Millard, 1980
Corhiza splendens Vervoort & Watson, 2003
Corhiza suensoni (Jäderholm, 1896)

Genus *DIPLOPTEROIDES* Peña Cantero & Vervoort 1999

Fig. 150A

Synonym: *Diplopteron* Nutting, 1900 (in part, not Allman, 1883).
Hydroid: colony with polysiphonic and unbranched stems; hydrocaulus with alternate, unbranched hydrocladia; one cauline hydrotheca at base of each hydrocladium; hydrocladia irregularly divided into internodes; nodes often absent; hydrocladia with regularly distributed hydrothecae and nematothecae; normally two pairs of nematothecae associated with

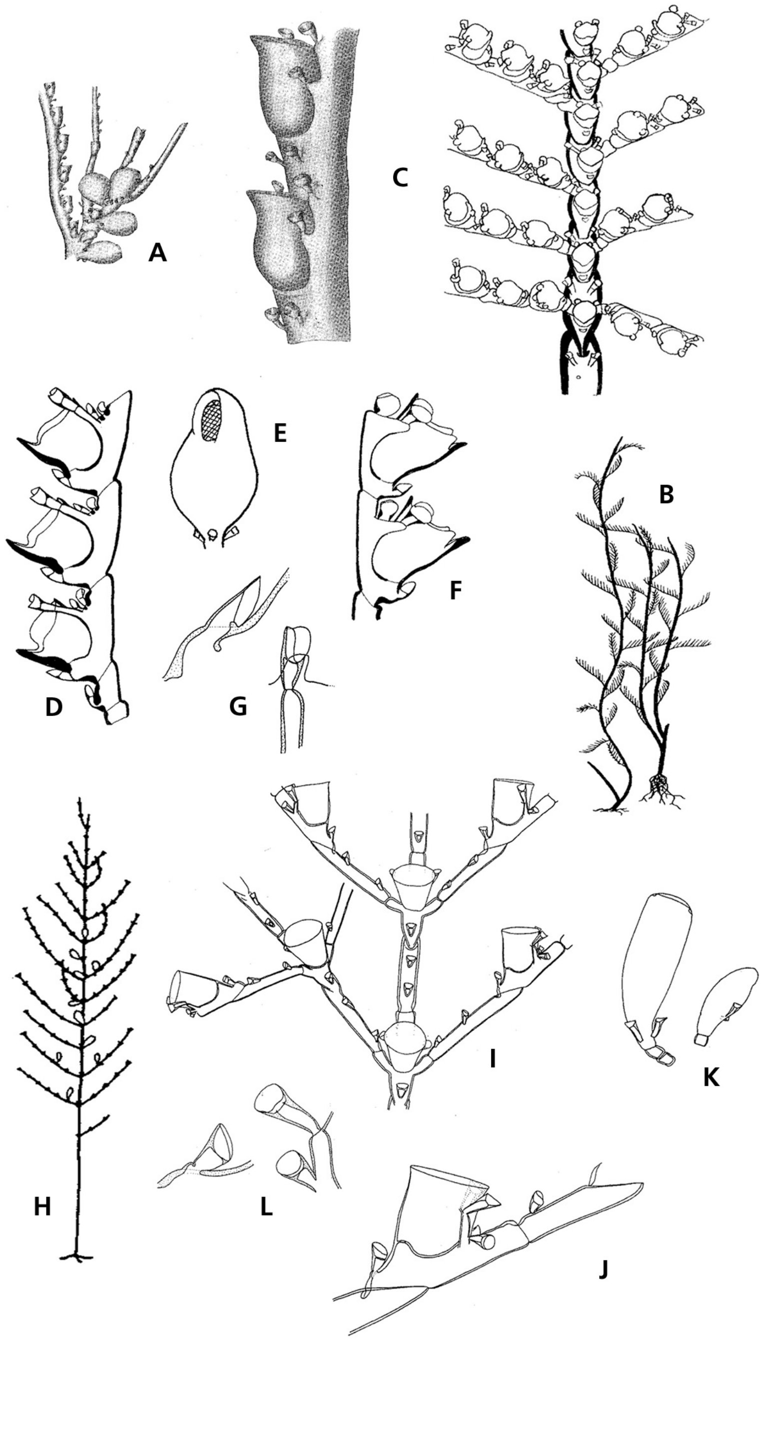


FIG. 150. Leptomedusae, Halopterididae. A, *Diploteroides grandis*, portion of hydrocladium with hydrothecae and nematothecae (right), hydrocladium, phylactocarps and gonothecae (left). B-G, *Gattya*: B, *Gattya heurteli*, general view of a colony; C-E, *Gattya conspecta*: C, part of stem in anterior view including first internode and hinge-joint; D, portion of hydrocadium; E, gonotheca; F, *Gattya humilis*, two hydrothecae; G, *Gattya aglaopheniaformis*, median inferior nematotheca (left), lateral nematotheca seen from inside hydrotheca (right). H-L, *Halopteris catharina*: H, normal plumose colony; I, part of caulus with opposite, branched hydrocladia; J, part of caulus with main segment and intersegment; K, gonothecae, female (left), male (right); L, median inferior nematotheca (left), pair of lateral nematothecae (right) (A after Nutting, 1900; B-F after Millard, 1975; G-L after Schuchert, 1997).

FIG. 150. *Leptomedusae, Halopterididae. A,* Diploteroides grandis, *portion d'un hydroclade avec hydrothèques et nématothèques (à droite), fragment d'un hydroclade avec phylactocarpes et gonothèques (à gauche). B-G,* Gattya : *B,* Gattya heurteli, *vue générale d'une colonie ; C-E,* Gattya conspecta *: C, vue d'avant d'un hydrocaule comprenant le premier internode et le joint d'articulation ; D, portion d'hydroclade ; E, gonothèque ; F,* Gattya humilis, *deux hydrothèques ; G,* Gattya aglaopheniaformis, *nématothèque médiane inférieure (à gauche), nématothèque latérale vue de l'intérieur de l'hydrothèque (à droite). H-L,* Halopteris catharina *: H, colonie plumeuse normale ; I, partie de l'hydrocaule avec des hydroclades opposés et branchus ; J, partie d'un hydroclade montant le segment principal et l'intersegment ; K, gonothèques, femelle (à gauche), mâle (à droite) ; L, nématothèque médiane inférieure (à gauche), paire de nématothèques latérales (à droite) (A d'après Nutting, 1900 ; B-F d'après Millard, 1975 ; G-L d'après Schuchert, 1997).*

each hydrotheca: one pair situated halfway along hydrothecal length and another pair flanking hydrothecal aperture; extra nematothecae occurring between hydrothecae; nematothecae two-chambered and movable; hydrothecae cup-shaped and completely adnate; gonophores as fixed sporosacs, gonothecae borne in clusters on accessory ramuli springing from hydrocladia and with numerous nematothecae and occasional hydrothecae.
Recent reference: Schuchert (1997).

Diplopteroides longipinna (Nutting, 1900)
Diplopteroides grandis (Nutting, 1900)
Diplopteroides quadricorne (Nutting, 1900)

Genus *GATTYA* Allman, 1886
Fig. 150B-G

Hydroid: cormoids simple, pinnate, arising either directly from hydrorhiza or from main axial tube of an erect, polysiphonic stem of stolon-like tubes; hydrocauli in monosiphonic colonies with hydrothecae; main axial tube in polysiphonic stems without hydrothecae or nematothecae; hydrocladia normally unbranched; hydrothecae cup-shaped, margin with more than one cusp; nematothecae two-chambered, movable or immovable; gonophores as fixed sporosacs, gonothecae of both sexes on same colony.
Recent references: Schuchert (1997); Gravier-Bonnet (1998).

Gattya aglaopheniaformis (Mulder & Trebilcock, 1909)
Gattya balei (Bartlett, 1907)
Gattya conspecta (Billard, 1907a)
Gattya heurteli (Billard, 1907b)
Gattya humilis Allman, 1886
Gattya multithecata (Jarvis, 1922)
Gattya trebilcocki Watson, 1973
Gattya tropicalis Millard & Bouillon, 1973
Gattya wimleni Gravier-Bonnet, 1998

Genus *HALOPTERIS* Allman, 1877
Figs 9I, R, 150H-L

Hydroid: colony typically erect, unbranched or branched, forming pinnate cormoids arising from a creeping hydrorhiza, often with a hinge-joint near base; hydrocaulus usually monosiphonic, rarely polysiphonic, bearing hydrothecae and pinnately arranged hydrocladia; in polysiphonic stems, all tubes can give rise to cormidia; hydrocladia almost always unbranched, alternate or in opposite pairs, or opposite basally and alternate distally, in one plane, sometimes (as secondary growth-form) arising independently from hydrorhiza; hydrothecae cup-shaped, on hydrocaulus and hydrocladia, margin entire or with one median abcauline cusp; nematothecae polymorphic, movable or immovable ones on a given colony, one- or two-chambered, lateral nematothecae typically borne on prominent peduncles adhering to hydrothecal wall; gonophores as fixed sporosacs, gonothecae arising from hydrocaulus or hydrocladia, solitary, with or without nematothecae.
Recent references: Hirohito (1995); Calder (1997); Schuchert (1997); Schuchert (2001a); Calder *et al.* (2003); Vervoort & Watson (2003).

Halopteris alternata (Nutting, 1900)
Halopteris billardi (Vannucci, 1951)
Halopteris buskii (Bale, 1884)
Halopteris campanula (Busk, 1852)
Halopteris carinata Allman, 1877
Halopteris catharina (Johnston, 1833)
Halopteris concava (Billard, 1911a)
Halopteris crassa (Billard, 1911a)
Halopteris diaphana (Heller, 1868)
Halopteris diaphragmata (Billard, 1911a)
Halopteris everta (Mulder & Trebilcock, 1909)
Halopteris gemellipara Millard, 1962
Halopteris geminata (Allman, 1877)
Halopteris glutinosa (Lamouroux, 1816)
Halopteris gracilis (Clarke, 1879)
Halopteris infundibulum Vervoort, 1966
Halopteris jedani (Billard, 1913)
Halopteris liechtensternii (Marktanner-Turneretscher, 1890)
Halopteris minuta (Trebilcock, 1928)
Halopteris opposita (Mulder & Trebilcock, 1911)

Halopteris peculiaris (Billard, 1913)
Halopteris plagiocampa (Pictet, 1893)
Halopteris platygonotheca Schuchert, 1997
Halopteris polymorpha (Billard, 1913)
Halopteris prominens Vervoort & Watson, 2003
Halopteris pseudoconstricta Millard, 1975
Halopteris regressa (Billard, 1918)
Halopteris rostrata Millard, 1975
Halopteris simplex (Warren, 1914)
Halopteris sulcata (Lamarck, 1816)
Halopteris tenella (Verrill, 1874)
Halopteris tuba (Kirchenpauer, 1876)
Halopteris valdiviae (Stechow, 1923b)
Halopteris violae Calder, Mallinson, Collins & Hickman, 2003
Halopteris zygocladia (Bale, 1914b)

Genus ***MONOSTAECHAS*** Allman, 1877

Fig. 151A-F

Hydroid: colony with or without erect stems; if present and polysiphonic, stem composed of intercommunicating tubes of equal diameter and importance, irregularly giving rise to hydrocladia; if stem absent, hydrocladia arising directly from hydrorhiza; hydrocladia branched in one plane or forming a sympodium, each successive hydrocladium originating from the posterior surface of the ahydrothecate segment of the previous hydrocladium, typically all branches directed towards same side or, rarely alternating, or helicoidal; hydrotheca cup-shaped, margin without cusps; nematothecae two-chambered, when known, movable; gonophores as fixed sporosacs, gonothecae of two sexes often present in the same colony.
Recent reference: Schuchert (1997).

Monostaechas faurei Millard, 1958
Monostaechas fisheri Nutting, 1905
Monostaechas natalensis Millard, 1958
Monostaechas quadridens (McCrady, 1859a)
Monostaechas sibogae Billard, 1913

Genus ***NUDITHECA*** Nutting, 1900

Fig. 151G-J

Hydroid: colony with branched, polysiphonic stems; hydrocladia arising from main axial tube with hydrothecae, branched, sometimes with heteromerous segmentation; hydrothecae without cusps, completely adnate; median inferior nematotheca movable, not fused to hydrotheca, lateral nematotheca immovable, fused to pedicel; gonophores as fixed sporosacs, gonothecae solitary, with 2 or 3 nematothecae.
Recent reference: Schuchert (1997).

Nuditheca dallii (Clark, 1876b)
Nuditheca dogieli Naumov, 1952
Nuditheca tetrandra Naumov, 1960

Genus ***PENTATHECA*** Naumov, 1955

Fig. 151K-L

Hydroid: colony with polysiphonic, pinnate stem; main axial tube bearing hydrothecae; stem occasionally branched; hydrocladia unbranched, giving off from two sides of the stem; hydrocladia homomerously segmented, each segment with a completely adnate hydrotheca and 2 widely separated pairs of lateral nematothecae, median nematothecae absent; hydrothecae with smooth rim; all nematothecae immovable, fused to pedicel; gonophores as fixed sporosacs, gonothecae solitary, with 2 nematothecae.
Recent reference: Schuchert (1997).

Pentatheca angulifera Naumov, 1955

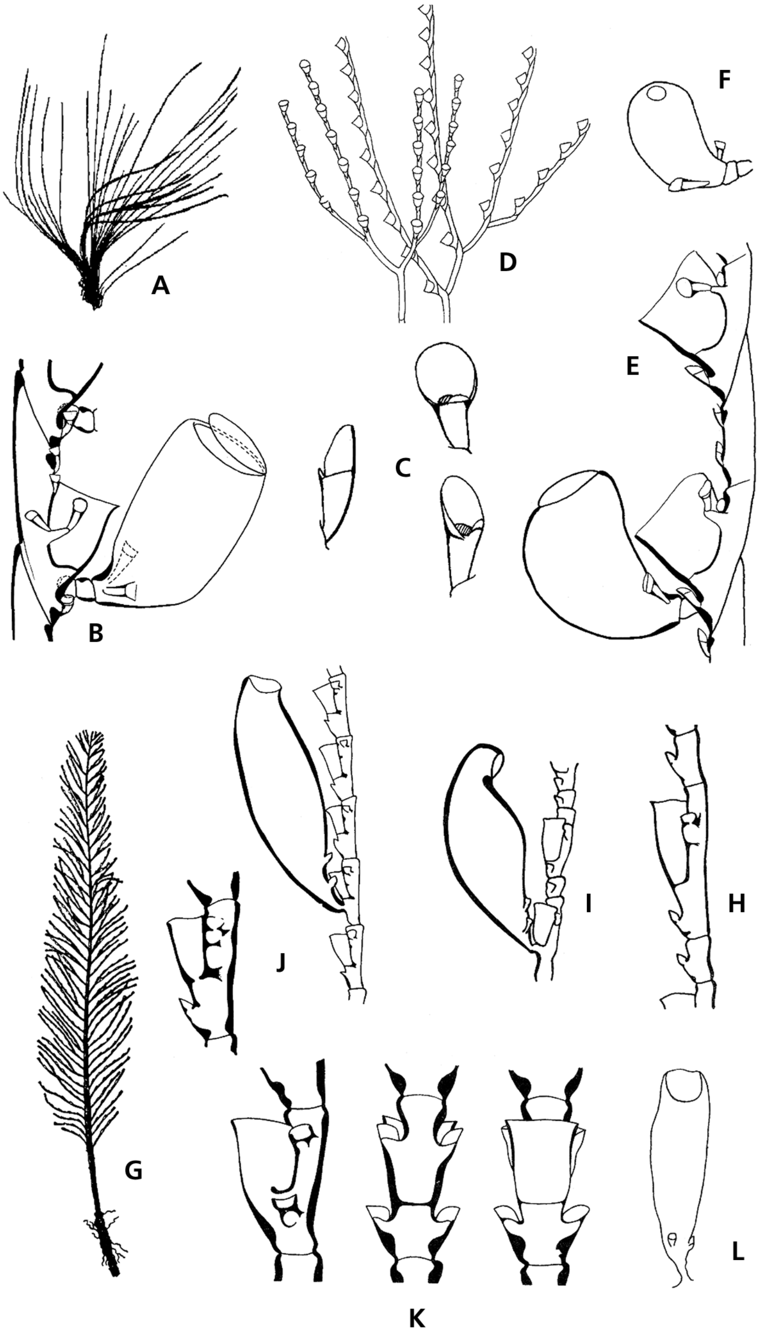


FIG. 151. Leptomedusae, Halopterididae. A-C, *Monostaechas natalensis*: A, general view of a colony; B, part of hydrocladium with female gonotheca; C, lateral nematothecae. D-F, *Monostaechas quadridens*: D, two stems, the one on left branching first dichotomously and then in a helicoid manner, the one on the right branching as a helicoid sympodium only; E, fragment of hydrocladium with hydrothecae, nematothecae and a female gonotheca; F, male gonotheca. G-I, *Nuditheca tetrandra*: G, general view of a colony; H, portion of a hydrocladium; I, part of hydrocladium with gonotheca. J, *Nuditheca dogieli*, segment of hydrocladium (left), hydrocladium with gonotheca (right). K-L, *Pentatheca angulifera*: K, segment of hydrocladium in various positions; L, gonotheca (A-F after Millard, 1975; G-L after Naumov, 1969).

FIG. 151. *Leptomedusae, Halopterididae. A-C,* Monostaechas natalensis : *vue générale d'une colonie ; B, partie d'hydroclade montrant une gonothèque femelle ; C, nématothèques latérales. D-F,* Monostaechas quadridens *: D, deux hydrocaules, celui de gauche se ramifiant d'abord de façon dichotome puis de façon helicoïdale, celui de droite se ramifiant seulement comme une colonie sympodiale helicoidale ; E, fragment d'hydroclade avec hydrothèques, nématothèques et une gonothèque femelle ; F, gonothèque mâle. G-I,* Nuditheca tetrandra : *G, vue générale d'une colonie ; H, portion d'hydroclade ; I, partie d'un hydroclade avec une gonothèque. J,* Nuditheca dogieli*, segment d'hydroclade (à gauche), hydroclade avec gonothèque (à droite). K-L,* Pentatheca angulifera : *K, segments d'hydroclades vues en différentes positions ; L, gonothèque (A-F d'après Millard, 1975 ; G-L d'après Naumov, 1969).*

Genus *POLYPLUMARIA* Sars, 1874

Fig. 152A-D

Hydroid: colony with erect, strongly ramified, pinnate stems, rigid in appearance, typically polysiphonic; branches of hydrocaulus opposite or nearly so; hydrocladia branched, regularly arranged, placed on an apophysis with a much developed, large "mamelon" (considered as an atrophied hydrotheca) on its superior surface; hydrothecal rim smooth; gonophores as fixed sporosacs, gonothecae with or without nematothecae.

Remarks: sometimes included in the Plumulariidae.

Recent references: Calder (1997); Schuchert (1997); Schuchert (2001a).

Polyplumaria arenaria Antsulevich, 1997
Polyplumaria cornuta (Bale, 1884)
Polyplumaria flabellata G.O. Sars, 1874
Polyplumaria gracilis (Naumov, 1960)
Polyplumaria gracillima (Sars, 1873)
Polyplumaria kossowskae (Billard, 1911a)
Polyplumaria sibogae Billard, 1913
Schizotricha pacificola Naumov, 1960 and *S. parvula* Nutting, 1900 are probably species of *Polyplumaria*

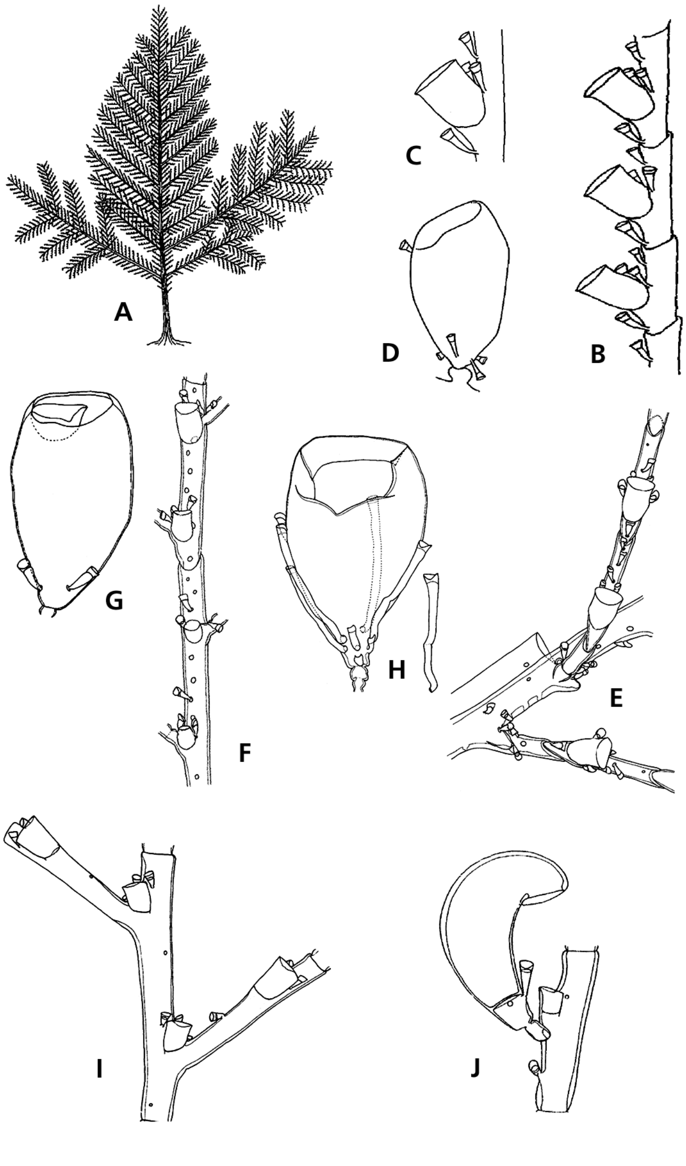


FIG. 152. Leptomedusae, Halopterididae. A-D, *Polyplumaria flabellata*: A, general view of a colony; B, detail of a hydrocladium; C, a hydrotheca and associated nematothecae; D, gonotheca. E-G, *Pseudoplumaria sabinae*: E, part of primary axis with a single secondary tube and insertion of two hydrocladia; F, part of a branch in frontal view showing transition of ''mamelon'' at axial apophysis to axial hydrotheca; G, gonotheca. H, *Pseudoplumaria marocana*, male gonotheca with nematothecae and an isolated gonothecal nemathoteca. I, *Schizotricha frutescens*, cauline internode with two cauline hydrothecae and the base of two hydrocladium. J, *Schizotricha falcata*, gonotheca (A-D after Cornelius, 1995; E-H after Ramil & Vervoort, 1992b; I after Peña Cantero & Vervoort, 1999; J after Peña Cantero, 1998: p. 78, fig. 1 i).

***FIG. 152.** Leptomedusae, Halopterididae. A-D,* Polyplumaria flabellata *: A, vue générale d'une colonie ; B, détail d'un hydroclade ; C, une hydrothèque et nématothèques associées ; D, gonothèque. E-G,* Pseudoplumaria sabinae *: E, partie d'un axe primaire avec un simple tube secondaire et l'insertion de deux hydroclades ; F, partie d'une branche en vue frontale montrant la transition d'un ''mamelon'' de l'apophyse axiale en une hydrothèque axiale ; G, gonothèque. H,* Pseudoplumaria marocana*, gonothèque mâle et ses nématothèques et une nématothèque isolée. I,* Schizotricha frutescens*, internode caulinaire avec hydrothèques caulinaires et la base de deux hydroclades. J,* Schizotricha falcata*, gonothèque (A-D d'après Cornelius, 1995 ; E-H d'après Ramil & Vervoort, 1992b ; I d'après Peña Cantero & Vervoort, 1999 ; J d'après Peña Cantero, 1998 : p. 78, fig. 1 i).*

Genus ***PSEUDOPLUMARIA*** Ramil & Vervoort, 1992

Fig. 152E-H

Hydroid: colony composed of rigid, strongly ramified, polysiphonic, occasionally forked hydrocaulus, with alternate or opposite branches; hydrocladia always unbranched, alternately arranged along axis, placed on an apophysis with a much developed, large "mamelon" (considered as an atrophied hydrotheca) on its superior surface; hydrotheca exclusively found on the hydrocladia, hydrothecal border smooth; mobile, immobile and reduced nematothecae two-chambered (bithalamic) present. Gonophores as fixed sporosacs, gonothecae single with a few nematothecae on basal region.
Remarks: sometimes included in the Plumulariidae.
Recent references: Calder (1997); Schuchert (1997).

Pseudoplumaria marocana (Billard, 1930a)
Pseudoplumaria sabinae Ramil & Vervoort, 1992b

Genus ***SCHIZOTRICHA*** Allman, 1883

Figs 152I-J, 153A-E

Hydroid: colony with polysiphonic, erect stem, which may be branched or unbranched, with one main axial tube bearing pinnately arranged hydrocladia and hydrothecae, and several undivided accessory tubes provided only with nematothecae; hydrocladia alternate, the majority branched sympodially from anterior or lateral surface immediately below hydrothecae; hydrotheca cup-shaped, with smooth rim; nematotheca 2-chambered and movable, lateral nematothecae not fused to their pedicel or to hydrothecae; gonophores as fixed sporosacs, gonothecae inserted on hydrocladia between hydrothecae and provided with nematothecae.
Recent references: Peña Cantero *et al.* (1996); Schuchert (1997); Peña Cantero & Vervoort (1999); Schuchert (2001a).

Schizotricha anderssoni Jäderholm, 1904a
Schizotricha dichotoma Nutting, 1900
Schizotricha falcata Peña-Cantero, 1998
Schizotricha frutescens (Ellis & Solander, 1786)
Schizotricha glacialis (Hickson & Gravely, 1907)
Schizotricha jaederholmi Peña-Cantero & Vervoort, 1996a
Schizotricha multifurcata Allman, 1883
Schizotricha nana Peña-Cantero, Svoboda & Vervoort, 1996
Schizotricha pacificola Naumov, 1960 [probably a species of *Polyplumaria*]
Schizotricha parvula Nutting, 1900 [probably a species of *Polyplumaria*]
Schizotricha philippina Hargitt, 1924
Schizotricha polaris Naumov, 1960
Schizotricha profunda (Nutting, 1900)
Schizotricha turqueti Billard, 1906
Schizotricha unifurcata Allman, 1883
Schizotricha variabilis (Bonnevie, 1899)
Schizotricha vervoorti Peña-Cantero, 1998

Family HEBELLIDAE Fraser, 1912

Hydroid: colony stolonal, hydrotheca campanulate with smooth margin, short or long distinct pedicel; hydrothecal base with annular perisarcal thickening and membranous diaphragm or thick diaphragm and no annular thickening; gonotheca solitary, with or without operculum, arising from hydrorhiza; exceptionally with nematothecae (*Bedotella*); gonophores as fixed sporosacs, or swimming gonophore, or eumedusoids, or free medusae.
Medusa: umbrella flat; manubrium short and flat, mouth with irregular lips; with marginal cordyli; with 4 or more branched radial canals; marginal tentacles hollow; "gonads" linear to sinuous on the radial canals; with or without marginal cirri; with or without adaxial ocelli; without statocysts.
Remarks: this family is usually included in the Lafœidae, but has often been separated as a subfamily by several authors (see Calder 1991; Boero *et al.* 1997 for a review). The family Hebellidae was established by Fraser (1912) to accomodate the following genera (see Calder 1991): *Bedotella*; *Halisiphonia*; *Hebella*; *Hebellopsis* and *Scandia*, whose

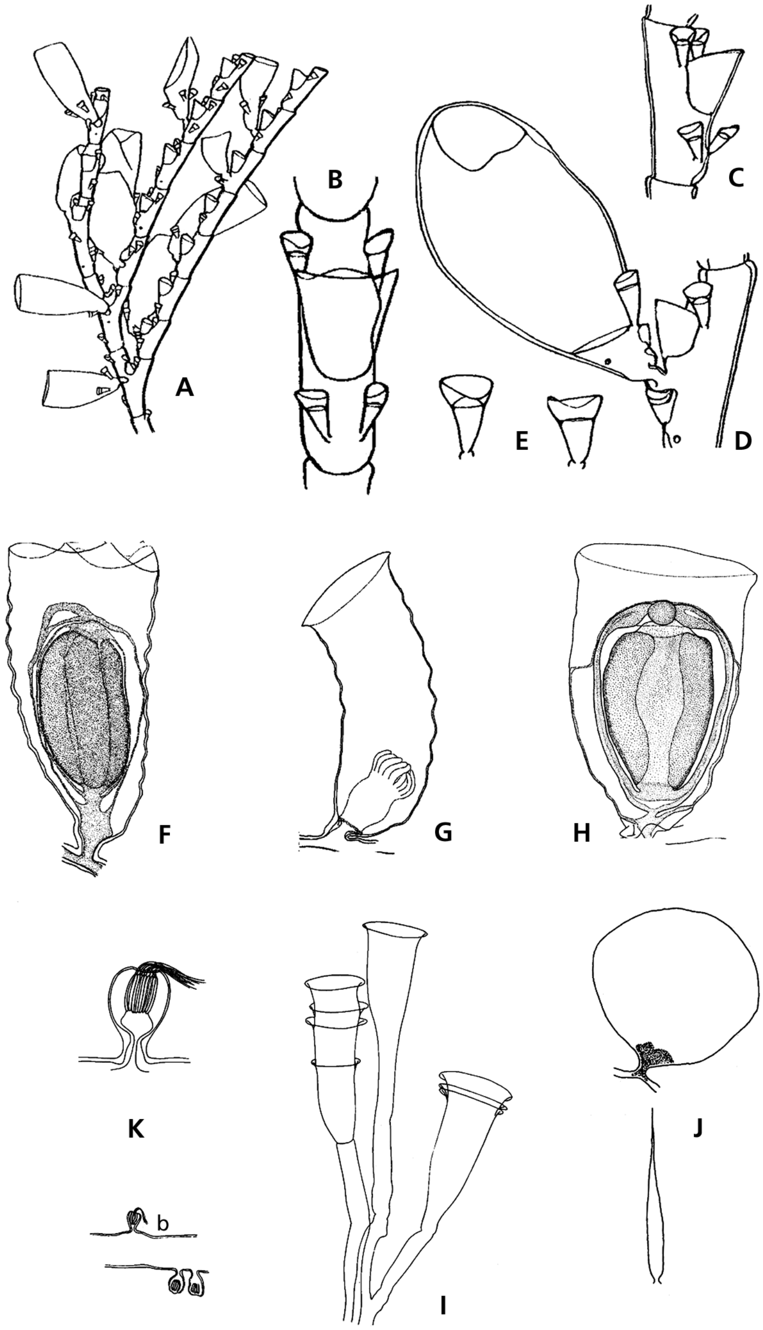


FIG. 153. Leptomedusae. A-E, Halopterididae (concluded), *Schizotricha vervoorti*: A, hydrocladia branching disposition; B-C, two hydrocladial internodes with hydrothecae and nematothecae; D, female gonotheca; E, nematothecae. F-G, Hebellidae, *Anthohebella tubitheca*: F, gonotheca containing one swimmimg sporosac; G, hydrotheca. H, *Anthohebella brevitheca*, gonotheca containing one swimmimg sporosac. I-K, *Bedotella armata*: I, part of rhizocaulomic colony with two renovated hydrothecae; J, gonotheca in frontal and lateral view; K, stolonal nematothecae (A-E after Peña Cantero, 1998: p. 80, figs 2 a, c, d, f, g, h; F-H after Boero *et al*., 1997; I & K after Ramil & Vervoort, 1992b; J after Álvarez Claudio, 1993).

***FIG. 153.** Leptomedusae. A-E, Halopterididae (fin),* Schizotricha vervoorti : *A, disposition des branches hydrocladiales; B-C, deux internodes hydrocladiaux avec hydrothèques et nématothèques ; D, gonothèque femelle ; E, nématothèque. F-G, Hebellidae,* Anthohebella tubitheca : *F, gonothèque contenant un ''sporosac libre nageur'' ; G, hydrothèque. H,* Anthohebella brevitheca, *gonothèque contenant un ''sporosac libre nageur''. I-K,* Bedotella armata : *I, partie d'une colonie rhizocaulomique montrant trois hydrothèques dont deux rénovées ; J, gonothèques en vue frontale et latérale ; L, nématothèques stolonaires (A-E d'après Peña Cantero, 1998 : p. 80, figs 2 a, c, d, f, g, h ; F-H d'après Boero* et al., *1997 ; I & K d'après Ramil & Vervoort, 1992a ; J d'après Álvarez Claudio, 1993).*

hydroids typically have stolonal colonies, campanulate hydrothecae with a diaphragm or an annular thickening or both, and single gonothecae. As stated by Calder (1991), in the Lafœidae, *Filellum* is stolonal, a diaphragm is present in *Abietinella*, *Cryptolaria* and *Zygophylax*, and single gonothecae are found in some species of *Cryptolarella*. We recognise what Calder (1991) considered as a subfamily of the Lafœidae, the Hebellinae, as a separate family: the Hebellidae. In fact, although certain of the hebellid characters are shared with the some lafœid genera, none of them have all those characters together; *Filellum* is stolonal but has no diaphragm and has aggregated gonothecae; some *Cryptollarella* have a single gonotheca, but they have no diaphragm and are erect; *Abietinella*, *Cryptolaria* and *Zygophylax* have a diaphragm but have erect colonies and coppinia.

Hebellid medusae, till recent years, were only known by juvenile indeterminable stages. De Andrade and Migotto (1997) reared immature medusae from a *Hebella* species, showing relationship with the Laodiceidae, perhaps with the medusa-based genus *Staurodiscus*, and Migotto & De Andrade (2000) elucidated the life cycle of *Hebella furax* that should be referred to genus *Toxorchis,* possibly to *T. kellnery*? (*Toxorchis* is here considered as congeneric with *Staurodiscus,* see below). The Laodiceidae contain two distinct groups of medusa genera, those with unbranched radial canals from which several life cycle are known, the hydroids being all "*Cuspidella*-like", and two genera with branched radial canals, whose life cycle was unknown till the observations of the authors cited above, and having *Hebella* hydroids. Those two particular genera are here included in the family Hebellidae. The Leptomedusae thus contain four families with cordyli or cordyli-like structure the Hebellidae, the Laodiceidae, the Teclaiidae and the Tiarannidae.

Recent references: Calder (1991); Migotto (1996); De Andrade & Migotto (1997); Boero *et al.* (1997); Migotto & De Andrade (2000); Watson (2000); Schuchert (2001a).

KEY TO HYDROIDS AND MEDUSAE

1. gonophores producing fixed sporosacs 2
– gonophores not producing fixed sporosacs; hydrothecae sharply separated from pedicel 4

2. colony with nematophores and nematothecae . . . . *Bedotella*
– colony without nematophores. 3

3. hydrotheca sharply separated from pedicel . . . . *Scandia*
– hydrotheca not sharply demarcated from pedicel . . . . *Halisiphonia*

4. gonophores swimming . . . . *Anthohebella*
– gonophores not as above 5

5. with eumedusoids or immature medusae . . . . *Hebella*
– with free mature medusae; some or all of the radial canals branched, branches joining or not ring canal . . . . *Staurodiscus*

Genus ***ANTHOHEBELLA*** Boero, Bouillon & Kubota, 1997

Fig. 153F-H

Hydroid: colony stolonal; hydrotheca on short pedicel, campanulate, usually with thin annular thickening and thin membranous diaphragm; gonophores swimming, with velum, 4 radial canals, 4 atentaculate marginal bulbs; "gonads" on spadix (manubrium); gonotheca solitary originating from hydrorhiza.

Remarks: Watson (2000) described a new species of *Anthohebella*, *A. darwinensis*, but the gonophores of this species are devoid of manubrium and no reference is made in the description to the position of the gonads, although the gonophore is considered as nearly mature. This species is here referred provisionally to *Anthohebella.*

Anthohebella brevitheca (Leloup, 1938b)
Anthohebella darwinensis Watson, 2000
Anthohebella najimaensis (Hirohito, 1995)
Anthohebella parasitica (Ciamician, 1880)
Anthohebella tubitheca (Millard & Bouillon, 1975)

Genus *BEDOTELLA* Stechow, 1913

Fig. 153I-K

Hydroid: colony stolonal or erect, branched, polysiphonic; hydrothecae campanulate, borne irregularly on all surface of branches and sometimes on hydrorhiza, free, non adherent, distinctly pedicellate, with thin diaphragm; margin even and slightly everted; nematophore in shortly globular pedunculate nematotheca on hydrocaulus and hydrocladia; gonophores as fixed sporosacs, gonothecae solitary, strongly compressed, disc-shaped, not aggregated.
Recent references: Ramil & Vervoort (1992b); Alvarez Claudio (1993).

Bedotella armata (Pictet & Bedot, 1900)

Genus *HALISIPHONIA* Allman, 1888

Fig. 154A

Hydroid: colony typically stolonal, anastomosing; hydrotheca long, funnel-shaped, pedicellate, gradually passing into pedicel usually as long or longer than hydrotheca, springing directly from hydrorhiza; a ring of slightly thickened perisarc at the margin of hydrotheca and pedicel; hydrotheca often regenerated; diaphragm as a very delicate membrane; gonophores described as fixed sporosacs, in *Halisiphonia artica* seems to produce a medusa, gonothecae solitary, strongly compressed, fan shaped, strongly resembling egg capsules of Gastropoda, attached to hydrorhiza by means of a very short pedicel.
Remarks: This genus was referred to the subfamily Hebellinae by Rees & Vervoort (1987).
Recent references: Rees & Vervoort (1987); Blanco *et al.* (1994); Schuchert (2001a).

Halisiphonia arctica Kramp, 1932a
Halisiphonia megalotheca Allman, 1888
Halisiphonia nana Stechow, 1921a
Halisiphonia spongicola Haeckel, 1889

Genus *HEBELLA* Allman, 1888

Fig. 154B-D

Synonym: *Hebellopsis* Hadzi, 1913.
Hydroid: colony stolonal; hydrotheca on short pedicel, campanulate to cylindrical, usually with annular thickening and membranous or perisarc-like diaphragm; gonophores either as liberable eumedusoids with mature "gonads" on radial canals, or as medusa already mature at liberation with 4 radial canals, each with a proximal gonad; 4 perradial atentaculate bulbs and 4 small interradial atentaculate bulbs; manubrium short; mouth and gastric cavity present; during life span some tentacles and more marginal bulbs may grow, or as juvenile immature free medusa.
Medusa: adult medusa unknown.
Remarks: The genus *Hebella* will probably have to be split in the future when more life cycles will be completely described, several hebelliform hydroids giving apparently rise to different medusa morphotypes. See also remarks under *Scandia*.
Recent references: Blanco *et al.* (1994); Altuna Prados (1996); Boero *et al.* (1997).

Hebella brochii (Hadzi, 1913)
Hebella contorta Marktanner-Turneretscher, 1890
Hebella crateroides Ritchie, 1909a
Hebella dispolians (Warren, 1909)
Hebella dyssymetra Billard, 1933
Hebella furax Millard, 1957 [probably a syn. of *Staurodiscus kellneri*]
Hebella laterocaudata Billard, 1942a
Hebella muscensis Millard & Bouillon, 1975
Hebella plana Ritchie, 1907b
Hebella scandens (Bale, 1888)

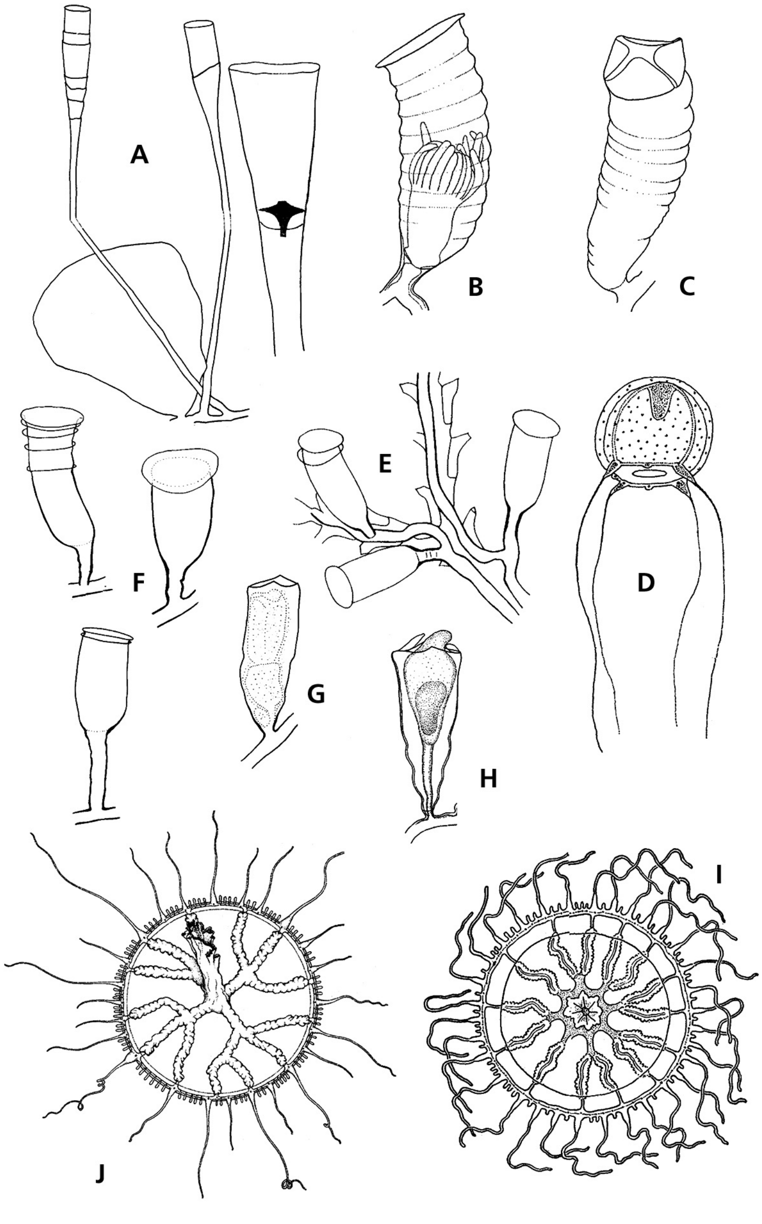


FIG. 154. Leptomedusae, Hebellidae. A, *Halisiphonia galatheae*, fragment of colony with two hydrothecae and gonotheca (left), hydrotheca with remnant of hydranth (right). B-D, *Hebella muscencis*: B, hydrotheca; C, gonotheca; D, newly released medusa. E, *Scandia mutabilis*, part of a colony on the hydrocaulus of *Dynamena crisioides*. F-I, *Staurodiscus kellneri*: F-H, hydroid: F, lateral view of hydrothecae showing variation of form, length and perisarc development, G-H, gonotheca; I, adult medusa. J, *Staurodiscus nigricans*, adult medusa (A after Vervoort, 1966; B-D, H after Boero *et al*., 1997; E after Migotto, 1996; F-G after Migotto & de Andrade, 2000; I after Kramp, 1959b; J after Bouillon, 1984b).

FIG. 154. *Leptomedusae, Hebellidae. A,* Halisiphonia galatheae*, fragment d'une colonie avec deux hydrothèques et une gonothèque (à gauche), hydrothèque avec le reste d'un hydranthe (à droite). B-D,* Hebella muscencis *: B, hydrothèque ; C, gonothèque ; D, méduse venant de se libérer. E,* Scandia mutabilis*, partie d'une colonie croissant sur l'hydrocaule d'une* Dynamena crisioides*. F-I,* Staurodiscus kellneri *: F-H, hydroïde : F, vue latérale de diverses hydrothèques montrant les variations de forme, de longueur et du développement du périsarc ; G-H, gonothèques ; I, méduse adulte. J,* Staurodiscus nigricans*, méduse adulte (A d'après Vervoort, 1966 ; B-D, H d'après Boero* et al.*, 1997 ; E d'après Migotto, 1996 ; F-G d'après Migotto & de Andrade, 2000 ; I d'après Kramp, 1959b ; J d'après Bouillon, 1984b).*

Genus *SCANDIA* Fraser, 1912

Fig. 154E

Synonym: *Croatella* Hadzi, 1916.
Hydroid: colony stolonal, sometimes sympodial, arising from a creeping hydrorhiza; hydrotheca large, campanulate, usually borne on long pedicels, with a basal rounded annular perisarcal thickening; gonophores fixed sporosacs, gonotheca solitary.
Remarks: *Scandia* differs from *Anthohebella* and *Hebella* in not being associated to supporting hydroids and in gonothecal content. It could be synonymized with *Hebella*.
Recent reference: Calder *et al.* (2003).

Scandia corrugata Fraser, 1938a
Scandia gigas (Pieper, 1884)
Scandia michaelsarsi (Leloup, 1935)
Scandia minor (Fraser, 1938a)
Scandia mutabilis (Ritchie, 1907a)
Scandia neglecta (Stechow, 1913b)

Genus *STAURODISCUS* Haeckel 1879

Fig. 154F-J

Synonym: *Toxorchis* Haeckel, 1879.
Hydroids: colony epizootic, *Hebella*-like; hydrothecae almost conical when growing on upper part of the host, cylindrical when growing on lower part of same host; asymmetrical to symmetrical; with everted margin, sharply or slightly oblique, with short to long, wrinkled or annulated pedicels; with membranous diaphragm (sometimes absent) and annular thickening; gonophores as free medusae; gonotheca as big or slightly bigger than hydrotheca, with four opercular flaps, on short pedicel, slightly undulated walls, truncated distally, tapering at base, containing up to three medusae.
Medusa: with 4 or more main primary radial canals, some or all branching one or more times, primary canal and some or all of the branches reaching circular canal; "gonads" on primary radial canals and branches; numerous tentacles and cordyli; with or without cirri; with or without ocelli.
Remarks: the life cycle *Hebella furax* Millard, 1957 has been elucidated by Migotto & De Andrade (2000); the hydroid giving rise to a *Staurodiscus* (*Toxorchis* type of medusa), presumably *Staurodiscus kellneri* Mayer, 1910. The differences between *Staurodiscus* and *Toxorchis* are ambiguous and tenuous, the main character being the supposed mode of ramification of the radial canals. In *Staurodiscus*, ramifications are described as branches formed after the development of the primary canal which first reach the circular canal, whereas in *Toxorchis* ramifications were believed to be bifurcation of the primary canal which himself never reached the circular canal (see Kramp 1962; Bouillon 1984a). Migotto & De Andrade (2000), studying the cycle of a *Toxorchis* medusa (obtained from *Hebella furax*), described a development of the radial canals and of their branches similar to that observed in *Staurodiscus*. There are presently no convincing reasons to separate the two genera.
Recent references: Boero *et al.* (1997); De Andrade & Migotto (1997); Migotto & De Andrade (2000).

Staurodiscus arcuatus Haeckel, 1879
Staurodiscus brooksi (Mayer, 1910)
Staurodiscus gotoi (Uchida, 1927b)
Staurodiscus heterosceles Haeckel, 1879 [doubtful status]
Staurodiscus kellneri Mayer, 1910 [*Hebella furax* Millard, 1957 may be a synonym]
Staurodiscus milleri (Bouillon, 1984)
Staurodiscus nigricans Agassiz & Mayer, 1899
Staurodiscus polynema (Kramp, 1959)
Staurodiscus quadristoma Bouillon, 1984b
Staurodiscus tetrastaurus Haeckel, 1879
Staurodiscus thalassinus (Péron & Lesueur, 1810a)
Staurodiscus vietnamensis Kramp, 1962

Family KIRCHENPAUERIIDAE Stechow, 1921

Hydroid: colony either with erect, branched or unbranched hydrocaulus, monosiphonic or polysiphonic or stolonal (*Ophinella*); issued from a creeping hydrorhiza; hydrocladia alternate, arising in polysiphonic hydrocauli from a single dominant axial tube; hydrothecae small, occurring only on hydrocladia, with or without marginal cusps, with or without an abcauline intrathecal septum, adnate or not; nematophores with nematothecae often rudimentary or occurring as naked sarcostyles; when present, nematothecae simple, typically one-chambered although two-chambered in some taxa (i.e. *Ventromma*), not fused to hydrothecae; paired lateral nematophores and nematothecae absent; gonophores as fixed sporosacs; gonotheca solitary, lacking nematothecae, on stem or hydrocladia, exceptionally on hydrorhiza (*Pycnotheca*).

Remarks: cnidome usually composed of microbasic mastigophores and sometimes pseudostenoteles, microbasic euryteles, and haplonemes. Stepanjants et al. (1997) described, in some specimens of *Wimveria*, desmoneme-like capsules from undischarged cnidocysts. The presence of desmonemes seems very doubtful in Leptomedusae and result presumably of contamination by cnidocysts issued from other species. The family Kirchenpaueriidae needs critical revision, the genera being not clearly defined and their diagnoses often overlapping. The genera *Naumovia*, *Oswaldella*, *Ventromma* and *Wimveria* present only slight differences and in the future they will probably be synonymized with *Kirchenpaueria*.

Recent references: Cornelius (1995); Migotto (1996); Calder (1997); Stepanjants *et al.* (1997); Peña Cantero & Marques (1999); Ansín Agís *et al.* (2001); Schuchert (2001a).

KEY TO HYDROIDS

1. hydrothecal aperture with cusps .... *Halicornopsis*
– hydrothecal aperture without cusps........ 2
2. hydrotheca with internal septum .... *Pycnotheca*
– hydrotheca without internal septum 3
3. colony stolonal, without distinct stem .... *Ophinella*
– colony with well defined stem 4
4. stem with nematophores........ 5
– stem without nematophores 6
5. nematotheca 2-chambered; no naked cauline nematophores; gonotheca annulated ..... *Ventromma*
– nematophores without two-chambered nematothecae; cauline nematophores naked or with nematothecae; gonophores not annulated .... *Kirchenpaueria*
6. hydrothecate hydrocladial internodes without mesial inferior nematophore .... *Naumovia*
– hydrothecate hydrocladial internodes with mesial inferior nematophore 7
7. hydrotheca adnate along most of adcauline wall .... *Oswaldella*
– hydrotheca free along most of adcauline wall .... *Wimveria*

Genus ***HALICORNOPSIS*** Bale, 1882

Fig. 155A-C

Hydroid: colony with erect stem, polysiphonic basally, monosiphonic in smaller and distal branches; hydrocladia alternate; hydrothecae shallow, on hydrocladia, with internal septum; hydrothecal rim with three pointed teeth, one on each side of hydrotheca and a large mesial abcauline one; mesial nematothecae 2-chambered, fixed, no lateral nematophores, nematothecae present also on stem and hydrocladia; gonophores as fixed sporosacs, gonotheca simple.

Remarks: this genus shares some characters with aglaopheniids.

Recent reference: Calder (1991).

Halicornopsis elegans (Lamarck, 1816)

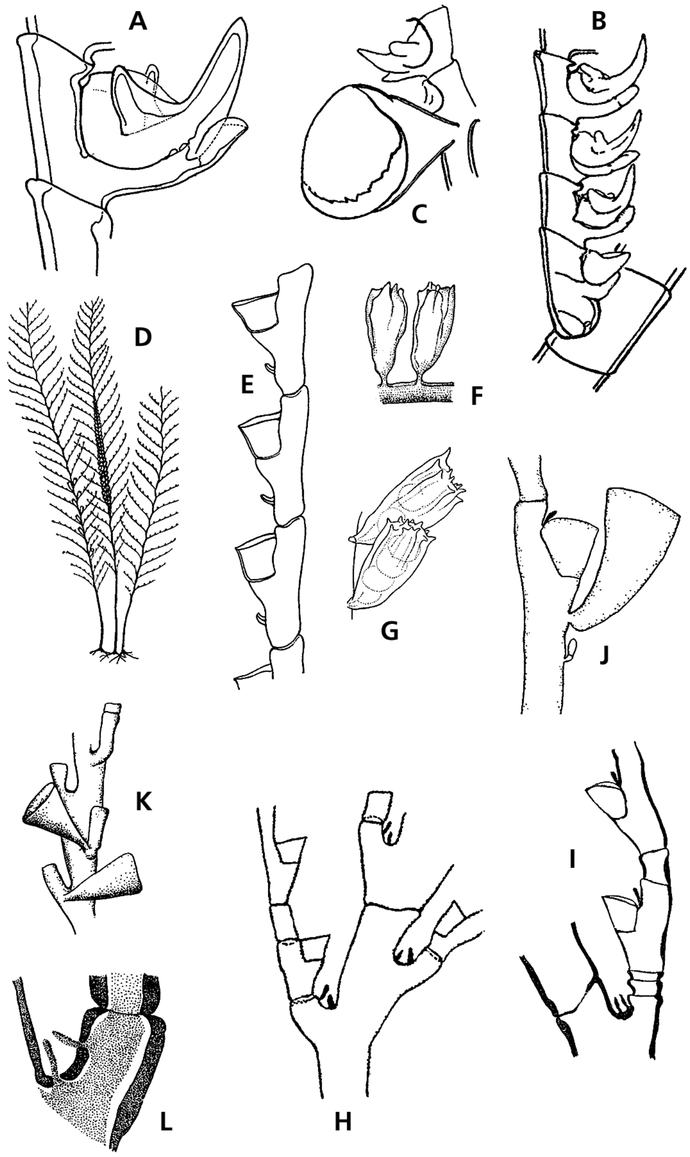


FIG. 155. Leptomedusae, Kirchenpaueriidae. A-C, *Halicornopsis elegans*: A, hydrotheca; B, portion of hydrocladium; C, gonotheca. D-G, *Kirchenpaueria pinnata*: D, general view of a colony; E, portion of a hydrocladium with hydrothecae and nematophores; F-G, two types of gonothecae. H-L, *Naumovia microtheca*: H, fragment of stem; I, portion of hydrocladium; J, hydrotheca, gonotheca and nematophores; K, schema of arrangement of cauline apophysis and gonothecae on the stem; L, scheme of arrangement of nematophores on cauline apophysis (A-C after Ralph, 1961a: p. 53, text-fig. 7 c, d, e; D-G after Leloup, 1952; H-L after Stepanjants *et al.*, 1997).

FIG. 155. *Leptomedusae, Kirchenpaueriidae. A-C,* Halicornopsis elegans : *A, hydrothèque ; B, portion d'un hydroclade ; C, gonothèque. D-G,* Kirchenpaueria pinnata : *D, vue générale d'une colonie ; E, portion d'un hydroclade avec hydrothèques et nématophores ; E-F, deux types de gonothèques. H-L,* Naumovia microtheca : *H, fragment d'une branche ; I, portion d'un hydroclade ; J, hydrothèque, gonothèque et nématophores ; K, schéma d'arrangement d'une apophyse caulinaire et des gonothèques ; L, schéma d'arrangement de nématophores sur une apophyse caulinaire (A-C d'après Ralph, 1961a : p. 53, text-fig. 7 c, d, e ; D-G d'après Leloup, 1952 ; H-L d'après Stepanjants* et al.*, 1997).*

Genus ***KIRCHENPAUERIA*** Jickeli, 1883

Figs 9S, 155D-G

Hydroid: stem unbranched, monosiphonic, with alternate, pinnate, unbranched hydrocladia, in simple forms arising directly from hydrorhiza; hydrotheca cup-shaped, without intrathecal septum, with even rim, partially or completely adnate; no cauline hydrothecae; nematotheca typically 1-chambered and movable, mesial nematothecae present or absent, sometimes poorly developed, reduced or even absent, nematophores with or without nematothecae present also on stem pending species; gonophores as fixed sporosacs, gonotheca solitary, not annulated, often with longitudinal ridges and spines.

Recent references: Cornelius (1995); Schuchert (2001a).

Kirchenpaueria adhaerens Millard, 1958
Kirchenpaueria biseptata Blackburn, 1938
Kirchenpaueria bonnevieae (Billard, 1906)
Kirchenpaueria curvata Jäderholm, 1904a
Kirchenpaueria fragilis (Hamann, 1882) [as *Plumularia*]
Kirchenpaueria magellanica (Hartlaub, 1905)
Kirchenpaueria moneroni (Antsulevich, 1980)
Kirchenpaueria pinnata (Linnaeus, 1758) [syn. *K. echinulata* (Lamarck, 1816)]
Kirchenpaueria similis (Hincks, 1861)
Kirchenpaueria tenuissima (Fraser, 1938c)
Kirchenpaueria ventruosa (Billard, 1911a)

Genus ***NAUMOVIA*** Stepanjants, Peña Cantero, Sheiko & Svoboda, 1997

Fig. 155H-L

Hydroid: colony with monosiphonic, unbranched stems, bearing alternately arranged apophyses in one or slightly different planes; stems without nematophores, cauline apophysis with two nematophores sometimes enclosed in 2-chambered nematothecae; hydrocladia unbranched, divided in ahydrothecate or hydrothecate internodes, these bearing one hydrotheca and a single mesial superior nematophore, sometimes with a thin nematotheca; hydrotheca with smooth rim, adnate; gonophores as fixed sporosacs, gonotheca arising from cauline apophysis.

Naumovia microtheca (Naumov, 1960)

Genus ***OPHINELLA*** Stechow, 1919

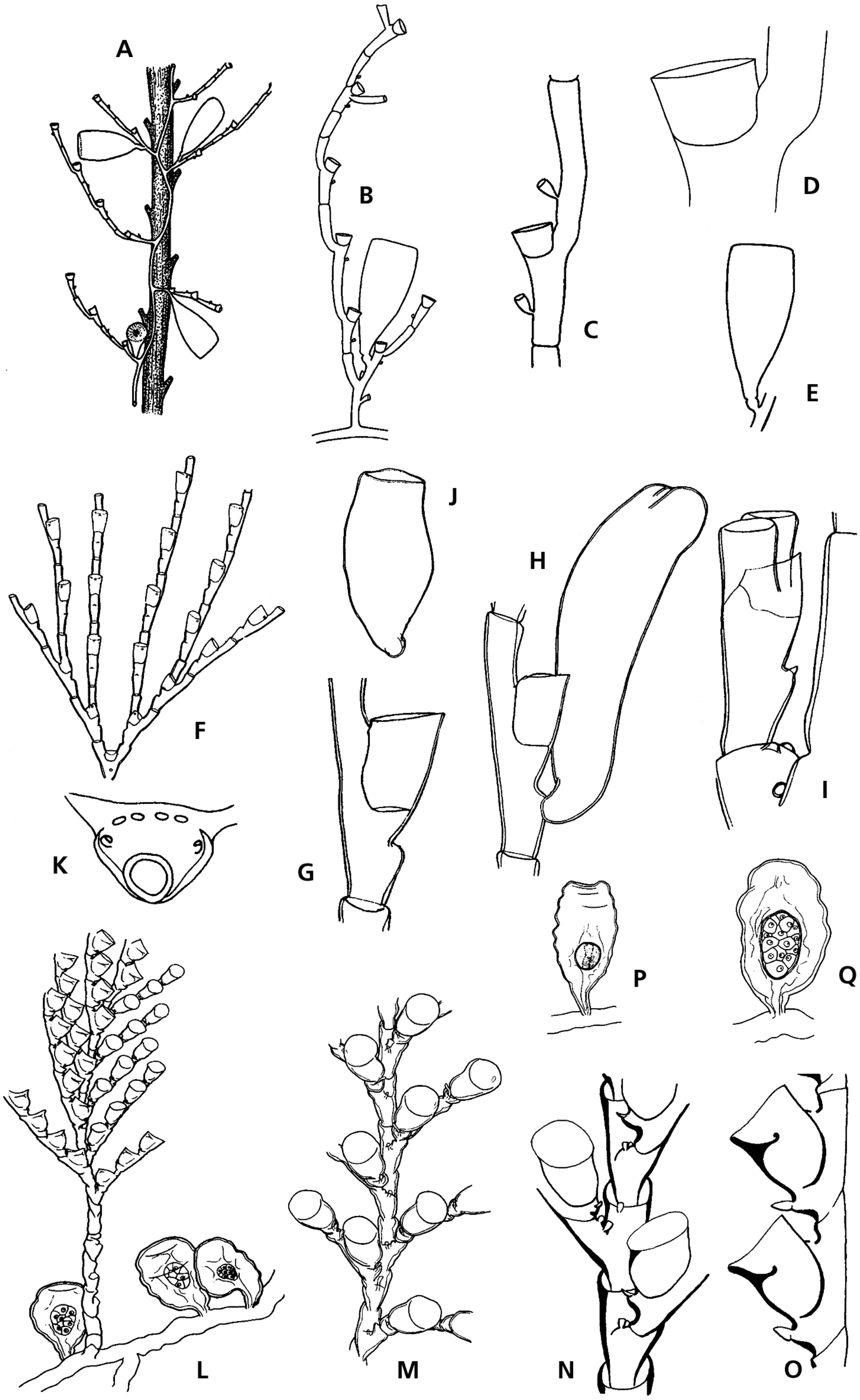
Fig. 156A-E

Hydroid: colony stolonal, reptant on other hydroids, stolons giving rise at various intervals to sub erected hydrocladia with hydrothecate and ahydrothecate internodes; many internodes bending abruptly outwards just below hydrothecae; hydrothecae small, free to half adnate, uniseriate; nematothecae short, barrel-shaped, typically two, one mesial above and one mesial below hydrothecae, nematophores very extensile, narrow capitate and armed terminally with prominent cnidocysts; gonophores as fixed sporosacs, gonothecae near base of hydrocladia.
Remarks: often included in the genus *Hydrodendron* (see Bouillon 1985a; Rees & Vervoort 1987); Cornelius (1995), however, allocated it to the Kirchenpaueriidae and is followed here.

Ophinella parasitica (G.O. Sars, 1874)

FIG. 156. Leptomedusae, Kirchenpaueriidae. A-E, *Ophinella parasitica*: A, colony overgrowing plumulariid hydroid; B, detail of a portion of colony; C, hydrocladia with hydrotheca and associated nematothecae; D, detail of hydrotheca; E, gonotheca. F-K, *Oswaldella stepanjantsae*: F, branch of a colony showing hydrocladial ramification and disposition of hydrothecae; G, hydrocladial internode with hydrotheca; H, hydrocladial internode with male gonotheca; I, first hydrocladial internode and cauline apophysis showing the two mamelons and one axillary nematophore; J, female gonotheca; K, cauline apophysis with two mamelons and four axillary nematophores (frontal view). L-Q, *Pycnotheca mirabilis*: L, part of hydrorhiza with hydrocaulus, hydrocladia and female gonothecae; M, part of hydrocaulus with origins of hydrocladia; N, detail of anterior view of stem; O, detail of hydrocadium with hydrotheca and nematotheca; P, male gonotheca; Q, female gonotheca (A-E after Cornelius, 1995; F-K after Peña Cantero *et al.,* 1997; L-M, P-Q after Hirohito, 1995; N-O after Millard, 1975).

FIG. 156. *Leptomedusae, Kirchenpaueriidae. A-E,* Ophinella parasitica : *A, colonie couvrant un hydroïde plumulariide ; B, détail d'une portion de colonie ; C, hydroclade portant une hydrothèque et ses nématothèques ; D, détail d'une hydrothèque ; E, gonothèque. F-K,* Oswaldella stepanjantsae : *F, branche d'une colonie montrant les ramifications hydrocladiales et la disposition des hydrothèques ; G, internode hydrocladial avec une hydrothèque ; H, internode hydrocladial avec une gonothèque mâle ; I, premier internode hydrocladial et apophyse caulinaire montrant les deux mamelons et un nématophore axillaire ; J, gonothèque femelle ; K, apophyse caulinaire avec deux mamelons et quatre nématophores axillaires (vue frontale). L-Q,* Pycnotheca mirabilis *: L, partie de l'hydrorhize avec un hydrocaule, des hydroclades et des gonothèques femelles ; M, portion d'hydrocaule avec les origines des hydroclades ; N, détail de la face antérieure d'un fragment d'hydrocaule ; O, détail d'un hydroclade avec hydrothèque et nématothèque ; P, gonothèque mâle ; Q, gonothèque femelle (A-E d'après Cornelius, 1995 ; F-K d'après Peña Cantero* et al.*, 1997 ; L-M, P-Q d'après Hirohito, 1995 ; N-O d'après Millard, 1975).*


A
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Genus *OSWALDELLA* Stechow, 1919

Fig. 156F-K

Hydroid: colony pinnate, stems branched or unbranched, mono- or polysiphonic, with two longitudinal rows of apophyses alternately arranged in one plane and giving rise to hydrocladia; apophyses with varied number of nematophores near axil with hydrocaulus; stem without nematophores; hydrocladia typically branched; hydrothecae cup-shaped or tubular, adnate along most of adcauline wall, without intrathecal septum; hydrothecate internodes with two mesial nematophores, one inferior with or without nematotheca and one superior naked; inferior nematophores inconspicuous, lateral nematophores absent; gonophores as fixed sporosacs, colony dioecious, gonothecae sexually dimorphic.
Remarks: the above diagnosis does not include the characters of *Oswaldella nova* (Jarvis 1922), with hydrocladia arising directly from a creeping stolon and with nematothecae on the apophyses carrying hydrocladia: its systematic position has to be reconfirmed.
Recent references: Peña Cantero *et al.* (1995), Peña Cantero & Vervoort (1998); Peña Cantero & Marques (1999).

Oswaldella antarctica (Jäderholm, 1904a)
Oswaldella bifurca (Hartlaub, 1904)
Oswaldella billardi Briggs, 1938
Oswaldella blanconae El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Oswaldella crassa Peña-Cantero & Vervoort, 1998
Oswaldella curiosa Peña-Cantero & Vervoort, 1998
Oswaldella delicata Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella elongata Peña-Cantero, Garcia-Carrascosa & Vervoort, 1995
Oswaldella encarnae Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella erratum Peña-Cantero & Vervoort, 1997
Oswaldella garciacarrascosai Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella gracilis Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella grandis Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella herwigi El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Oswaldella incognita Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella nova (Jarvis, 1922) [position doubtful]
Oswaldella obscura Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella rigida Peña-Cantero, Svoboda & Vervoort, 1997a
Oswaldella shetlandica Stepanjants, 1979
Oswaldella stepanjantsae El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Oswaldella terranovae Peña-Cantero & Vervoort, 1996b
Oswaldella tottoni Peña-Cantero & Vervoort, 1996b
Oswaldella vervoorti Peña-Cantero & Garcia-Carrascosa, 1998

Genus *PYCNOTHECA* Stechow, 1919

Fig. 156L-Q

Synonym: *Diplocheilus* Allman, 1883.
Hydroid: stem monosiphonic, unbranched or sparsely branched, bearing alternate unbranched hydrocladia; nematothecae on apophysis of hydrocladia; hydrotheca cup-shaped, with strong abcauline intrathecal septum and even rim, partially adnate; hydrothecate internodes usually with a mesial inferior fixed nematotheca and a mesial superior sarcostyle; gonophores as fixed sporosacs, gonothecae transversally annulated, on hydrorhiza, with acrocyst.
Recent reference: Hirohito (1995).

Pycnotheca mirabilis (Allman, 1883) [syn. *P. allmani* Torrey, 1902]
Pycnotheca producta (Bale, 1882)

Genus *VENTROMMA* Stechow, 1923

Fig. 157A-E

Hydroid: colony erect, monosiphonic or polysiphonic, with branched or unbranched hydrocauli arising from creeping hydrorhiza; hydrocladia alternate, typically unbranched; hydrothecae only on hydrocladia, cup-shaped, margin entire, without intrathecal septum; nematophores usually with small, 2-chambered nematothecae, hydrothecate internodes with a median inferior and a median superior nematotheca, no lateral nematophores and nematothecae; nematophores or nematothecae also on stems; gonophores as fixed sporosacs, gonotheca solitary, with transverse annulations.
Remarks: often regarded as congeneric with *Kirchenpaueria* Jickeli, 1883.
Recent reference: Calder *et al.* (2003).

Ventromma halecioides (Alder, 1859)
Ventromma plumularioides (Clark, 1876b)

Genus *WIMVERIA* Stepanjants, Svoboda, Peña-Cantero & Sheiko, 1998

Fig. 157F-K

Hydroid: stem monosiphonic, internodes without nematophores, with one apophysis, cauline apophyses arranged in different planes, with nematophores and "mamelons"; hydrocladia forked, with ahydrothecate and hydrothecate internodes; hydrothecae deep, cylindrical, with even rim, without intrathecal septum, free along most adcauline wall, hydrothecal aperture strongly abcaulinely directed; hydrothecate internodes with two mesial nematothecae, one below the other above hydrothecae, typically one-chambered, thin, sometimes absent; gonophores as fixed sporosacs, gonotheca on cauline apophysis.

Wimveria divergens (Naumov, 1960)

Family LAFOEIDAE A. Agassiz, 1865

Hydroid: colonial, either erect or stolonal, arising from creeping hydrorhiza; hydrotheca from tubular to campanulate, radially or bilaterally symmetrical, usually adherent, seldom pedicellate, margin entire, operculum usually absent, with or without diaphragm, without annular perisarcal thickening; hydranth with or without abcauline diverticulum; nematophores present or absent; cnidome: microbasic mastigophores; gonophores as fixed sporosacs; gonothecae aggregated into coppinia or scapus, exceptionally solitary (Figs 6N, $10D^1$, D^2).
Recent references: Calder (1991); Ramil & Vervoort (1992a); Blanco *et al.* (1994); Cornelius (1995); Hirohito (1995); Calder & Vervoort (1998); Schuchert (2001a).

KEY TO HYDROIDS

1. hydrotheca with operculum .... *Abietinella*
– hydrotheca without operculum........ 2

2. hydrotheca stalked 3
– hydrotheca not stalked, usually adherent........ 4

3. hydrothecae in two longitudinal rows; with diaphragm or reduced annulus; nematophores and nematothecae usually present .... *Zygophylax*
– hydrothecae irregularly on all sides; with no diaphragm or annular thickening; without nematophores .... *Lafoea*

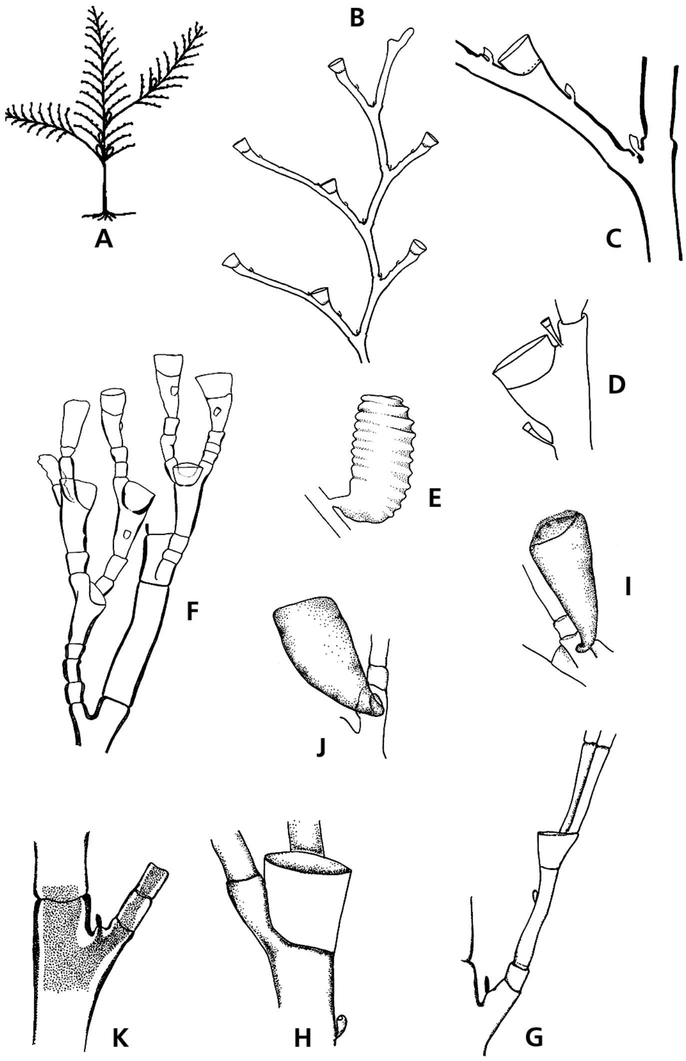


FIG. 157. Leptomedusae, Kirchenpaueriidae. A-E, *Ventromma halecioides*: A, general view of a colony; B, part of hydrocaulus with both monothecate and bithecate hydrocladia; C, hydrocaulus and part of a hydrocladium; D, hydrotheca and associated nematothecae; E, gonotheca. F-K, *Wimveria divergens*: F, portion of a colony; G, section of a stem with cauline apophysis and nematophores; H, portion of hydrocladia with hydrotheca; I-J, gonothecae; K, cauline apohysis with nematophore (A, D-E after Cornelius, 1995; C after Calder, 1997; F-K after Stepanjants *et al*., 1998).

FIG. 157. *Leptomedusae, Kirchenpaueriidae. A-E,* Ventromma halecioides *: A, vue générale d'une colonie ; B, partie d'un hydrocaule avec des hydroclades portant soit une soit deux hydrothèques ; C, hydrocaule et une portion d'hydroclade ; D, hydrothèque avec ses nématothèques associées ; E, gonothèque. F-K,* Wimveria divergens *: F, portion d'une colonie ; G, section d'un hydrocaule avec une apophyse caulinaire et des nématophores ; H, portion d'un hydroclade avec une hydrothèque ; I-J, gonothèques ; K, apophyse caulinaire avec un nématophore (A, D-E d'après Cornelius, 1995 ; C d'après Calder, 1997 ; F-K d'après Stepanjants* et al.*, 1998).*

4. colony stolonal; hydrotheca adherent to hydrorhiza .... *Filellum*
– colony with erect, branching stem 5

5. hydrotheca adherent to stem or branch 6
– hydrotheca sessile, usually not adhering to stem or branch .... *Billardia*

6. diaphragm between hydrotheca and stem apophysis; normally with nematophores and nematothecae .... *Cryptolaria*
– normally no diaphragm and no nematophores 7

7. hydrothecae alternate, in two longitudinal rows .... *Acryptolaria*
– hydrothecae not alternate, on all surface of the stem, though they may be alternate in some regions; gonothecae solitary or in pairs .... *Cryptolarella*

Genus *ABIETINELLA* Levinsen, 1913

Fig. 158A-D

Hydroid: colony normally erect, rarely stolonal, strongly pinnate, main stem branched, mono-to polysiphonic; hydrocladia and hydrothecae rigorously alternate in one plane; hydrotheca tubular, with not well demarcated pedicel, with diaphragm, two one-chambered nematothecae, one on each side of supporting apophyses; hydrothecal rim circular, slightly flared, tilted so that plane of aperture is almost perpendicular to main axis of hydrocladium; hydrotheca with a one-valved, thin, disc-shaped, terminal operculum, attached to adcauline wall, close to rim, often lost; hydranth with abcauline caecum?; gonophores as fixed sporosacs, gonothecae aggregated in coppinia with defensive structures.

Remarks: it is uncertain whether this genus belongs to this family; the presence of coppinia is a clear lafœid feature, but the hydrothecal operculum is not.

Recent references: Rees & Vervoort (1987); Peña Cantero & Garcia-Carrascosa (1993).

Abietinella operculata (Jäderholm, 1903)

Genus *ACRYPTOLARIA* Norman, 1875

Fig. 158E-I

Hydroid: colony normally erect, stolonal when young, more or less alternately branched; hydrocaulus and hydrocladia polysiphonic, with an axial tube overgrown by accessory tubes; all branches with two longitudinal rows of alternate hydrothecae, sessile, tubular, adnate to axial tube or immersed basally in accessory tubes, curving outwards and becoming free distally; diaphragm absent; nematophores absent; gonophores as fixed sporosacs, gonothecae aggregated in coppinia.

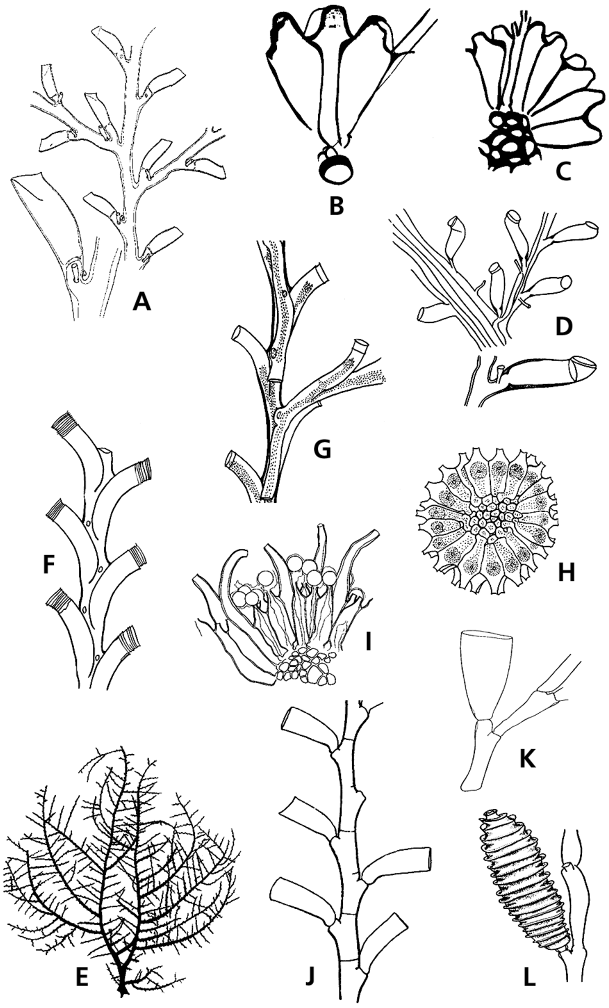


FIG. 158. Leptomedusae, Lafœidae. A-D, *Abietinella operculata*: A, monosiphonic fragment of colony (above), hydrotheca with pair of basal nematothecae (below); B-C, details of coppinia; D, detail of colony. E-I, *Acryptolaria conferta*: E, colony, general view of heavy form; F, part of stem; G, portion of stem showing branching portions of peripheral tubes in position; H, coppinia with female gonothecae; I, cross section of a part of coppinia with female gonophores and modified hydrothecae. J-L, *Billardia*: J, *Billardia novaezealandiae*, branch of a colony; K-L, *Billardia subrufa*: K, monosiphonic fragment with hydrotheca; L, gonotheca (A & K after Vervoort, 1972; B-C after Peña & García-Carrascosa, 1993; D & L after Stepanjants, 1979; E-H after Millard, 1975; I after Hirohito, 1995; J after Ralph, 1957: p. 817, text-fig. 1 a).

FIG.158. *Leptomedusae, Lafœidae. A-D,* Abietinella operculata : *A, fragment de colonie monosiphonique (au-dessus), hydrothèque avec une paire de nématothèques basilaires (au-dessous) ; B-C, détails d'une coppinia ; D, détail d'une colonie. E-I,* Acryptolaria conferta : *E, colonie, vue générale d'une forme massive ; F, portion d'une branche ; G, portion d'une branche montrant la position des tubes péripheraux ; H, coppinia avec des gonothèques femelles ; I, section d'une partie de coppinia avec des gonophores femelle et des hydrothèques modifiées. J-K,* Billardia : *J,* Billardia novae-zealandiae, *branche d'une colonie ; K-L,* Billardia subrufa : *K, fragment monosiphonique avec des hydrothèques ; L, gonothèque (A & K d'après Vervoort, 1972 ; B-C d'après Peña & García-Carrascosa, 1993 ; D & L d'après Stepanjants, 1979 ; E-H d'après Millard, 1975 ; I d'après Hirohito, 1995 ; J d'après Ralph, 1957 : p. 817, text-fig. 1 a).*

Remarks: Stepanjants (1979) described an operculum in *Acryptolaria operculata*.
Recent references: Schuchert (2001a, 2003).

Acryptolaria abies (Allman, 1877)
Acryptolaria andersoni Totton, 1930
Acryptolaria angulata (Bale, 1914b)
Acryptolaria arboriformis (Ritchie, 1911)
Acryptolaria conferta (Allman, 1877)
Acryptolaria corniformis Naumov & Stepanjants, 1962
Acryptolaria elegans (Allman, 1877)
Acryptolaria flabellum (Allman, 1888)
Acryptolaria gracilis (Allman, 1888)
Acryptolaria longitheca (Allman, 1877)
Acryptolaria minima Totton, 1930
Acryptolaria normani Nutting, 1927
Acryptolaria operculata Stepanjants, 1979 [doubtful status]
Acryptolaria patagonica El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Acryptolaria pulchella (Allman, 1888)
Acryptolaria rectangularis (Jarvis, 1922)
Acryptolaria symmetrica (Nutting, 1905)

Genus ***BILLARDIA*** Totton, 1930

Fig. 158J-L

Hydroid: colony erect, sympodially branched or stolonal; hydrocaulus strongly polysiphonic in large colonies; hydrothecae sessile, alternate, on hydrocauli and hydrocladial short apophyses, sometimes slightly adnate, abruptly curved at base, more tubular than bell-shaped, margin entire, circular, without diaphragm or annular thickening, sometimes a basal septum; hypostome dome-shaped; gonophores as fixed sporosacs, gonothecae compressed, annulated; replacing hydrothecae, but larger.
Remarks: systematic position unclear, included in the Campanulariidae by many authors, considered a member of the Lafœidae or of the Syntheciidae by others.
Recent references: Bouillon (1985a); Calder (1991); Vervoort & Watson (2003).

Billardia hyalina Vervoort & Watson, 2003
Billardia intermedia Blanco, 1967
Billardia novaezealandiae Totton, 1930
Billardia subrufa (Jäderholm, 1904a)

Genus ***CRYPTOLARELLA*** Stechow, 1913

Fig. 159A-C

Hydroid: colony normally erect, stolonal in young stages; erect stems polysiphonic and branched; hydrothecae arising from axial tube of stem, irregularly and on all surfaces, tubular, partly adnate, without diaphragm; no nematophores; gonophores as fixed sporosacs, gonothecae not aggregated, solitary or in pairs, contents not known.

Cryptolarella abyssicola (Allman, 1888)
Cryptolarella contorta (Allman, 1888)

Genus ***CRYPTOLARIA*** Busk, 1857

Fig. 159D-I

Hydroid: colony normally erect, pinnate, stolonal in young stages; main stem polysiphonic, occasionally forked; hydrocladia sub-alternate, all in one plane; main axis with 2 or 4 longitudinal rows of sub-opposite hydrothecae; hydrothecae tubular, without pedicel, directly on apophysis, adcauline wall adherent to hydrocladia for some distance at least in some part of colony, usually curved outwards, separated from apophysis by a distinct diaphragm; nematohores and nematothecae present; gonophores as fixed sporosacs, gonothecae aggregated to form a coppinia.
Recent references: Rees & Vervoort (1987); Calder *et al.* (2003).

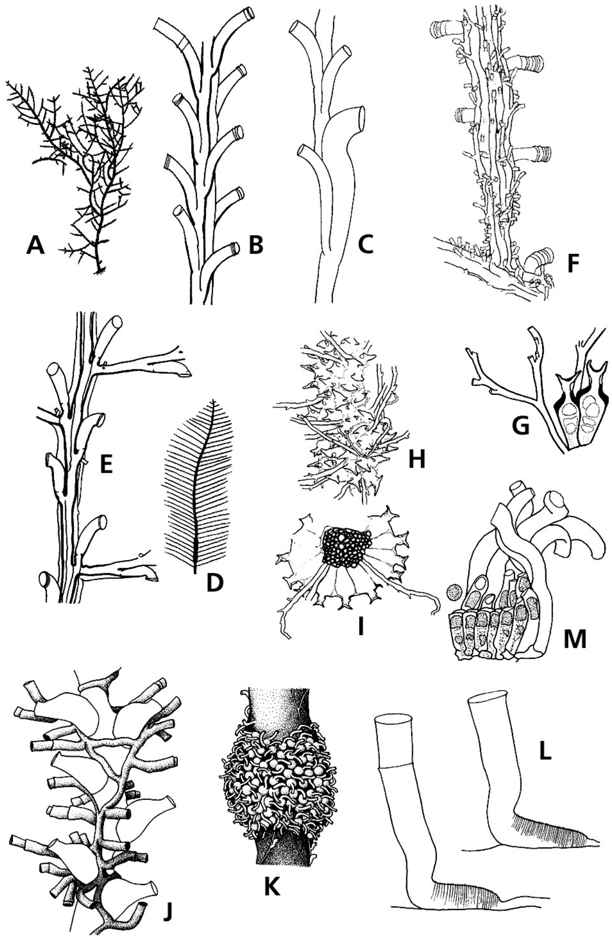


FIG. 159. Leptomedusae, Lafœidae. A-C, *Cryptolarella abyssicola*: A, general view of colony; B, part of stem; C, monosiphonic fragment with gonotheca. D-I, *Cryptolaria*: D-G, *Cryptolaria pectinata*: D, stem with basal coppinia; E, detail of stem from distal region to show axillary hydrothecae and origin of hydrocladia; F, detail of a origin of a hydrocladium showing hydrothecae and nematothecae; G, part of coppinia showing female gonotheca and nematotheca; H-I, *Cryptolaria exserta*: H, surface view of coppinia showing the branched nematothecae; I, cross section of a part of a coppinia. J-M, *Filellum*: J-K, *Filellum serpens*: J, general view of a colony; K, coppinia and a few hydrothecae; L-M, *Filellum serratum*: L, large hydrothecae; M, part of coppinia showing gonothecae and accessory tubes (A-B, D-E, G, L-M after Millard, 1975; C after Vervoort, 1966; F, H-I after Hirohito, 1995; J-K after Cornelius, 1995).

***FIG. 159.** Leptomedusae, Lafœidae. A-C,* Cryptolarella abyssicola : *A, vue générale d'une colonie ; B, partie d'une branche ; C, fragment monosiphonique avec une gonothèque. D-I,* Cryptolaria : *D-G,* Cryptolaria pectinata : *D, hydrocaule avec une coppinia basale ; E, détail d'une branche de la région distale montrant des hydrothèques axilliaires et l'origine des hydroclades ; F, détail de l'origine d'un hydroclade montrant les hydrothèques et les nématothèques ; G, partie d'une coppinia montrant les gonothèques femelles et les nématothèques ; H-I,* Cryptolaria exserta : *H, vue d'une coppinia montrant les nématothèques ramifiées ; I, section transversale d'une portion de coppinia. J-M,* Filellum : *J-K,* Filellum serpens : *J, vue générale d'une colonie ; K, coppinia et quelques hydrothèques associées ; L-M,* Filellum serratum : *L, larges hydrothèques ; M, partie d'une coppinia montrant les gonothèques les tubes accessoires (A-B, D,-E, G, L-M d'après Millard, 1975 ; C d'après Vervoort, 1966 ; E, H-I d'après Hirohito, 1995 ; J-K d'après Cornelius, 1995).*

Cryptolaria chazaliei (Versluys, 1899) [doubtful status]
Cryptolaria exserta Busk, 1858
Cryptolaria pectinata (Allman, 1888)
Cryptolaria prima Busk, 1857
Cryptolaria profunda Naumov, 1960
Cryptolaria rigida (Fraser, 1940b)
Cryptolaria spinosa Millard, 1980

Genus ***FILELLUM*** Hincks, 1868

Fig. 159J-M

Synonym: *Reticularia* Thomson, 1853, non M'Coy, 1844 [Brachiopoda].

Hydroid: colony stolonal, stolon filiform, creeping on substrate, usually over other hydroids, irregularly branched; hydrotheca sessile, tubular, arising singly from hydrorhiza, adnate basally, curving centrally and becoming free and bending upwards in varying degrees distally; no diaphragm and operculum; no nematophores and nematothecae; gonophores as fixed sporosacs, gonothecae either closely aggregated, with lateral walls contiguous, touching each other, or weakly aggregated, being isolated, not in close contact; coppinia usually hermaphrodite, with or without modified hydrothecal protective tubes.

Recent references: Peña Cantero *et al.* (1998); Schuchert (2001a).

Filellum adhaerens (Nutting, 1901)
Filellum antarcticum (Hartlaub, 1904)
Filellum contortum (Nutting, 1905)
Filellum disaggregatum Peña-Cantero, Garcia-Carrascosa & Vervoort, 1998
Filellum parasiticum (Antsulevich, 1987)
Filellum serpens (Hassall, 1848)
Filellum serratum (Clarke, 1879)
Filellum tubiforme Shidlovskii, 1902 [probably a syn. of *F. serpens*]

Genus ***GRAMMARIA*** Stimpson, 1853

Figs 5J, 160A-D

Hydroid: colony erect, with polysiphonic branched stems; hydrothecae usually arranged in three or more longitudinal rows, lacking diaphragm and operculum, at least partially tubular, basally submerged in hydrocauli and hydrocladia, curving outward, distal end free or totally sunk, sometimes only mouth margin projecting to the outside, mouth rim even or recurved; nematophores absent; gonophores as fixed sporosacs, gonothecae protected in coppinia.
Recent reference: Schuchert (2001a).

Grammaria abietina (M. Sars, 1850)
Grammaria borealis (Levinsen, 1893b) [as *Cryptolaria*]
Grammaria elegans Fraser, 1943
Grammaria gracilis Stimpson, 1853
Grammaria immersa Nutting, 1901a
Grammaria rigida Fraser, 1943
Grammaria scandens Stechow, 1913a [probably a syn. of *G. borealis*]

Genus ***LAFOEA*** Lamouroux, 1821

Figs 6N, 160E-J

Hydroid: colony occasionally stolonal but usually erect, branched, with polysiphonic hydrocaulus, terminal branches of hydrocaulus monosiphonic; hydrothecae irregularly arranged, tubular to deeply campanulate, radially to bilaterally symmetrical, pedicellate, usually free from stem or stolon, pedicel generally spirally twisted, sometimes absent, not always well defined, diaphragm absent, hydrothecal base indistinctly separated from pedicel by ring of small desmocytes; gonophores as fixed sporosacs, gonothecae aggregated in coppinia with modified tubes.
Recent references: Schuchert (2001a, 2003).

Lafoea adnata Fraser, 1925
Lafoea benthophila Ritchie, 1909
Lafoea coalescens Allman, 1877
Lafoea dumosa (Fleming, 1820)
Lafoea grandis Hincks, 1874 [probably a syn. of *L. dumosa*]
Lafoea regia Fraser, 1948
Lafoea symmetrica Bonnevie, 1899
Lafoea tenellula Allman, 1877
Lafoea weddelli Blanco, 1991

Genus ***ZYGOPHYLAX*** Quelch, 1885

Fig. 160K-O

Hydroid: colony erect, pinnate or flabellate, rarely stolonal; stem occasionally forked, polysiphonic with the exception of distal parts; hydrocladia in most species in one plane but sometimes in various planes; hydrothecae arising from stem, branches and hydrocladia, alternately in two longitudinal rows and from the axial tube when polysiphonic, tubular to deep campanulate, never adherent, usually merging into a pedicel of various length, with distinct diaphragm often reduced to mere annulus; abcauline caecum present (?); nematothecae generally present on hydrothecal apophyses and on hydrocladial tubes; gonophores as fixed sporosacs, gonothecae arranged in coppinia or scapus.
Recent references: Rees & Vervoort (1987); Schuchert (2001a, 2003); Vervoort & Watson (2003).

Zygophylax abyssicola (Stechow, 1926)
Zygophylax adhaerens (Fraser, 1938a)
Zygophylax africana Stechow, 1923a
Zygophylax antipathes (Lamarck, 1816)
Zygophylax arborescens (Leloup, 1931)
Zygophylax armata (Ritchie, 1907b)
Zygophylax bathyphila Leloup, 1940a
Zygophylax biarmata Billard, 1905
Zygophylax bifurcata Billard, 1942b
Zygophylax binematophoratus Vervoort & Watson, 2003
Zygophylax brevitheca Jäderholm, 1919
Zygophylax brownei Billard, 1924b
Zygophylax carolina (Fraser, 1911)
Zygophylax concinna (Ritchie, 1911)
Zygophylax convallaria (Allman, 1877) [syn. *Z. cervicornis* (Nutting, 1905)]
Zygophylax crassicaulis (Fraser, 1943)
Zygophylax crassitheca (Fraser, 1941)
Zygophylax crozetensis Millard, 1977b
Zygophylax curvitheca Stechow, 1913a
Zygophylax cyathifera (Allman, 1888)
Zygophylax echinata Calder & Vervoort, 1998
Zygophylax elegans (Fewkes, 1881a)
Zygophylax elongata Ramil & Vervoort, 1992
Zygophylax flexilis (Pictet & Bedot, 1900) [doubtful status]
Zygophylax geminocarpa Millard, 1958
Zygophylax geniculata (Clarke, 1894)
Zygophylax infundibulum Millard, 1958
Zygophylax junceoides (Borradaile, 1905)
Zygophylax kurilensis Antsulevich, 1988c
Zygophylax leloupi Ramil & Vervoort, 1992a
Zygophylax levinseni (Saemundsson, 1911)
Zygophylax millardae Rees & Vervoort, 1987
Zygophylax pacifica Stechow, 1920
Zygophylax parapacificus Vervoort & Watson, 2003
Zygophylax pinnata (Sars, 1874)
Zygophylax polycarpa Vervoort & Watson, 2003
Zygophylax profunda Quelch, 1885a
Zygophylax pseudafricanus Vervoort & Watson, 2003
Zygophylax recta Jarvis, 1922
Zygophylax reflexa (Fraser, 1948)
Zygophylax rigida (Fraser, 1948)
Zygophylax rufa (Bale, 1884)
Zygophylax sagamiensis Hirohito, 1983
Zygophylax sibogae Billard, 1918
Zygophylax stechowi (Jäderholm, 1919)
Zygophylax tizardensis Kirkpatrick, 1890b
Zygophylax tottoni Rees & Vervoort, 1987
Zygophylax unilateralis Totton, 1930
Zygophylax valdiviae Stechow, 1923b

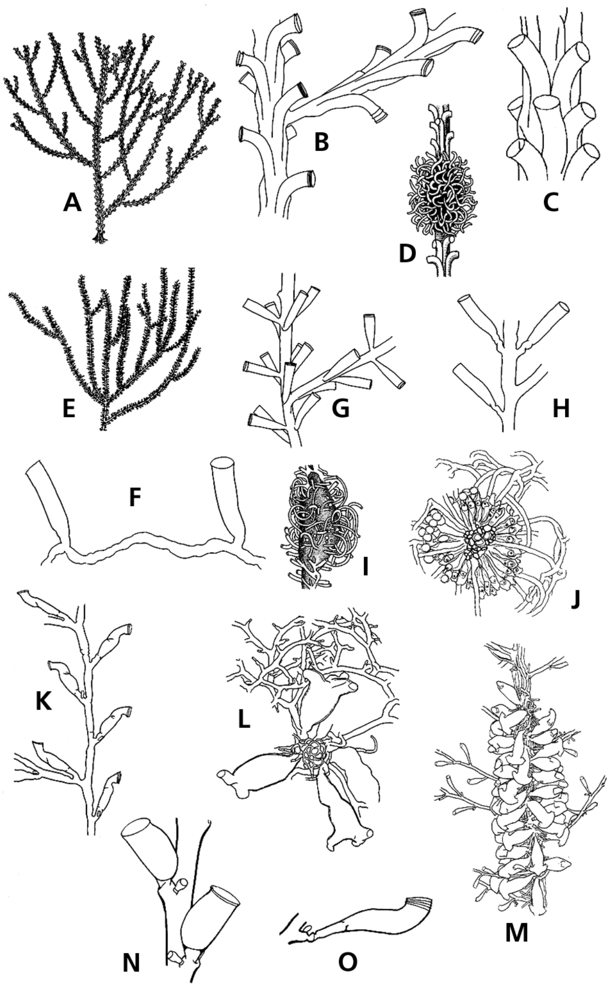


FIG. 160. Leptomedusae, Lafœidae. A-D *Grammaria abietina*: A, general view of a colony; B, detail of a branch; C, hydrothecae; D, coppinia. E-J, *Lafoea*: E, G-J, *Lafoea dumosa*: E, general view of an erected colony; G-H, detail of a branches of an erected colony with stalked and unstalked hydrothecae; I, coppinia and a few hydrothecae; J, cross section of a coppinia with female gonophores and tubular hydrothecae. F, *Lafoea tenellula*, part of a stolonal colony. K-O, *Zygophylax*: K-L, *Zygophylax tizardensis*: K, portion of stem; L, part of coppinia; M, *Zygophylax convallaria,* scapus with branched nematothecae; N, *Zygophylax geminocarpa*, part of hydrocladium; O, *Zygophylax infundibulum*, hydrothecae (A-B, D-E, G-I after Cornelius, 1995; C after Naumov, 1969; F, J & M after Hirohito, 1995; K-L after Vervoort, 1987: p. 97, fig. 10.9 (A), (B); N-O after Millard, 1975).

***FIG. 160.** Leptomedusae, Lafœidae. A-D,* Grammaria abietina *: A, vue générale d'une colonie ; B, détail d'une branche ; C, groupe d'hydrothèques ; D, coppinia. E-J,* Lafoea *: E, G-J,* Lafoea dumosa *: E, vue générale d'une colonie érigée ; G-H, détails de branches de colonie érigée avec des hydrothèques pédonculées et sessiles ; I, coppinia et quelques hydrothèques associées ; J, section transversale d'une coppinia avec des gonophores femelles et des hydrothèques tubulaires. F,* Lafoea tenellula*, partie d'une colonie stoloniale. K-O,* Zygophylax *: K-L,* Zygophylax tizardensis *: K, portion d'une branche ; L, partie d'une coppinia ; M,* Zygophylax convallaria*, scapus avec des némato-thèques ramifiées ; N,* Zygophylax geminocarpa*, partie d'un hydroclade ; O,* Zygophylax infundibulum*, hydrothèque (A-B, D-E, G-I d'après Cornelius, 1995 ; C d'après Naumov, 1969 ; F, J & M d'après Hirohito, 1995 ; K-L d'après Vervoort, 1987 : p. 97, fig. 10.9 (A), (B) ; N-O d'après Millard, 1975).*

Family LAODICEIDAE Agassiz, 1862

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

Medusa: with marginal cordyli with or without cnidocysts; with 4 or 8, simple radial canals; marginal tentacles hollow; "gonads" on radial canals, on radial canals and lobes of manubrium or into manubrial pouches; with or without marginal cirri; with or without adaxial ocelli; without statocysts.

Recent references: Bouillon *et al.* (1991); Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

When known, the hydroids have a "*Cuspidella* " facies; indistinguishable from each other and inadequate for diagnosis.

KEY TO MEDUSAE

1. cordyli with zooxanthellae .... *Wuvula*
– cordyli without zooxanthellae 2

2. radial canals closed 3
– radial canals as open grooves forming large cruciform mouth .... *Staurophora*

3. with 4 radial canals 4
– with 8 simple, unbranched radial canals .... *Melicertissa*

4. manubrium with perradial lobes or pouches 5
– 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*

5. manubrium with funnel-shaped lobes; radial canals with "gonads" placed in lateral diverticula; without cirri and ocelli .... *Ptychogena*
– 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, Pagès, Gili, Palanques, Puig & Heussner, 2000

Fig. 161A-B

Hydroid: unknown.
Medusa: well developed manubrial perradial pouches; 4 radial canals; 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.

Guillea canyonincolae Bouillon, Pagès, Gili, Palanques, Puig & Heussner, 2000

Genus *LAODICEA* Lesson, 1843

Figs 35F-G, 41, 161C-G

Hydroid: "*Cuspidella*" type, see family characters; hydrotheca sessile.
Medusa: 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.
Recent reference: Bouillon *et al.* (1991).

Laodicea brevigona Allwein, 1967
Laodicea chapmani Günther, 1903 [doubtful status]
Laodicea cruciata (Forskål, 1775) [doubtful status]
Laodicea eucope (Haeckel, 1879) [doubtful status]
Laodicea fertilis (Lendenfeld, 1885b)
Laodicea fijiana Agassiz & Mayer, 1899
Laodicea indica Browne, 1906
Laodicea marama Agassiz & Mayer, 1899
Laodicea minuscula Vannucci, 1957
Laodicea neptuna Mayer, 1900a [doubtful status]
Laodicea ocellata Babnik, 1948 [doubtful status]
Laodicea pulchra Browne, 1902
Laodicea undulata (Forbes & Goodsir, 1851) [*Ptychogena longigona* Maas, 1893 is probably a synonym]

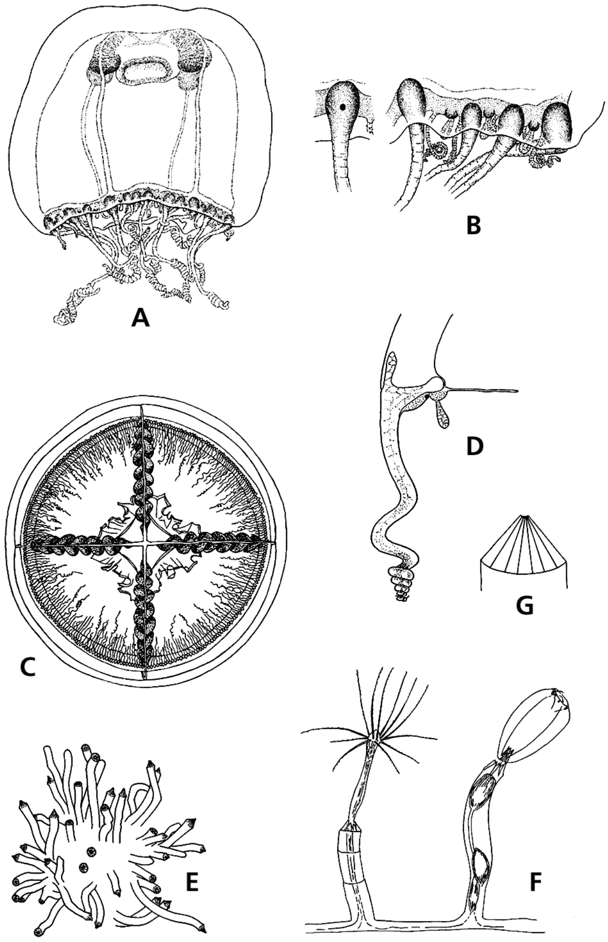


FIG. 161. Leptomedusae, Laodiceidae. A-B, *Guillea canyonincolae*: A, general view of a mature medusa; B, details of the umbrella margin, adaxial view of a marginal tentacle showing ocellus (left), abaxial view showing cordyli and lateral spiral cirri (right). C-G, *Laodicea undulata*: C, adult medusa; D, diagrammatic vertical section of margin at tentacular level showing the velum, a cordylus, an ocellus and an adaxial spur; E, part of a hydroid colony; F, hydrotheca and hydranth (left), gonotheca with medusa buds and a young medusa (right); G, diagram of closed operculum (A-B after Bouillon *et al.*, 2000; C after Kramp, 1959b; D after Russell,1953; E-F after Russell, 1936a; G after Cornelius, 1995).

FIG. 161. *Leptomedusae, Laodiceidae. A-B,* Guillea canyonincolae : *A, vue générale d'une méduse mature ; B, détails du bord exombrellaire, vue adaxiale d'un tentacule marginal montrant l'ocelle (à gauche), vue abaxiale montrant les cordyles et les cirres spiralés latéraux (à droite). C-G,* Laodicea undulata : *C, méduse adulte ; D, section verticale diagrammatique au niveau d'un tentacule marginal montrant le velum, un cordyle, un ocelle et un éperon adaxial ; E, partie d'une colonie d'hydroïdes ; F, hydrothèque et son hydranthe (à gauche), gonothèque avec des bourgeons médusaires et libérant une jeune méduse (à droite) ; G, diagramme d'un opercule fermé (A-B d'après Bouillon* et al., *2000 ; C d'après Kramp, 1959b ; D d'après Russell, 1953 ; E-F d'après Russell, 1936a ; G d'après Cornelius, 1995).*

Genus ***MELICERTISSA*** Haeckel, 1879

Fig. 162A

Hydroid: unknown.
Medusa: with 8 simple radial canals; with adaxial ocelli; with or without cirri.

Melicertissa adriatica Neppi, 1915
Melicertissa clavigera Haeckel, 1879
Melicertissa malayica (Maas, 1905)
Melicertissa mayeri Kramp, 1959b
Melicertissa orientalis Kramp, 1961a
Melicertissa platygastra Nair, 1951
Melicertissa rosea Bouillon, 1984b
Melicertissa sp. – Kramp, 1965a

Genus ***PTYCHOGENA*** A. Agassiz, 1865

Fig. 162B-D

Hydroid: "*Cuspidella*"-like.
Medusa: with 4 radial canals giving rise to lateral diverticula, in which the "gonads" are located; manubrium with funnel-shaped perradial lobes; no cirri; no ocelli.

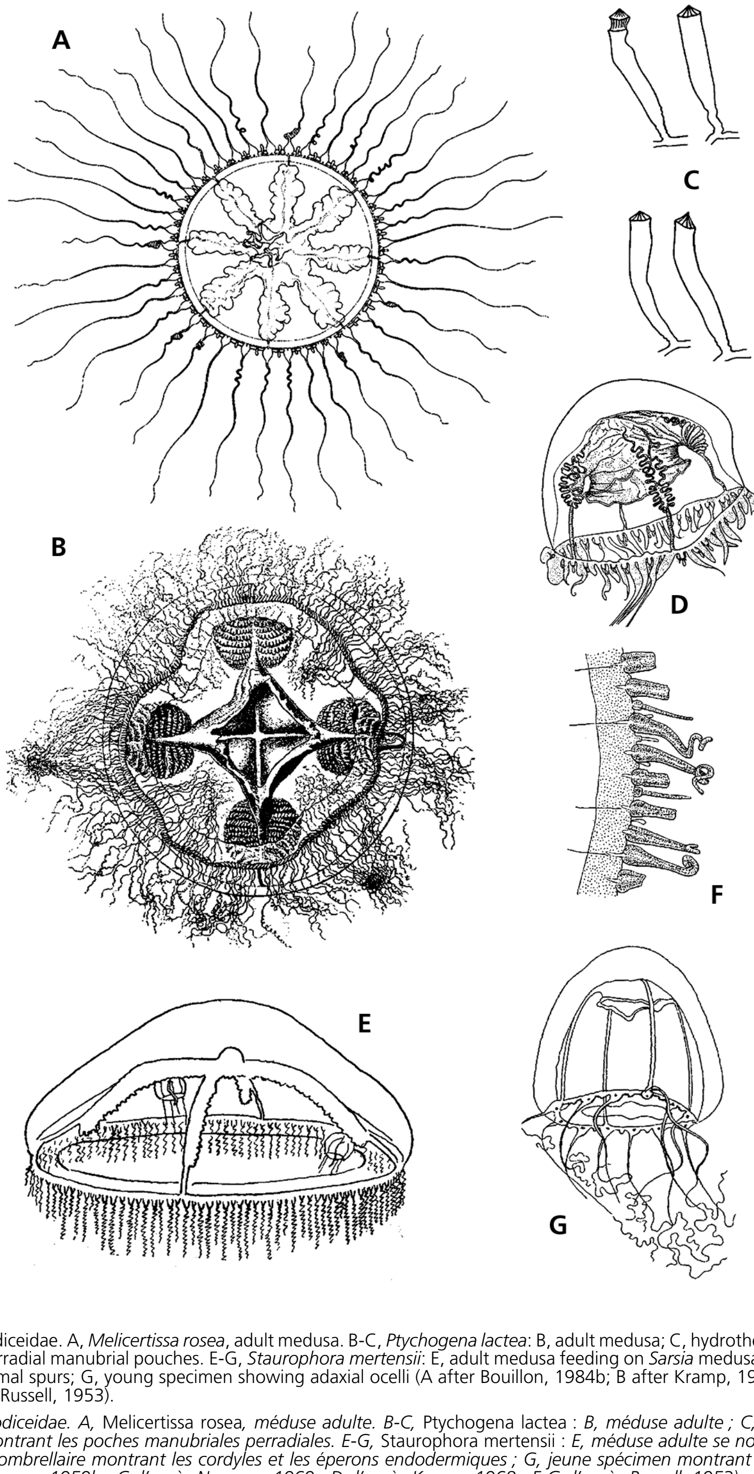


FIG. 162. Leptomedusae, Laodiceidae. A, *Melicertissa rosea*, adult medusa. B-C, *Ptychogena lactea*: B, adult medusa; C, hydrothecae. D, *Ptychogena californica*, adult medusa showing the perradial manubrial pouches. E-G, *Staurophora mertensii*: E, adult medusa feeding on *Sarsia* medusa; F, portion of umbrella margin showing cordyli and endodermal spurs; G, young specimen showing adaxial ocelli (A after Bouillon, 1984b; B after Kramp, 1959b; C after Naumov, 1969; D after Kramp, 1968; E-G after Russell, 1953).

FIG. 162. *Leptomedusae, Laodiceidae. A,* Melicertissa rosea, *méduse adulte. B-C,* Ptychogena lactea : *B, méduse adulte ; C, hydrothèques. D,* Ptychogena californica*, méduse adulte montrant les poches manubriales perradiales. E-G,* Staurophora mertensii : *E, méduse adulte se nourrissant de méduses du genre* Sarsia ; *F, portion du bord exombrellaire montrant les cordyles et les éperons endodermiques ; G, jeune spécimen montrant les ocelles adaxiaux (A d'après Bouillon, 1984b ; B d'après Kramp, 1959b ; C d'après Naumov, 1969 ; D d'après Kramp, 1968 ; E-G d'après Russell, 1953).*

Remarks: the cycle of *Ptychogena* is not firmly established yet; using zoogeographical arguments Naumov (1960) and Calder (1970) proposed a peduncled "*Cuspidella*"-like hydroid as probably representing the polyp of *Ptychogena lactea*.

Ptychogena antarctica Browne, 1907b
Ptychogena aurea Vanhöffen, 1912 [probably a syn. of *Chromatonema rubrum*]
Ptychogena californica Torrey, 1909
Ptychogena crocea Kramp & Damas, 1925
Ptychogena hyperborea Kramp, 1942
Ptychogena lactea Agassiz, 1865
Ptychogena longigona Maas, 1893 [probably a syn. of *Laodicea undulata*]

Genus ***STAUROPHORA*** Brandt, 1834

Figs 162E-G, 163A-C

Hydroid: typical cuspidellid polyp, hydrotheca sessile; gonothecae unknown. Doubtfully identified as *Cuspidella humilis* by Naumov (1951).
Medusa: manubrium cross-shaped; 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; no cirri; with adaxial ocelli.

Staurophora mertensii Brandt, 1834

Genus ***WUVULA*** Bouillon, Seghers & Boero, 1988

Fig. 163D-E

Hydroid: unknown.
Medusa: more than 4 radial canals, sometimes partially ramified; numerous cordyli modified in vesicles enclosing zooxanthellae; adaxial papillae on marginal tentacular bulbs, on cordyliform vesicles and rudimentary bulbs when present; no ocelli.

Wuvula ochracea (Mayer, 1910)
Wuvula fabietti Bouillon, Seghers & Boero, 1988b

Family LINEOLARIIDAE Allman, 1864

Hydroid: colony stolonal, growing on an underlying sheet of perisarc; hydrothecae sessile or shortly pedicellate, adherent to substrate, deep, tubular to sac-like, margin upturned, even or lobate, operculum a single flap or conical, formed of converging segments demarcated from margin; nematophores present or absent; gonophores as fixed sporosacs, gonothecae sessile, adherent to substrate
Recent reference: Watson (1992).

KEY TO HYDROIDS

1. hydrotheca shortly but distinctly pedicellate .... *Agglutinaria*
– hydrotheca not pedicellate 2

2. operculum pyramidal, segmented; with nematophores .... *Nicoliana*
– operculum as single flap; without nematophores .... *Lineolaria*

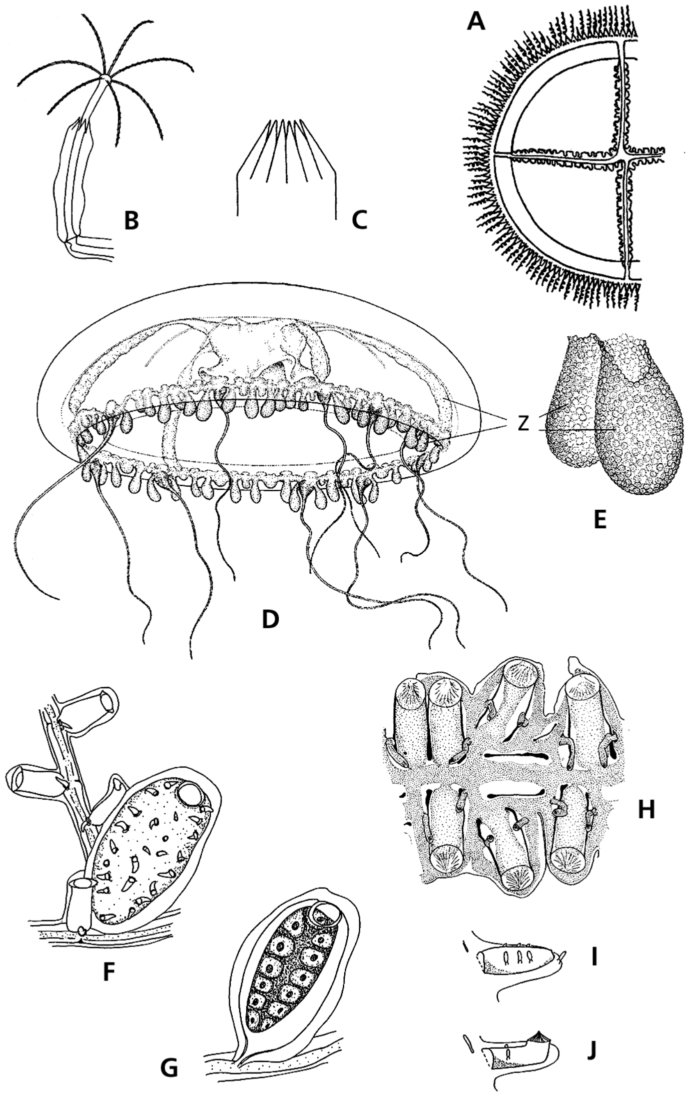


FIG. 163. Leptomedusae, Laodiceidae. A-C, *Staurophora mertensii*: A, immature medusa showing the mouth and radial canals combined to form a large gastric cross reaching from centre nearly to umbrella margin; B, hydrotheca and hydranth; C, diagram of operculum. D-E, *Wuvula fabietti*: D, adult medusa; E, cordyliform vesicles with zooxanthellae. Lineolariidae. F-G, *Lineolaria spinulosa*: F, part of colony with empty gonotheca; G, female gonophores inside gonotheca (spines not shown). H-J, *Nicoliana gravierae*: H, surface view of a colony growing on weed; I, lateral view of gonotheca; J, lateral view of hydrotheca (A after Kramp, 1959; B-C after Naumov, 1969; D-E after Bouillon *et al*., 1988; F-G, I-J after Watson, 1992; H after Millard & Bouillon, 1974). Z = zooxanthellae.

FIG. 163. *Leptomedusae, Laodiceidae. A-C,* Staurophora mertensii : *A, méduse immature montrant la bouche et les canaux radiaires combinés pour former une large croix gastrique atteignant presque le bord exombrellaire ; B, hydrothèque et hydranthe ; C, diagramme de l'opercule. D-E,* Wuvula fabietti : *D, méduse adulte ; E, vesicules cordyliformes contenant des zooxanthelles. Lineolariidae. F-G,* Lineolaria spinulosa : *F, partie d'une colonie avec une gonothèque vide ; G, gonophore femelle dans sa gonothèque (épines non montrées). H-J,* Nicoliana gravierae : *H, vue apicale d'une colonie poussant sur une algue ; I, vue latérale d'une gonothèque ; J, vue latérale d'une hydrothèque (A d'après Kramp, 1959 ; B-C d'après Naumov, 1969 ; D-E d'après Bouillon* et al., *1988 ; F-G, I-J d'après Watson, 1992 ; H d'après Millard & Bouillon, 1974). Z = zooxanthelles.*

Genus ***AGGLUTINARIA*** Antsulevich, 1987

Hydroid: colony stolonal, extending along the trunk and arms of the hydrozoan *Abietinaria abietina*; hydrothecae pedicellate, pedicel and most part of hydrotheca adnate to hydrorhiza and substratum; hydrotheca tubular, without diaphragm, a little swollen near the base and rim; distal part the hydrotheca, usually free and separated from the substrate by an acute angle, or adhering to the substrate; rim of the hydrotheca even, semicircular in shape, placed almost perpendicular to substrate; operculum with one adcauline valve; gonophores and gonothecae unknown.

Agglutinaria operculata Antsulevich, 1987

Genus ***LINEOLARIA*** Hincks, 1861

Fig. 163F-G

Hydroid: colony stolonal, usually on weeds; hydrotheca sessile, tubular or sac-shaped, adherent to substrate for part or all its length, free part bending up almost at right angles to the attached region; no diaphragm; hydrothecal margin elliptical to circular, with two opposite lobes; operculum of a single flap; gonophores as fixed sporosacs, gonothecae sessile, adherent to substrate

Recent references: Antsulevich (1987); Calder (1991); Watson (1992).

Lineolaria flexuosa Bale, 1884
Lineolaria spinulosa Hincks, 1861b

Genus ***NICOLIANA*** Watson, 1992

Fig. 163H-J

Hydroid: colony stolonal, living on weeds; hydrotheca sessile, deep, cylindrical to sac-like, adhering to substrate for most of length, then bending upward, margin circular, with a peaked operculum of delicate converging segments demarcated from margin; nematophores present, on hydrorhiza, flanking the hydrothecae; gonophores as fixed sporosacs, gonothecae sessile adherent to substrate.

Recent reference: Millard, 1975.

Nicoliana gravierae (Millard, 1975)

Family LOVENELLIDAE Russell, 1953

Hydroid: colony stolonal or erect, sympodial; hydrotheca pedicellate, elongate, everted-conical to bell-shaped, with diaphragm; operculum conical, formed either by many triangular plates on embayments in shallowly cusped hydrothecal margin and well demarcated from hydrothecal wall by noticeable crease line, or by a folded continuation of the hydrothecal wall, lacking hinge-like base; hydrothecae may renovate, but often collapsing, disintegrating in old specimens, just a crumpled collar-shaped sheath remaining around hydranth base; hydranth with endodermal epithelium differentiated into distinct parts, upper one digestive, basal one formed by chordal cells; with or without intertentacular web; gonophores as free medusae, gonothecae peduncled.

Medusa: manubrium short; no gastric peduncle; no excretory pores; 4 simple radial canals; marginal tentacles hollow, with lateral cirri; no 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.

Remarks: the family Lovenellidae was created by Russell (1953) for Leptomedusae with lateral cirri, 4 radial canals, no marginal cirri, peduncle and excretory pores, *Lovenella*-like hydroids with a well demarcated operculum and hydrothecal margin embayments. Russell (1953) distinguished *Lovenella*, with an indefinite number of statocysts, from *Eucheilota* with usually 8 statocyst. Kramp (1959a) adopted these views and later (Kramp 1959b; 1961b; 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 embayments that should be typical of *Lovenella*, having an operculum in continuation with the hydrotheca. He consequently resurrected the genus *Dipleuron* for this species (Calder 1991). Bouillon (1985a), considering the impossibility to integrate the diagnostic characters of the polyps and medusae, separated Kramp’s Lovenellidae in three families: the Cirrholoveniidae with medusae with marginal cirri and “cuspidellid” hydroids; the Eucheilotidae with medusae with lateral cirri, 8 statocysts and “campanulinid" hydroids with a well demarcated operculum but without hydrothecal embayments; and the Lovenellidae with lateral cirri, an indefinite number of statocysts and a "*Lovenella*" type of hydroid, with a well demarcated operculum with embayments of hydrothecal margin. The study of " Lovenellidae" life cycles, however, shows that if the medusae of this family present clear diagnostic characters, their hydroids are puzzling, all belong to a "campanulinid" type but their opercular structures present differences even within the same genus. It is thus hopeless to refer with confidence one or another type of opercular structure to a family-group taxon, particularly to a medusa-based family. After Kramp (1919; 1932b), too a great importance has been given to the opercular structures of the Campanulinida. Opercula can be different within the same family (see, for instance, the Tiaropsidae and the Lineolariidae) or even within the same genus: in *Phialella*, for instance, some species have opercular flaps demarcated from hydrothecae and other do not (Boero 1987), and even different hydrothecae on the same hydrocaulus may present the two opercular types. Opercular structure, thus, 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 colony growth, as shown by Werner (1968a; b) in *Eucheilota maculata* and *Eutonina indicans* or can even be absent in some species of a normally operculate genus (many Eirenidae), only a little more than a collar remaining at the base of the hydrothecae of fully developed hydranths, looking like a haleciid theca (see for instance Werner 1968a, Fig. 14). The family Eucheilotidae is consequently considered as synonym of the Lovenellidae and the genera *Eucheilota* and *Lovenella* are again included in the Lovenellidae, being defined as above for the medusa stage, the hydroid being characterised by "campanulinid polyps" with an operculum well or not well demarcated from the hydrotheca, with hydrothecae having or not marginal embayments, or reduced to a basal collar; usually with an intertentacular web; cnidome generally with merotrichous haplonemes. The family Cirrholoveniidae, with marginal cirri and "cuspidellid" type of hydroids, is kept as valid. Two genera, *Hydranthea* with free eumedusoids and *Campalecium* with newly released medusae of *Eucheilota* type 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 similar to reduced stages of Lovenellidae, but might well represent the basal state from which paedomorphic species with fixed gonophores and reduced hydrotheca originated the Haleciidae.

Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000), Schuchert (2001a, 2003).

KEY TO HYDROIDS

1. hydroid of "*Campanulina*" facies 2
– hydroid with reduced hydrotheca, of "Haleciid" facies 3

2. hydranth with intertentacular web.......... *Eucheilota*
– hydranth without intertentacular web .... *Lovenella*

3. gonophores producing eumedusoids; gonothecae on hydrorhiza, reduced or absent .... *Hydranthea*
– gonophores producing free medusae; gonothecae growing from pedicel just under hydrothecae .... *Campalecium*

KEY TO MEDUSAE

1. without statocyst .... *Paralovenia*
– with statocysts.......... 2

2. with usually no more than 8 statocysts.......... *Eucheilota*
– with an indefinite number of statocysts (16-32) .... *Lovenella*

Genus ***EUCHEILOTA*** McCrady, 1859

Figs 164C-K, 165A

Hydroid: colony of "campanulinid" type; hydrotheca with diaphragm, hydrotheca often reduced to a collar-shaped sheath around base of adult hydranths, operculum well developed, base not demarcated; hydranth with intertentacular web; gonotheca long, pedicellate on erect stems, with one to five medusa buds.
Medusa: with usually 8 statocysts.
Recent references: Ramil (1988); Cornelius (1995); Bouillon & Boero (2000).

Eucheilota bakeri (Torrey, 1909)
Eucheilota birabeni Tundisi, 1962
Eucheilota comata (Bigelow, 1909)
Eucheilota diademata Kramp, 1959a
Eucheilota duodecimalis Agassiz, 1862
Eucheilota flevensis Van Kampen, 1922
Eucheilota foresti Goy, 1979
Eucheilota macrogona Zhang & Lin, 1984
Eucheilota maculata Hartlaub, 1894
Eucheilota menoni Kramp, 1959a
Eucheilota minima Bouillon, 1984b
Eucheilota multicirris Xu & Huang, 1990a
Eucheilota paradoxica Mayer, 1900a [syn. *E. taiwanensis* Xu & Huang, 1990]
Eucheilota tropica Kramp, 1959a
Eucheilota ventricularis McCrady, 1859a
Eucheilota sp. – Kramp, 1959
Eucheilota sp. – Bouillon & Barnett, 1999

Genus ***HYDRANTHEA*** Hincks, 1868

Fig. 165B-D

Hydroid: colony stolonal, hydrotheca short, collar-shaped, on short pedicel; hydranth elongated, large, with intertentacular web with merotrichous haploneme cnidocysts; gonophores as eumedusoid, only short-lived male free eumedusoids known; without tentacles; with four radial canals; "gonads" on radial canals, 8 statocysts; gonothecae reduced or absent; when present, attached to hydrorhiza.
Recent references: Cornelius (1995); Bouillon & Boero (2000).

Hydranthea aloysii (Zoja, 1893)
Hydranthea diaphana (Hadzi, 1912) [doubtful status]
Hydranthea margarica (Hincks, 1862)
Hydranthea phialiformis Antsulevich, 1983

Genus ***LOVENELLA*** Hincks, 1868

Figs 9O, 165E-J

Synonym: *Mitrocomium* Haeckel, 1879
Hydroid: colony "*Campanulina*" type; stolonal or upright and sympodial; hydrotheca pedicellate, usually elongate, everted-conical to bell-shaped; operculum conical, formed either by many triangular plates with embayments 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; diaphragm present; in sime species the hydrotheca is reduced to a collar shaped sheath around base of adult hydranths (haleciid type); hydranths with or without intertentacular web; no nematophores.
Medusa: with an indefinite number of statocysts.
Remarks: all *Lovenella*-like hydroids with unknown cycle must be included in the Campanulinidae *incertae sedis*.

Lovenella annae (Lendenfeld, 1885b) [doubtful status]
Lovenella assemblies (Browne, 1905a)
Lovenella bermudensis (Fewkes, 1883)
Lovenella chiquitita Millard, 1957
Lovenella cirrata (Haeckel, 1879)
Lovenella clausa (Lovén, 1836)
Lovenella corrugata Thornely, 1908 [doubtful status]
Lovenella gracilis Clarke, 1882
Lovenella grandis Nutting, 1901b [doubtful status]
Lovenella haichangensis Xu & Huang, 1983a
Lovenella nodosa Fraser, 1938a
Lovenella producta (Sars, 1874) [doubtful status]
Lovenella rugosa Fraser, 1938b [doubtful status]

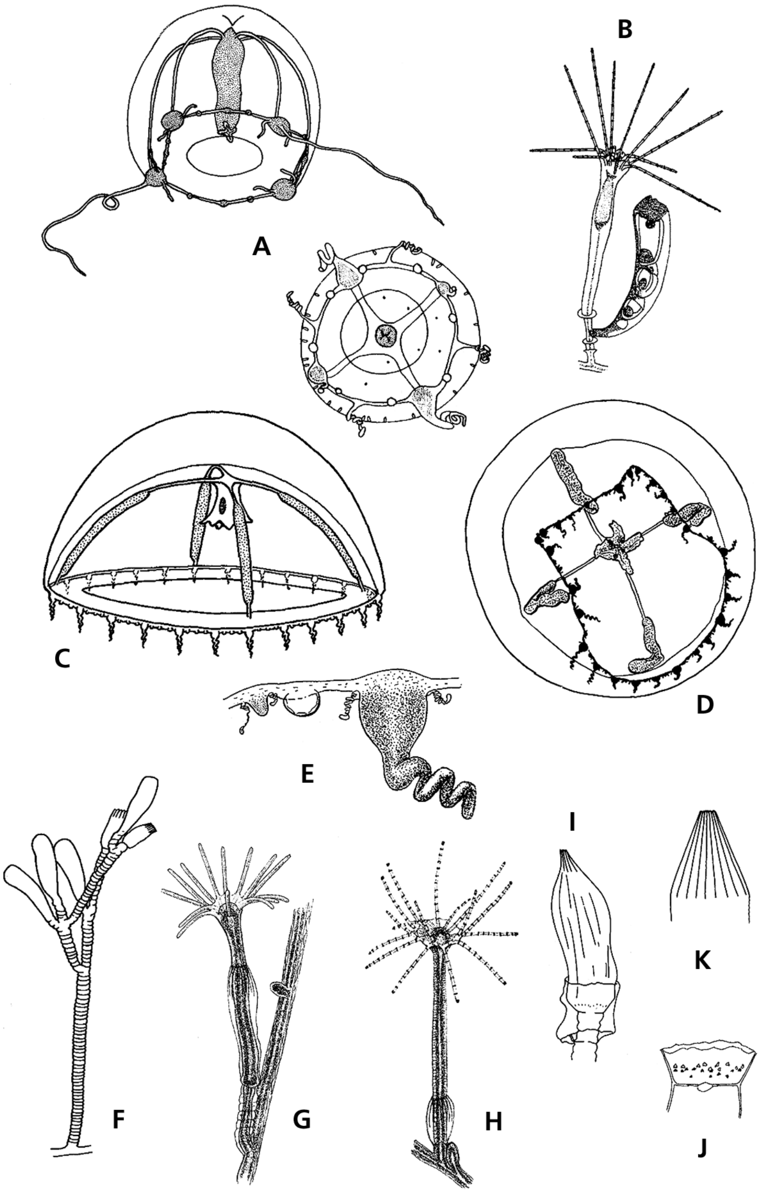


FIG. 164. Leptomedusae, Lovenellidae. A-B, *Campalecium medusiferum*: A, juvenile medusae showing the lateral cirri; B, hydranth and gonotheca. C-K, *Eucheilota maculata*: C-D, adult medusae; E, part of umbrella margin showing the base of a marginal tentacles, the lateral cirri and the statocysts; F, part of a hydroid colony; G, detail of a juvenile hydranth with its complete hydrotheca; H, fully developed hydranth with reduced hydrotheca. I, empty hydrotheca; J, operculum of the hydrotheca of a juvenile hydranth; K, remains of the hydrotheca of fully grown hydranth, haleciid stage (A above after Boero, 1980; A below & B after Boero, 1981; C after Russell, 1963; D-E after Russell, 1953; F-I & K after Werner, 1968; J after Cornelius, 1995).

FIG. 164. *Leptomedusae, Lovenellidae. A-B,* Campalecium medusiferum : *A, méduses juvéniles montrant les cirres latéraux ; B, hydranthe et gonothèque. C-K,* Eucheilota maculata : *C-D, méduses adultes ; E, bord exombrellaire montrant la base d'un tentacule marginal, les cirres latéraux et un statocyste ; F, partie d'une colonie d'hydroïdes ; G, détail d'un hydranthe juvénile avec son hydrothèque complète ; H, hydranthe complètement développé avec son hydrothèque réduite ; I, hydrothèque vide ; J, opercule de l'hydrothèque d'un hydranthe juvénile ; K, restes de l'hydrothèque d'un hydranthe adulte, stade haléciide (A au-dessus d'après Boero, 1980 ; A au-dessous & B d'après Boero, 1981 ; 3 d'après Russell, 1963 ; D-E d'après Russell, 1953 ; F-I & K d'après Werner, 1968 ; J d'après Cornelius, 1995).*

Genus ***PARALOVENIA*** Bouillon, 1984

Fig. 165L

Hydroid: unknown.

Medusa: 2 opposite perradial tentacles with large bulbs without cirri; 2 small non-tentacular bulbs with 6 lateral cirri; no rudimentary bulbs and statocysts.

Paralovenia bitentaculata Bouillon, 1984c

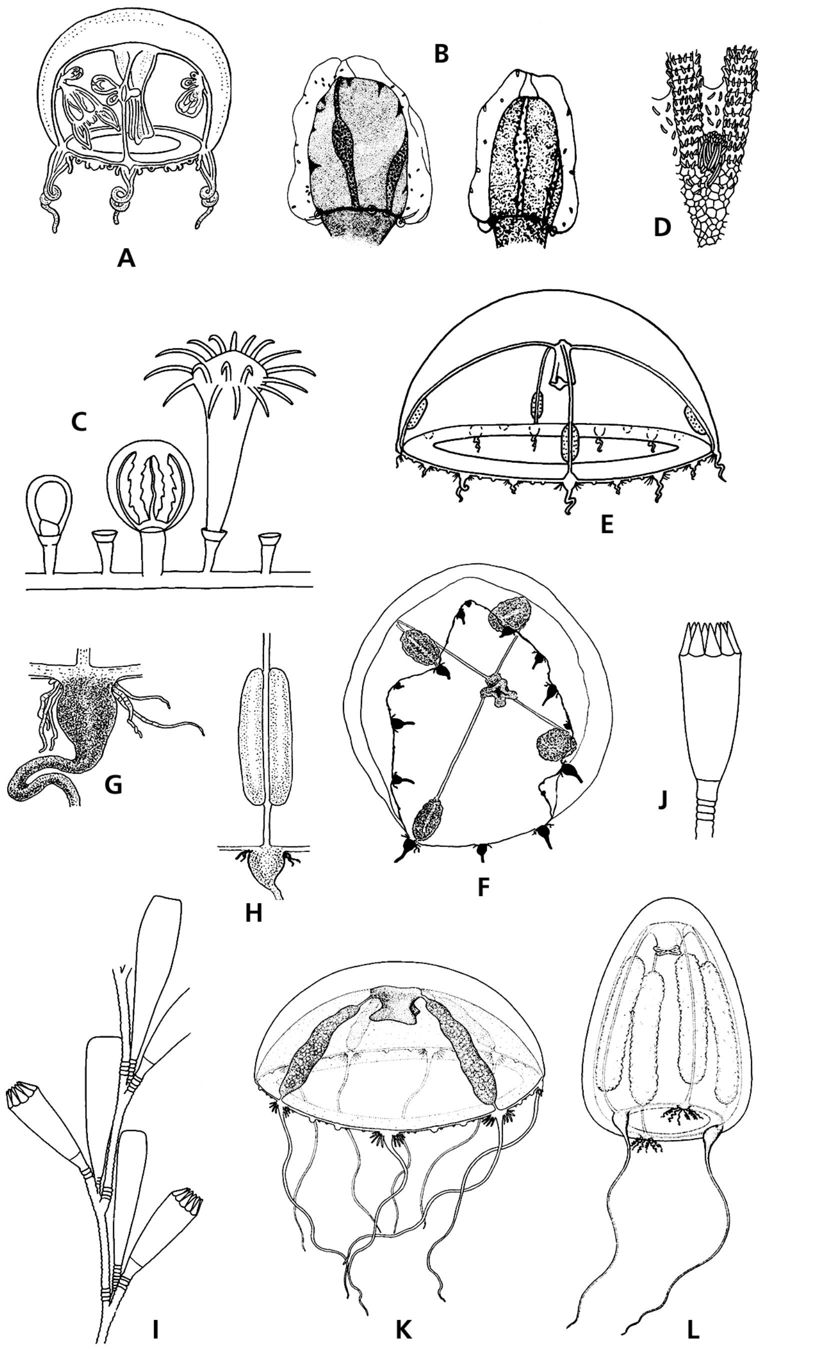


FIG. 165. Leptomedusae, Lovenellidae. A, *Eucheilota paradoxica,* medusa with medusa-buds on radial canals. B-D, *Hydranthea margarica*: B, male medusoid; C, part of a colony with a hydranth and a medusoid; D, two tentacle bases and intervening web. E-J, *Lovenella clausa*: E-F, aspects of fully grown medusae; G, detail of umbrella margin showing a marginal tentacle and its lateral cirri; H, subumbrellar view of a gonad; I, part of hydroid colony; J, hydrotheca. K, *Lovenella cirrata*, adult medusa. L, *Paralovenia bitentaculata*, adult medusa (A, after Kramp, 1959b; B after Boero & Sarà, 1987; C, I-J after Cornelius, 1995; D after Huvé, 1954; E & G after Russell, 1963; F & H after Russell, 1953; K after Pagès *et al*., 1992; L after Bouillon, 1984b).

***FIG. 165.** Leptomedusae, Lovenellidae. A,* Eucheilota paradoxica*, méduse développant des bourgeons médusaires sur les canaux radiaires. B-D,* Hydranthea margarica : *B, médusoïdes mâles ; C, partie d'une colonie montrant un hydranthe et des médusoïdes ; D, deux bases tentaculaires avec une membrane intertentaculaire. E-J,* Lovenella clausa : *E-F, aspects de méduses matures ; G, détail du bord exombrellaire montrant un tentacule marginal et ses cirres latéraux ; H, vue sous-ombrellaire d'une gonade ; I, portion d'une colonie d'hydroïdes ; J, hydrothèque. K,* Lovenella cirrata*, méduse adulte. L,* Paralovenia bitentaculata*, méduse adulte (A après Kramp, 1959b ; B d'après Boero & Sarà, 1987 ; C, I-J d'après Cornelius, 1995 ; D d'après Huvé, 1954; E & G d'après Russell, 1963 ; F & H d'après Russell, 1953 ; K d'après Pagès* et al.*, 1992 ; L d'après Bouillon, 1984b).*

Lovenellidae *incertae sedis*:

Genus ***CAMPALECIUM*** Torrey, 1902

Fig. 164A-B

Hydroid: colony typically stolonal, pedicel of varied length bearing terminal hydranth, often secondary pedicels forming sympodial branches; hydrotheca collar-shaped, shallow (often regenerated, with a distinct diaphragm, large desmocytes; hydranth relatively large, elongated, cylindrical, not retractable into hydrotheca; up to 30 amphicoronate tentacles; with or without intertentacular web; gonophores giving rise to free medusae; gonothecae clavate or rounded arising beneath hydrothecal pedicel, each with several medusa buds.
Medusa: only medusa buds or juvenile medusae of *Eucheilota* type presently known, pending the species.
Recent references: Watson (1993); Bouillon & Boero (2000); Boero, unpublished observations; Schuchert (2003).

Campalecium alcoicum Watson, 1993
Campalecium medusiferum Torrey, 1902
Campalecium simplex (Pictet, 1893) n. comb. [as *Halecium*]

Family MALAGAZZIIDAE Bouillon, 1984

Hydroid: of "campanulinid" type; colony stolonal; hydrotheca shortly pedicellate, with a conical operculum formed by numerous convergent segments not clearly demarcated from hydrothecal wall; hydranth with intertentacular web; gonotheca claviform, arising from stolon.
Medusa: manubrium small; no gastric peduncle; 4-8, sometimes up to 12 radial canals; "gonads" completely surrounding radial canals, separated from manubrium; adaxial excretory papillae; no permanent rudimentary marginal bulbs (all bulbs potentially transforming into tentacles); closed statocysts; no ocelli and cirri.

KEY TO HYDROIDS

Hydroids only known in some *Malagazzia* and *Octophialucium*, from rearing experiments, both of "*Campanulina*" facies indistinguishable at present stage of knowledge.

KEY TO MEDUSAE

1. normally 4 radial canals (sometimes up to 10, asymmetrically arranged) 3
– normally 8 or more, symmetrically arranged, radial canals 2

2. mouth with 4 lips . . . . *Octocanna*
– mouth with 8 lips . . . . *Octophialucium*

3. rounded "gonads"; no excretory papillae . . . . *Tetracanna*
– linear "gonads"; excretory papillae . . . . *Malagazzia*

Genus ***MALAGAZZIA*** Bouillon, 1984

Fig. 166A-C

Hydroid: See family characters.
Medusa: normally 4 radial canals; manubrium with 4 lips; gonad linear or ribbon-like.

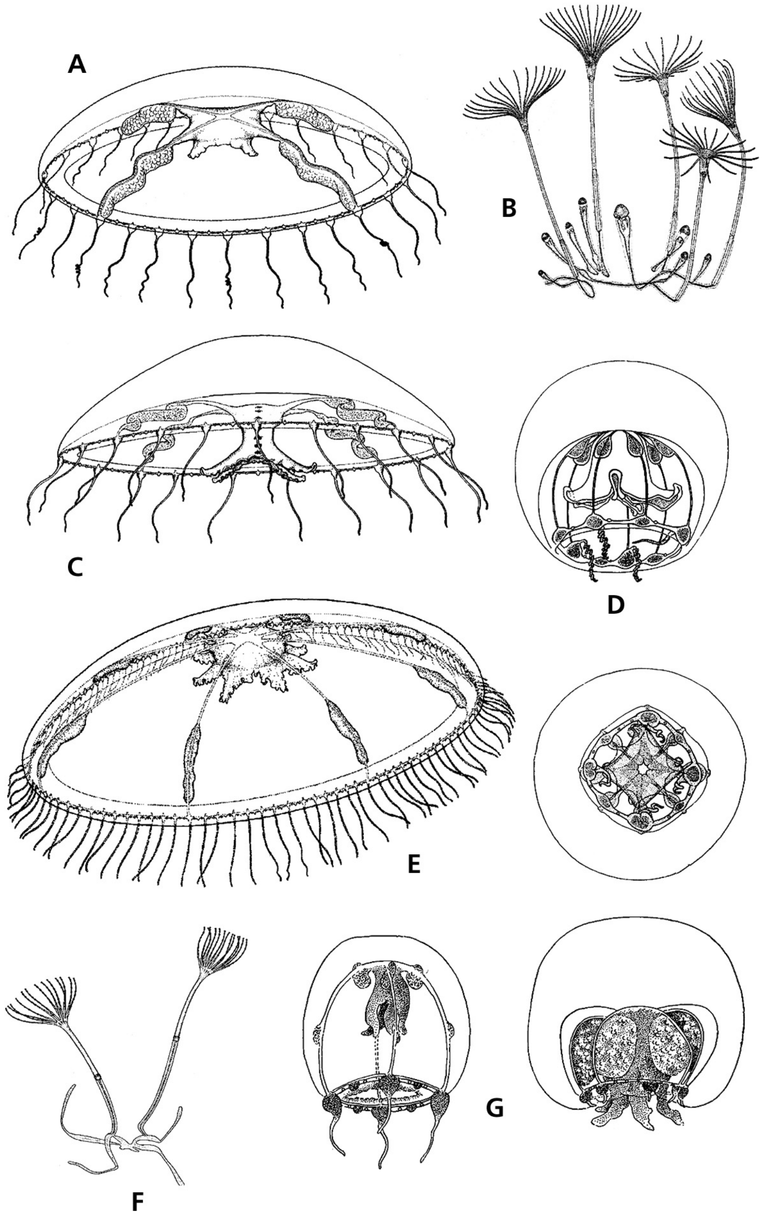


FIG.166. Leptomedusae, Malagazziidae. A-B, *Malagazzia condensum*: A, fully-grown medusa; B, hydroid colony. C, *Malagazzia multitentaculata*, adult medusa. D, *Octocanna haeckeli*, adult medusae, lateral view (above), oral view (below). E-F, *Octophialucium aphrodite*: E, adult medusa; F, part of a hydroid colony. G, *Tetracanna octonema*, young specimen (left), mature specimen (right) (A-C, E-F after Bouillon, 1984b; D after Vannucci & Soares Moreira 1966b; G after Goy, 1979).

FIG. 166. *Leptomedusae, Malagazziidae. A-B,* Malagazzia condensum : *A, méduse adulte ; B, colonie d'hydroïdes. C,* Malagazzia multitentaculata, *méduse adulte. D,* Octocanna haeckeli, *méduses adultes, vue latérale (au-dessus), vue orale (au-dessous). E-F,* Octophialucium aphrodite : *E, méduse adulte ; F, fragment de colonie d'hydroïdes. G,* Tetracanna octonema, *jeune spécimen (à gauche), méduse mature (à droite) (A-C, E-F d'après Bouillon, 1984b ; D d'après Vannucci & Soares Moreira 1966b ; G d'après Goy, 1979).*

Malagazzia carolinae (Mayer, 1900b)
Malagazzia condensum (Kramp, 1953)
Malagazzia curviductum (Xu & Zhang, 1978)
Malagazzia cyphogonia (He & Xu, 1982)
Malagazzia multitentaculatum (Menon, 1932)
Malagazzia taeniogonia (Chow & Huang, 1958)

Genus ***OCTOCANNA*** Haeckel, 1879

Fig. 166D

Hydroid: unknown.
Medusa: 8 radial canals; 8 "gonads" on radial canals; 4 hollow marginal tentacles and 4 small, non-tentacular marginal bulbs; 4 long oral lips; excretory pores on small adradial papillae.

Octocanna haeckeli Vannucci & Soares Moreira, 1966b
Octocanna octonema Haeckel, 1879
Octocanna polynema Haeckel, 1879

Genus ***OCTOPHIALUCIUM*** Kramp, 1955

Fig. 166E-F

Hydroid: of "campanulinid" type, see family characters.
Medusae: normally 8 radial canals; 8 "gonads" on radial canal; mouth with 8 lips.

Octophialucium aphrodite (Bigelow, 1919)
Octophialucium bigelowi Kramp, 1955
Octophialucium funerarium (Quoy & Gaimard, 1827)
Octophialucium indicum (Kramp, 1958)
Octophialucium krampi Bouillon, 1984b
Octophialucium medium Kramp, 1955
Octophialucium mollis Bouillon, 1984b
Octophialucium solidum (Menon, 1932)

Genus ***TETRACANNA*** Goy, 1979

Fig. 166G

Hydroid: unknown.
Medusae: 4 radial canals; 8 marginal tentacles; 4 long oral 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).

Tetracanna octonema Goy, 1979

Family MELICERTIDAE Agassiz, 1862

Hydroid: colony stolonal, with branching stolon and erect shoots bearing one, sometimes two, hydranths; perisarc thinning away completely below hydranth base, no hydrotheca; hydranth naked, large, broad in the middle, thin below, tapering gently above, with narrow, amphicoronate tentacles; no intertentacular web; gonophores borne on hydranth column, no gonothecae (hydroid known only in *Melicertum*).
Medusa: base of manubrium attached over its whole surface; 8 simple or bifurcated radial canals; marginal tentacles hollow; no cirri, statocysts and cordyli; with or without ocelli.

KEY TO HYDROIDS
(see above)

KEY TO MEDUSAE

1. radial canals bifurcated .... *Netocertoides*
– radial canals simple 2
2. 8 radial canals, 4 developed centripetally from circular canal .... *Melicertoides*
– all radial canals arise from manubrium 3
3. 8 large marginal tentacles and a few rudimentary bulbs .... *Orchistomella*
– numerous marginal tentacles .... *Melicertum*

Genus ***MELICERTOIDES*** Kramp, 1959

Fig. 167A

Hydroid: unknown.
Medusa: 8 simple radial canals, 4 primary and 4 secondary, the latter developed centripetally from circular canal; "gonads" adjacent to manubrium.

Melicertoides centripetalis Kramp, 1959a
Melicertoides octolabiatis Xu, Huang & Chen, 1991 [juvenile medusae]

Genus ***MELICERTUM*** L. Agassiz, 1862

Fig. 167B-D

Hydroid: see family characters.
Medusa: 8 simple radial canals, 4 primary and 4 secondary, all arising from manubrium; "gonads" on radial canals, separated from manubrium; no ocelli?

Melicertum campanula (Fabricius, 1780)
Melicertum georgicum Agassiz, 1862
Melicertum octocostatum (Sars, 1835)
Melicertum panocto (Haeckel, 1879) [doubtful status]

Genus ***NETOCERTOIDES*** Mayer, 1900

Fig. 167E

Hydroid: unknown.
Medusa: 8 main radial canals bifurcating once, all arising from manubrium; "gonads" on main radial canals adjacent to manubrium.

Netocertoides brachiatus Mayer, 1900a

Genus ***ORCHISTOMELLA*** Kramp, 1959

Fig. 167F

Hydroid: unknown.
Medusa: 8 or more radial canals, all arising from manubrium; with or without ocelli, "gonads" unknown.

Orchistomella applanata Kramp, 1959a
Orchistomella graeffei (Neppi & Stiasny, 1911) [probably a juvenile *Aequorea*]
Orchistomella tentaculata (Mayer, 1900b) [probably a juvenile *Aequorea*]

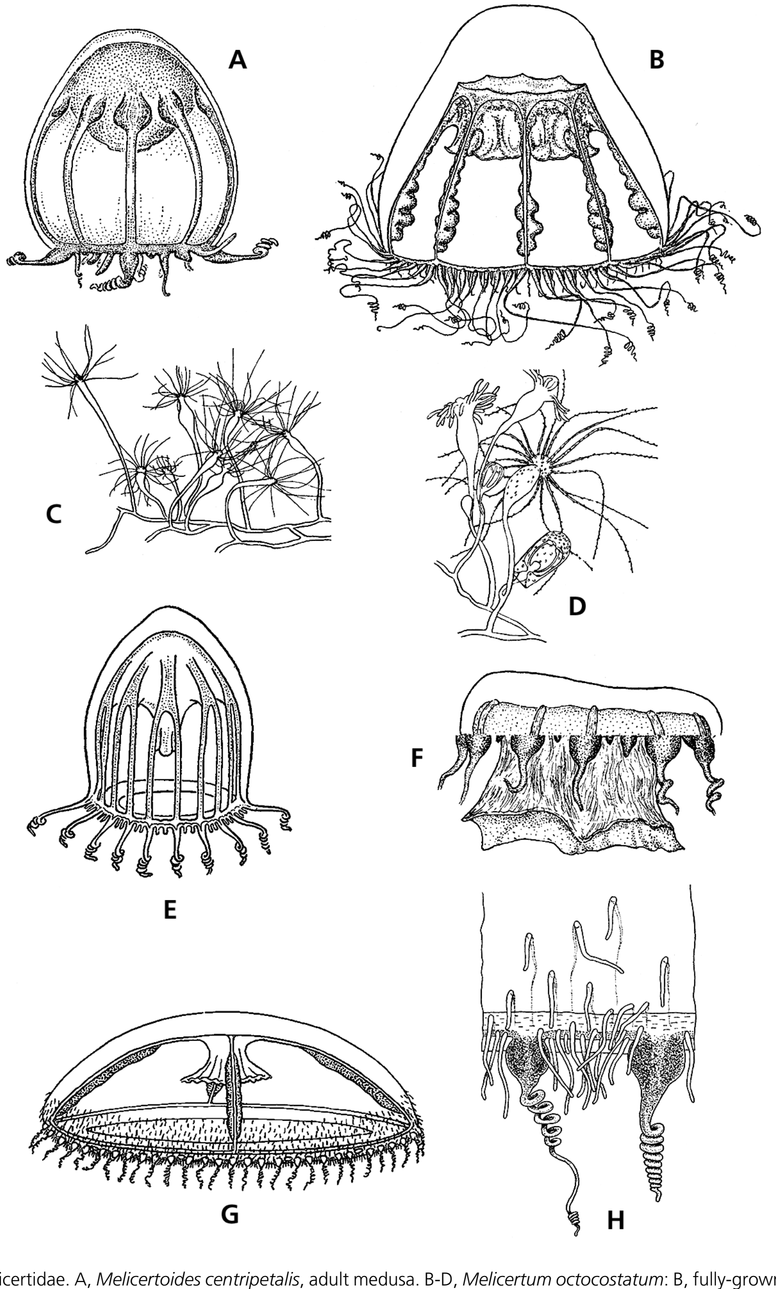


FIG. 167. Leptomedusae, Melicertidae. A, *Melicertoides centripetalis*, adult medusa. B-D, *Melicertum octocostatum*: B, fully-grown medusa; C, hydroid colony; D, hydroid colony with medusa buds. E, *Netocertoides brachiatus*, adult medusa. F, *Orchistomella applanata*, medusa. Mitrocomidae. G-H, *Cosmetira pilosella*: G, fully grown medusa; H, detail of umbrella margin showing two marginal tentacles and the flexile cirri, the older cirri extending up unto exumbrellar surface (A-B, E-F after Kramp, 1968; C-D & H after Russell, 1953; G after Cornelius 1995).

FIG. 167. *Leptomedusae, Melicertidae. A,* Melicertoides centripetalis*, méduse adulte. B-D,* Melicertum octocostatum : *B, méduse adulte ; C, colonie d'hydroïdes ; D, colonie d'hydroïdes avec bourgeons médusaires. E,* Netocertoides brachiatus*, méduse adulte. F,* Orchistomella applanata*, méduse Mitrocomidae. G-H,* Cosmetira pilosella : *G, méduse adulte ; H, détail du bord exombrellaire montrant deux tentacules marginaux et les cirres marginaux souples, les cirres les plus âgés s'étendent sur la surface latérale exombrellaire (A-B, E-F d'après Kramp, 1968 ; C-D & H d'après Russell, 1953 ; H d'après Cornelius 1995).*

Family MITROCOMIDAE Haeckel, 1879

Hydroid: poorly known, stolonal; 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 usually amphicoronate tentacle whorl; no intertentacular web; no nematophores; gonophores as free medusae, gonotheca scarcely pedicellate, on hydrorhiza.

Medusa: bases of manubrium attached to subumbrella along continuation of radial canals; 4 or more simple radial canals; marginal tentacles hollow; marginal cirri present in some genera; "gonads" oval or linear, only on radial canals; open statocysts; no ocelli.

Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

(see above)

KEY TO MEDUSAE

1. radial canals "S" shaped .... *Cyclocanna*
– radial canals straight 2

2. 4 radial canals 3
– 12 to 16 radial canals .... *Halopsis*

3. marginal cirri 5
– no marginal cirri........ 4

4. numerous open statocysts .... *Foersteria*
– only 8 open statocysts .... *Cosmetirella*

5. flexile cirri, with cnidocysts throughout their length, 8 marginal statocysts........ *Cosmetira*
– spiral marginal cirri with terminal cnidocyst cluster 6

6. 8-16 open statocysts .... *Mitrocomella*
– numerous (20-160) open statocysts .... *Mitrocoma*

Genus ***COSMETIRA*** Forbes, 1848

Figs 25K, 26P, 27B, 167G-H, 168A

Hydroid: colony stolonal, of "*Cuspidella*" type, operculum with numerous sharp pointed, triangular flaps, meeting centrally and presenting no clear limits with hydrothecal margin; gonotheca similar to hydrotheca, on hydrorhiza.

Medusa: 4 radial canals; 8 open statocysts; no ocelli; flexile cirri with numerous cnidocysts throughout their length, usually straight, exceptionally, in young specimens, spirally coiled.

Cosmetira pilosella (Forbes, 1848)

Genus ***COSMETIRELLA*** Browne, 1910

Fig. 168B

Hydroid: unknown.

Medusa: 4 radial canals; 8 open statocysts; no marginal cirri; no ocelli.

Cosmetirella davisi (Browne, 1902)

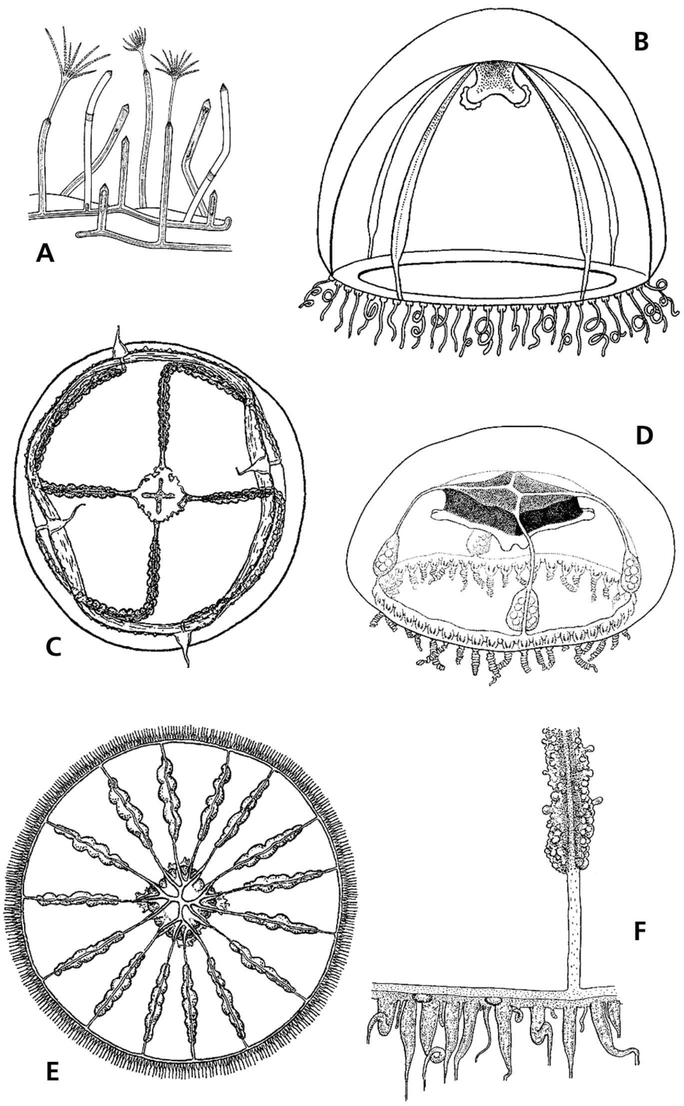


FIG. 168. Leptomedusae, Mitrocomidae. A, *Cosmetira pilosella*, part of a hydroid colony. B, *Cosmetirella davisi*, adult medusa. C, *Cyclocanna welshi*, adult medusa. D, *Foersteria antoniae*, fully grown medusa. E-F, *Halopsis ocellata* : E, general view of an adult medusa; F, portion of umbrella margin showing distal end of radial canal and gonad, tentacles and statocysts (A after Rees, 1941a; B after Kramp, 1968; C & E after Kramp, 1959b; D after Gili *et al*., 1998; F after Russell, 1953).

FIG. 168. *Leptomedusae, Mitrocomidae. A,* Cosmetira pilosella, *portion d'une colonie d'hydroïdes. B,* Cosmetirella davisi, *méduse adulte. C,* Cyclocanna welshi, *méduse adulte. D,* Foersteria antoniae, *méduse adulte. E-F,* Halopsis ocellata *: E, vue générale d'une méduse adulte; F, portion du bord exombrellaire montrant les extrémités distales d'un canal radiaire et d'une gonade ainsi que des tentacules, des cirres spiralés marginaux et des statocystes ouverts (A d'après Rees, 1941a ; B d'après Kramp, 1968 ; C & E after Kramp, 1959b ; D d'après Gili* et al.*, 1998 ; F d'après Russell, 1953).*

Genus ***CYCLOCANNA*** Bigelow, 1918

Fig. 168C

Hydroid: unknown.
Medusa: 4 radial canals, each bent like an S; 8 open statocysts; no ocelli.

Cyclocanna welshi Bigelow, 1918

Genus ***FOERSTERIA*** Arai & Brinckmann-Voss, 1980

Fig. 168D

Hydroid: unknown.
Medusa: 4 radial canals; numerous open statocysts; no marginal cirri.

Foersteria antoniae Gili, Bouillon, Pagès, Palanques, Puig & Heussner, 1998
Foersteria araiae Gili, Bouillon, Pagès, Palanques & Puig, 1999
Foersteria bruuni (Navas, 1969)
Foersteria purpurea (Foerster, 1923) [as *Staurophora*]

Genus ***HALOPSIS*** A. Agassiz, 1863

Fig. 168E-F

Hydroid: unknown.
Medusa: more than 8 radial canals; marginal cirri spirally coiled; numerous (about 80) statocysts.

Halopsis ocellata Agassiz, 1863

Genus ***MITROCOMA*** Haeckel, 1864

Fig. 27F, 169A-E

Hydroid: colony of "*Cuspidella*" type, operculum with numerous sharp, pointed, triangular flaps, meeting centrally and presenting no clear limits with hydrothecal margin.
Medusa: 4 radial canals; numerous open statocysts; marginal cirri.

Mitrocoma annae Haeckel, 1864
Mitrocoma cellularia (Agassiz, 1865)
Mitrocoma discoidea Torrey, 1909
Mitrocoma minervae Haeckel, 1879 [doubtful status]

Genus ***MITROCOMELLA*** Haeckel, 1879

Figs 27D, 169F-J

Hydroid: colony of "*Cuspidella*" type; operculum pleated, presenting no clear limits with the hydrothecal margin; gonangia unknown.
Medusa: 4 radial canals; marginal cirri spirally coiled or not; 8, 12 or 16 (exceptionally up to 19) statocysts.

Mitrocomella brownei (Kramp, 1930)
Mitrocomella cruciata (Agassiz, 1865)
Mitrocomella frigida (Browne, 1910)
Mitrocomella fulva Browne, 1903
Mitrocomella grandis Kramp, 1965a
Mitrocomella millardae Pagès, Gili & Bouillon, 1992
Mitrocomella niwai Bouillon & Barnett, 1999
Mitrocomella polydiademata (Romanes, 1876a)
Mitrocomella sinuosa (Foerster, 1923)

Family OCTOCANNOIDIDAE Bouillon, Boero & Seghers, 1991 [as Octocannoidae]

Hydroid: unknown.
Medusa: 8 simple radial canals; 8 marginal tentacles; 16-32 short club-shaped "tentaculae", all marginal structures with black pigmented spots; manubrium short; mouth with 8 simple lips; no gastric peduncle and excretory papillae; "gonads" consisting of two lateral halves; with numerous statocysts, no ocelli.

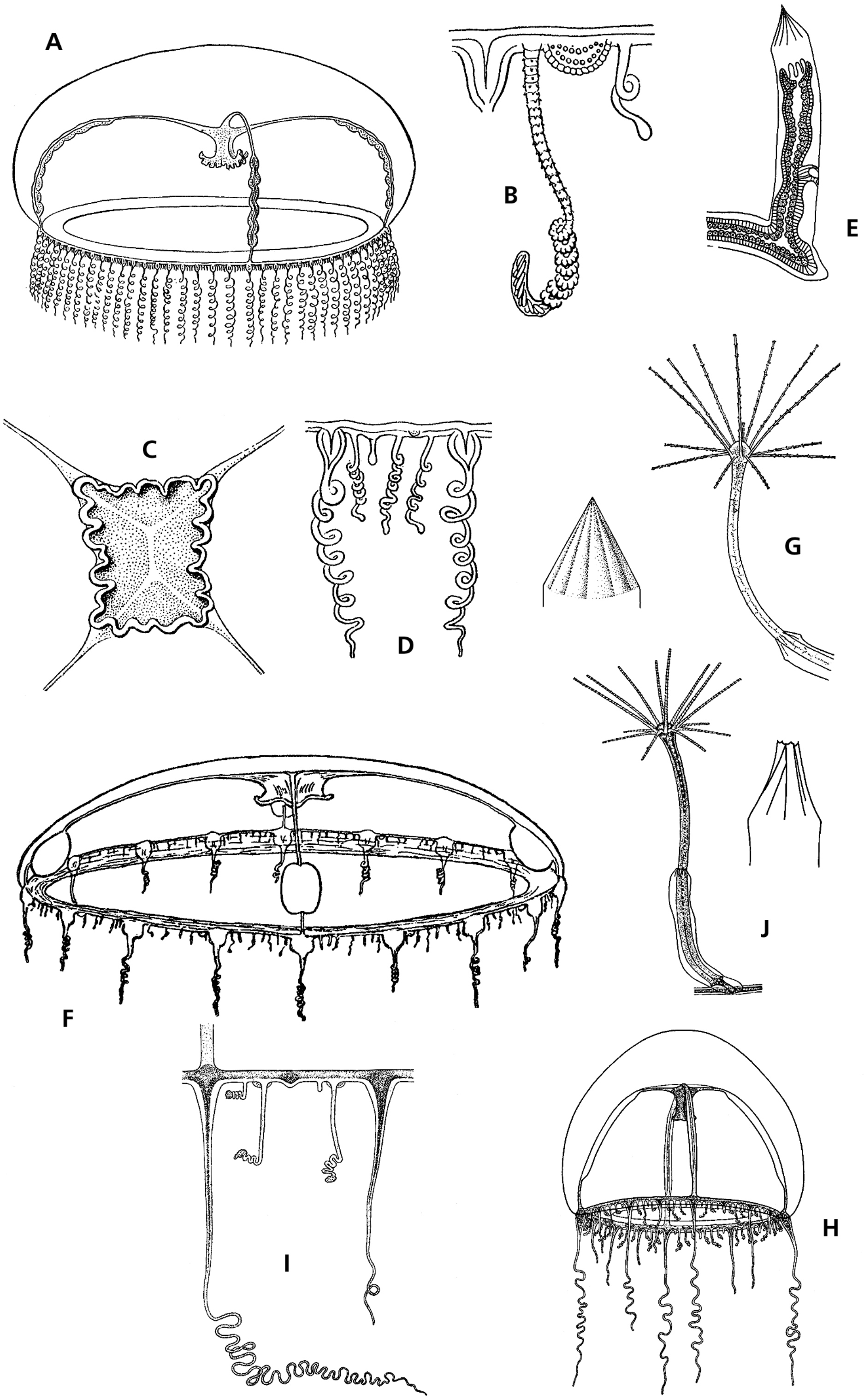


FIG. 169. Leptomedusae, Mitrocomidae. A-E, *Mitrocoma annae*: A, general view of an adult medusa; B & D, portions of umbrella margin showing spiral cirri and open statocysts; C, oral view of open mouth; E, hydranth. F-G, *Mitrocomella brownei*: F, general view of an adult medusa; G, diagram of operculum (left), hydranth (right). H-J, *Mitrocomella polydiademata*: H, mature medusa ; I, portion of umbrella margin showing an open statocyst, the spiral cirri and tentacles ; J, fully grown polyp (left), closed operculum showing the pleated structure (right) (A-D after Mayer, 1910; E after Metschnikoff, 1886; F after Kramp, 1959b; G left after Cornelius, 1995, G right after Russell, 1953; H-J after Edwards, 1973).

FIG. 169. *Leptomedusae, Mitrocomidae. A-E,* Mitrocoma annae : *A, vue générale d'une méduse adulte ; B & D, portions du bord exombrellaire montrant les cirres spiralés et les statocystes ouverts ; C, vue orale de la bouche ouverte ; E, hydranthe. F-G,* Mitrocomella brownei : *F, vue générale d'une méduse adulte ; G, diagramme de l'opercule (à gauche), hydranthe (à droite). H-J,* Mitrocomella polydiademata : *H, méduse mature ; I, portion du bord exombrellaire montrant un statocyste ouvert, les cirres spiralés et les tentacules ; J, polype adulte (à gauche), opercule fermé montrant sa structure plissée (à droite) (A-D d'après Mayer, 1910 ; E d'après Metschnikoff, 1886 ; F d'après Kramp, 1959b ; G à gauche d'après Cornelius, 1995, G à droite d'après Russell, 1953 ; H-J d'après Edwards, 1973).*

Genus *OCTOCANNOIDES* Menon, 1932

Fig. 170A-B

See family characters.

Octocannoides ocellata Menon, 1932

Family ORCHISTOMATIDAE Bouillon, 1984

Hydroid: unknown.

Medusa: manubrium very short; gastric peduncle large; mouth with 8-30 sinuous or crenulated lips; 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, cordyli, excretory pores or papillae.

Genus *ORCHISTOMA* Haeckel, 1879

Figs 27E, 170C-E

Hydroid: unknown.

Medusa: see family characters.

Orchistoma agariciforme Keller, 1884
Orchistoma collapsa (Mayer, 1900a)
Orchistoma manam Bouillon, 1984b
Orchistoma nubiae Bouillon, 1984b
Orchistoma pileus (Lesson, 1843)

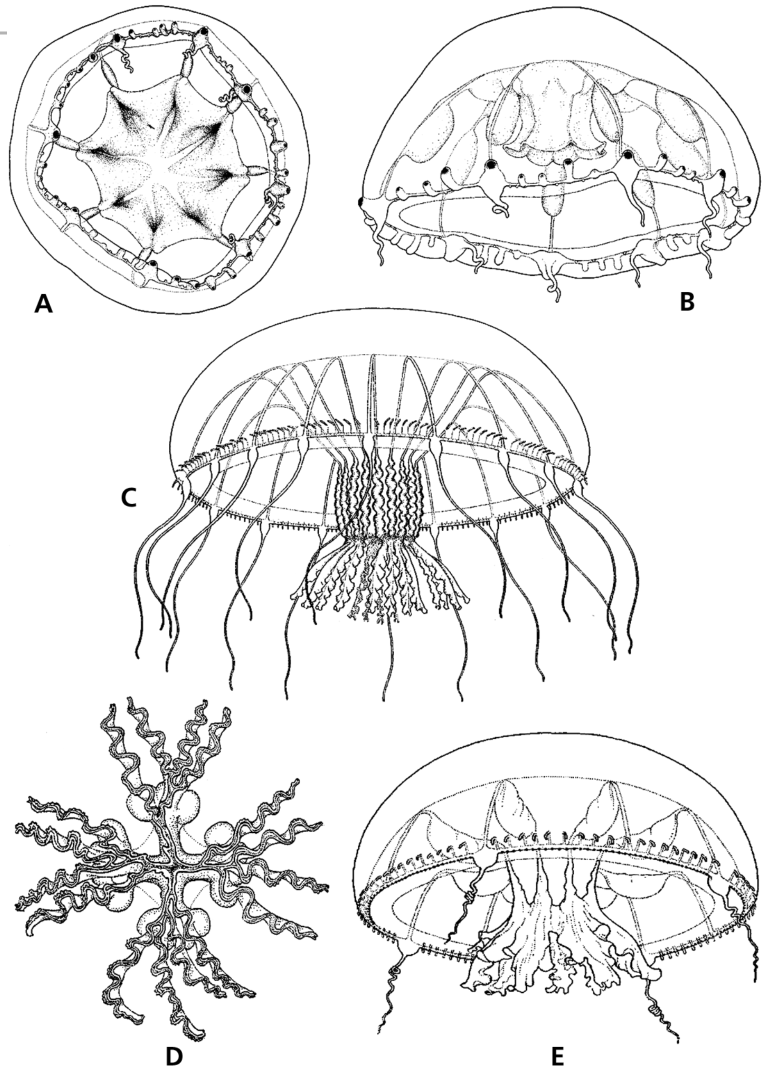


FIG.170. Leptomedusae, Octocannoidae. A-B, *Octocannoides ocellata*, adult medusa: A, oral subumbrellar view; B, lateral view. C-E, Orchistomidae. C-D, *Orchistoma agariciforme*: C, general view of an adult medusa; D, detail of lips, mouth and manubrium; E, *Orchistoma manam*, fully-grown medusa (A-B after Bouillon *et al*., 1991; C-E after Bouillon, 1984b).

FIG. 170. *Leptomedusae, Octocannoidae. A-B,* Octocannoides ocellata*, méduse adulte : A, vue orale sous-ombrellaire ; B, vue latérale. C-E, Orchistomidae. C-D,* Orchistoma agariciforme : *C, vue générale d'une méduse adulte ; D, détail des lèvres de la bouche et du manubrium ; E,* Orchistoma manam*, méduse adulte (A-B d'après Bouillon* et al.*, 1991 ; C-E d'après Bouillon, 1984b).*

Family PHIALELLIDAE Russell, 1953

Hydroid: colony stolonal or erect, arising from a creeping hydrorhiza, sympodial; hydrotheca pedicellate, tubular to deeply campanulate, persistent, with a cone-shaped operculum formed by separate triangular flaps demarcated or not from hydrothecal margin by a basal crease line; diaphragm present; gonophores as free medusae, gonotheca usually stolonal, sometimes on erect shoot.
Medusa: manubrium small; no gastric peduncle; 4 radial canals; "gonads" on radial canals, separated from manubrium and divided into two lateral parts by a median groove; tentacles hollow, smooth or moniliform; no excretory pores, lateral or marginal cirri; 8 closed statocysts, usually each on a bulbous-like swellings; without ocelli.
Recent references: Boero (1987); Calder (1991); Schuchert (2001a).

Genus ***PHIALELLA*** Browne, 1902
Figs 25D, 171A-I

Hydroid: colony stolonal or erect; when erect, branches irregularly flexuose; stem and pedicels annulated almost throughout, not divided in internodes; hydrotheca minute, campanulate, with diaphragm, on ringed pedicels; operculum with opercular flaps demarcated or not from hydrothecae; hydranth extensile, without intertentacular web, with amphicoronate tentacles; gonophores as free medusae, gonothecae arising from short annulated pedicel on hydrorhiza or stem.
Medusa: see family characters.
Remarks: for geographical reasons, Rees & Thursfield (1965) suggested that the hydroid-based *Opercularella* (*Phialella*) *chilensis* Hartlaub (1904) could correspond to the medusa-based *P. falklandica*.
Recent reference: Blanco *et al.* (2000).

Phialella annulata (von Lendenfeld, 1885a) [doubtful status]
Phialella dissonema (Haeckel, 1879) [doubtful status]
Phialella falklandica Browne, 1902
Phialella fragilis (Uchida, 1938)
Phialella hyalina (Lendenfeld, 1885b) [doubtful status]
Phialella macrogona Xu, Huang & Wang, 1985
Phialella parvigastra (Mayer, 1900a)
Phialella quadrata (Forbes, 1848)
Phialella turrita (Hincks, 1868) [only medusa buds known]
Phialella zappai Boero, 1987

Phialellidae *incertae sedis*:
All the Phialellidae-like hydroids described with an unknown cycle or juvenile medusa buds must be included in the Campanulinidae *incertae sedis*.

Family PLUMULARIIDAE McCrady, 1859

Hydroid: colony upright, monosiphonic or polysiphonic, arising from creeping, rootlike, or disc-shaped hydrorhiza; hydrocauli branched or unbranched, hydrocladia alternate, opposite or in verticils, arising in polysiphonic hydrocauli from a single axial tube; hydrothecae typically small, uniseriate, usually at least partially adnate, occurring only on hydrocladia, with or without marginal cusps; nematophores with well developed nematothecae, not as naked sarcostyles; all nematothecae (axillar, cauline or hydrothecal) usually two-chambered (bithalamic) and movable, a minimum of three nematothecae adjacent to hydrothecae, one mesial inferior and a pair of lateral ones; gonophores as fixed sporosacs, exceptionally as swimming gonophores; gonothecae solitary, without nematothecae; with or without phylactocarps. (Figs 4E, 9, 20).
Recent references: Cornelius (1995); Hirohito (1995); Migotto (1996); Calder (1997); Calder & Vervoort (1998); Peña Cantero & Vervoort (1999); Watson (2000); Angis Agís *et al.* (2001); Schuchert (2001a).

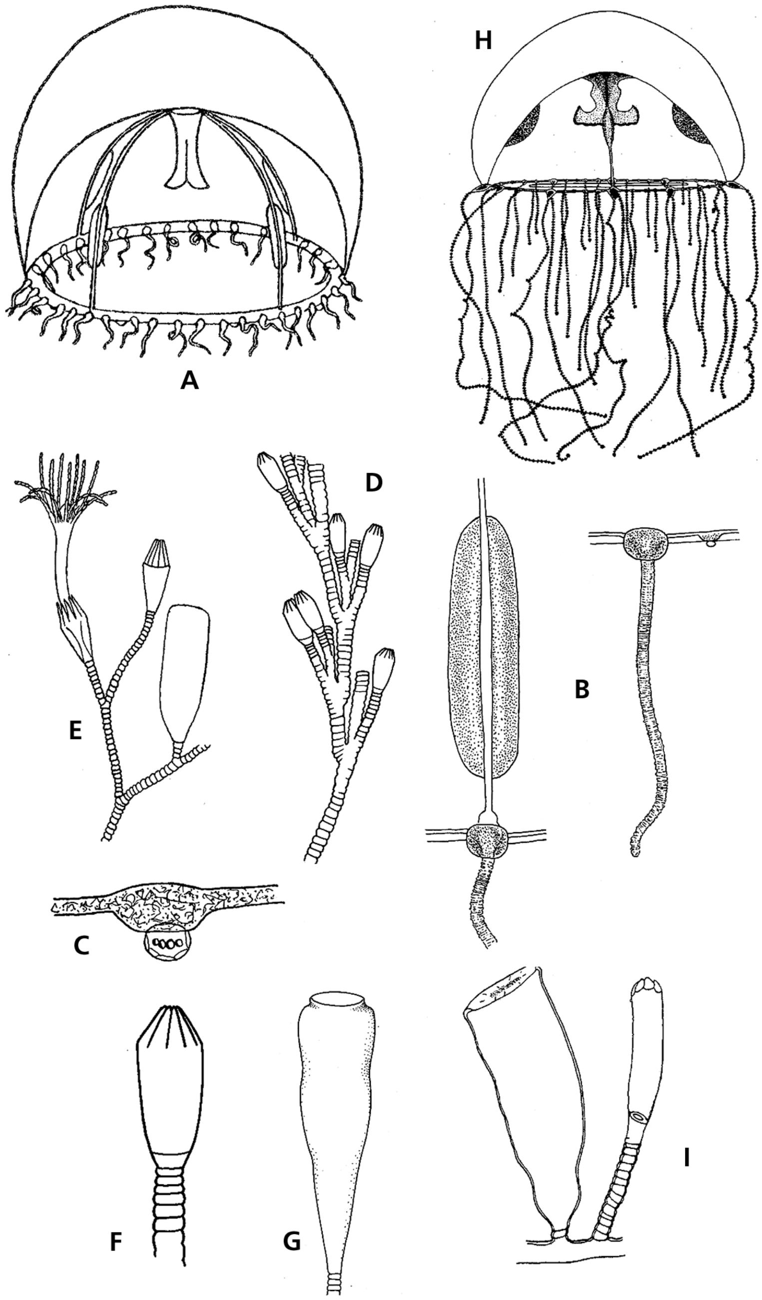


FIG. 171. Leptomedusae, Phialelliidae. A-G, *Phialella quadrata*: A, fully grown medusa; B, male gonad with the characteristic median groove (left), marginal tentacle and statocysts (right); C, detail of a statocyst with the typical phialellid cushion-like swelling; D, general view of a colony; E, part of a hydroid colony with gonothecae and hydrothecae, opercula of the hydrothecae with or without a crease line on the same hydrocaulus; F, hydrotheca with a pleated operculum not delimited basally by a crease line; G, gonotheca. H-I, *Phialella zappai*: H, adult medusa; I, gonotheca and hydrotheca with an operculum delimited basally by a crease line (A after Kramp, 1959b ; B-E, Russell, 1953; F-G after Cornelius, 1995; H-I after Boero, 1987).

***FIG. 171.** Leptomedusae, Phialelliidae. A-G,* Phialella quadrata *: A, méduse adulte ; B, ''gonade'' mâle montrant la séparation médiane caractéristique (à gauche), tentacule marginal et un statocyste (à droite) ; C, détail d'un statocyste présentant le coussinet basal typique des phialellides ; D, vue générale d'une colonie ; E, partie d'une colonie d'hydroïdes avec des gonothèques et des hydrothèques, sur le même hydrocaule, les valves operculaires des hydrothèques sont soit nettement délimitées basalement ou ne représente que la partie distale plissée de l'hydrothèque ; F, hydrothèque avec un opercule plissé non délimité par une ligne basale ; G, gonothèque. H-I,* Phialella zappai *: H, méduse adulte ; I, gonothèque et hydrothèque avec un opercule à valves délimitées basalement par une nette ligne de démarcation (A d'après Kramp, 1959b ; B-E d'après Russell, 1953 ; F-G d'après Cornelius, 1995 ; H-I d'après Boero, 1987).*

KEY TO HYDROIDS

1. hydrocladia with a single, terminal hydrotheca 2
– hydrocladia with two or more hydrothecae 3

2. nematothecae bithalamic, movable; gonotheca usually large, ovate, truncated distally and tapering at base, with wide terminal opening .... *Monotheca*
– nematothecae monothalamic and immovable, gonotheca cowl-shaped .... *Monothecella*

3. gonophores protected by phylactocarps 4
– gonophores not protected by phylactocarps 5

4. gonophores borne on specialised, modified branches, springing from front of main stem, their axis with a series of whorls of modified hydrocladia arranged in verticils, each ramified in several terminal processes armed with nematophores on adcauline side (phylactocarps) .... *Callicarpa*
– gonophores borne on the distal part of ordinary branches where hydrocladia become modified into protective nematophorous branchlets (phylactocarps) disposed in more or less regular verticils enclosing the gonophores .... *Hippurella*

5. hydrocladial branchlets reduced to spines at their end .... *Cladacanthella*
– hydrocladial branchlets not reduced to spines at their end 6

6. stem and branches bearing hydrocladia in alternate verticils, forming a double number of longitudinal rows .... *Nemertesia*
– hydrocladia not arranged in verticils 7

7. hydrocladia giving off from all sides, each with a single basal hydrotheca beyond which the hydrocladium is produced into a long slender flagelliform process bearing nematophores .... *Sibogella*
– hydrocladia arranged in alternate pairs to form two longitudinal rows 8

8. hydrothecal margin even; hydrocauli monosiphonic, colony small .... *Plumularia*
– hydrothecal margin toothed; hydrocauli polysiphonic; colony large .... *Dentitheca*

Remarks: the division of the Plumulariidae in 9 genera could be simplified, for instance the monohydrothecate forms (*Monotheca* and *Monothecella*) could easily be, as some authors did (see Millard 1975; Bouillon 1985a; Hirohito 1995), included in the genus *Plumularia*. The type of nematothecae is also taken as a differentiating character: bithalamic, monothalamic, movable, immovable are variable characters inside the Plumulariidae, even as defined hereunder. The genera *Callicarpa* and *Hippurella* could be treated as one genus, *Hippurella* having priority: the difference between them consisting mainly in the degree of development of the "pseudocorbula" along the sexual hydrocladia. In such case the Plumulariidae should be reduced to five genera: *Cladacanthella*, *Dentitheca, Nemertesia*, *Plumularia* and *Sibogella.*

Genus ***CALLICARPA*** Fewkes, 1881

Fig. 172A-B

Hydroid: colony erect, polysiphonic, unbranched; hydrocladia alternate, pinnate; hydrotheca deep, cylindrical, hydrothecal rim even; lateral hydrothecal nematophores large, trumpet-shaped, mesial one on a small protuberance; gonophores as fixed sporosacs, borne on specialised, modified, branches springing from the front of the main stem, their axis bearing a series of whorls of modified hydrocladia arranged in verticils, each ramified in several terminal processes supplied with nematophores on adcauline side (phylactocarps), the whole having the appearance of a spike of wheat (pseudo corbula), gonophores growing in the axils of modified hydrocladia.

Callicarpa chazaliei Versluys, 1899
Callicarpa gracilis Fewkes, 1881

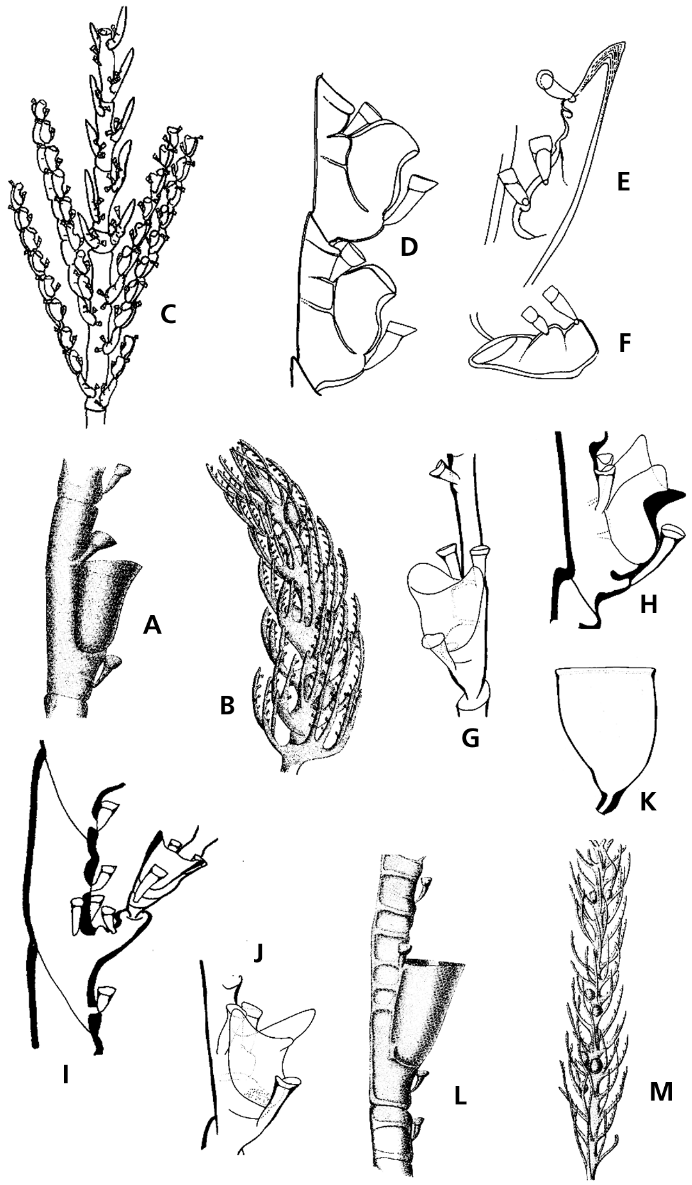


FIG. 172. Leptomedusae, Plumulariidae. A-B, *Callicarpa gracilis*: A, hydrocladial internode; B, phylactocarps. C-F, *Cladacanthella scabra*: C, hydrocladiate part of stem with cauline spurs; D, hydrocladial internodes; E, cauline spur; F, apophysis of branch. G-K, *Dentitheca bidentata*: G & J, fronto-lateral view of an internode, hydrothecae showing the lateral and abcauline lobes; H, lateral view of an internode showing hydrotheca and nematothecae; I, part of stem in lower region showing origin of hydrocladium; K, gonotheca. L-M, *Hippurella longicarpa*: L, hydrocladial internode; M, phylactocarps and gonangia (A-B, L-M after Nutting, 1900; C-F after Watson, 2000; G-H, J-K after Migotto & Marques, 1999b; I after Millard, 1975).

***FIG. 172.** Leptomedusae, Plumulariidae. A-B,* Callicarpa gracilis : *A, internode hydrocladial ; B, phylactocarpes. C-F,* Cladacanthella scabra : *C, partie d'une branche avec hydroclades et éperons caulinaires ; D, internodes hydrocladiaux ; E, éperon caulinaire ; F, apophyse d'une branche. G-K,* Dentitheca bidentata : *G & J, vues fronto-latérale d'un internode, hydrothèques montrant les lobes latéraux et abcaulinaires ; H, vue latérale d'un internode montrant une hydrothèques et les nématothèques ; I, fragment d'hydrocaule de la région basilaire montrant l'origine d'un hydroclade ; K, gonothèque. L-M,* Hippurella longicarpa : *L, internode hydrocladial ; M, phylactocarpes et gonanges (A-B, L-M d'après Nutting, 1900 ; C-F d'après Watson, 2000 ; G-H, J-K d'après Migotto & Marques, 1999b ; I d'après Millard, 1975).*

Genus ***CLADACANTHELLA*** Calder, 1997

Fig. 172C-F

Synonym: *Acanthella* Allman, 1883, an invalid junior homonym of *Acanthella* Schmidt, 1862 [Porifera]. The type and only species, *Acanthella effusa*, is a synonym of *Plumularia scabra* Lamarck, 1816 (see Bale 1919: 342-343; Bouillon 1985a: 170; Watson 2000: 52-53; Schuchert 2003: 212-213). Calder (1997) proposed the replacement name *Cladacanthella* nom. nov. considering it distinguishable from the other Plumulariidae by having a lobed hydrothecal rim and hydrocladia reduced to spines at the ends of branches, we follow this opinion here.

Hydroid: colony erect, branched, monosiphonic; hydrocladia pinnately disposed, hydrocladial branchlets reduced to spines at their end; hydrotheca pitcher-shaped, completely adnate; hydrothecal margin with two large triangular lateral lobes and an abcauline lobe margin (see Allman 1883: Plate VI); three hydrothecal nematothecae present; gonophores inserted in upper axil of apophyses, ovoid, flattened, distal, truncated and oblique.

Cladacanthella scabra (Lamarck, 1816) [syn. *Acanthella effusa* Allman, 1883]

Genus *DENTITHECA* Stechow, 1919

Fig. 172G-K

Hydroid: colony unbranched, unfascicled, pinnate, bearing alternate hydrocladia; hydrocladia bearing hydrothecae on anterior surface; three nematothecae on each internode apophysis, hydrothecae with strong perisarc, adnate, margin with 2 large triangular lateral lobes and an acauline lobe; 3 hydrothecal nematothecae, all nematothecae two-chambered, movable; gonophore as solitary fixed sporosacs, exceptionally swimming gonophores, gonothecae arising from axils of hydrocladia, inverted, conical, with truncated apex, smooth.
Recent references: Migotto (1997); Migotto & Marques (1999); Gravier & Migotto (2000).

Dentitheca alata (Bale, 1888) [as *Plumularia*]
Dentitheca bidentata (Jäderholm, 1920)
Dentitheca habereri (Stechow, 1909) [as *Plumularia*]
Dentitheca hertwigi (Stechow, 1909)

Genus *HIPPURELLA* Allman, 1877

Fig. 172L-M

Hydroid: colony erect, polysiphonic, ramified; hydrocladia pinnate, at least in the proximal part of the colony, distally scattered or in verticils; hydrothecal rim even; gonophores as fixed sporosacs, borne on the distal part of ordinary branches where hydrocladia become modified into protective nematophorous branchlets (phylactocarps) disposed in more or less regular verticils enclosing the gonophores like a corbula (pseudocorbula).

Hippurella annulata Allman, 1877
Hippurella elegans Fraser, 1937a
Hippurella longicarpa Nutting, 1900

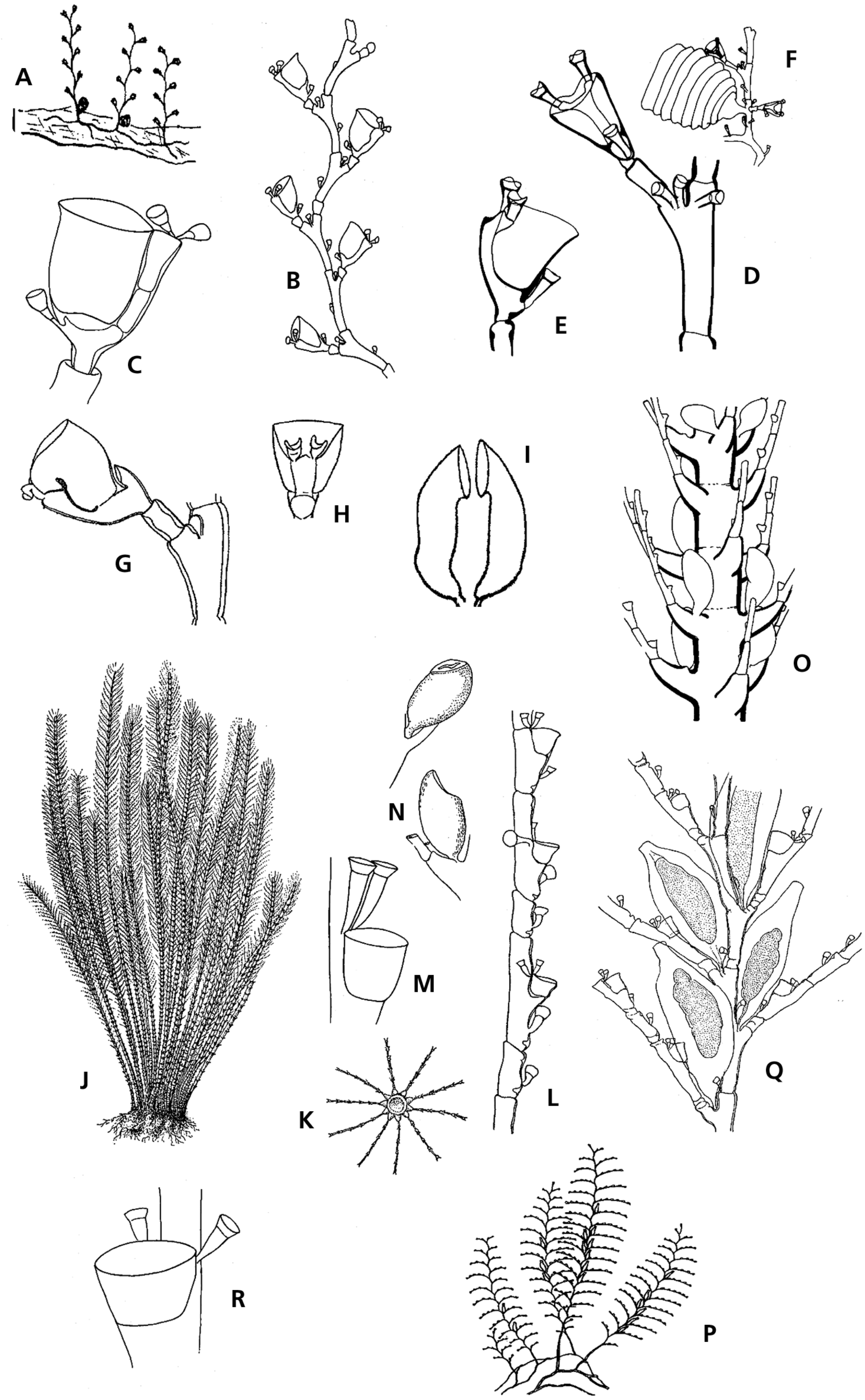
Genus *MONOTHECA* Nutting, 1900

Fig. 173A-F

Hydroid: colony minute, erect, monosiphonic, with unbranched or sparingly branched stems; hydrocladia alternate, typically unbranched, short, each with two internodes: a basal ahydrothecate one and second, bearing the terminal ,hydrotheca; hydrotheca large, only on hydrocladia, margin more or less entire, sinuous; adcauline side completely adnate

FIG. 173. Leptomedusae, Plumulariidae. A-F, *Monotheca*: A, *Monotheca pulchella*, three colonies rising from creeping stolon; B-C, *Monotheca obliqua*: B, part of stem; C, hydrotheca and associated nematothecae; D-F, *Monotheca margaretta*: D, part of stem; E, lateral view of a hydrotheca; F, basal part of stem with gonotheca. G-I, *Monothecella compressa*: G, lateral view of hydrotheca; H, frontal view of hydrotheca; I, gonothecae. J-O, *Nemertesia*: J-N, *Nemertesia antennina*: J, general view of a colony; K, transversal section of a hydrocaulus showing arrangement of hydrocladia (number of rows not constant); L, part of hydrocladium; M, hydrotheca and nematothecae; N, gonothecae; O, *Nemertesia ramosa*, part of hydrocaulus with three hydrocladia per whorl and gonothecae (nematothecae omitted). P-R, *Plumularia setacea*: P, general view of a colony; Q, detail of a hydrocaulus showing hydrocladia and gonothecae; R, hydrotheca and lateral nematothecae (A after Medel & Vervoort, 1995; B-C, M, P & R after Cornelius, 1995; D-F after Migotto, 1996; G-I after Bale, 1884; J-L, N & Q after Leloup, 1952; O after Millard, 1975).

***FIG. 173.** Leptomedusae, Plumulariidae. A-F,* Monotheca : *A,* Monotheca pulchella*, trois colonies issues d'un stolon rampant ; B-C,* Monotheca obliqua : *B, partie d'hydrocaule ; C, hydrothèque et nématothèques associées ; D-F,* Monotheca margaretta *: D, fragment d'une branche ; E, vue latérale d'une hydrothèque ; F, portion basale d'une branche avec une gonothèque. G-I,* Monothecella compressa *: G, vue latérale d'une hydrothèque ; H, vue frontale d'une hydrothèque ; I, gonothèques. J-O,* Nemertesia : *J-N,* Nemertesia antennina *: J, vue générale d'une colonie ; K, section transversale d'un hydrocaule montrant l'arrangement des hydroclades (nombre de rangées non constante) ; L, fragment d'hydroclade ; M, hydrothèque et nématothèques ; N, gonothèque. O,* Nemertesia ramosa*, partie d'un hydrocaule avec trois hydroclades par rangée et des gonothèques (nématothèques non dessinées). P-R,* Plumularia setacea *: P, vue générale d'une colonie ; Q, détail d'un hydrocaule montrant des hydroclades et des gonothèques ; R, hydrothèque et nématothèques latérales (A d'après Medel & Vervoort, 1995 ; B-C, M, P & R d'après Cornelius, 1995 ; D-F d'après Migotto, 1996 ; G-I d'après Bale, 1884 ; J-L, N & Q d'après Leloup, 1952 ; O d'après Millard, 1975).*


A
B
C
D
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to internode, hydrothecate internode with a single median inferior nematotheca and a terminal pair of lateral nematothecae above hydrothecae, cauline nematothecae present or not, nematothecae ordinarily bithalamic, movable; gonophore as solitary fixed sporosacs or swimming gonophores (*M. obliqua*, *M. margaretta*), gonothecae at base of hydrocladium, usually large, ovate, truncated distally and tapering at base, with wide terminal opening, usually lacking nematothecae, not protected.

Remarks: Some *Monotheca* may occasionally have 2-3 hydrothecae per hydrocladium. *Monotheca* has often been treated as a synonym of *Plumularia* (see Millard 1975; Bouillon 1985a; Hirohito 1995).

Recent references: Medel & Vervoort (1995); Migotto (1996); Calder (1997); Gravier & Migotto (2000).

Monotheca flexuosa (Bale, 1894)
Monotheca hyalina (Bale, 1882)
Monotheca margaretta Nutting, 1900
Monotheca obliqua (Johnston, 1847)
Monotheca posidoniae Picard, 1952 [probably a syn. of *M. obliqua*]
Monotheca pulchella (Bale, 1882)
Monotheca spinulosa (Bale, 1882)
Monotheca vervoorti Leloup, 1971

Genus ***MONOTHECELLA*** Stechow, 1923

Fig. 173G-I

Hydroid: colony normally erect, arising from a creeping hydrorhiza; hydrocauli mostly monosiphonic, branched or unbranched, hydrocladia alternate, typically unbranched, pinnately arranged and with a single terminal hydrotheca; hydrothecal margin more or less entire; hydrothecate internode with a single median inferior nematotheca and a terminal pair of lateral nematothecae above hydrotheca; nematotheca monothalmic and immovable; gonophores as fixed sporosac, gonothecae cowl-shaped.

Remarks: Often included in the synonymy of *Plumularia*.

Monothecella aurita Bale, 1888 [as *Plumularia*]
Monothecella australis Kirchenpauer, 1876 [as *Plumularia*]
Monothecella compressa Bale, 1882 [as *Plumularia*]

Genus ***NEMERTESIA*** Lamouroux, 1812

Figs 9K, 10F, 173J-O

Synonym: *Sciurella* Allman, 1883.

Hydroid: colony monosiphonic or polysiphonic, branched or unbranched; hydrocladia arranged in verticils in mature colonies, number of hydrocladia per verticil typically increasing with age, young colonies sometimes just biseriate, pinnate; hydrocladia of one verticil typically alternating with those above and below, forming twice (or more) the number of longitudinal rows, increasing progressively up the colony; hydrothecae cup-shaped, margin even; hydrothecal nematothecae two-chambered, movable; gonophores as fixed sporosacs; gonotheca unprotected, usually borne on hydrocladial apophysis, without nematothecae

Remarks: Allman (1871-1872) reported reduced medusoids in *Nemertesia antennina* but his observation has not been confirmed by futher studies (see Millard 1975; Hughes 1977).

Recent references: Schuchert (2001a; 2003); Vervoort & Watson (2003).

Nemertesia alternata (Fraser, 1938a)
Nemertesia americana (Nutting, 1900)
Nemertesia antennina (Linnaeus, 1758)
Nemertesia belini Bedot, 1916
Nemertesia ciliata Bale, 1914b
Nemertesia compacta (Fraser, 1938c)
Nemertesia constricta (Fraser, 1948)
Nemertesia cymodocea (Busk, 1851)
Nemertesia dissimilis (Fraser, 1943)
Nemertesia disticha (Heller, 1868)
Nemertesia elongata Totton, 1930
Nemertesia fascicularis (Allman, 1883)
Nemertesia fraseri Ramil & Vervoort, 1992a
Nemertesia geniculata (Nutting, 1900)
Nemertesia gracilis Fraser, 1948
Nemertesia hartlaubi (Ritchie, 1907b)

Nemertesia hexasticha Kirchenpauer, 1876
Nemertesia inconstans (Fraser, 1948)
Nemertesia indivisa (Allman, 1883)
Nemertesia intermedia Kirchenpauer, 1876
Nemertesia irregularis (Quelch, 1885a)
Nemertesia japonica (Stechow, 1907)
Nemertesia mutabilis (Fraser, 1948)
Nemertesia norvegica (Sars, 1874)
Nemertesia pacifica (Nutting, 1927)
Nemertesia parva (Fraser, 1948)
Nemertesia pinnata (Nutting, 1900)
Nemertesia pinnatifida Vervoort & Watson, 2003
Nemertesia polygeniculata Rho & Park, 1984
Nemertesia polynema (Fraser, 1948)
Nemertesia ramosa (Lamarck, 1816)
Nemertesia rugosa (Nutting, 1900)
Nemertesia septata (Fraser, 1938c)
Nemertesia simplex (Allman, 1877)
Nemertesia sinuosa (Fraser, 1947)
Nemertesia tetraseriata (Fraser, 1938a)
Nemertesia tetrasticha (Meneghini, 1845)
Nemertesia ventriculiformis (Marktanner-Turneretscher, 1890)
Nemertesia verticillata (Fraser, 1925)
Nemertesia vervoorti El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]

Genus ***PLUMULARIA*** Lamarck, 1816

Figs 9B, 10E, 173P-R, 174A-E

Hydroid: colony normally erect (stolonal when epizootic), arising from a creeping hydrorhiza or from anchoring filaments; hydrocauli mostly monosiphonic, branched or unbranched, giving off alternate apophyses; hydrocladia typically unbranched, pinnately arranged or sometimes occurring in gradual spiral, but not in verticils, divided into internodes; hydrothecae occurring only on hydrocladia, typically two or more per hydrocladium, small, typically cup-shaped, partly or almost totally adnate, margin entire, even; with or without intrathecal septum; axil and cauline nematothecae variable in number, three hydrothecal nematothecae, one median and two lateral ones, flanking each hydrotheca, ordinarily bithalamic and movable; gonophores as solitary, unprotected, fixed sporosacs, neither armed with nematothecae, sometimes with acrocyst.

Recent references: Schuchert (2001a); Calder *et al.* (2003); Vervoort & Watson (2003).

Plumularia acutifrons Fraser, 1938
Plumularia adjecta Fraser, 1948
Plumularia aglaophenoides Nutting, 1927
Plumularia altitheca Nutting, 1900
Plumularia angusta Stechow, 1923c
Plumularia annuligera Quelch, 1885b
Plumularia anonyma Vervoort & Watson, 2003
Plumularia antonbrunni Millard, 1967
Plumularia attenuata Allman, 1877
Plumularia australiensis Watson, 1973
Plumularia badia Kirchenpauer, 1876
Plumularia bedoti Billard, 1911a
Plumularia biarmata Fraser, 1938a
Plumularia branchiata Totton, 1930
Plumularia caliculata Bale, 1888
Plumularia camarata Nutting, 1927
Plumularia campanuloides Billard, 1911a
Plumularia canariensis Izquierdo, Garcia-Corrales & Bacallado, 1986
Plumularia caulitheca Fewkes, 1881
Plumularia congregata Vervoort & Watson, 2003
Plumularia corrugatissima Mulder & Trebilcock, 1915
Plumularia crater Billard, 1911a
Plumularia crateriformis Mulder & Trebilcock, 1911
Plumularia cylindrica Kirchenpauer, 1876
Plumularia defecta Fraser, 1938a
Plumularia delicata Nutting, 1905
Plumularia dendritica Nutting, 1900
Plumularia diploptera Totton, 1930
Plumularia dolichotheca Allman, 1883
Plumularia duseni Jäderholm, 1904b
Plumularia epibracteolosa Watson, 1973
Plumularia excavata Mulder & Trebilcock, 1911
Plumularia exilis Fraser, 1948
Plumularia falcicula Ramil & Vervoort, 1992
Plumularia filicaulis Kirchenpauer, 1876
Plumularia filicula Allman, 1877
Plumularia flabellata Nutting, 1927
Plumularia floridana Nutting, 1900
Plumularia galapagensis Calder, Mallinson, Collins & Hickman, 2003 [syn. *Plumularia tenuissima* Fraser, 1938c]
Plumularia goldsteini Bale, 1882
Plumularia goodei Nutting, 1900
Plumularia gracilis (Fraser, 1948)
Plumularia hargitti Nutting, 1927
Plumularia indica Mammen, 1965
Plumularia insignis Allman, 1883
Plumularia insolens Fraser, 1948
Plumularia integra Fraser, 1948
Plumularia inverta (Fraser, 1948)

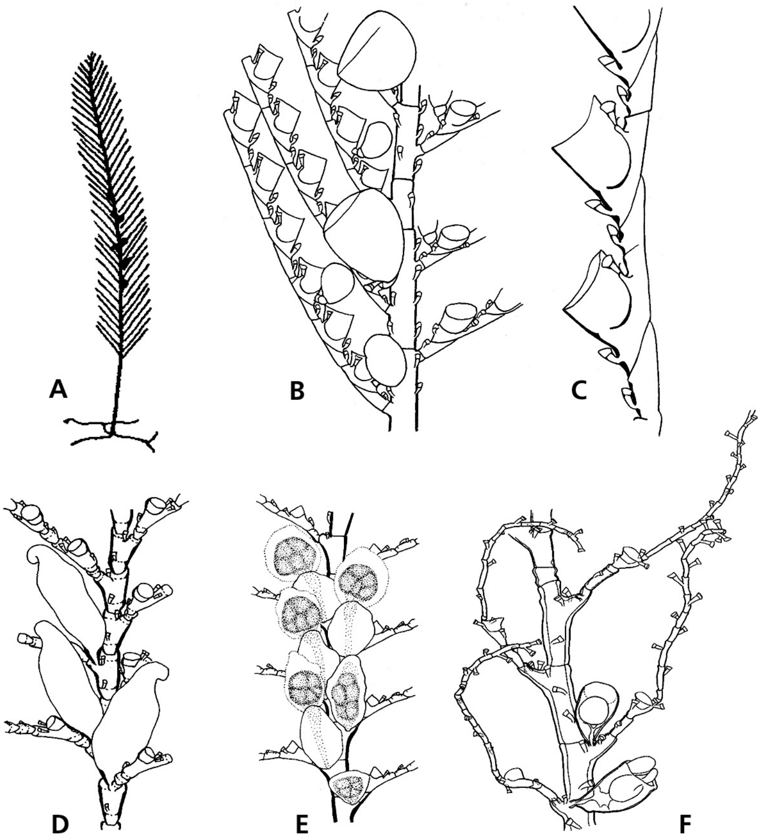


FIG. 174. Leptomedusae, Plumulariidae. A-E, *Plumularia*: A-C, *Plumularia wasini*: A, general view of a fertile stem; B, anterior view of hydrocaulus showing male (small) and female (large) gonothecae and origins of hydrocladia; C, hydrocladia showing hydrothecae and associated nematothecae; D, *Plumularia laginifera*, hydrocaulus showing female gonothecae and origins of hydrocladia; E, *Plumularia warreni*, lower part of hydrocaulus showing female gonothecae and their acrocysts. F, *Sibogella erecta*, part of hydrocaulus with hydrocladia and gonothecae (A-E after Millard, 1975; F after Hirohito, 1995).

FIG. 174. *Leptomedusae, Plumulariidae. A-E,* Plumularia *: A-C,* Plumularia wasini *: A, vue générale d'une branche fertile ; B, vue antérieure d'un hydrocaule montrant les petites gonothèques mâles et les gonothèques femelles plus volumineuses ainsi que l'origine des hydroclades ; C, hydroclade montrant des hydrothèques et leurs nématothèques associées ; D,* Plumularia laginifera*, portion d'hydrocaule montrant les gonothèques femelles et l'origine des hydroclades ; E,* Plumularia warreni*, partie inférieure d'un hydrocaule montrant les gonothèques femelles et leurs acrocystes. F,* Sibogella erecta*, partie d'hydrocaule montrant les hydroclades et les gonothèques (A-E d'après Millard, 1975 ; F d'après Hirohito, 1995).*

Plumularia irregularis Fraser, 1948
Plumularia jaederholmi (Stechow, 1912)
Plumularia jordani Nutting, 1905
Plumularia kirkpatricki Billard, 1908
Plumularia lagenifera Allman, 1886
Plumularia leloupi Blanco & Bellusci, 1971b
Plumularia linkoi Naumov, 1960
Plumularia macrotheca Allman, 1877
Plumularia megalocephala Allman, 1877
Plumularia meganema Fraser, 1948
Plumularia meretriacia Watson, 1973
Plumularia michaelseni Stechow, 1924
Plumularia micronema Fraser, 1938b
Plumularia mobilis Fraser, 1948
Plumularia mossambicae Millard, 1975
Plumularia mula Totton, 1925
Plumularia multiramosa Fraser, 1948
Plumularia mutabilis Fraser, 1948
Plumularia nodosa Stechow, 1924
Plumularia obesa Blackburn, 1938
Plumularia orientalis Billard, 1911a
Plumularia parva Fraser, 1948
Plumularia paucinema Fraser, 1940a
Plumularia paucinoda Nutting, 1900
Plumularia polycladia Mammen, 1967
Plumularia polynema Fraser, 1941
Plumularia procumbens Spencer, 1891
Plumularia propinqua Fraser, 1938a
Plumularia providentiae Jarvis, 1922
Plumularia ramulifera Allman, 1871
Plumularia reversa Fraser, 1948
Plumularia rotunda Mulder & Trebilcock, 1911
Plumularia rugosa Kirchenpauer, 1876
Plumularia sargassi Vanhöffen, 1910
Plumularia septata Fraser, 1938b
Plumularia setacea (Linnaeus, 1758)
Plumularia setaceiformis Mulder & Trebilcock, 1915
Plumularia setaceoides Bale, 1882
Plumularia siliculata (Mammen, 1967)
Plumularia spiralis Billard, 1911a
Plumularia spiralis Milstein, 1976 [invalid name: junior homonym of *P. spiralis* Billard, 1911]
Plumularia spirocladia Totton, 1930
Plumularia strictocarpa Pictet, 1893

Plumularia strobilophora Billard, 1913
Plumularia stylifera Allman, 1883
Plumularia syriaca Billard, 1931
Plumularia tenuissima Totton, 1930
Plumularia togata Watson, 1973
Plumularia tubacarpa Watson, 2000
Plumularia undulata Yamada, 1950
Plumularia variabilis Quelch, 1885a
Plumularia varians Billard, 1911a
Plumularia venusta Fraser, 1948
Plumularia virginiae Nutting, 1900
Plumularia warreni Stechow, 1919a
Plumularia wasini Jarvis, 1922
Plumularia wattsi Bale, 1887
Plumularia wilsoni Bale, 1926

Genus ***SIBOGELLA*** Billard, 1911

Fig. 174F

Hydroid: colony polysiphonic ramified; branches scattered over hydrocaulus, bearing hydrocladia given off in all directions, not arranged in verticils, each bearing a single basal hydrotheca beyond which the hydrocladium is produced into a long slender flagelliform process bearing nematophores; hydrothecae with one median and two lateral nematophores, cauline nematophores present; gonophores as isolated fixed sporosacs, gonothecae piriform on apophyses at base of hydrocladia.
Remarks: often considered as congeneric with *Nemertesia*.
Recent references: Hirohito (1995); Calder (1997).

Sibogella erecta Billard, 1911b

Family SERTULARIIDAE Lamouroux, 1812

Hydroid: colony erect, exceptionally stolonal; hydrothecae bi- or multiseriate, exceptionally apparently uniseriate through secondary modification, sessile through adnate to wholly sunk within perisarc, or exceptionally pedicellate, radially to bilaterally symmetrical, rim usually cusped, operculum of 1-4 flaps; diaphragm in the few pedicellate forms, others having a clearly defined basal floor pierced by narrow and eccentric hydropore (exception: *Sertularella diaphana*); hydranth completely retractable in hydrotheca, in some species with abcauline gastric caecum when hydranth contracts and mantle (ectodermal lamella); cnidome: generally small and often large microbasic mastigophores and sometimes haplonemes; gonophore as fixed sporosacs, exceptionally as swimming gonophores (*Amphisbetia operculata*), gonothecae solitary, usually sexually dimorphic, on stem or branches, acrocyst often present, in *Fraseroscyphus* gonothecae arising from within hydrothecal cavity. (Fig. 6C-H, I-M, P).
Remarks: the Sertulariidae is the most speciose hydrozoan family and sertulariid species are generally easily recognised at family level. Genera, however, are poorly differentiated from each other. Generic diagnoses are mostly based on colony form (stolonal or erect) and on skeletal characters such as hydrothecal shape, position, structure, and number hydrothecal teeth, number of opercular flaps, etc.; some of these characters, however, are variable even in a single colony. Hydranth characters such as the presence of an abcauline caecum, or of an annular ectodermal fold (see glossary) have been given great generic importance; these structures, however, have not been systematically investigated throughout the family.
The Sertulariidae comprise more than 500 species, an amazing number if compared to the 800 valid species of medusae described for the whole superclass Hydrozoa! It is reasonable to suppose that population variations of a single species might have been given specific rank. The description of new genera and species should be based on studies on specific population variations, on external and internal hydranth morphology, on cnidome, and on life cycles.
Recent references: Vervoort (1993) (list); Cornelius (1995); Hirohito (1995); Migotto (1996); Calder & Vervoort (1998); Watson (2000); Schuchert (2001a, 2003), Vervoort & Watson (2003).

KEY TO HYDROIDS

1. hydrotheca pedicellate 2
– hydrotheca not pedicellate 3

2. colony stolonal . . . . . . *Calamphora*
– colony with upright stem; hydrotheca with 3 or 4 teeth, operculum with 3 or 4 valves . . *Parascyphus*

3. hydrotheca with more than 4 marginal teeth 4
– hydrotheca with no marginal teeth or with 4 or less 5

4. hydrotheca with internal ridges or septa . . . . . . *Crateritheca*
– hydrotheca without internal ridges or septa . . . . . . *Stereotheca*

5. Hydrothecal operculum in form of pyramid consisting in 3 or 4 valves, hydrothecal margin with 3 or 4 teeth of equal size 6
– hydrothecal operculum not in form of pyramid, margin not as above; with no teeth, 2 teeth or 3 to 4 teeth not equal in size 14

6. hydrothecae arranged in more than 2 longitudinal rows in at least some parts of stem . *Dictyocladium*
– hydrothecae alternate and arranged in 2 longitudinal rows only 7

7. hydrotheca with 4 marginal teeth and operculum with 4 valves 8
– hydrotheca with 3 marginal teeth and operculum of 3 valves 9

8. hydrothecae all alternate . . . . . . *Sertularella*
– hydrothecae in pairs and in alternate verticils . . . . . . *Caminothujaria*

9. hydrothecae alternate or subalternate 10
– hydrothecae opposite 13

10. hydrothecal rim with 3 teeth, one adcauline and two lateroabcauline 11
– hydrothecal rim with 3 teeth, one abcauline and two lateroadcauline; gonothecae varied, either free on base of hydrothecae, or developing on secondary tubules, with which they may be adnate or even coalesced . . . . . . *Gonaxia*

11. hydrothecae subalternate; gonothecae arising from aperture of most basal hydrothecae . . . . . . *Fraseroscyphus*
– hydrothecae alternate; gonothecae borne on internodes of stem or/and hydrocladia 12

12. distinct main stem in zigzag, internodes with apophyses carrying two hydrocladia; gonothecae smooth with no distal neck . . . . . . *Antarctoscyphus*
– no distinct stem or lacking apophysis and paired hydrocladia if main stem present; gonothecae with tubular neck . . . . . . *Symplectoscyphus*

13. no abcauline caecum . . . . . . *Tamarisca*
– abcauline caecum . . . . . . *Geminella*

14. operculum of 2 valves, the adcauline one sometimes divided in two; hydrotheca with two marginal teeth (and sometimes a minute one as well) 15
– operculum of one valve or deciduous; hydrothecal margin generally not cusped (except in *Diphasia tetraglochina*) 18

15. bases of hydrothecae forming one longitudinal row, their distal ends bending alternately to right and left; adcauline valve of operculum large . . . . . . *Hydrallmania*
– bases of hydrothecae forming two longitudinal rows, more or less on the side of the stem 16

16. marginal teeth of hydrothecae near abcauline edge; adcauline opercular valve larger than abcauline, retracted hydranth with abcauline caecum . . . . . . *Amphisbetia*
– marginal teeth of hydrothecae more or less midway between adcauline and abcauline edge; abcauline opercular valve larger than adcauline 17

17. retracted hydranth without abcauline caecum; hydrothecal pairs typically (though, not always) grouped . . . . . . *Dynamena*
– retracted hydranth with abcauline caecum; hydrothecal pairs never grouped . . . . . . *Sertularia*

18. operculum delicate, fragmenting at eruption of hydranth .... *Tasmanaria*
– operculum forming a robust valve, not fragmenting at eruption of hydranth 19

19. operculum adcauline.. 20
– operculum abcauline... 23

20. operculum divided in two folded wings along sagittal plane .... *Papilionella*
– operculum not divided in two folded wings along sagittal plane 21

21. hydrotheca expanding distally; retracted hydranth without abcauline caecum .... *Diphasia*
– hydrotheca not expanding distally.. 22

22. retracted hydranth without abcauline caecum; hydrothecae all on one surface of hydrocladium...... .... *Idiellana*
– retracted hydranth with abcauline caecum; hydrothecae on lateral surface of hydrocladium........... .... *Abietinaria*

23. at least some hydrothecae in more than two longitudinal rows .... *Staurotheca*
– hydrothecae normally in two longitudinal rows... 24

24. retracted hydranth with abcauline caecum .... *Thuiaria*
– retracted hydranth without abcauline caecum 25

25. hydrothecae in opposite or subopposite pairs, partly or completely adnate to stem, hydrothecal rim without marginal cusps .... *Salacia*
– hydrothecae in opposite pairs, adnate to stem and partly to each other, hydrothecal rim with 2 small teeth .... *Hypopyxis*

Genus ***ABIETINARIA*** Kirchenpauer, 1884

Figs 4A-D, 5M, 6L, 175A-C

Hydroid: colony erect, imperfectly pinnate, monosiphonic; hydrocaulus different in structure than hydrocladia; hydrocladia alternate with some secondary branches; hydrothecae flask-shaped, bulbous below, sessile, partly adnate, biseriate; alternate to subalternate, on hydrocaulus, hydrocladia and in axils; hydrothecal aperture circular, even with no marginal teeth, with one flapped large adcauline operculum; retracted hydranth with abcauline caecum; gonophores as solitary fixed sporosacs, gonothecae somewhat inconspicuous.

Abietinaria abietina (Linnaeus, 1758)
Abietinaria alexanderi Nutting, 1904
Abietinaria alternitheca (Kudelin, 1914)
Abietinaria anguinea (Trask, 1857)
Abietinaria annulata (Kirchenpauer, 1884)
Abietinaria compressa (Mereshkovskii, 1878a)
Abietinaria crassiparia Naumov, 1960
Abietinaria cruciformis Antsulevich, 1987
Abietinaria derbeki (Kudelin, 1914)
Abietinaria elsaeoswaldae Stechow, 1923a
Abietinaria expansa Fraser, 1948
Abietinaria filicula (Ellis & Solander, 1786)
Abietinaria fusca (Johnston, 1847)
Abietinaria gagarae Naumov, 1960
Abietinaria gigantea (Clark, 1876)
Abietinaria gracilis Nutting, 1904
Abietinaria greenei (Murray, 1860)
Abietinaria immersa Vervoort, 1993
Abietinaria inconstans (Clark, 1876)
Abietinaria interversa (Pictet & Bedot, 1900)
Abietinaria juniperus Kirchenpauer, 1884
Abietinaria kincaidi (Nutting, 1901c)
Abietinaria laevimarginata (Ritchie, 1907) [syn. *Sertularia linearis* Warren, 1908]
Abietinaria macrotheca Naumov, 1960
Abietinaria melo Kirchenpauer, 1884
Abietinaria merkii Kirchenpauer, 1884
Abietinaria pacifica Stechow, 1923a
Abietinaria pulchra (Nutting, 1904)
Abietinaria raritheca Naumov, 1960
Abietinaria rigida Fraser, 1911
Abietinaria smirnowi (Kudelin, 1914)
Abietinaria spasskii Fenyuk, 1947
Abietinaria spiralis Naumov, 1960
Abietinaria thuiarioides (Clark, 1876)
Abietinaria traski (Torrey, 1902)
Abietinaria trigona Antsulevich, 1987
Abietinaria turgida (Clark, 1876)
Abietinaria variabilis (Clark, 1876) [syn. *Salacia cartilaginea* (Kirchenpauer, 1884)]

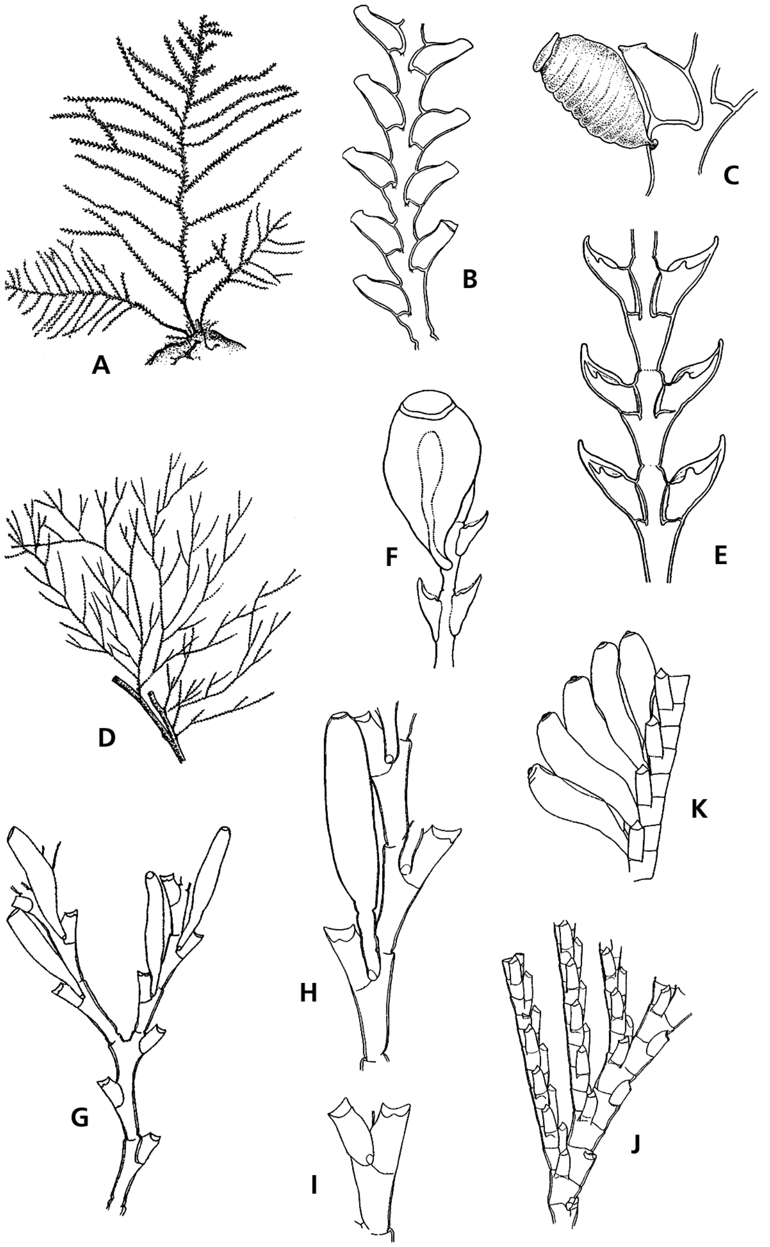


FIG. 175. Leptomedusae, Sertulariidae. A-C, *Abietinaria abietina*: A, general view of a colony; B, detail of a hydrocladium; C, hydrotheca and gonotheca. D-F, *Amphisbetia operculata*: D, view of a colony; E, detail of a hydrocladium; F, part of hydrocladium and gonotheca. G-K, *Antarctoscyphus*: G-I, *Antarctoscyphus asymmetricus*: G, fragment of a lateral branch showing the branching, the arrangement of the hydrothecae and male gonothecae; H, hydrothecae and male gonothecae; I, additional hydrothecae; J-K, *Antarctoscyphus encarnae*: J, lateral branch showing three secondary branches and the arrangement of the hydrothecae; K, gonothecae (A-F after Leloup, 1952; G-K after Peña Cantero *et al.*, 1997: p. 28, figs a, d, e; p. 29, figs 2 a, d).

FIG. 175. *Leptomedusae, Sertulariidae. A-C,* Abietinaria abietina *: A, vue générale d'une colonie ; B, détail d'un hydroclade ; C, hydrothèque et gonothèque. D-F,* Amphisbetia operculata *: D, vue générale d'un fragment de colonie ; E, détail d'un hydroclade ; F, partie d'hydroclade et gonothèque. G-K,* Antarctoscyphus *: G-I,* Antarctoscyphus asymmetricus *: G, fragment d'une branche latérale montrant les ramifications, la position des hydrothèques et des gonothèques mâles ; H, hydrothèques et gonothèques mâles ; I, hydrothèques ; J-K,* Antarctoscyphus encarnae *: J, branche latérale montrant trois branches secondaires et la disposition des hydrothèques ; K, gonothèques (A-F d'après Leloup, 1952 ; G-K d'après Peña Cantero* et al.*, 1997 : p. 28, figs a, d, e ; p. 29, figs 2 a, d).*

Genus *AMPHISBETIA* L. Agassiz, 1862

Figs 56E-F, 175D-F

Hydroid: colony erect, usually branched, monosiphonic; hydrothecae opposite and biseriate, roughly tubular and partly adnate, with 2 long sharp abcauline marginal cusps and sometimes a small adcauline one; operculum of 2 unequal valves, larger one adcauline, smaller one abcauline; retracted hydranth with abcauline caecum; gonophores as fixed sporosacs, or swimming gonophores (*Amphisbetia operculata*), gonothecae solitary, large, usually ovate.
Recent reference: Calder *et al.* (2003).

Amphisbetia aperta (Allman, 1886)
Amphisbetia avia Watson, 1975
Amphisbetia bidens (Bale, 1884)
Amphisbetia bispinosa (Gray, 1843)
Amphisbetia brevis Stechow, 1923c
Amphisbetia clarki (Mereshkovsky, 1878a)
Amphisbetia elegans (Kirchenpauer, 1884)
Amphisbetia episcopus (Allman, 1876)
Amphisbetia erecta (Fraser, 1938b)
Amphisbetia fasciculata (Kirchenpauer, 1864)
Amphisbetia furcata (Trask, 1857)
Amphisbetia geminata (Bale, 1884)
Amphisbetia grossedentata (Kirchenpauer, 1864)
Amphisbetia heteromorpha (Allman, 1886)
Amphisbetia irregularis (Von Lendenfeld, 1885a)
Amphisbetia macrocarpa (Bale, 1884)
Amphisbetia maplestonei (Bale, 1884)
Amphisbetia mccallumi (Bartlett, 1907)
Amphisbetia megalocarpa (Allman, 1886)
Amphisbetia minima (Thompson, 1879)
Amphisbetia minuscula (Bale, 1919)
Amphisbetia minuta (Bale, 1882)
Amphisbetia nasonovi (Kudelin, 1913)
Amphisbetia norte El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Amphisbetia olseni Watson, 1973
Amphisbetia operculata (Linnaeus, 1758)
Amphisbetia pacifica Stechow, 1931
Amphisbetia recta (Bale, 1882)
Amphisbetia rectitheca (Ritchie, 1907b)
Amphisbetia simplex (Von Lendenfeld, 1885b)
Amphisbetia trispinosa (Coughtrey, 1875)
Amphisbetia trochocarpa (Allman, 1886)

Genus *ANTARCTOSCYPHUS* Peña Cantero, Garcia Carrascosa & Vervoort, 1997

Fig. 175G-K

Hydroid: colony erect, of varied appearance; stem distinct with internodes disposed in zigzag fashion; main stem either monosiphonic or polysiphonic; internode apophyses alternate, each giving rise to a pair of lateral hydrocladia, one hydrotheca at axil between them; hydrocladia unbranched or branched; one hydrotheca per hydrocladial internode, hydrothecae alternately arranged but with strong tendency towards unilateral disposition; hydrotheca mainly tubular, adcauline wall free or partly adnate; hydrothecal margin with three cusps; internal teeth absent or sometimes present, operculum composed of three flaps; gonophores as fixed sporosacs, colony dioecious, gonothecae with smooth walls and no distal neck, sexually dimorphic, on internodes at base of hydrothecae, female ones with acrocyst.
Remarks: very close to *Symplectoscyphus*.
Recent references: Peña Cantero, Svoboda & Vervoort (1999).

Antarctoscyphus admirabilis Peña Cantero, Svoboda & Vervoort, 1999
Antarctoscyphus asymmetricus Peña-Cantero, Garcia-Carrascosa & Vervoort, 1997
Antarctoscyphus biformis (Jäderholm, 1905)
Antarctoscyphus elongatus (Jäderholm, 1904a)
Antarctoscyphus encarnae Peña-Cantero, Garcia-Carrascosa & Vervoort, 1997
Antarctoscyphus fragilis Peña Cantero, Svoboda & Vervoort, 1999
Antarctoscyphus grandis (Blanco 1977a)
Antarctoscyphus gruzovi (Stepanjants, 1979)
Antarctoscyphus mawsoni (Briggs, 1939)
Antarctoscyphus spiralis (Hickson & Gravely, 1907)

Genus *CALAMPHORA* Allman, 1888

Fig. 176A-C

Hydroid: colony stolonal, hydrothecae and gonothecae arising directly from hydrorhiza; hydrotheca pedicellate, barrel-shaped, with 4 marginal teeth and a pyramid-shaped operculum of 4 triangular valves; diaphragm present, retracted hydranth with abcauline caecum; gonophores as solitary fixed sporosacs.

Remarks: closely related to *Sertularella*, the two often considered as congeneric. They are mainly differentiated by colony form, stolonal in *Calamphora* and erect in *Sertularella*, and by pedicellate hydrothecae in the first genus and sessile in the second. Vervoort (1968) argued, however, that *S. tenella* can have both erect and pedicellate forms. *Calamphora* is also close to *Symmetroscyphus* by its stolonal pedicellate form and its four-cusped rim and four-flapped operculum, *Symmetroscyphus* having a centrally located rather than eccentric hydropore, an annular ectodermal fold instead of an abcauline caecum, being thus radially instead bilaterally symmetrical and the mantle (ectodermal lamella) forms an aggregation of large cnidocysts (see Thyroscyphidae). *Calamphora* is retained here as a separate genus, the inclusion of pedicellate forms in the diagnosis of *Sertularella* would considerably alter its meaning and, giving no importance to the presence or absence of a pedicel, would also question the validity of the family Thyroscyphidae.

Calamphora campanulata (Warren, 1908)
Calamphora parvula Allman, 1888
Calamphora solitaria (Nutting, 1904)

Genus *CAMINOTHUJARIA* Campenhausen, 1896

Fig. 176D-G

Hydroid: colony erect, basally polysiphonic and distally monosiphonic, hydrocladia and axial hydrothecae in one plane; axial hydrothecae in group of 3; hydrocladial hydrothecae in alternate pairs and/or in verticils of 3 or 4; hydrothecae partly adnate, hydrothecal rim with 4 teeth, operculum of 4 flaps; adnate portion of axial hydrothecae with an adcauline perisarcal process; retracted hydranth with abcauline caecum; gonophores as fixed isolated sporosacs.

Remarks: the unique species of this genus has been confused and included in almost all the sertulariid genera (see Billard 1925a; Vervoort 1993), it is very close to *Sertularella*, differing only by the arrangement of some hydrothecae in opposite disposition or in verticils composed of 3 or 4 thecae.

Recent references: Vervoort (1993); Schuchert (2003).

Caminothujaria molukkana Campenhausen, 1896

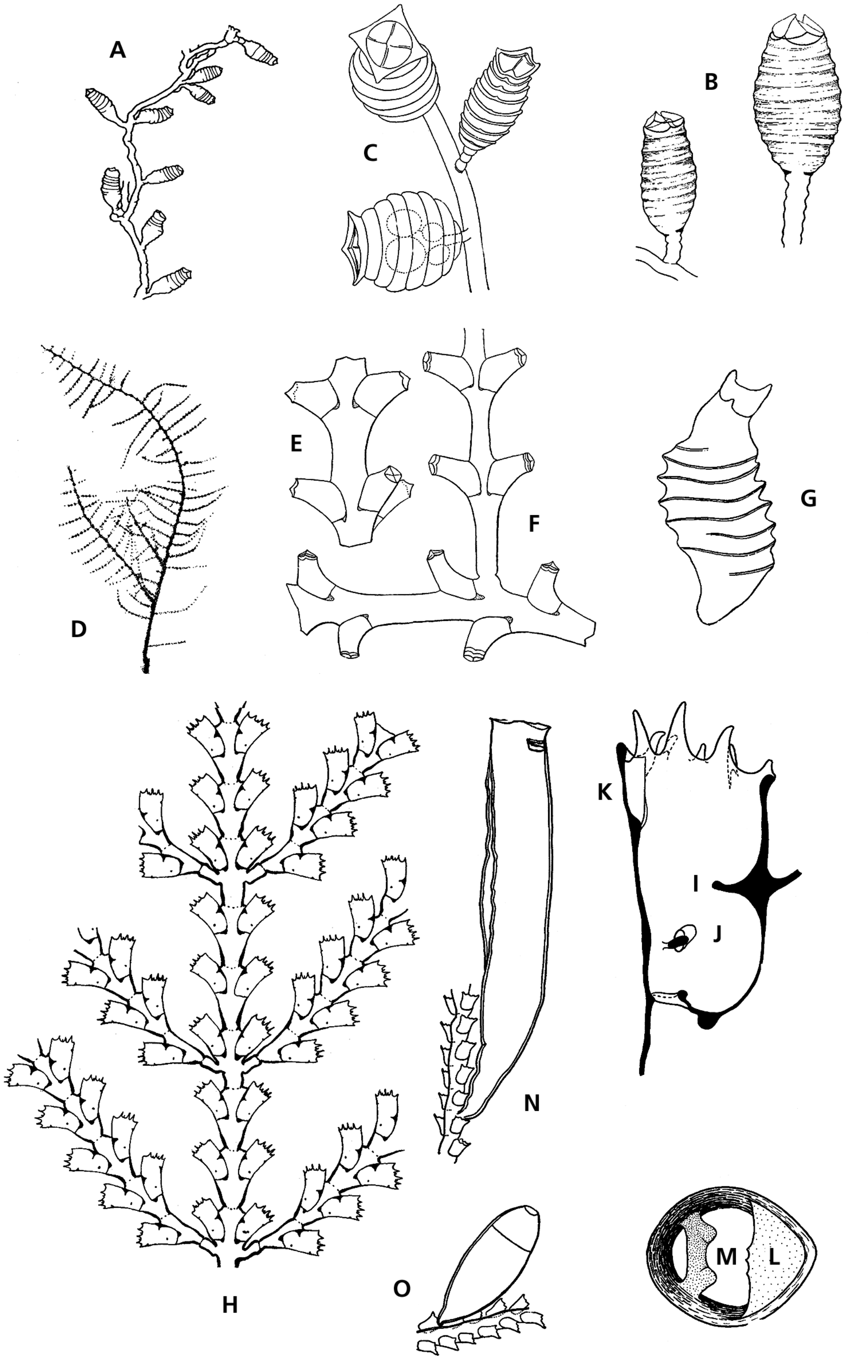
Genus *CRATERITHECA* Stechow, 1921

Fig. 176H-O

Hydroid: colony erect, monosiphonic, pinnate; hydrocaulus and hydrocladia bearing 2 or more (up to 11) longitudinal rows of hydrothecae; hydrotheca sessile, at least partly adnate, with more than 4 marginal teeth (5-15), with prominent

FIG. 176. Leptomedusae, Sertulariidae. A-C, *Calamphora campanulata*: A, general view of a part of a colony; B, two hydrothecae; C, piece of colony with hydrotheca and gonothecae. D-G, *Caminothujaria molukkana*: D, general view of a colony; E, part of hydrocladium with a verticil and a pair of hydrotheca; F, hydrocaulus with the base of a hydrocladium; G, gonotheca. H-O, *Crateritheca*: H-M, *Crateritheca acanthostoma*: H, part of hydrocaulus with the origins of hydrocladia; I-K, hydrotheca in side view, adcauline side on right: I, adcauline septum; J, lower abcauline septum; K, upper abcauline septum; L-M, transverse section of a hydrothecae at deeper level viewed from above showing: L, adcauline septum; M, lower abcauline septum; N, *Crateritheca zelandica*, female gonophore; O, male gonophore (A after Hirohito, 1974; B after Leloup, 1937; C after Mammen, 1965; D-G after Billard, 1925a; H-M after Millard, 1975; N-O after Ralph, 1961b: p. 759, text-fig. 3 i, k).

FIG. 176. *Leptomedusae, Sertulariidae. A-C,* Calamphora campanulata : *A, vue générale d'une partie de colonie ; B, vue de deux hydrothèques ; C, fragment d'une colonie avec une hydrothèque et des gonothèques. D-G,* Caminothujaria molukkana : *D, vue générale d'une colonie ; E, partie d'hydroclade avec un verticille et une paire d'hydrothèques ; F, portion d'hydrocaule avec la base d'un hydroclade ; G, gonothèque. H-O,* Crateritheca : *H-M,* Crateritheca acanthostoma : *H, portion d'hydrocaule avec les origines des hydroclades ; I-K, vue latérale d'une hydrothèque, le côté adcaulinaire droite : I, septum adcaulinaire ; J, septum abcaulinaire basal ; K, septum abcaulinaire supérieur ; L-M, section transversale médio-basale d'une hydrothecae vue du dessus et montrant : L, le septum adcaulinaire ; M, le septum abcauline basal ; N,* Crateritheca zelandica*, gonophore femelle ; O, gonophore mâle (A d'après Hirohito, 1974 ; B d'après Leloup, 1937 ; C d'après Mammen, 1965 ; D-G d'après Billard, 1925a ; H-M d'après Millard, 1975 ; N-O d'après Ralph, 1961b : p. 759, text-fig. 3 i, k).*


A
C
B
D
E
F
G
H
N
K
I
J
O
M
L

abcauline and adcauline intrathecal septa and often with external longitudinal ridges; operculum reduced, either absent altogether, or consisting of a single membranous valve; retracted hydranth with abcauline caecum; gonophores as solitary fixed sporosacs.
Recent reference: Vervoort & Watson (2003).

Crateritheca acanthostoma (Bale, 1882)
Crateritheca bidens Vervoort & Watson, 2003
Crateritheca crenata (Bale, 1884)
Crateritheca insignis (Thompson, 1879)
Crateritheca novaezelandiae (Thompson, 1879)
Crateritheca zelandica (Gray, 1843)

Genus ***DICTYOCLADIUM*** Allman, 1888
Fig. 177A-C

Hydroid: colony flabellate, monosiphonic, irregularly sub-dichotomously branched; hydrothecae either alternate or sub-opposite; axis and branches twisted between each successive pair of hydrothecae; in species with sub-opposite hydrothecae, alternate "pairs" staggered, giving the impression of four longitudinal rows; in species with alternate hydrothecae, this arrangement is less distinct and only visible in older parts of colony; hydrothecae cylindrical, major part of adcauline wall adnate, distal portion curved; hydrothecal rim with 3 acute cusps separated by embayments, one adcauline and two lateral ones; 3 opercular flaps, corresponding to cusps; gonophores as fixed sporosacs, gonotheca arising from apophysis on the inner surface of branches at short distance above their bifurcation, globular, with short pedicel and apical tube, with distinct hyaline flap; perisarc of gonotheca forming spiral external folds.
Recent references: Vervoort (1993); Vervoort & Watson (2003).

Dictyocladium amplexum Vervoort & Watson, 2003
Dictyocladium biseriale Vervoort, 1993
Dictyocladium coactum Stechow, 1923a
Dictyocladium dichotomum Allman, 1888
Dictyocladium flabellum Nutting, 1904
Dictyocladium thuja Vervoort & Watson, 2003

Genus ***DIPHASIA*** Agassiz, 1862
Figs 9H, 10B, 177D-K

Hydroid: colony erect, pinnately branched or unbranched; hydrocaulus mono- or polysiphonic; hydrocaulus, and hydrocladia when present, with hydrothecae in 2, rarely 3 longitudinal rows; hydrotheca tubular, sessile, adnate to partly sunk, usually expanding distally, in opposite to alternate pairs, hydrothecal margin sprout-shaped, even or with 2 to 4 teeth, operculum of one adcauline flap; gonophores as fixed sporosacs; gonothecae sometimes with spines forming brood chambers (marsupium) in females.
Recent references: Calder (1991); Cornelius (1995); Hirohito (1995); Schuchert (2001a).

Diphasia attenuata (Hincks, 1866)
Diphasia bipinnata Allman, 1886 [doubtful status]
Diphasia cauloatheca Billard, 1920
Diphasia corniculata (Murray, 1860)
Diphasia cristata Billard, 1920
Diphasia delagei Billard, 1912
Diphasia densa (Stechow, 1923c)
Diphasia digitalis (Busk, 1852)
Diphasia dubia Hargitt, 1927
Diphasia fallax (Johnston, 1847) [syn. *D. wandeli* Levinsen, 1893b]
Diphasia heurteli Billard, 1924b
Diphasia inornata Nutting, 1927
Diphasia margareta (Hassall, 1841)
Diphasia minuta Billard, 1920
Diphasia mutulata (Busk, 1852)
Diphasia nigra (Pallas, 1766)
Diphasia nuttingi Stechow, 1913a
Diphasia orientalis Billard, 1920
Diphasia paarmani Nutting, 1904
Diphasia palmata Nutting, 1905
Diphasia pinaster (Cuvier, 1830) [syn. *D. alata* (Hincks, 1855)]
Diphasia robusta Fraser, 1943
Diphasia rosacea (Linnaeus, 1758)
Diphasia scalariformis Kirkpatrick, 1890a
Diphasia subcarinata (Busk, 1852)
Diphasia tetraglochina Billard, 1907b
Diphasia thornelyi Ritchie, 1909a
Diphasia tropica Nutting, 1904
Diphasia varians Jarvis, 1922

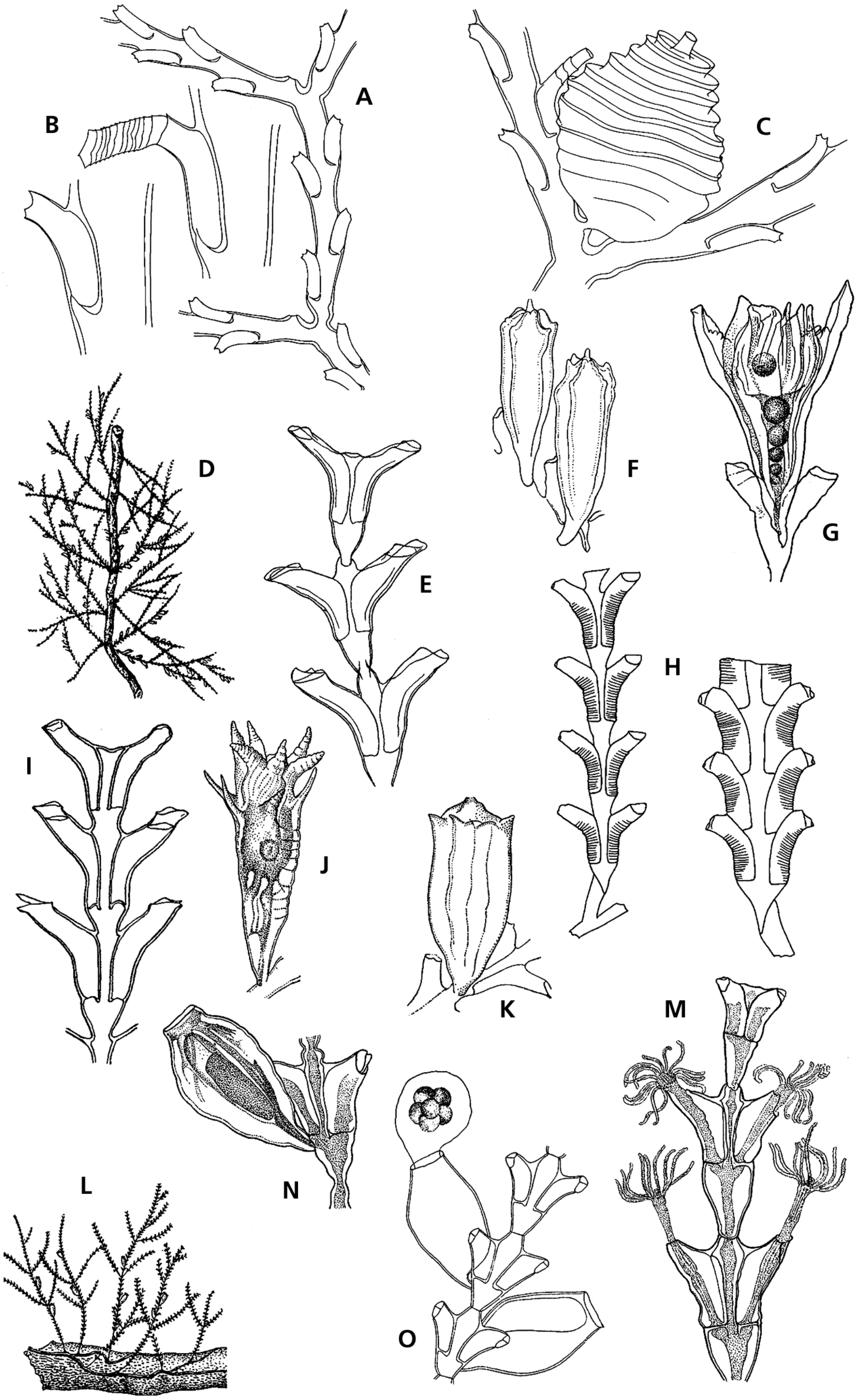


FIG. 177. Leptomedusae, Sertulariidae. A-C, *Dictyocladium biseriale*: A, part of axis to show bifurcations; B, hydrothecae, the right one repeatedly renovated; C, gonotheca at bifurcation. D-K, *Diphasia*: D-G, *Diphasia rosacea*: D, general view of a colony; E, detail of hydrocladium; F, male gonotheca; G, female gonotheca; H, *Diphasia delagei*, two different colonies; I-K, *Diphasia attenuata*: I, hydrocladium; J, female gonotheca; K, male gonotheca. L-O, *Dynamena pumila*: L, general view of a colony; M, hydrocladium with expanded hydranths; N, gonotheca; O, detail of hydrocladium with gonothecae, the left one with an acrocyst (A-C after Vervoort, 1993; D-G, I-N after Leloup, 1952; H after Cornelius, 1995; O after Vervoort, 1946).

FIG. 177. *Leptomedusae, Sertulariidae. A-C,* Dictyocladium biseriale : *A, partie de l'hydrocaule montrant les bifurcations ; B, hydrothèques, celle de droite rénovée plusieurs fois ; C, gonothèque située au niveau d'une bifurcation. D-K,* Diphasia : *D-G,* Diphasia rosacea : *D, vue générale d'une colonie ; E, détail d'une hydroclade ; F, gonothèque mâle ; G, gonothèque femelle ; H,* Diphasia delagei, *deux portions de colonies différentes ; I-K,* Diphasia attenuata : *I, détail d'un hydroclade ; J, gonothèque femelle ; K, gonothèque mâle. L-O,* Dynamena pumila : *L, vue générale d'une colonie ; M, portion d'hydroclade avec des hydranthes en extension ; N, gonothèque ; O, détail d'un fragment d'hydroclade avec deux gonothèques, celles de gauche avec un acrocyste (A-C d'après Vervoort, 1993 ; D-G, I-N d'après Leloup, 1952 ; H d'après Cornelius, 1995 ; O d'après Vervoort, 1946).*

Genus ***DYNAMENA*** Lamouroux, 1812

Figs 2B, 10C, 47A, 154E, 177L-O, 178A-C

Hydroid: colony erect, branched or unbranched, monosiphonic; hydrocaulus, and hydrocladia when present, with hydrothecae in two longitudinal rows; hydrothecae tubular, sessile, partly to completely adnate, usually expending distally, in opposite to sub-opposite pairs, occasionally in groups of 2 or more pairs per internode; hydrothecal margin tridentate; median adcauline tooth smaller and less conspicuous than lateral teeth; operculum of 2 flaps, adcauline one usually smaller than abcauline one and divided into two parts by a median line; some species with mantle (ectodermal lamella), with or without distal batteries of large cnidocysts; gonophores as fixed sporosacs, planula often brooded in an external acrosyst, gonothecae solitary.

Recent references: Calder (1991); Cornelius (1995); Hirohito (1995); Schuchert (2001a, 2003); Calder *et al.* (2003).

Dynamena anceps (Fraser, 1938a) [as *Sertularia*]
Dynamena bilamellata Watson, 2000
Dynamena brevis (Fraser, 1935)
Dynamena cornicina McCrady, 1859a
Dynamena crisiodes Lamouroux, 1824a
Dynamena dalmasi (Versluys, 1899)
Dynamena decipiens (Levinsen, 1913)
Dynamena dispar (Fraser, 1938a)
Dynamena disticha (Bosc, 1802)
Dynamena griffini Hargitt, 1924
Dynamena heterodonta (Jarvis, 1922)
Dynamena japonica Stechow, 1920
Dynamena moluccana (Pictet, 1893)
Dynamena nanshaenensis Tang, 1991a
Dynamena obliqua Lamouroux, 1816
Dynamena ogasawarana Hirohito, 1974
Dynamena pumila (Linnaeus, 1758)
Dynamena quadridentata (Ellis & Solander, 1786)
Dynamena stabilis (Fraser, 1948)
Dynamena tropica Stechow, 1926

Genus ***FRASEROSCYPHUS*** Boero & Bouillon, 1993

Fig. 178D-F

Hydroid: colony erect, hydrocaulus unbranched, monosiphonic; hydrothecae nearly tubular, partly adnate, usually alternate, many not in one plane, converging in one direction; hydrothecal rim with 3 well-marked, sharp teeth, two latero-abcauline cusps larger than median one, cusps reduced in old colonies; operculum of 3 flaps; distal clinging organ often present; base of stem with two or 3 annular hinge joints; hydranth with abcauline caecum; gonotheca solitary, smooth, arising from the aperture of the most basal hydrotheca sometimes gonothecae partially encircled by upper hydrothecae.

Fraseroscyphus sinuosus (Fraser, 1948)

Genus ***GEMINELLA*** Billard, 1925

Fig. 178G-J

Hydroid: colony erect, irregularly branched, monosiphonic; hydrothecae partly adnate, single, alternate or in (sub)-opposite pairs, becoming opposite during development; hydrothecal rim with 3 teeth, an adcauline one and 2 lateral ones near abcauline side; operculum of 3 triangular flaps; retracted hydranth with abcauline caecum; gonophores as solitary, fixed sporosacs.

Remarks: *Geminella* has been treated as a subgenus of *Sertularella* by Bouillon, 1985a; of *Tridentata* by Calder, 1991; and has been retained by Vervoort (1993) for sertulariids with three cusped hydrothecal rim, an operculum with three flaps and single alternate or (sub)opposite hydrothecae becoming opposite in the course of development. *Geminella* has great affinities with *Tamarisca* in having a tricuspid hydrothecal rim and an operculum of three valves, but *Geminella* has an abcauline caecum when contracted, *Tamarisca* does not. *Geminella* is also close to *Symplectoscyphus*, bearing a three-cusped

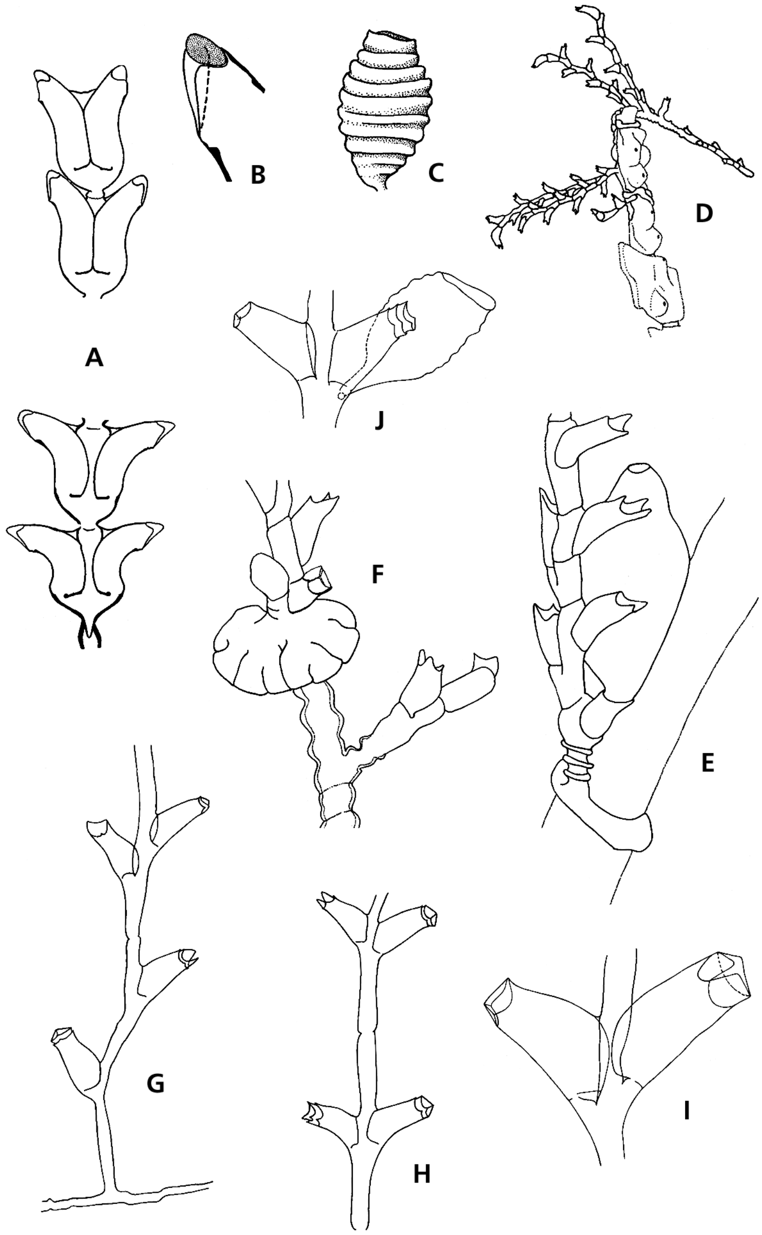


FIG. 178. Leptomedusae, Sertulariidae. A-C, *Dynamena cornicina*: A, the upper two and lower two pairs of hydrothecae of a simple stem; B, margin of hydrothecae with operculum, abcauline valve in broken line; C, gonotheca. D-F, *Fraseroscyphus sinuosus*: D, newly settled colony after attachment of clinging organ; E, lower part of colony with gonotheca originating from within basal hydrotheca and showing the clinging organ; F, tip of a colony with clinging organ. G-J, *Geminella ceramenis*: G, basal part of axis with dispersed hydrotheca; H, part of axis with (sub)opposite hydrothecae; I, detail of pair of sub-opposite hydrothecae; J, (damaged) gonotheca and its insertion on axis (A-C after Millard, 1975; D-F after Boero & Bouillon, 1993; G-J after Vervoort, 1993).

FIG. 178. *Leptomedusae, Sertulariidae. A-C,* Dynamena cornicina : *A, les deux paires d'hydrothèques supérieures et les deux paires d'hydrothèques inférieures d'une même branche d'une colonie ; B, bord marginal d'une hydrothèque montrant l'opercule et la valve abcaulinaire en ligne pointillée ; C, gonothèque. D-F,* Fraseroscyphus sinuosus : *D, colonie venant de s'établir par attachement de son organe fixation ; E, partie inférieure d'une colonie montrant une gonothèque prenant naissance de l'hydrothèque la plus basale et l'organe de fixation ; F, sommet d'une colonie avec organe de fixation. G-J,* Geminella ceramenis : *G, partie basale de l'axe d'une colonie avec des hydrothèques dispersées ; H, partie basale de l'axe d'une colonie avec des hydrothèques sub-opposées ; I, détail d'une paire d'hydrothèques sub-opposées ; J, gonothèque (endommagée) et son insertion sur un axe (A-C d'après Millard, 1975 ; D-F d'après Boero & Bouillon, 1993 ; G-J d'après Vervoort, 1993).*

hydrothecal rim, an opercular apparatus of 3 flaps having an abcauline caecum, but the two differ by the position of the hydrothecae that are alternate in *Symplectoscyphus*. Calder (1991) referred *Geminella* to *Tridentata* because of the tridentate hydrothecal wall and opposite hydrothecae, *Tridentata* is here considered as congeneric with *Sertularia* in having only two opercular flaps and small median adcauline tooth.

We concur with Vervoort (1993) in keeping *Geminella* as a separate genus although the differences between *Geminella* and *Symplectoscyphus* are not very convincing.

Geminella ceramensis (Billard, 1925b)

Genus ***GONAXIA*** Vervoort, 1993

Fig. 179A-C

Hydroid: colony erect, usually thick, polysiphonic, regularly pinnate; hydrocladia straight, supported by distinct apophyses; hydrocladia with varied number of alternate biseriate hydrothecae, axial and axillary hydrothecae present in varied arrangement, all hydrothecae strictly in one plane; hydrothecae tubiform, basal part sunken in varied degree into hydrocladium, more distal part either perpendicular or directed obliquely upwards; hydrothecal aperture perpendicular to axis, hydrothecal rim with 3 marginal teeth of varied development, an abcauline one and two lateral ones near adcauline part of hydrotheca; operculum composed by 3 triangular flaps, usually only visible in young hydrothecae; in some species, proximal portion of hydrothecae with external spur on each side; hydranth with small abcauline caecum; gonophores as styloid sporosacs, gonothecae smooth, varied in shape, either free on base of hydrothecae, elongate spindle-shaped, with short peduncle and widened basal circular disk, or developing on secondary tubules, to which they may be adnate or even coalescent; some species may have gonothecae intermediate between these two extremes.

Recent reference: Vervoort & Watson (2003).

Gonaxia amphorifera Vervoort, 1993
Gonaxia ampullacea Vervoort, 1993
Gonaxia anonyma Vervoort, 1993
Gonaxia australis Vervoort & Watson, 2003
Gonaxia bulbifera Vervoort, 1993
Gonaxia compacta Vervoort, 1993
Gonaxia complexa Vervoort, 1993
Gonaxia constricta (Totton, 1930)
Gonaxia crassa Vervoort, 1993
Gonaxia crassicaulis Vervoort, 1993
Gonaxia crusgalli Vervoort, 1993
Gonaxia elegans Vervoort, 1993
Gonaxia errans Vervoort, 1993
Gonaxia grandis Vervoort & Watson, 2003
Gonaxia immersa Vervoort & Watson, 2003
Gonaxia intercalata Vervoort & Watson, 2003
Gonaxia intermedia Vervoort, 1993
Gonaxia pachyclados Vervoort, 1993
Gonaxia perplexa Vervoort, 1993
Gonaxia persimilis Vervoort, 1993
Gonaxia robusta Vervoort, 1993
Gonaxia scalariformis Vervoort, 1993
Gonaxia similis Vervoort, 1993
Gonaxia sinuosa Vervoort, 1993
Gonaxia stricta Vervoort, 1993
Gonaxia tasmanica Watson & Vervoort, 2001

Genus ***HYDRALLMANIA*** Hincks, 1868

Fig. 179D-G

Hydroid: colony erect, monosiphonic; hydrocaulus giving off spirally-arranged pinnate branches bearing alternate hydrocladia; hydrothecae sessile, partially adnate, secondarily arranged along one side of hydrocladia and appearing uniseriate though slightly inclined alternately to the left and right, contiguous, in groups of 3-10; young colonies and occasional branches of mature ones with alternate and biseriate arrangement; hydrotheca with two marginal cusps often ill-defined or absent; operculum of two delicate flaps; retracted hydranth with abcauline caecum; gonophores as solitary fixed sporosacs.

Recent reference: Schuchert (2001a).

Hydrallmania distans Nutting, 1899
Hydrallmania falcata (Linnaeus, 1758)
Hydrallmania franciscana (Trask, 1857)
Hydrallmania plumulifera (Allman, 1877)

Genus ***IDIELLANA*** Cotton & Godfrey, 1942

Fig. 179H-L

Hydroid: colony erect, monosiphonic, pinnate; hydrocladia alternate, unbranched; hydrocaulus with 3 hydrothecae, an axillary one and an alternate, non contiguous pair above; hydrocladia with a double row of alternate, or subalternate,

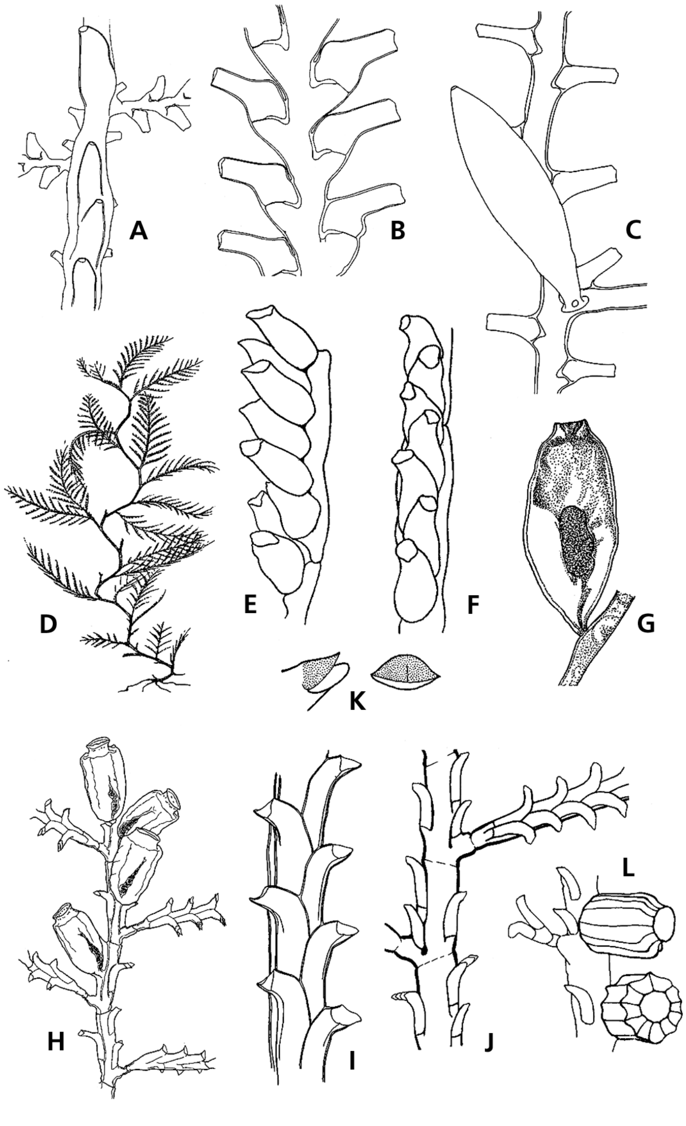


FIG. 179. Leptomedusae, Sertulariidae. A-C, *Gonaxia*: A-B, *Gonaxia ampullacea*: A, part of hydrocladium with gonothecae; B, detail of a section of hydrocladia; C, *Gonaxia similis*, monosiphonic distal portion of a colony with gonotheca. D-G, *Hydrallmania falcata*: D, general view of a colony; E, lateral view of a hydrocladium; F, frontal view of a hydrocladium; G, gonotheca. H-L, *Idiellana pristis*: H, general view of a portion of hydrocaulus with origins of hydrocladia and female gonothecae; I, detail of an anterior view of hydrocladia; J, part of hydrocaulus with origin of an hydrocladia and renovated hydrothecae; K, lateral and abcauline views of operculum; L, basal part of stem with two gonothecae (A-C after Vervoort, 1993; D-G after Leloup, 1952; H-I after Hirohito, 1995; J-K after Millard, 1975; L after Migotto, 1996).

***FIG. 179.** Leptomedusae, Sertulariidae. A-C,* Gonaxia : *A-B,* Gonaxia ampullacea : *A, portion d'un hydroclade avec des gonothèques ; B, détail d'une portion d'hydroclade ; C,* Gonaxia similis, *portion distale d'une colonie monosiphonique montrant une gonothèque. D-G,* Hydrallmania falcata : *D, vue générale d'une colonie ; E, vue latérale d'un hydroclade ; F, vue frontale d'un hydroclade ; G, gonothèque. H-L,* Idiellana pristis : *H, vue générale d'une portion d'hydrocaule montrant les origines des hydroclades ainsi que des gonothèques femelles ; I, détail d'une vue de la face antérieure d'une hydroclade ; J, partie d'hydrocaule montrant l'origine d'un hydroclade et des hydrothèques renovées ; K, vues latérales et abcaulinaire d'un opercule ; L, partie basilaire d'une branche avec deux gonothèques (A-C d'après Vervoort, 1993 ; D-G d'après Leloup, 1952 ; H-I d'après Hirohito, 1995 ; J-K d'après Millard, 1975 ; L d'après Migotto, 1996).*

contiguous, overlapping hydrothecae on one face; hydrothecae sessile, tubular, curved outwards, with two lateral lobes, no internal teeth; operculum of one adcauline flap with a median ridge; gonophores as solitary fixed sporosacs.
Recent references: Hirohito (1995); Migotto (1996).

Idiellana lepida Watson, 2000
Idiellana pristis (Lamouroux, 1816)

Genus ***PAPILIONELLA*** Antsulevich & Vervoort, 1993

Fig. 180A-C

Hydroid: colony erect, arborescent to irregularly pinnate; hydrocladia alternate, hydrothecae on hydrocaulus and hydrocladia, completely sunk into cladial perisarc, alternate, vertically contiguous, biseriate, tubular, gradually narrowing

towards rim, not inflated; hydrothecal rim free, sinuous without teeth, occasionally slightly quadrangular in one plane; operculum formed by one composite flap attached on adcauline side, divided in 2 folded wings along sagittal plane, its shape suggesting a butterfly; retracted hydranth with abcauline caecum?; gonophores unknown.
Remarks: this genus is here retained for the sole species *P. pterophora*.

Papilionella pterophora Antsulevich & Vervoort, 1993

Genus ***PARASCYPHUS*** Ritchie, 1911

Fig. 180D-G

Hydroid: colony erect, unbranched or sparsely branched; hydrothecae in 2 alternate rows, adcauline wall free from stem, directly on apophysis or on short pedicels issued from apophyses renovations, elongated, more or less tubular, slightly curved, adcauline wall swollen, bilaterally symmetrical; hydrothecal margin with 3 to 4 teeth; operculum pyramidal, of 3 to 4 valves; diaphragm either absent, small or incomplete; retracted hydranth with abcauline caecum; gonophores as fixed sporosacs, gonothecae on stem.

Parascyphus repens (Jäderholm, 1904a)
Parascyphus simplex (Lamouroux, 1816)

Genus ***SALACIA*** Lamouroux, 1816

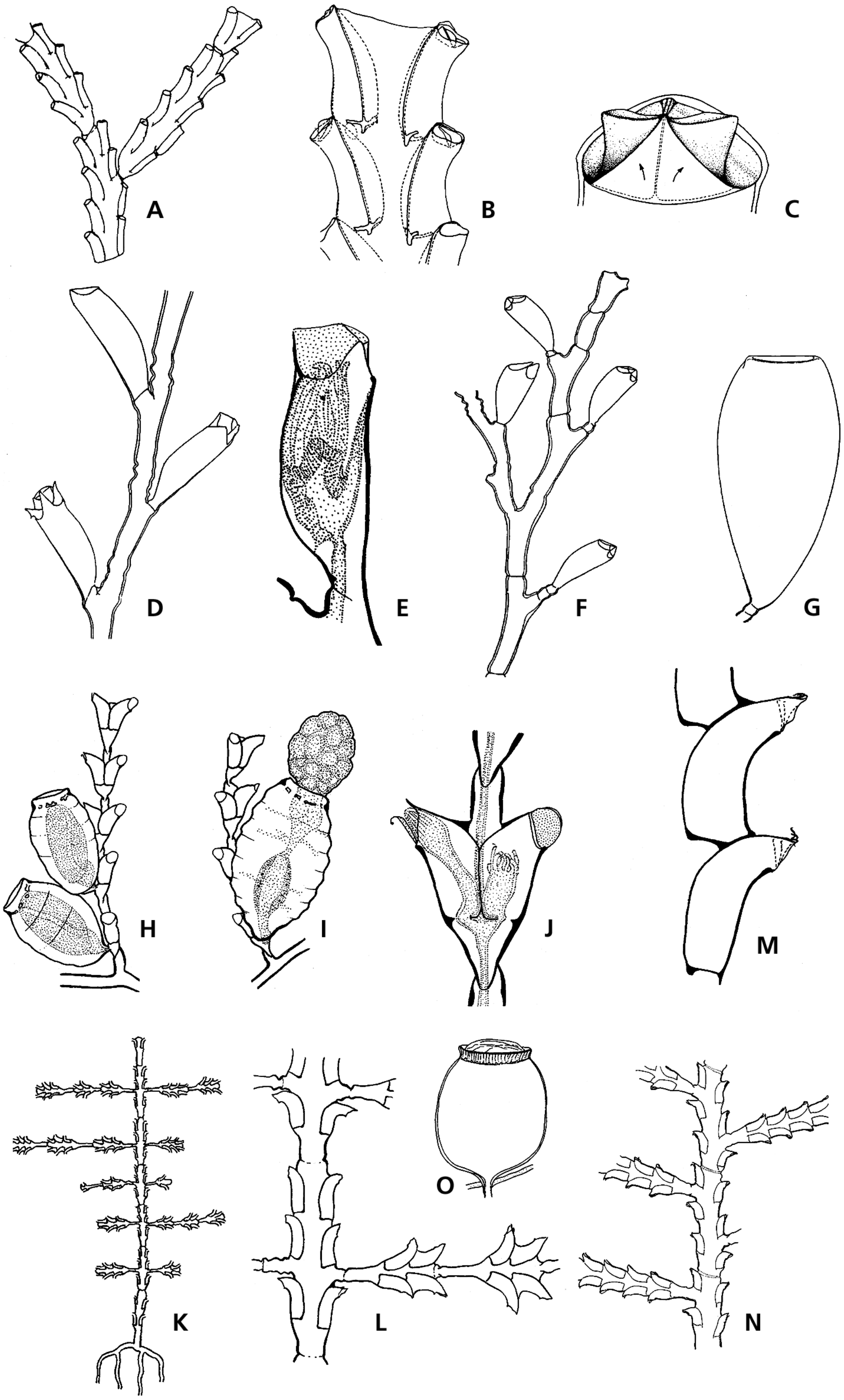
Fig. 180H-O

Synonym: *Dymella* Stechow, 1923.
Hydroid: colony erect, monosiphonic; hydrocladia, when present, either opposite or alternate and of different structure than hydrocaulus, internodes being of irregular length; hydrothecae on hydrocaulus and hydrocladia, in 2 longitudinal rows, in opposite or subopposite pairs, sessile, partly or completely adnate, without marginal cusps, hydrothecal aperture triangular, operculum with single abcauline circular flap; retracted hydranth without abcauline caecum; gonophores as solitary fixed sporosacs.
Recent references: Calder (1991); Hirohito (1995), Schuchert (2003); Vervoort & Watson (2003).

Salacia alata Watson, 2000
Salacia alba (Fraser, 1911)
Salacia bicalycula (Coughtrey, 1876)
Salacia bidentata Watson, 2000
Salacia buski (Allman, 1876a)
Salacia coronata (Allman, 1874a)
Salacia desmoides (Torrey, 1902)
Salacia dichotoma (Allman, 1888)
Salacia disjuncta Millard, 1964
Salacia distans (Bale, 1914b)
Salacia farquhari (Bale, 1924)
Salacia flavidula Watson, 2000

FIG. 180. Leptomedusae, Sertulariidae. A-C, *Papilionella pterophora*: A, portion of a colony showing structure of internodes and ramification; B, top part of a branch showing young hydrothecae with their operculum; C, semi-diagrammatic drawing of top part of hydrotheca to demonstrate the folding and mode of operation of opercular apparatus. D-G, *Parascyphus*: D-E, *Parascyphus simplex*: D, portion of an erect stem; E, hydrotheca and hydranth showing the abcauline caecum; F-G, *Parascyphus repens*: F, monosiphonic fragment of a colony; G, gonotheca. H-O, *Salacia*: H-J, *Salacia desmoides*: H, part stem with male gonothecae; I, part of stem with female gonotheca and acrocyst; J, hydrothecae with hydranths and opercula, no abcauline caecum; K-M, *Salacia disjuncta*: K, part of a colony; L, portion of hydrocaulus with origins of hydrocladia; M, hydrothecae; N-O, *Salacia tetracythara*: N, part of hydrocaulus with origins of hydrocladia; O, gonotheca (A-C after Antsulevich & Vervoort, 1993; D after Ralph, 1961b: p. 754, text-fig. 1 b; E, H-M after Millard 1975; F-G after Vervoort, 1972; N after Hirohito, 1995; O after Watson, 2000).

FIG. 180. *Leptomedusae, Sertulariidae. A-C,* Papilionella pterophora *: A, portion d'une colonie montrant la structure des internodes et d'une ramification ; B, partie supérieure d'une branche montrant de jeunes hydrothèques avec leurs opercules ; C, dessin semi-diagrammatique de la partie supérieure d'une hydrothèque montrant les plis et le mode opératoire de l'opercule. D-G,* Parascyphus : *D-E,* Parascyphus simplex : *D, portion d'une branche dressée ; E, hydrothèque et son hydranthe montrant le caecum abcaulinaire ; F-G,* Parascyphus repens : *F, fragment d'une colonie monosiphonique ; G, gonothèque. H-O,* Salacia : *H-J,* Salacia desmoides : *H, partie d'une branche avec des gonothèques mâles ; I, partie d'une branche avec une gonothèques femelle et son acrocyste ; J, hydrothèques avec leurs hydranthes et opercules mais sans caecum abcaulinaire ; K-M,* Salacia disjuncta : *K, partie d'une colonie ; L, portion d'hydrocaule montrant l'origine des hydroclades ; M, hydrothèques ; N-O,* Salacia tetracythara : *N, fragment d'hydrocaule montrant l'origine des hydroclades ; O, gonothèque (A-C d'après Antsulevich & Vervoort, 1993 ; D d'après Ralph, 1961b : p. 754, text-fig. 1 b ; E, H-M d'après Millard 1975 ; F-G d'après Vervoort, 1972 ; N d'après Hirohito, 1995 ; O d'après Watson, 2000).*


A
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Salacia fraseri Calder, 1991
Salacia hexodon (Busk, 1852)
Salacia macer Vervoort & Watson, 2003
Salacia marktanneri Stechow, 1913a
Salacia obliquanoda (Mulder & Trebilcock, 1914)
Salacia punctagonangia (Hargitt, 1924) [as *Sertularella*]
Salacia pyriformis (Fraser, 1936b)
Salacia ramosissima (Allman, 1885)
Salacia sibogae Billard, 1924b
Salacia sinuosa (Bale, 1884)
Salacia spiralis (Trebilcock, 1928)
Salacia tetracythara Lamouroux, 1816

Genus *SERTULARELLA* Gray, 1848

Figs 6I, P, 7D, 22, 23, 181A-K

Hydroid: colony erect, branched or unbranched, monosiphonic or polysiphonic; hydrocaulus and hydrocladia, when present, with two longitudinal rows of alternate, sessile hydrothecae; hydrothecal margin with 4 teeth; submarginal teeth present or absent, operculum pyramidal, composed of 4 triangular valves; retracted hydranth with abcauline caecum; gonophores as solitary fixed sporosacs, acrocyst in some species.

Remarks: the number of inner teeth may sometimes vary in the same colony; namely in *S. miurensis*, where they can vary from 0 to 5 (Hirohito 1995).

Recent references: Ramil, Parapar & Vervoort (1992); Vervoort (1993) (list); Hirohito (1995); Calder *et al.* (2003); Schuchert (2003); Vervoort & Watson (2003).

Sertularella acutidentata Billard, 1919b
Sertularella africana Stechow, 1919a
Sertularella agulhenis Millard, 1964
Sertularella albida Kirchenpauer, 1884
Sertularella ampullacea Fraser, 1938a
Sertularella anguina Vervoort, 1993
Sertularella annulata (Allman, 1888)
Sertularella annulaventricosa Mulder & Trebilcock, 1915
Sertularella antarctica Hartlaub, 1901a
Sertularella arbuscula (Lamouroux, 1816)
Sertularella areyi Nutting, 1904
Sertularella argentina El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella avrilia Watson, 1973
Sertularella billardi Vervoort, 1993
Sertularella bipectinata Vervoort, 1993
Sertularella blanconae El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella brandti Linko, 1912
Sertularella capensis Millard, 1957
Sertularella catena (Allman, 1888)
Sertularella clarki Mereschkowsky, 1878a
Sertularella clausa (Allman, 1888)
Sertularella complexa Nutting, 1904
Sertularella conella Stechow, 1920
Sertularella congregata Millard, 1964
Sertularella conica Allman, 1877
Sertularella costata Leloup, 1940
Sertularella crassa Billard, 1919b
Sertularella crassicaulis (Heller, 1868)
Sertularella crassiuscula Bale, 1924
Sertularella craticula Naumov, 1960
Sertularella crenulata Nutting, 1905
Sertularella cruzensis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella cubica García, Aguirre & Gonzalez, 1980
Sertularella decipiens Billard, 1919b
Sertularella diaphana (Allman, 1886)
Sertularella dubia Billard, 1907b
Sertularella ellisii (Deshayes & Milne Edwards, 1836)
Sertularella erecta Naumov & Stepanjants, 1962
Sertularella exigua Thompson, 1879
Sertularella exilis Fraser, 1938a
Sertularella falsa Millard, 1957
Sertularella flabellum (Allman, 1885)
Sertularella fuegonensis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella fusiformis (Hincks, 1861)
Sertularella fusoides Stechow, 1926
Sertularella gaudichaudi (Lamouroux, 1824a)
Sertularella gayi (Lamouroux, 1821)
Sertularella geniculata Hincks, 1874
Sertularella geodiae Totton, 1930
Sertularella gigantea Mereschkowsky, 1878b
Sertularella gilchristi Millard, 1964
Sertularella goliathus Stechow, 1923a
Sertularella helenae Vervoort, 1993
Sertularella hermanosensis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella humilis Fraser, 1943
Sertularella implexa (Allman, 1888)
Sertularella inabai Stechow, 1913a
Sertularella inconstans Billard, 1919b
Sertularella integra Allman, 1876a
Sertularella intricata Billard, 1919a
Sertularella japonica Stechow, 1926

Sertularella jorgensis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella keiensis Billard, 1925a
Sertularella lagena (Allman, 1876)
Sertularella lata Bale, 1882
Sertularella laxa Allman, 1888
Sertularella leiocarpa (Allman, 1888)
Sertularella leiocarpoides Vervoort, 1993
Sertularella levigata Stechow, 1931
Sertularella magna Nutting, 1904
Sertularella mediterranea Hartlaub, 1901a
Sertularella megastoma Nutting, 1904
Sertularella megista Stechow, 1923a
Sertularella microtheca Leloup, 1974
Sertularella millardi Stepanjants, 1979
Sertularella minuscula Billard, 1925b
Sertularella mirabilis Jäderholm, 1896
Sertularella miurensis Stechow, 1921c
Sertularella mutsuensis Stechow, 1931
Sertularella natalensis Millard, 1968
Sertularella novaecaledoniae Vervoort, 1993
Sertularella nuttingi Billard, 1914
Sertularella ornata Broch, 1933
Sertularella ornata Fraser, 1937a [doubtful status]
Sertularella paessleri Hartlaub, 1901a
Sertularella parvula Mammen, 1965
Sertularella patagonica (D'Orbigny, 1846)
Sertularella paucicostata Vervoort, 1993
Sertularella peculiaris Leloup, 1974
Sertularella pellucida Jäderholm, 1907
Sertularella peregrina Bale, 1926
Sertularella picta (Meyen, 1834)
Sertularella pinnata Clark, 1876b
Sertularella polyzonias (Linnaeus, 1758)
Sertularella producta Allman, 1888
Sertularella pseudocostata Vervoort, 1993
Sertularella pulchra Stechow, 1923a
Sertularella quadrata Nutting, 1895
Sertularella quadridens (Bale, 1884)
Sertularella quadrifida Hartlaub, 1901a
Sertularella quinquelaminata Stechow, 1931
Sertularella ramosa Thompson, 1879
Sertularella richardsoni Ralph, 1961b
Sertularella robusta Coughtrey, 1876
Sertularella robustoides Mulder & Trebilcock, 1915
Sertularella rugosa (Linnaeus, 1758)
Sertularella sagamina Stechow, 1921c
Sertularella sanmatiasensis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella similis Fraser, 1948
Sertularella simplex (Hutton, 1873)
Sertularella sinensis Jäderholm, 1896
Sertularella solidula Bale, 1882
Sertularella spinosa Kirchenpauer, 1884
Sertularella spirifera Stechow, 1931

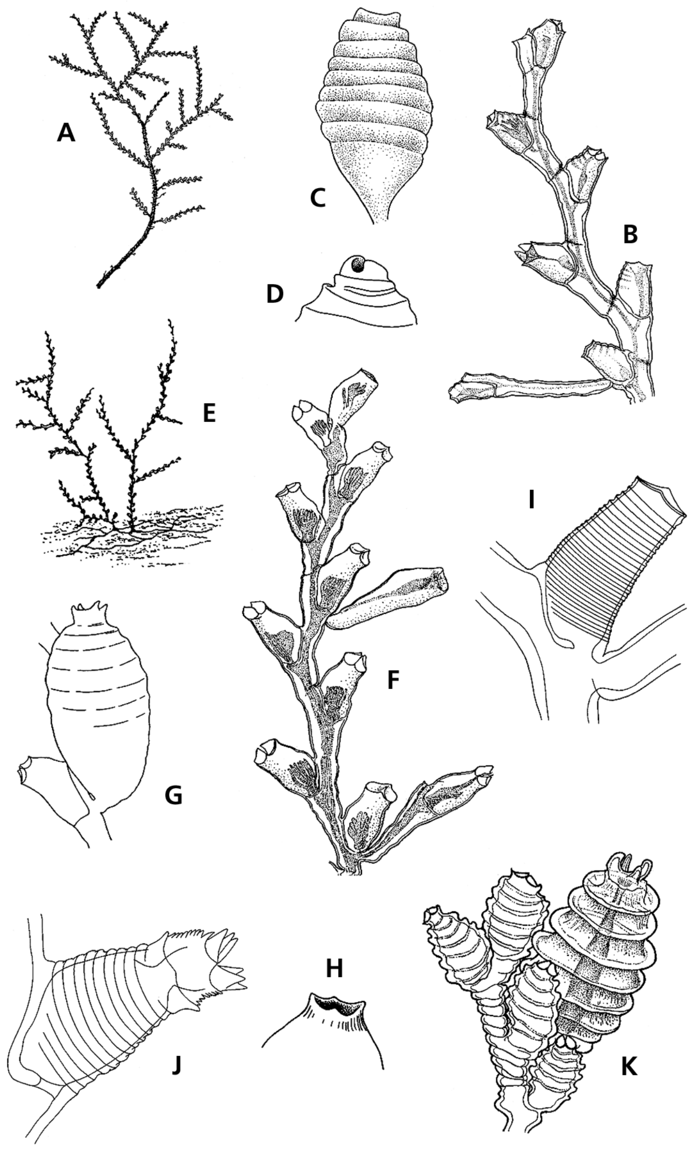


FIG. 181. Leptomedusae. A-K, Sertulariidae, *Sertularella*. A-D, *Sertularella gayi*: A, general view of a colony; B, detail of a hydrocladium; C, gonotheca; D, end of a gonotheca. E-H, *Sertularella polyzonias*: E, general view of a colony; F, detail of a hydrocladium; G, gonotheca; H, detail of end of gonotheca. I, *Sertularella crenulata*, axillary hydrotheca. J, *Sertularella sinensis*, hydrocladial hydrotheca with much renovated distal portion. K, *Sertularella rugosa*, hydrothecae and gonotheca (A-C, E-G & K after Leloup, 1952; D, H after Cornelius, 1995; I-J after Vervoort, 1993).

FIG. 181. *Leptomedusae. A-K, Sertulariidae,* Sertularella. *A-D,* Sertularella gayi : *A, vue générale d'une colonie ; B, détail d'un hydroclade ; C, gonothèque ; D, partie apicale d'une gonothèque. E-H,* Sertularella polyzonias : *E, vue générale d'une colonie ; F, détail d'un hydroclade ; G, gonothèque ; H, détail de l'extrémité d'une gonothèque. I,* Sertularella crenulata*, hydrothèque axillaire. J,* Sertularella sinensis*, hydrothèque hydrocladiale avec de multiples rénovations de la portion distale. K,* Sertularella rugosa*, hydrothèques et gonothèque (A-C, E-G & K d'après Leloup, 1952 ; D, H d'après Cornelius, 1995 ; I-J d'après Vervoort, 1993).*

Sertularella stolonifera Vervoort & Watson, 2003
Sertularella striata Stechow, 1923b
Sertularella tanneri Nutting, 1904
Sertularella tasmanica Bale, 1915
Sertularella tenella (Alder, 1856a) [perhaps a syn. of *S. rugosa*]
Sertularella thecocarpa Jarvis, 1922
Sertularella tilesii Kirchenpauer, 1884
Sertularella tongensis Stechow, 1919a
Sertularella tridentata (Lamouroux, 1816)
Sertularella undulitheca Vervoort, 1959
Sertularella unituba Calder, 1991
Sertularella uruguayensis Mañon-Garzon & Milstein, 1973
Sertularella valdiviae Stechow, 1923b
Sertularella vervoorti El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Sertularella wallacei Stechow, 1926
Sertularella whitei Rees & Vervoort, 1987
Sertularella xantha Stechow, 1923a
Sertularella zenkevitchi Naumov, 1960

Genus ***SERTULARIA*** L., 1758

Figs 6K, 182A-L

Synonym: *Tridentata* Stechow, 1920, sometimes kept as a separate genus.
Hydroid: colony erect, arborescent, pinnate or simple, monosiphonic; hydrothecae borne on stem and branches, sessile, partly adnate, oppositely or alternately in two longitudinal rows, hydrothecal margin with two lateral cusps about midway of abcauline and adcauline edges and, in some species, a third median adcauline one; operculum non pyramidal, two-valved, adcauline valve smaller than abcauline; retracted hydranth with abcauline caecum, in some species mantle or ectodermal lamella present, with or without distal batteries of large cnidocysts; gonophore as fixed sporosacs, sometimes planula brooded in external acrocyst, exceptionally as swimming gonophores (*Sertularia marginata*).
Recent references: Medel *et al.* (1991); Medel & Vervoort (1998); Calder *et al.* (2003); Schuchert (2003).

Sertularia albimaris Mereshkovsky, 1878b [syn. *S. inflata* Schydlowsky, 1902]
Sertularia argentea Linnaeus, 1758
Sertularia australis (Kirchenpauer, 1864)
Sertularia bicuspidata Lamarck, 1816
Sertularia bilateralis (Brooks, 1880)
Sertularia billardi Bale, 1915
Sertularia borneensis Billard, 1925b
Sertularia brashnikowi Kudelin, 1914
Sertularia brunnea (Stechow, 1923c)
Sertularia camtschatika Winogradow, 1947
Sertularia carolinensis Verrill, 1872
Sertularia ceylonensis Stechow, 1921a
Sertularia conferta (Kirchenpauer, 1864)
Sertularia converrucosa Naumov, 1960
Sertularia cupressina Linnaeus, 1758
Sertularia cupressoides Clark, 1876b
Sertularia distans (Lamouroux, 1816) [syn. *S. gracilis* Hassall, 1848]
Sertularia divergens Lamouroux, 1816
Sertularia dohrni Stechow, 1923c
Sertularia drachi Vannucci, 1949
Sertularia dubia Hargitt, 1924
Sertularia elongata Stechow & Müller, 1923
Sertularia fabricii Levinsen, 1893b
Sertularia fissa Thornely, 1904
Sertularia flexilis Thompson, 1879
Sertularia flowersi Nutting, 1904
Sertularia frigida Stechow, 1921a
Sertularia funafutiensis Stechow, 1923b
Sertularia gracillima Bale, 1926
Sertularia hattorii Leloup, 1940b
Sertularia heteroclada (Jäderholm, 1902b)
Sertularia humilis (Armstrong, 1879)
Sertularia intermedia Levinsen, 1913
Sertularia latiuscula Stimpson, 1854
Sertularia ligulata Thornely, 1904
Sertularia linkoi Kudelin, 1914
Sertularia littoralis Thornely, 1900
Sertularia loculosa Busk, 1852
Sertularia longa (Millard, 1958)
Sertularia maccallumi Bartlett, 1907
Sertularia malayensis Billard, 1925b
Sertularia marginata (Kirchenpauer, 1864)
Sertularia mediterranea (Marktanner-Turneretscher, 1890)
Sertularia mertoni Stechow & Müller, 1923
Sertularia mirabilis (Verrill, 1873)
Sertularia nana (Hartlaub, 1901a)
Sertularia notabilis Fraser, 1947
Sertularia nuttingi Levinsen, 1913
Sertularia orthogonalis Gibbons & Ryland, 1989
Sertularia palkensis Mammen, 1965
Sertularia perpusilla Stechow, 1919a
Sertularia plumosa (Clark, 1876b)
Sertularia pusilla Bale, 1915
Sertularia robusta (Clark, 1876b)
Sertularia rugosissima Thornely, 1904

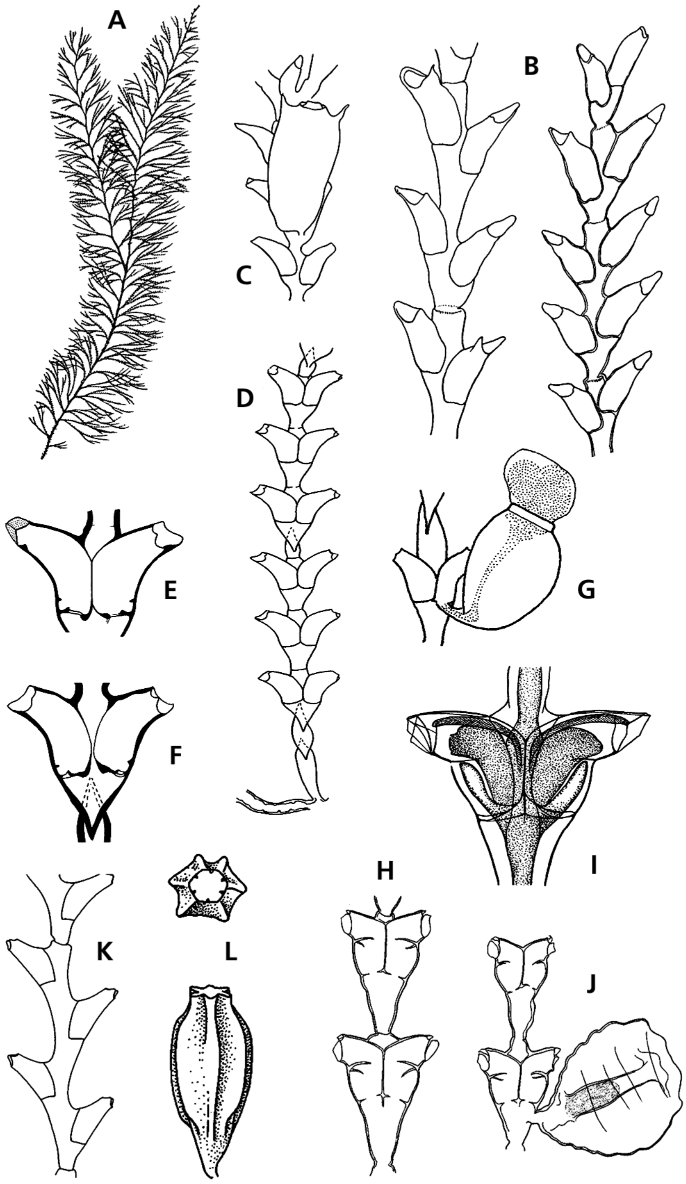


FIG. 182. Leptomedusae, Sertulariidae. A-C, *Sertularia argentea*: A, general view of a colony; B, two aspects of hydrocladia; C, part of hydrocladia with gonotheca. D-G, *Sertularia distans*: D, view of a part of stem; E, hydrothecae from middle part of stem; F, hydrotheca of lower part of stem; G, gonotheca. H-J, *Sertularia ligulata*: H, pairs of hydrothecae; I, pair of hydrothecae with hydranths and ligulae; J, part of stem with male gonotheca. K-L, *Sertularia tenera*: K, detail of hydrocladia; L, gonotheca with polygonal cross-section (A-C after Leloup, 1952; D-G after Millard, 1975; H & J after Hirohito, 1995; I after Leloup, 1937; K-L after Cornelius, 1995).

FIG. 182. *Leptomedusae, Sertulariidae. A-C,* Sertularia argentea : *A, vue générale d'une colonie ; B, deux aspects d'hydroclades ; C, fragment d'hydroclade avec une gonothèque. D-G,* Sertularia distans : *D, vue d'une portion de branche ; E, hydrothèques de la partie médiane d'une branche ; F, hydrothèques de la partie basale d'une branche ; G, gonothèque. H-J,* Sertularia ligulata : *H, paire d'hydrothèques ; I, paire d'hydrothèques avec leurs hydranthes et ligules ; J, partie d'une branche avec des gonothèques mâles. K-L,* Sertularia tenera : *K, détail d'une hydroclade ; L, gonothèque de section polygonale (A-C d'après Leloup, 1952 ; D-G d'après Millard, 1975 ; H & J d'après Hirohito, 1995 ; I d'après Leloup, 1937 ; K-L d'après Cornelius, 1995).*

Sertularia schmidti Kudelin, 1914
Sertularia secunda Heller, 1868
Sertularia similis Clark, 1876
Sertularia simplex (Fraser, 1938a)
Sertularia stabilis Fraser, 1948
Sertularia staurotheca Naumov, 1960
Sertularia stechowi Hirohito, 1995
Sertularia suensoni Levinsen, 1913
Sertularia tatarica Kudelin, 1914
Sertularia tenera Sars, 1874
Sertularia tenuis Bale, 1884
Sertularia tolli (Jäderholm, 1908)
Sertularia trigonostoma Busk, 1852
Sertularia tumida Allman, 1877
Sertularia turbinata (Lamouroux, 1816)
Sertularia unguiculata Busk, 1852
Sertularia vervoorti Migotto & Calder, 1998
Sertularia westindica (Stechow, 1920)

Genus *STAUROTHECA* Allman, 1888

Fig. 183A-G

Hydroid: colony bushy or palmate; hydrothecae tubular, curved slightly or distinctly outwards, with circular aperture, partly to almost completely adnate, arranged in 2 longitudinal rows or in series alternately crossing at right angles (=decussate) composed of pairs or verticils of hydrothecae, the number of longitudinal hydrothecal rows being so twice the number of hydrothecae found in verticil pairs; along length of stem and main hydrocladia the number of series of hydrothecae decreases or remain constant; decussate pairs of opposite, subopposite or even alternate hydrothecae may occur in distal hydrocladial branches; operculum one-flapped, deciduous and with indistinct point of attachment, diaphragm frequently mushroom-shaped; cnidome: microbasic mastigophores; gonophores as solitary fixed sporosacs, gonothecae on hydrocauli and hydrocladia inserted directly under a hydrotheca.

Remarks: the species formerly referred to the genus *Selaginopsis* Allman, 1876 found in the southern hemisphere have been included by Peña Cantero *et al.* (1997b) in *Staurotheca* while the northern hemisphere ones have been placed in *Thuiaria*; this proposal based mainly on geographical distribution is provisionally followed here.

Recent references: Peña Cantero *et al.* (1997b); Peña Cantero *et al.* (1999); Vervoort & Watson (2003).

Staurotheca affinis (Jäderholm, 1904a)
Staurotheca amphorophora Naumov & Stepanjants, 1962
Staurotheca antarctica Hartlaub, 1904
Staurotheca australis Peña Cantero, Svoboda & Vervoort, 1997b
Staurotheca compressa Briggs, 1938 (1939)
Staurotheca cornuta Peña Cantero, Garcia-Carrascosa & Vervoort, 1999
Staurotheca dichotoma Allman, 1888
Staurotheca frigida Peña Cantero, Svoboda & Vervoort, 1997b
Staurotheca glomulosa Peña Cantero, Svoboda & Vervoort, 1997b
Staurotheca jaederholmi Stechow, 1920
Staurotheca juncea (Vanhöffen, 1910)
?*Staurotheca megalotheca* Vervoort & Watson, 2003
Staurotheca multifurcata Peña Cantero, Garcia-Carrascosa & Vervoort, 1999
Staurotheca nonscripta Peña Cantero, Svoboda & Vervoort, 1997b
Staurotheca pachyclada (Jäderholm, 1904)
Staurotheca plana Peña Cantero, Svoboda & Vervoort, 1997b
Staurotheca polarsterni Peña Cantero, Svoboda & Vervoort, 1997b
Staurotheca stolonifera (Hartlaub, 1904)
Staurotheca tubifera Blanco, 1971
Staurotheca undosiparietina (Stepanjants, 1979)
Staurotheca urceolifera (Kirchenpauer, 1884)
Staurotheca vanhoeffeni (Peña Cantero & Garcia-Carrascosa, 1994)

Genus *STEREOTHECA* Stechow, 1919

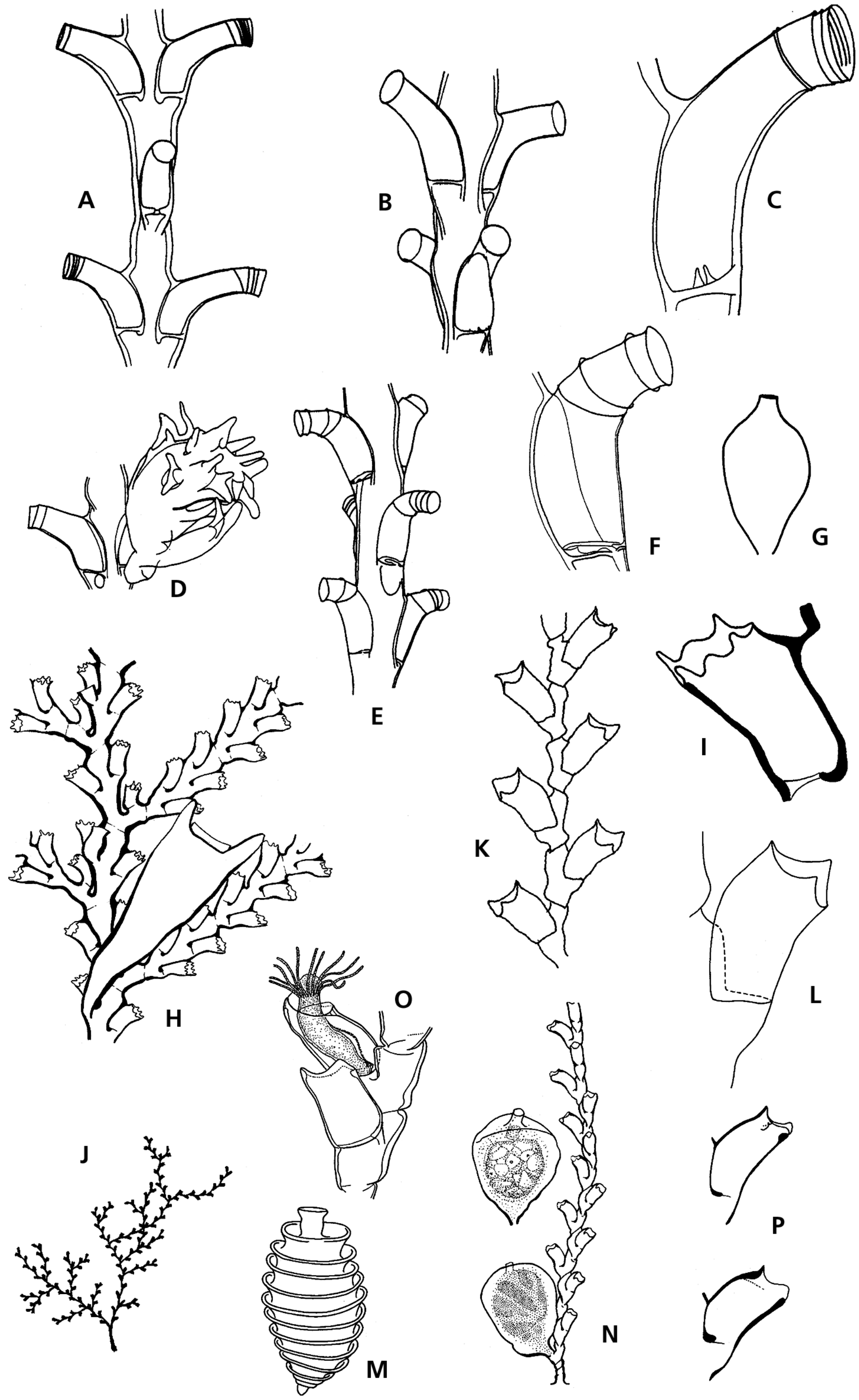
Fig. 183H-I

Hydroid: colony stiff, erect, monosiphonic, pinnate; hydrocladia opposite, subopposite or alternate; hydrocaulus and hydrocladia bearing two longitudinal rows of alternate hydrothecae in one plane; hydrothecae sessile, adnate half to three-quarters of adcauline height, with more than four (up to 16 usually 6) well developed marginal teeth, with no intrathecal septa and no external longitudinal ridges; no operculum; hydranth not described; gonophores as solitary fixed sporosacs.

Stereotheca elongata (Lamouroux, 1816)

FIG. 183. Leptomedusae, Sertulariidae. A-G, *Staurotheca*: A-D, *Staurotheca antarctica*: A-B, fragment of hydrocladium showing the arrangement of hydrothecae in decussate pairs; C, detail of hydrotheca; D, female gonotheca; E-G, *Staurotheca dichotoma*: E, part of hydrocladium showing the arrangement of the hydrothecae in decussate pairs; F, detail of hydrotheca; G, gonotheca. H-I, *Stereotheca elongata*: H, part of hydrocaulus showing origins of hydrocladia and gonotheca; I, detail of hydrotheca. J-P, *Symplectoscyphus*: J-M, *Symplectoscyphus tricuspidatus*: J, general view of a part of a colony; K, detail of hydrocladium; L, hydrotheca; M, gonotheca; N-P, *Symplectoscyphus macrogonus*: N, stem with hydrothecae and male gonothecae, left isolated female gonotheca;O, two hydrothecae, one with hydranth; P, hydrothecae (A-G after Peña Cantero *et al.*, 1997; H-I, N & P after Millard, 1975; J-L after Cornelius, 1995; O after Ralph, 1961b: p. 799, text-fig. 14 b).

FIG. 183. *Leptomedusae, Sertulariidae. A-G,* Staurotheca : *A-D,* Staurotheca antarctica : *A-B, fragments d'hydroclade montrant l'arrangement des hydrothèques en paires décussées ; C, détail d'une hydrothèque ; D, gonothèque femelle ; E-G,* Staurotheca dichotoma : *E, partie d'un hydroclade montrant l'arrangement des hydrothèques en paires décussées ; F, détail d'une hydrothèque ; G, gonothèque. H-I,* Stereotheca elongata *: H, partie d'un hydrocaule montrant l'origine des hydroclades et une gonothèque ; I, détail d'une hydrothèque. J-P,* Symplectoscyphus : *J-M,* Symplectoscyphus tricuspidatus : *J, vue générale d'un fragment de colonie ; K, détail d'un hydroclade ; L, détail d'une hydrothèque ; M, gonothèque. N-P,* Symplectoscyphus macrogonus : *N, branche avec des hydrothèques et une gonothèque mâle, à gauche une gonothèque femelle isolée ; O, deux hydrothèques, dont une avec un hydranthe ; P, hydrothèques (A-G d'après Peña Cantero* et al.*, 1997 ; H-I, N & P d'après Millard, 1975 ; J-L d'après Cornelius, 1995 ; O d'après Ralph, 1961b : p. 799, text-fig. 14 b).*


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P

Genus ***SYMPLECTOSCYPHUS*** Marktanner-Turneretscher, 1890

Figs 6J, 9J, 183J-P

Hydroid: colony erect, branched or unbranched; no distinct stem or no apophyses and paired hydrocladia if main stem present; hydrocaulus and hydrocladia bearing alternate hydrothecae in two longitudinal rows; hydrotheca sessile, generally cylindrical, with 3 marginal teeth, an adcauline median one and two latero-abcauline ones; operculum of three triangular flaps, pyramidal; in some species an oblique septum supporting the hydranth on the intrathecal wall at the base of hydrotheca; retracted hydranth with abcauline caecum; gonophores as solitary fixed sporosacs, gonothecae normally having spiral or circular ribs, with distal tubular neck.

Remarks: this genus is very close to *Antarctoscyphus*.

Recent references: Vervoort (1993); Peña Cantero *et al.* (1997); Schuchert (2001a); Vervoort & Watson (2003).

Symplectoscyphus adpressa (Ritchie, 1911)
Symplectoscyphus aggregatus (Jäderholm, 1917)
Symplectoscyphus amoenus Vervoort & Watson, 2003
Symplectoscyphus amphorifera (Allman, 1877)
Symplectoscyphus anae Peña Cantero, Svoboda & Vervoort, 2002
Symplectoscyphus arboriformis (Marktanner-Turneretscher, 1890)
Symplectoscyphus articulatus (Allman, 1888)
Symplectoscyphus bathyalis Vervoort, 1972
Symplectoscyphus bathypacificus Vervoort, 1993
Symplectoscyphus candelabrum Vervoort & Watson, 2003
Symplectoscyphus chubuticus El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus columnarius (Briggs, 1914)
Symplectoscyphus commensalis Vervoort, 1993
Symplectoscyphus confusus Totton, 1930
Symplectoscyphus cumberlandicus (Jäderholm, 1905)
Symplectoscyphus curvatus (Jäderholm, 1917)
Symplectoscyphus densestriatus Tang, 1991b
Symplectoscyphus dentiferus (Torrey, 1902)
Symplectoscyphus divaricatus (Busk, 1852)
Symplectoscyphus effusus Vervoort, 1993
Symplectoscyphus elegans (Nutting, 1904)
Symplectoscyphus epizoicus Watson, 1973
Symplectoscyphus epizooticus Totton, 1930
Symplectoscyphus erectus (Fraser, 1938b)
Symplectoscyphus erectus (Naumov & Stepanjants, 1962) [preoccupied by *S. erectus* (Fraser, 1838b)]
Symplectoscyphus exochus Blanco, 1982
Symplectoscyphus exsertus (Allman, 1888)
Symplectoscyphus filiformis (Allman, 1888)
Symplectoscyphus flexilis (Hartlaub, 1901a)
Symplectoscyphus frigidus Peña Cantero, Svoboda & Vervoort, 2002
Symplectoscyphus fuscus (Trebilcock, 1928)
Symplectoscyphus glacialis (Jäderholm, 1904)
Symplectoscyphus hero Blanco, 1977a
Symplectoscyphus howensis Vervoort & Watson, 2003
Symplectoscyphus hozawai Stechow, 1931
Symplectoscyphus huanghaiensis Tang & Huang, 1986
Symplectoscyphus hydrallmaniaeformis (Kudelin, 1914)
Symplectoscyphus incisus (Fraser, 1938a)
Symplectoscyphus indivisus (Bale, 1882)
Symplectoscyphus infractus (Kirchenpauer, 1884)
Symplectoscyphus interruptus (Pfeffer, 1889)
Symplectoscyphus irregularis (Trebilcock, 1928)
Symplectoscyphus johnstoni (Gray, 1843)
Symplectoscyphus laevis (Bale, 1882)
Symplectoscyphus leloupi El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus levinseni (Nutting, 1904)
Symplectoscyphus liouvillei (Billard, 1914)
Symplectoscyphus longitheca (Bale, 1888)
Symplectoscyphus macrocarpa (Billard, 1918)
Symplectoscyphus macrogonus (Trebilcock, 1928)
Symplectoscyphus macroscyphus Vervoort & Watson, 2003
Symplectoscyphus macrotheca (Bale, 1882)
Symplectoscyphus magellanicus (Marktanner-Turneretscher, 1890)
Symplectoscyphus margaritaceus (Allman, 1885)
Symplectoscyphus marionensis Millard, 1971
Symplectoscyphus millardi (Stepanjants, 1979)
Symplectoscyphus milneanus (D'Orbigny, 1846)
Symplectoscyphus minutus (Nutting, 1904)
Symplectoscyphus modestus (Hartlaub, 1901a)
Symplectoscyphus monopleura (Hartlaub, 1901a)
Symplectoscyphus multinoda (Fraser, 1948)
Symplectoscyphus neglectus (Thompson, 1879)
Symplectoscyphus nesioticus Blanco, 1977b
Symplectoscyphus odontiferus Vervoort & Watson, 2003
Symplectoscyphus pallidus (Kirchenpauer, 1884)
Symplectoscyphus paraglacialis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus paulensis Stechow, 1923b
Symplectoscyphus pedrensis (Torrey, 1904)
Symplectoscyphus pedunculatus (Billard, 1919)
Symplectoscyphus pinnatus (Clark, 1876b)
Symplectoscyphus plectilis (Hickson & Gravely, 1907)
Symplectoscyphus pluma (Hartlaub, 1901a)
Symplectoscyphus procera (Trebilcock, 1928)
Symplectoscyphus pseudocolumnarius Vervoort, 1993
Symplectoscyphus pseudodivaricatus Ralph, 1961
Symplectoscyphus pulchellus (Jäderholm, 1904)
Symplectoscyphus pushi (Stepanjants, 1979)
Symplectoscyphus pygmaeus (Bale, 1882)

Symplectoscyphus ralphae Vervoort, 1993
Symplectoscyphus rentoni (Bartlett, 1907)
Symplectoscyphus ritchiei (Briggs, 1915)
Symplectoscyphus rostratus Watson, 1973
Symplectoscyphus rubellus (Kirchenpauer, 1884)
Symplectoscyphus salvadorensis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus secundus (Kirchenpauer, 1884)
Symplectoscyphus sibogae (Billard, 1924b)
Symplectoscyphus singularis El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus sinuosus (Fraser, 1948)
Symplectoscyphus sofiae Peña Cantero, Svoboda & Vervoort, 2002
Symplectoscyphus spiraliformis Vervoort & Watson, 2003
Symplectoscyphus spiritualis Totton, 1930
Symplectoscyphus subarticulatus (Coughtrey, 1875)
Symplectoscyphus subdichotomus (Kirchenpauer, 1884)
Symplectoscyphus tricuspidatus (Alder, 1856a)
Symplectoscyphus trimucronatus (Allman, 1885)
Symplectoscyphus tropicus (Hartlaub, 1901a)
Symplectoscyphus tuba Totton, 1930
Symplectoscyphus turgidus (Trask, 1857)
Symplectoscyphus unilateralis (Lamouroux, 1824b)
Symplectoscyphus valdesicus El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus vanhoeffeni Totton, 1930
Symplectoscyphus variabilis (Bale, 1888)
Symplectoscyphus vervoorti El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Symplectoscyphus watsonae Vervoort, 1993
Symplectoscyphus weddelli Peña Cantero, Svoboda & Vervoort, 2002

Genus ***TAMARISCA*** Kudelin, 1914

Fig. 184A-E

Hydroid: colony ramified in one plane, with robust monosiphonic stems, hydrocladia widely spaced, usually alternate but sometimes opposite; hydrothecae sub-opposite, in two rows on hydrocaulus and hydrocladia, tubular, sessile, partly adnate; hydrothecal rim with 3 equal cusps; operculum pyramidal with 3 flaps; gonothecae in upper part of hydrocaulus and hydrocladia, dimorphic, very distinctive, male one kit-shaped, tapering to short pedicel, female one conical, with distal end bearing three large flattened segments, each deeply divided into lobes, two of them covering the gonothecal aperture like a sloping roof, the third bending inwards (marsupium).
Recent references: Cornelius (1995); Schuchert (2001a).

Tamarisca tamarisca (Linnaeus, 1758)

Genus ***TASMANARIA*** Watson & Vervoort, 2001

Fig. 184F-H

Hydroid: colonies large, arborescent, planar or plumose; hydrocaulus polysiphonic, perisarc thick; hydrothecae biseriate, alternate or subalternate, immersed in hydrocladia and branches; margin of hydrotheca circular, rim even, operculum of one delicate concave or convex valve fragmenting at eruption of hydranth, gonothecae large piriform, borne singly on branches.
Recent reference: Vervoort & Watson (2003).

Tasmanaria aegis Watson & Vervoort, 2001
Tasmanaria edentulata (Bale, 1924) [also known as *Sertularella edentula*]
Tasmanaria monticola Watson & Vervoort, 2001
Tasmanaria pacifica Vervoort & Watson, 2003

Genus ***THUIARIA*** Fleming, 1828

Figs 5N, 6M, 184I-P

Hydroid: colony pinnate, palmate or bottle-brush-shaped; hydrocladia subopposite, alternate, or all around stem; hydrothecae on hydrocaulus and hydrocladia, cylindrical, broadened in lower part, narrowed toward aperture; partly or completely adnate or totally sunk in cladia, hydrothecal rim usually circular (except in *T. gonorhiza*, where it is sinuous), hydrothecal operculum of a single abcauline attached flap; hydrothecae multiseriate, on hydrocaulus in two opposite, subopposite or alternate longitudinal rows, (except in a few species like: *T. artica*, with 4 longitudinal rows, and *T. zachsi*, with 6 to 8 longitudinal rows) falling in the same plane, on hydrocladia, with a similar distribution to hydrocauli or as verticils formed by three or more hydrothecae, verticils alternately crossing in right angles, the number of longitudinal rows of hydrothecae being so twice the number of hydrothecae (up to 13 rows recorded); retracted hydranth with abcauline caecum; gonophores as fixed solitary sporosacs, in many species female ones forming a marsupium (acrocyst), in other species female ones with distal spines forming an external brood chamber (pseudomarsupium), gonothecae on hydrocauli and hydrocladia, inserted directly under a hydrotheca.

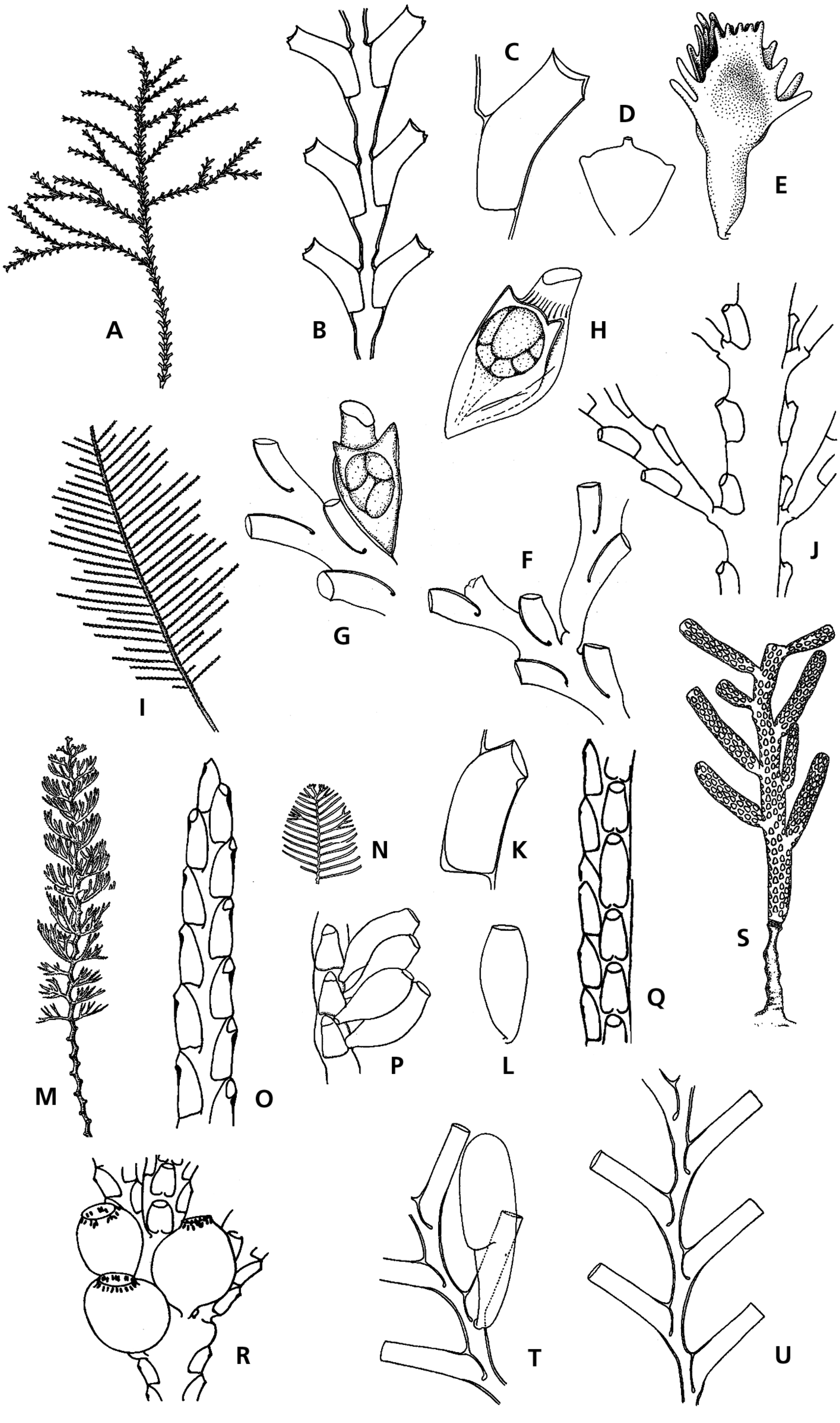
Remarks: see *Staurotheca*.

Recent references: Cornelius (1995); Peña Cantero *et al.* (1997b); Calder *et al.* (2003).

Thuiaria abyssicola (Billard, 1925a)
Thuiaria acutiloba Kirchenpauer, 1884
Thuiaria affinis (Jäderholm, 1905)
Thuiaria alternans Naumov, 1952
Thuiaria alternitheca Levinsen, 1893b
Thuiaria arctica (Bonnevie, 1899) [probably a syn. of *T. hartlaubi*]
Thuiaria articulata (Pallas, 1766)
Thuiaria bidentata (Allman, 1876)
Thuiaria breitfussi (Kudelin, 1914)
Thuiaria carica Levinsen, 1893c
Thuiaria cedrina (Linnaeus, 1758)
Thuiaria constans (Fraser, 1948) [doubtful status]
Thuiaria cornigera Kudelin, 1914
Thuiaria coronifera Allman, 1876
Thuiaria cupressoides (Lepechin, 1783)
Thuiaria cylindrica Clark, 1876
Thuiaria derbeki Kudelin, 1914
Thuiaria decemserialis (Mereshkovsky, 1878a)
Thuiaria desmoides (Torrey, 1902)
Thuiaria diffusa (Allman, 1885)
Thuiaria distans Fraser, 1914a
Thuiaria excepticea Fenyuk, 1947
Thuiaria gonorhiza Naumov, 1952
Thuiaria hartlaubi (Nutting, 1904)
Thuiaria hippuris Allman, 1874b
Thuiaria insociabilis Fraser, 1948
Thuiaria invicea Naumov, 1960
Thuiaria involuta Naumov, 1960
Thuiaria kudelini Naumov, 1960
Thuiaria kurilae Nutting, 1904
Thuiaria laxa Allman, 1874b
Thuiaria lebedi Naumov, 1960
Thuiaria mereschkowskii Kudelin, 1914
Thuiaria nivea Fenyuk, 1947
Thuiaria obsoleta (Lepechin, 1781)
Thuiaria ochotensis (Mereshkovsky, 1878a)
Thuiaria opercolata Watson, 2000
Thuiaria pinaster (Lepechin, 1783)
Thuiaria pinna Naumov, 1960
Thuiaria plumiformis (Nutting, 1904)
Thuiaria plumularoides Watson, 2000
Thuiaria purpurea (Linnaeus, 1758)
Thuiaria sachalini Kudelin, 1914
Thuiaria shetlandica Naumov & Stepanjants, 1972
Thuiaria stelleri Kirchenpauer, 1884
Thuiaria subthuja Fenyuk, 1947
Thuiaria tetrastriata Naumov, 1960
Thuiaria thuja (Linnaeus, 1758)
Thuiaria thujarioides (Clark, 1876b)
Thuiaria trilateralis Fraser, 1936a
Thuiaria triserialis (Mereshkovsky, 1878a)
Thuiaria variabilis Broch, 1918
Thuiaria vervoorti El Beshbeeshy, 1991 [name not available; not published in the sense of the Code]
Thuiaria wulfiusi Naumov, 1960
Thuiaria zachsi Fenyuk, 1947

FIG. 184. Leptomedusae, Sertulariidae. A-E, *Tamarisca tamarisca*: A, general view of a colony; B, detail of a hydrocladium; C, detail of hydrotheca; D, male gonotheca; E, female gonotheca. F-H, *Tasmanaria aegis*: F, monosiphonic part of branch; G, gonotheca adpressed to branch; H, anterior view of female gonotheca. I-P, *Thuiaria articulata*: I, view of a part of colony; J, detail of stem; K, hydrotheca; L, gonotheca; M-P, *Thuiaria thuja*: M, general view of a colony; N, young colony, note pinnate shape; O, detail of hydrocladium; P, gonothecae. Q-R, *Thuiaria cedrina*: Q, part of branch with hydrothecae; R, proximal part of branch with hydrothecae and gonothecae. S, *Thuiaria zachsi*, colony showing the numerous rows of hydrothecae. T-U, *Gigantotheca maxima*: T, part of stem with hydrothecae and gonotheca; U, part of stem with hydrothecae (A-E, I-L, N-O after Cornelius, 1995; F-H after Watson & Vervoort, 2001; M & P after Leloup, 1952; Q-S after Naumov, 1969; T-U after Vervoort & Watson, 2003).

***FIG. 184.** Leptomedusae, Sertulariidae. A-E,* Tamarisca tamarisca : *A, vue générale d'une colonie ; B, détail d'un hydroclade ; C, hydrothèque ; D, gonothèque male ; E, gonothèque femelle. F-H,* Tasmanaria aegis *: F, partie d'une branche monosiphonique ; G, gonothèque appliquée sur une branche ; H, vue antérieure d'une gonothèque femelle. I-P,* Thuiaria articulata *: I, colonie ; J, détail d'une branche ; K, hydrothèque ; L, gonothèque ; M-P,* Thuiaria thuja *: M, vue générale d,une colonie ; N, jeune colonie, notez la forme pinnée ; O, détail d'un hydroclade ; P, gonothèques. Q-R,* Thuiaria cedrina : *Q, partie d'une branche avec des hydrothèques ; R, portion proximale d'une branche avec des hydrothèques et des gonothèques. S,* Thuiaria zachsi*, colonie montrant les nombreuses rangées d'hydrothèques. T-U,* Gigantotheca maxima : *T, portion d'une branche avec des hydrothèques et une gonothèque ; U, partie d'une branche avec des hydrothèques (A-E, I-L, N-O d'après Cornelius 1995 ; F-H d'après Watson & Vervoort, 2001 ; M & P d'après Leloup, 1952 ; Q-S d'après Naumov, 1969 ; T-U d'après Vervoort & Watson, 2003).*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Sertulariidae *incertae sedis*:

Genus ***GIGANTOTHECA*** Vervoort and Watson, 2003

Fig. 184T-U

Hydroid: large, loosely branched, fan-shaped colonies; principal branches on lower, weakly polysiphonic, part of colony, with isolated secondary tubules running up the branches; nodes absent or indistinct. Hydrothecae large, biseriate, alternate, tubiform, only a fraction of abcauline wall adnate, margin circular, rim non-everted, operculum unknown, base of hydrotheca open. Stem between insertions of hydrothecae geniculate. Gonothecae large, club- to slipper-shaped, with slit-like apical aperture, folds or ornamentation may surround gonothecal aperture. Insertion of gonothecae on front of colony by means of short pedicel attaching to branch or stem directly under hydrothecal base, leaving distinct scar when shed.

Remarks: Vervoort & Watson (2003) considered this genus as a large sertulariid with colony structure similar to that of large species of *Sertularella*, but with much bigger, tubiform hydrothecae and much differing gonothecae. The opercular system of this genus being unknown, it is impossible to ascribe it with certainty to the Sertulariidae. Consequently, we consider *Gigantotheca* as *incertae sedis*, pending more information.

Recent reference: Vervoort & Watson (2003).

Gigantotheca maxima Vervoort and Watson, 2003
Gigantotheca raukumarai Vervoort and Watson, 2003

Genus ***HYPOPYXIS*** Allman, 1888

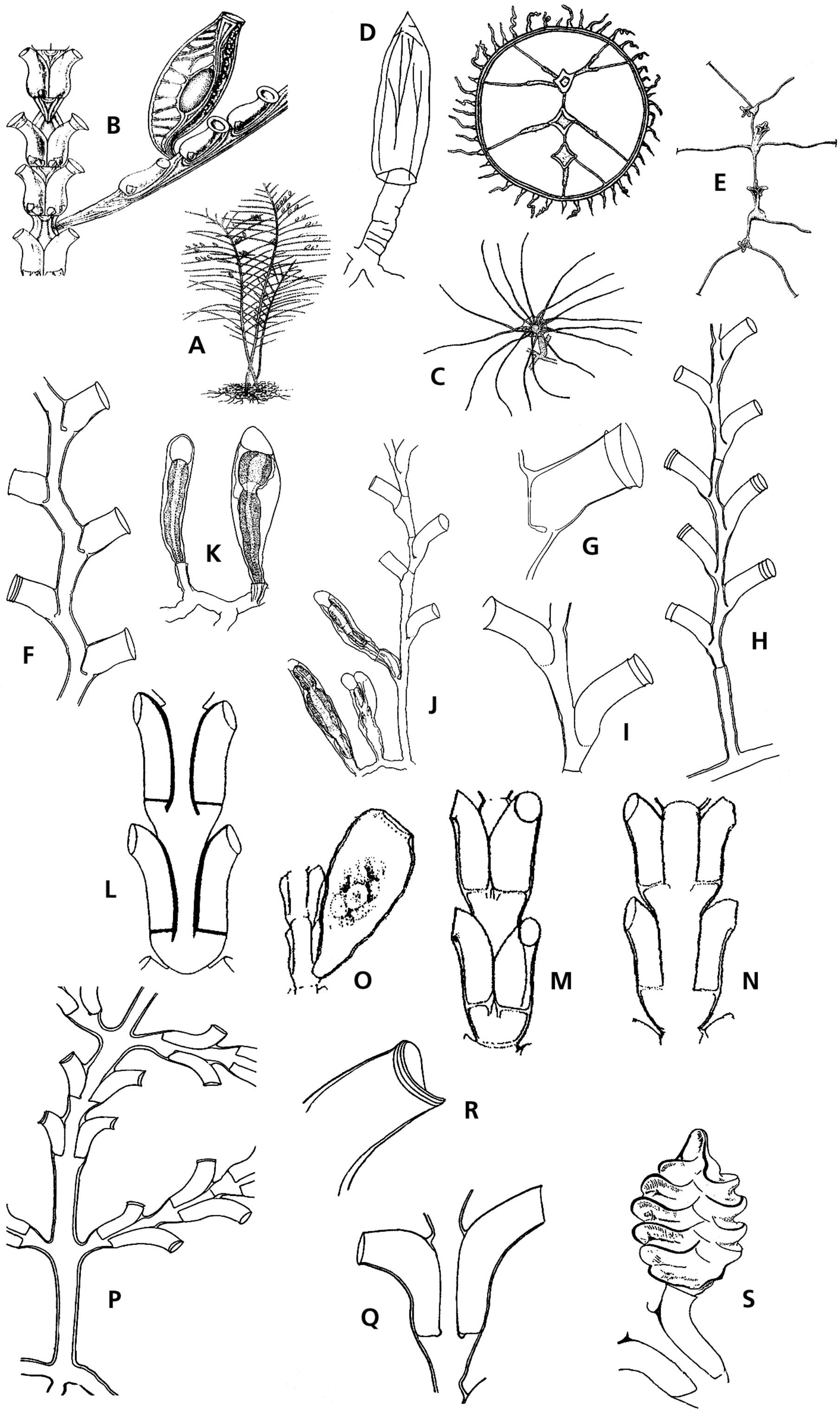
Fig. 185A-B

Hydroid: Colony erect, monosiphonic, sparingly branched, with pinnately, alternate hydrocladia; hydrothecae on hydrocauli and hydrocladia, sessile, opposite, in distant pairs, those of each pair disposed in a same frontal side and adnate one another along a great part of their length, free distal part diverging, hydrothecal rim with two small teeth or lobes, operculum with one abcauline valve; hydranth with one pair of small cup-shaped, laterally compressed appendages, attached in front at the hydrotheca base (nematophores?); gonophores as fixed sporosacs, gonothecae very large, elongate-ovate, smooth, with a number of irregular processes projecting into interior for some distance below rim, arising in front of the pinna in intervals of the pairs of hydrothecae.

Hypopyxis labrosa Allman, 1888

FIG. 185. Leptomedusae. A-B, Sertulariidae, *Hypopyxis labrosa*: A, colony; B, detail of a branch showing the cup shaped appendages in front of the hydrothecae and the gonothecae. C-E, Sugiuridae, *Sugiura chengshanensis*: C, expanded hydranth; D, hydrotheca and portion of hydrocaulus; E, medusa (right), radial canals, blind canals and manubria (left). F-S, Syntheciidae. F-G, *Hincksella cylindrica*: F, fragment of a colony; G, detail of a renovated hydrotheca; H-K, *Hincksella cylindrica* var. *pusilla*: H, basal part of a colony; I, two hydrothecae; J, part of hydrocaulus and hydrorhiza both with gonothecae; K, gonothecae on hydrorhiza. L-O, *Parathuiaria polycarpa*: L, internode with two pairs of hydrothecae; M, anterior face of an internode; N, posterior face of an internode; O, gonotheca. P-S, *Synthecium elegans*: P, hydrorhiza, hydrocaulus and origins of hydrocladia; Q, part of hydrocladia with two hydrothecae; R, margin of hydrotheca; S, gonotheca issued from within hydrothecae (A-B after Allman, 1888; C-D after Sugiura, 1973; E left after Chiu, 1954, E right after Uchida, 1925; F-I after Vervoort, 1959; J-K after Hirohito, 1995; L-O after Leloup, 1974; P-S after Ralph, 1958: p. 351, text-fig. 17 a, b, c, d).

FIG. 185. *Leptomedusae. A-B, Sertulariidae,* Hypopyxis labrosa : *A, colonie ; B, détail of d'une branche montrant les appendices cupulaires situé face à la base des hydrothèques et de la gonothèque. C-E, Sugiuridae,* Sugiura chengshanensis : *C, hydranthe en extension ; D, hydrothèque et portion de l'hydrocaule ; E méduse (à droite), canaux radiaires, canaux aveugles et manubrium (à gauche). F-S, Syntheciidae. F-G,* Hincksella cylindrica *: F, fragment d'une colonie ; G, détail d'une hydrothèque rénovée ; H-K,* Hincksella cylindrica *var.* pusilla : *H, partie basale d'une colonie ; I, deux hydrothèques ; J, partie d'un hydrocaule et de l'hydrorhize tous les deux avec des gonothèques ; K, gonothèques sur l'hydrorhize ; L-O,* Parathuiaria polycarpa : *L, internode avec deux paires d'hydrothèques ; M, face antérieure d'un internode ; N, face postérieure d'un internode ; O, gonothèque. P-S,* Synthecium elegans : *P, hydrorhize, hydrocaule et origine des hydroclades ; Q, partie des hydroclades avec deux hydrothèques ; R, bord marginal d'une hydrothèque ; S, gonothèque issue d'une hydrothèque (A-B d'après Allman, 1888 ; C-D d'après Sugiura, 1973 ; E gauche d'après Chiu, 1954, E droite d'après Uchida, 1925 ; F-I d'après Vervoort, 1959 ; J-K d'après Hirohito, 1995 ; L-O d'après Leloup, 1974 ; P-S d'après Ralph, 1958 : p. 351, text-fig. 17 a, b, c, d).*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Family SUGIURIDAE Bouillon, 1984

Hydroid: colony stolonal; hydrotheca cylindrical, tapering apically, on a short pedicel; operculum pyramidal, formed by numerous convergent flaps not demarcated by a basal crease line; hydranth with intertentacular web; gonothecae unknown.
Medusa: umbrella more or less elliptical, with up to 6 manubria (exceptionally 9), generally with 4 radial canals per well developed manubrium, in mature animals usually all joining circular canal but often incomplete and blind canals; no centripetal canals, all canals formed centrifugally from manubria; 2-6 ovoid "gonads" distally or in the middle of some canal, ovoid; marginal tentacles numerous; numerous statocyst; asexual reproduction by fission.

Genus ***SUGIURA*** Bouillon, 1984

Fig. 185C-E

See family characters.

Sugiura chengshanense (Ling, 1937)

Family SYNTHECIIDAE Marktanner-Turneretscher, 1890

Hydroid: colony erect, unbranched or with pinnately arranged hydrocladia, arising from a creeping hydrorhiza, commonly monopodial with terminal growing points, hydrothecae sessile, bilaterally symmetrical, in two or more longitudinal rows on hydrocaulus and hydrocladia, alternate or opposite, partly adnate, no real diaphragm but with a definite basal floor perforated by a distinct hydropore, hydrothecal rim even, operculum and nematophores absent; gonophore as fixed sporosacs, gonothecae arising from within hydrothecal cavity or from fenestrae below hydrothecae or from hydrorhiza.
Remarks: according to Broch (1918) the hydrotheca of the Syntheciidae is lined by an ectodermal lamella and the hydranths should possess an abcauline caecum (*Synthecium hians*) but those characters have not been verified for all species.
Recent references: Calder (1991); Watson (2000); Schuchert (2003).

KEY TO HYDROIDS

1. hydrothecae alternate on hydrocaulus and hydrocladia, forming two longitudinal rows . . . *Hincksella*
– hydrothecae in opposite pairs on hydrocaulus and hydrocladia, forming two longitudinal rows . . . 2

2. gonothecae springing from within hydrothecae . . . . *Synthecium*
– gonothecae borne from fenestrae below hydrothecae . . . . *Parathuiaria*

Genus ***HINCKSELLA*** Billard, 1918

Fig. 185F-K

Hydroid: colony erect, branched or unbranched, monosiphonic or polysiphonic; hydrocaulus may bear alternate hydrocladia; two alternate rows of sessile hydrothecae on hydrocaulus and hydrocladia, tubular, partly adnate, margin entire; no operculum; gonophores as solitary fixed sporosacs, gonothecae springing from within hydrothecal cavity, from a fenestra below hydrotheca or from hydrorhiza.
Recent reference: Calder *et al.* (2003).

Hincksella corrugata Millard, 1958
Hincksella cylindrica (Bale, 1888)
Hincksella echinocarpa (Allman, 1888)
Hincksella fallax (Hartlaub, 1904)
Hincksella indiana Millard, 1967
Hincksella projecta (Fraser, 1938a)
Hincksella pusilla (Ritchie, 1910)
Hincksella sibogae Billard, 1918

Genus ***PARATHUIARIA*** Leloup, 1974

Fig. 185L-O

Hydroid: colony erect, monosiphonic; hydrocaulus with opposite or alternate hydrocladia; hydrothecae in opposite pairs on hydrocaulus and hydrocladia, more or less disposed in a same frontal side, tubular, partly adnate, slightly twisted to one side; hydrothecal rim circular; gonophores as solitary fixed sporosacs, arising from base of hydrothecae.

Parathuiaria polycarpa (Kirchenpauer, 1884)

Genus ***SYNTHECIUM*** Allman, 1872

Figs 185P-S, 186A-D

Hydroid: colony erect, branched or unbranched, mono- or polysiphonic; hydrocaulus bearing hydrocladia usually in opposite pairs; two longitudinal rows of opposite to subopposite sessile hydrothecae on hydrocaulus and hydrocladia, usually tubular, partly adnate, margin entire; hydranths with abcauline caecum in some species; gonophores as solitary fixed sporosacs, gonothecae generally dioecious arising from within hydrothecal cavity.
Recent references: Schuchert (2003); Vervoort & Watson (2003).

Synthecium alternans Allman, 1888
Synthecium brucei Vervoort & Watson, 2003
Synthecium campylocarpum Allman, 1888
Synthecium carinatum Totton, 1930
Synthecium crassum (Fraser, 1940)
Synthecium dentigerum Jarvis, 1922
Synthecium elegans Allman, 1872
Synthecium evansi (Ellis & Solander, 1786)
Synthecium flabellum Hargitt, 1924
Synthecium formosum (Fewkes, 1881)
Synthecium gordoni Vervoort & Watson, 2003
Synthecium hians Millard, 1957
Synthecium longithecum Totton, 1930
Synthecium marginatum (Allman, 1877)
Synthecium megathecum Billard, 1925b
Synthecium orthogonium (Busk, 1852)
Synthecium patulum (Busk, 1852)
Synthecium rigidum Fraser, 1938a
Synthecium robustum Nutting, 1904
Synthecium samauense Billard, 1925a
Synthecium singulare Billard, 1925a
Synthecium subventricosum Bale, 1914a
Synthecium symmetricum Fraser, 1938a
Synthecium tottoni Ralph, 1958
Synthecium tubiger Jarvis, 1922
Synthecium tubithecum (Allman, 1877)

Family TECLAIIDAE Bouillon, Pages, Gili, Palanques, Puig & Heussner, 2000

Hydroid: Unknown.
Medusa: 4 simple radial canals; hollow tentacles; 4 simple lips; elongated "gonads" forming linear sacs on radial canals, separated from manubrium; one to three cordyliform structures between successive tentacles; with or without open statocysts.

KEY TO MEDUSAE

1. open statocysts . . . . *Parateclaia*
– no statocysts . . . . *Teclaia*

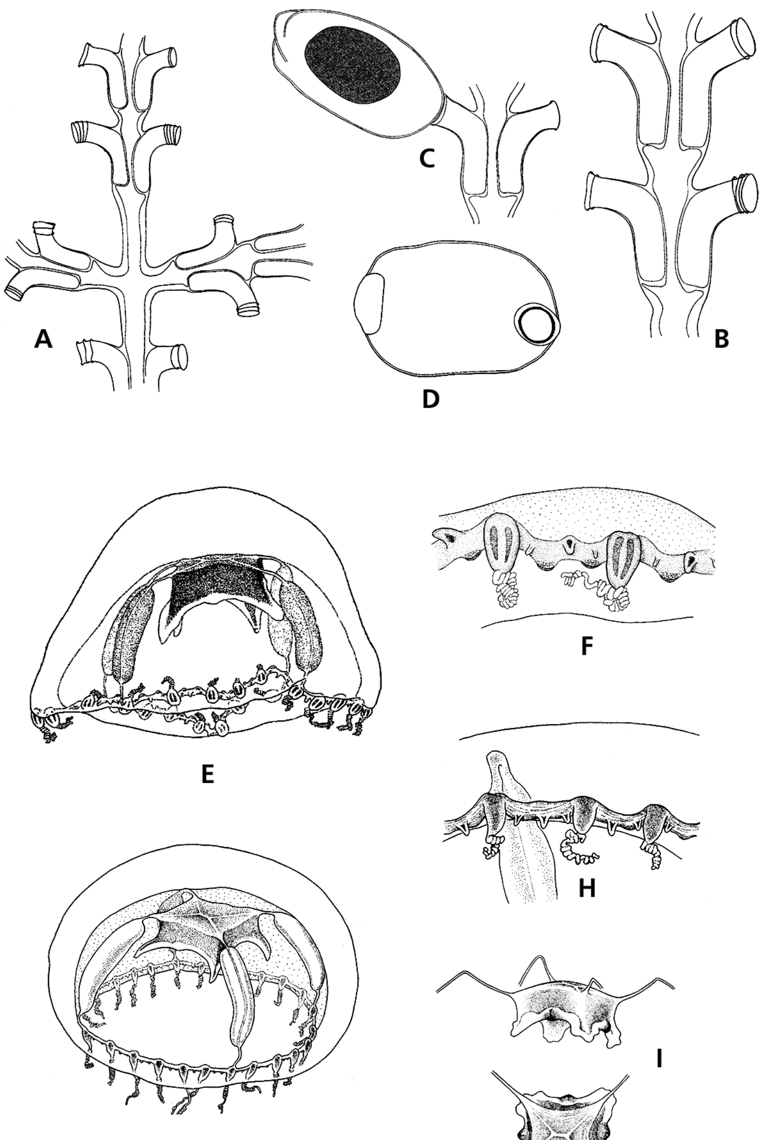


FIG. 186. Leptomedusae. A-D, Syntheciidae, *Synthecium samauense*: A, hydrocaulus with origins of two hydrocladia; B, hydrocladium with two pairs of hydrothecae; C, female gonotheca, lateral view; D, female gonotheca, frontal view. E-F, Teclaiidae, *Parateclaia euromarge*: E, general view of a fully grown medusa; F, detail of the abaxial side of umbrella margin showing the elongated marginal bulbs, the cordyliform marginal structures and the open statocysts. G-I, *Teclaia rencincolae*: G, adult medusae; H, detail of the marginal border showing the tentacles, the cordyliform structures and the distal part of a radial canal with a fragment of gonad; I, details of the manubrium (A-D after Vervoort & Vasseur, 1977; E-F after Bouillon *et al*., 2000; G-I after Gili *et al*., 1999).

FIG. 186. *Leptomedusae. A-D, Syntheciidae,* Synthecium samauense : *A, hydrocaule avec les origines de deux hydrocades ; B, hydroclade avec deux paires d'hydrothèques ; C, gonothèque femelle, vue latérale ; D, gonothèque femelle, vue frontale. E-F, Teclaiidae,* Parateclaia euromarge *: E, vue générale d'une méduse adulte ; F, détail de la face abaxiale du bord exombrellaire montrant les bulbes marginaux allongés les structures cordyliformes marginales et les statocystes ouverts. G-I,* Teclaia rencincolae *: G, méduse adulte ; H, détail du bord marginal exombrellaire montrant les tentacules, les structures cordyliformes et la partie distale d'un canal radiaire avec un fragment de ''gonade'' ; I, détail du manubrium (A-D d'après Vervoort & Vasseur, 1977 ; E-F d'après Bouillon* et al.*, 2000 ; G-I d'après Gili* et al.*, 1999).*

Genus ***PARATECLAIA*** Bouillon, Pagès & Gili, 2001

Fig. 186E-F

Hydroid: unknown.
Medusa: with open statocysts.

Parateclaia euromarge Bouillon, Pagès & Gili, 2001

Genus ***TECLAIA*** Gili, Bouillon, Pagès, Palanques & Puig, 1999

Fig. 186G-I

Hydroid: unknown.
Medusa: without statocysts.

Teclaia recincolae Gili, Bouillon, Pagès, Palanques & Puig, 1999

Family THYROSCYPHIDAE Stechow, 1920

Hydroid: colony stolonal or erect, arising from a creeping hydrorhiza, commonly monopodial, with terminal growing points; hydrothecae radially to bilaterally symmetrical, pedicellate, or both sessile and pedicellate in the same colony, or sessile but adnate only at diaphragm level (?); hydrothecal margin either entire or with 2 to 4 teeth; operculum of one, 3 or 4 valves and either persistent or shed early; annular perisarcal diaphragm usually present; hydranths with mantle (ectodermal lamella) and a basal annular ectodermal fold; cnidome: microbasic and macrobasic mastigophores; gonophores as fixed sporosacs (Fig. 7F).

Remarks: Calder (1991) considered that the presence of an ectodermal lamina or mantle lining the interior of the hydrotheca could be diagnostic of the Thyroscyphidae, but this structure is polyphyletic, being also present in some Aglaopheniidae and amongst the Sertulariidae, for instance in some *Dynamena, Sertularella* and *Sertularia*, and so is not a family or generic character (see also *Cnidoscyphus* below). We concur, however, with Calder that the presence of an ectodermal annular ectodermal fold is, at the state of our knowledge on hydranth structure, a good diagnostic character for delimitation of the Thyroscyphidae. The genera with an abcauline caecum previously included in this family are considered here as belonging to the Sertulariidae.

Recent references: Calder (1991); Migotto (1996); Schuchert (2003).

KEY TO HYDROIDS

1. colony usually stolonal 2
– colony erect 3

2. hydrotheca with 4 teeth and operculum with 4 flaps .... *Symmetroscyphus*
– hydrotheca with 3 teeth and operculum with 3 flaps .... *Uniscyphus*

3. hydrotheca pedicellate .... *Thyroscyphus*
– hydrotheca sessile or both sessile and pedicellate 4

4. hydrotheca sessile .... *Sertularelloides*
– sessile and pedicellate hydrothecae in the same colony .... *Thyroscyphoides*

Genus *SERTULARELLOIDES* Leloup, 1937

Fig. 187A-D

Hydroid: colony erect, simple, monosiphonic, arising from a strong ramified fasciculate hydrorhiza; hydrocauli monosiphonic, split in slender internodes with a hydrotheca near distal end; hydrocladia alternate in the same plane and with same structure than the hydrocauli, arising immediately under a cauline hydrotheca; hydrothecae large, cylindrical, alternate, sessile or on renovate apophyses in old colonies, adcauline adnate portion much reduced; hydrothecal rim quadrangular, with 4 teeth separated by shallow embayments; operculum with 4 low flaps, which do not close the aperture of the hydrotheca, diaphragm present; hydranth with a basal annular ectodermal fold; gonophores as fixed solitary sporosacs, gonothecae larger than hydrothecae, arising just below a hydrotheca, pedicellate, elongate and quadrangular apex with 4 marginal cusps.

Remarks: *Sertularelloides mercatoris* Leloup, 1937 the type and only species of this genus, is conspecific with the nominal species *Sertularella cylindritheca* Allman, 1888. Microscopical examination of the type material of *Sertularelloides* and of specimens of *Sertularella cylindritheca* from the "Institut Royal des Sciences naturelles de Belgique" shows the presence of an annular membrane, already described in the latter species by Vervoort (1959). For this reason we follow here Vervoort (1959) and Calder (1991), in considering this species a member of the Thyroscyphidae.

Recent references: Calder (1991); Medel *et al.* (1991); Ramil & Vervoort (1992a); Migotto (1996); Medel & Vervoort (1998); Watson (2000).

Sertularelloides cylindritheca (Allman, 1888)

Genus *SYMMETROSCYPHUS* Calder, 1986

Fig. 187E-F

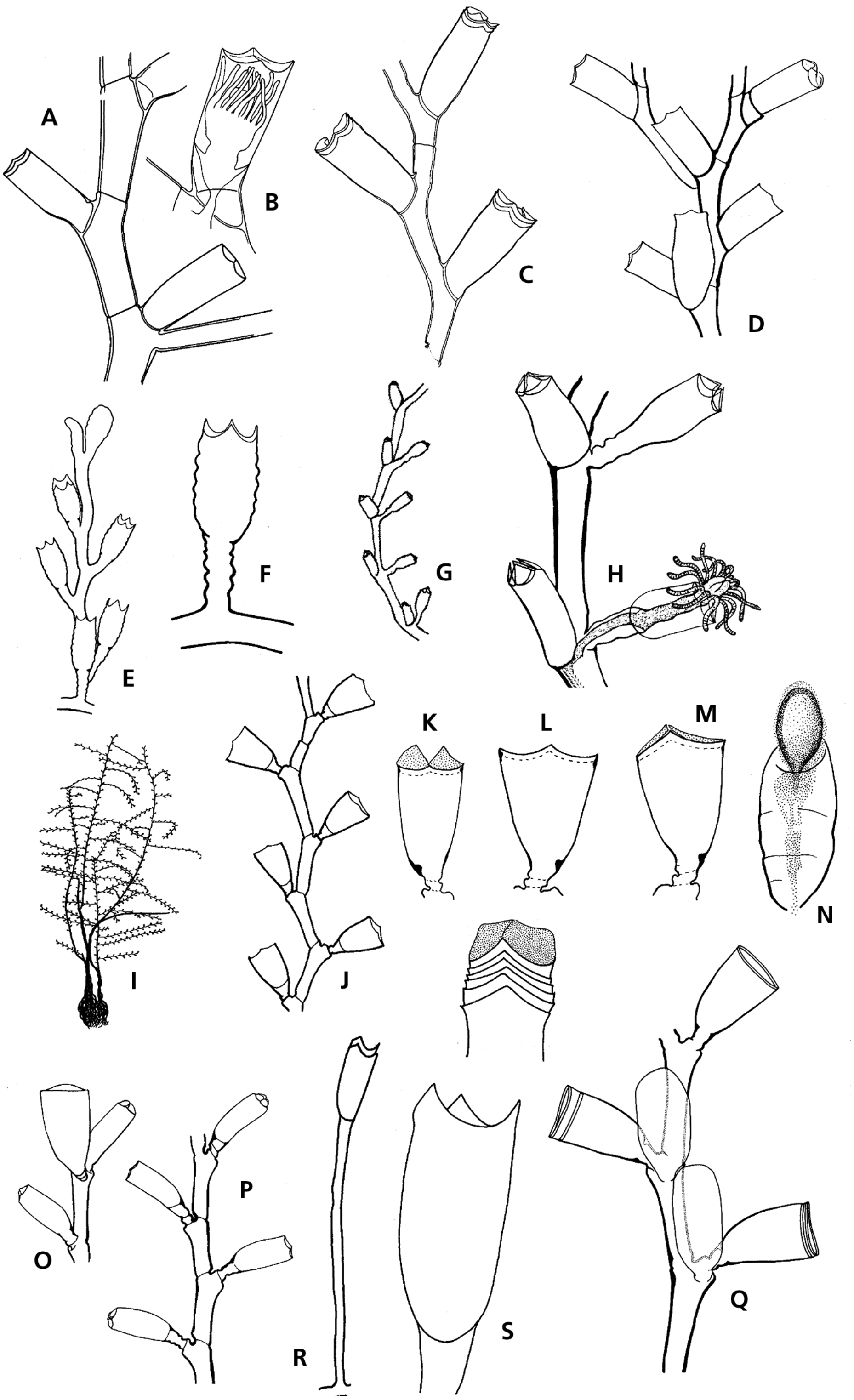
Hydroid: colony usually stolonal; hydrothecae pedicellate, radially symmetrical, barrell-shaped; hydrothecal margin with 4 teeth; operculum pyramidal, composed of 4 triangular valves with rounded bases; diaphragm with centrally located hydropore; hydranth with mantle or ectodermal lamella and basal annular ectodermal fold (ectodermal lamella), with aggregation of large cnidocysts also present in body wall; gonophores unknown.

Recent reference: Vervoort & Watson (2003).

Symmetroscyphus australis Vervoort & Watson, 2003
Symmetroscyphus intermedius (Congdon, 1907)

FIG. 187. Leptomedusae, Thyroscyphidae. A-D, *Sertularelloides cylindritheca*: A, some internodes from the higher part of a colony; B, hydrotheca with hydranth showing the basal annular ectodermal fold; C, fragment of axis; D, part of stem with hydrothecae and one gonotheca. E-F, *Symmetroscyphus intermedius*: E, part of colony with hydrocaulus; F, part of stolonal colony. G-H, *Thyroscypoides biformis*: G, branchlet with hydrothecae; H, detail of branchlet with hydrothecae and a hydranth, note the annular fold. I-Q, *Thyroscyphus*. I-N, *Thyroscyphus aequalis*: I, a general view of a colony; J, hydrocladium; K-M, different aspects of hydrothecae; N, male gonotheca; O-P, *Thyroscyphus ramosus*: O, fragment of stem with two hydrothecae and a gonotheca; P, part of stem showing internodes and hydrothecae; Q, *Thyroscyphus marginatus*, part of hydrocaulus with hydrothecae and gonothecae. R-T, *Uniscyphus fragilis*: R, hydrotheca with pedicel; S, hydrotheca; T, distal end of hydrotheca with regenerated margins and operculum. (A-B after Vervoort, 1959; C after Ramil & Vervoort, 1992a; D, O-P after Migotto, 1996; E-F & Q after Calder, 1991; G-H after Naumov, 1969; I-N after Millard, 1975; R-T after Millard, 1977a).

FIG. 187. *Leptomedusae, Thyroscyphidae. A-D,* Sertularelloides cylindritheca *: A, quelques internodes de la partie supérieure d'une colonie ; B, hydrothèque contenant son hydranthe pourvu du repli ectodermique annulaire basal ; C, fragment d'une branche ; D, partie d'une branche avec des hydrothèques et une gonothèque. E-F,* Symmetroscyphus intermedius *: E, partie d'un hydrocaule érigé ; F, fragment d'une colonie stolonaire. G-H,* Thyroscypoides biformis *: G, branche avec des hydrothèques ; H, détail d'une branche avec des hydrothèques dont l'une renferme un hydranthe, notez le repli annulaire. I-Q,* Thyroscyphus*. I-N,* Thyroscyphus aequalis *: I, vue générale d'une colonie ; J, hydroclade ; K-M, aspects différent de trois hydrothèques ; N, gonothèque mâle ; O-P,* Thyroscyphus ramosus *: O, fragment d'une branche montrant deux hydrothèques et une gonothèque ; P, partie d'une branche montrant les internodes et les hydrothèques ; Q,* Thyroscyphus marginatus *: portion d'un hydrocaule avec des hydrothèques et des gonothèques. R-T,* Uniscyphus fragilis *: R, hydrothèque et son pédicelle ; S, hydrothèque ; T, partie distale d'une hydrothèque ayant le bord marginal rénové et pourvu de son opercule (A-B d'après Vervoort, 1959 ; C d'après Ramil & Vervoort, 1992a ; D, O-P d'après Migotto, 1996 ; E-F & Q d'après Calder, 1991 ; G-H d'après Naumov, 1969 ; I-N d'après Millard, 1975 ; R-T d'après Millard, 1977a).*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Genus ***THYROSCYPHOIDES*** Naumov, 1955

Hydroid: colony erect, monosiphonic, irregularly branched; hydrothecae in two rows on hydrocaulus and hydrocladia, of two types, those of one row sessile, those of the other, opposite row on a well-developed pedicel; all hydrothecae with a rim with 4 teeth and an operculum consisting of 4 triangular valves; gonophores unknown.

Thyroscyphoides biformis Naumov, 1955 [syn. *Symplectoscyphus naumovi* Blanco, 1969]

Genus ***THYROSCYPHUS*** Allman, 1877

Figs 7F, 187I-Q

Synonym: *Cnidoscyphus* Splettstösser, 1929.
Hydroid: colony erect, branched, monosiphonic or polysiphonic; hydrothecae large, pedicellate, cone-shaped, campanulate, to nearly cylindrical, alternately arranged on opposite side of hydrocaulus and hydrocladia; hydrothecal adcauline wall usually more protuberant than abcauline wall; margin entire or with 4 teeth; diaphragm present; operculum of one or 4 valves either shed early or persistent; hydranth with mantle (ectodermal lamella) and basal annular ectodermal fold, with or without distal batteries of large cnidocysts, abcauline caecum absent; gonophores as fixed sporosacs.
Remarks: *Cnidoscyphus* was included by Millard (1975), Bouillon (1985a) and Calder (1991) in the genus *Thyroscyphus*. Vervoort (1993) nevertheless, retained the genus *Cnidoscyphus* for the species having large cnidocysts in the distal part of the mantle or ectodermal lamella; this character, being also found in some *Dynamena*, *Sertularia, Symmetroscyphus* and *Thyroscyphus*, has no generic diagnostic value and *Cnidoscyphus* is thus kept here as congeneric with *Thyroscyphus*.

Thyroscyphus aequalis (Warren, 1908)
Thyroscyphus balei Calder, 1983
Thyroscyphus bedoti Splettstösser, 1929
Thyroscyphus fruticosus (Esper, 1793)
Thyroscyphus intermedius Congdon, 1907
Thyroscyphus longicaulis Splettstösser, 1929
Thyroscyphus macrocytharus (Lamouroux, 1824a)
Thyroscyphus marginatus (Allman, 1877)
Thyroscyphus ramosus Allman, 1877
Thyroscyphus scorpioides Vervoort, 1993
Thyroscyphus sibogae Billard, 1930b
Thyroscyphus torresii (Busk, 1852)

Genus ***UNISCYPHUS*** Millard, 1977

Fig. 187R-T

Hydroid: colony stolonal, pedicellate hydrothecae arising from creeping hydrorhiza; pedicel long, slender; hydrotheca cylindrical, with 3 marginal teeth and pyramidal operculum of 3 flaps seated in bays between teeth; gonophores and gonothecae unknown.
Remarks: Millard (1977a) noted that hydranths of type material were badly preserved, and that, although difficult to ascertain, no abcauline caecum could be seen; we follow Calder (1991) in including *Uniscyphus* in the Thyroscyphidae.

Uniscyphus fragilis Millard, 1977a

Family TIARANNIDAE Russell, 1940

Hydroid: colony erect or 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, thus all imparting a bilateral symmetry to the distal part of hydrotheca; gonophores as free medusae or fixed sporosacs, gonothecae usually resembling hydrothecae, but larger.
Medusa: no apical projection; no gastric peduncle; manubrium wide, cross-shaped, with 4 perradial pouches joined to subumbrella; mouth with 4 simple or crenulated lips; 4

simple radial canals; "gonads" folded on interradial walls of manubrium and/or on perradial manubrial pouches; marginal tentacles numerous, hollow; hollow cordyli-like structures bearing cnidocysts; no ocelli (Fig. 6O).

Recent references: Pagès *et al.* (1991; 1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Schuchert (2001a).

KEY TO POLYPS

1. colony stolona . . . . *Modeeria*
– colony erect 2

2. hydrothecae adnate . . . . *Stegella*
– hydrothecae pedicellate or pedicellate and adnate in the same colony . . . . *Stegopoma*

KEY TO MEDUSAE

1. "gonads" on perradial manubrial pouches only 2
– "gonads" on manubrium and perradial gastric pouches . . . . *Modeeria*

2. "gonads" longitudinally split . . . . *Krampella*
– "gonads" not longitudinally split 3

3. 4 simple, smooth, "gonads" on walls of perradial manubrial pouches . . . . *Margalefia*
– "gonads" in 8 adradial rows of 10-16 sac-like invaginations on each side of perradial manubrial pouches . . . . *Chromatonema*

Genus *CHROMATONEMA* Fewkes, 1882

Fig. 188A-B

Hydroid: unknown.
Medusa: "gonads" represented by 8 (10-16) series of sac-like invaginations from the surface of perradial pouches, separated in interradii; 20-24 marginal tentacles; 1-2 cordylus-like structure between successive tentacles.

Chromatonema erythrogonon (Bigelow, 1909) [probably a syn. of *C. rubrum*]
Chromatonema rubrum Fewkes, 1882a [syn. *C. hertwigi* (Vanhöffen, 1911)]
See also *Ptychogena aurea* Vanhöffen, 1912.

Genus *KRAMPELLA* Russell, 1957

Fig. 188C-D

Hydroid: unknown.
Medusa: 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 5 cirrus-like tentaculae between successive marginal tentacles.
Recent reference: Gili *et al.* (1998).

Krampella dubia Russell, 1957
Krampella tardenti Gili, Bouillon & Pagès, 1998

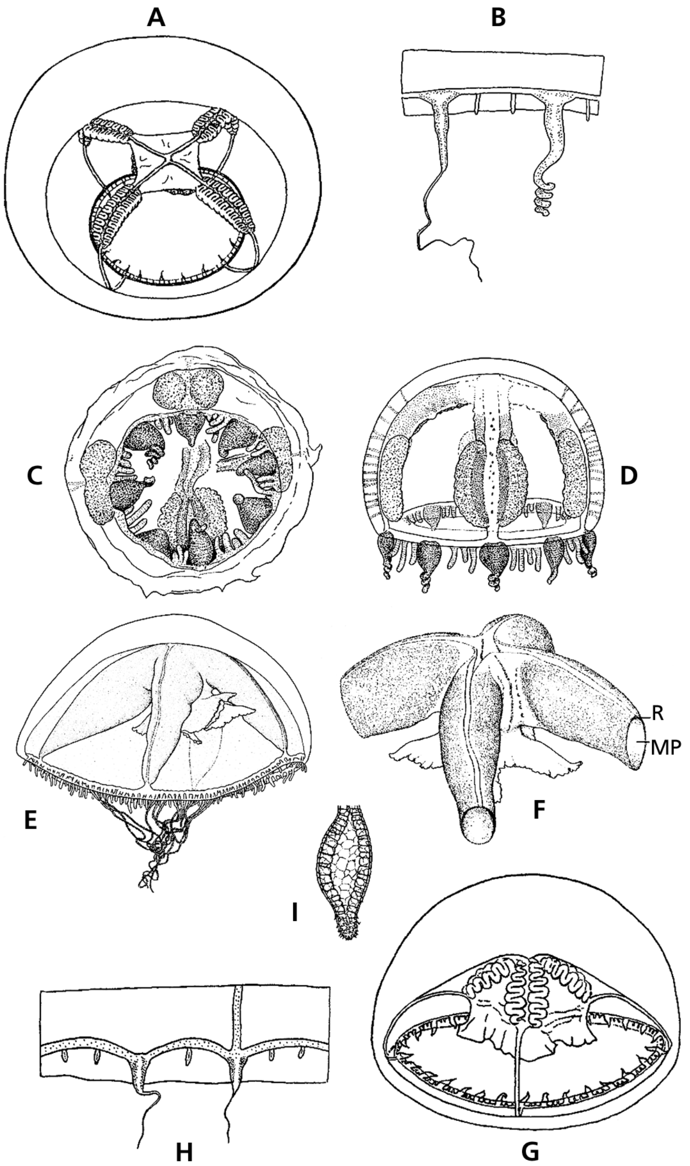


FIG. 188. Leptomedusae, Tiarannidae. A-B, *Chromatonema rubrum*: A, adult medusae seen obliquely from above; B, portion of umbrella margin with marginal tentacles and cordyli. C-D, *Krampella dubia*: C, oral view of adult medusa; D, lateral view of adult medusa. E-F, *Margalefia intemedia*: E, fully grown medusa; F, detail of the gonads and manubrium. G-I, *Modeeria rotunda*: G, adult medusa; H, portion of umbrella margin with marginal tentacles and cordyli; I, detail of a cordylus (A-B after Russell, 1953; C-D after Russell, 1970b; E-F after Pagès *et al*., 1991; G-H after Kramp, 1920; I after Kramp, 1919). MP = manubrial pouches; R = radial canal.

FIG. 188. *Leptomedusae, Tiarannidae. A-B,* Chromatonema rubrum *: A, méduse adulte, vue apicale oblique ; B, portion du bord marginal exombrellaire montrant les tentacules marginaux et les cordyles. C-D,* Krampella dubia *: C, vue orale d'une méduse adulte ; D, vue latérale d'une méduse adulte. E-F,* Margalefia intemedia *: E, méduse adulte ; F, détails des ''gonades'' et du manubrium. G-I,* Modeeria rotunda *: G, méduse adulte ; H, portion du bord marginal exombrellaire montrant les tentacules marginaux et les cordyles ; I, détail d'un cordyle (A-B d'après Russell, 1953 ; C-D d'après Russell, 1970b ; E-F d'après Pagès* et al.*, 1991 ; G-H d'après Kramp, 1920 ; I d'après Kramp, 1919). MP = poches manubriales ; R = canal radiaire.*

Genus ***MARGALEFIA*** Pagès, Bouillon & Gili, 1991

Fig. 188E-F

Hydroid: unknown.

Medusa: 4 long and large perradial manubrial pouches extending almost to circular canal; "gonads" simple, smooth, undivided on all the surface of perradial manubrial pouches; up to 150 marginal tentacles; one cordylus-like structure between every three marginal tentacles.

Margalefia intermedia Pagès, Bouillon & Gili, 1991

Genus *MODEERIA* Forbes, 1848

Figs 6O, 188G-I, 189A-F

Synonym: *Tiaranna* Hartlaub, 1913

Hydroid: colony stolonal creeping; polyps arising singly at frequent intervals from stolon; hydrothecae not sharply demarcated from smooth pedicel of variable length; hydrothecae smooth, deep and tubular, with margin produced on two sides; operculum of two longitudinally pleated membranes seated in the embayments of the margin and meeting another like a gable, "*Stegopoma*-like"; diaphragm absent or very thin; gonophores giving rise to free medusae, gonothecae similar to hydrothecae but larger, with short pedicel, or non existent, with up to 4 developing medusae.

Medusa: "gonads" transversally folded on interradial walls of manubrium and extending outwards along both sides of perradial pouches; 16-28 marginal tentacles; 2-3 spindle-shaped cordylus-like appendages between successive tentacles.

Recent references: Gili *et al.* (1989); Ramil & Vervoort (1992a); Hirohito (1995); Brinckmann-Voss & Arai (1998); Schuchert (2001a).

Modeeria ducalis (Forbes & Goodsir, 1851) [doubtful status]
Modeeria globulosa (Forbes, 1848) [doubtful status]
Modeeria rotunda (Quoy & Gaimard, 1827) [syn. *M. formosa* Forbes, 1848]
Modeeria sagamina (Uchida, 1947b) [as *Tiaranna*; doubtful status, probably a syn. of *M. rotunda*]

Genus *STEGOLARIA* Stechow, 1913

Fig. 189G-K

Hydroid: colony erect, stem giving rise to alternate or subalternate side branches all in the same plane, flabelliform and strongly polysiphonic, distal parts often monosiphonic and geniculate; hydrothecae in two alternate rows in the same plane as ramifications, tubular, curved outwards, adnate to stem or branch for 2/3 of height and immersed among peripheral tubes in well developed colonies; no diaphragm or perisarcal thickening but abcauline wall with an indentation; operculum of *Stegopoma* type, consisting of two pleated valves seated in the embayments between two gable-like processes of hydrothecal margin; gonophores as fixed sporosacs, gonophore with up to six ova gonothecae sac shaped, completely adnate to hydrocaulus or hydrocladia, aperture facing away from branch with a circular operculum of fragile converging segments.

Remarks: this genus is very similar, if not congeneric, with *Stegopoma* and is retained exclusively because of its peculiar gonothecae and typically unpedicellate hydrothecae. However, some *Stegopoma* have adnate gonothecae, including the type species *Stegopoma plicatile*! Furthermore, some pedicellate hydrothecae have been illustrated by Watson & Vervoort (2001) in *Stegolaria geniculata.*

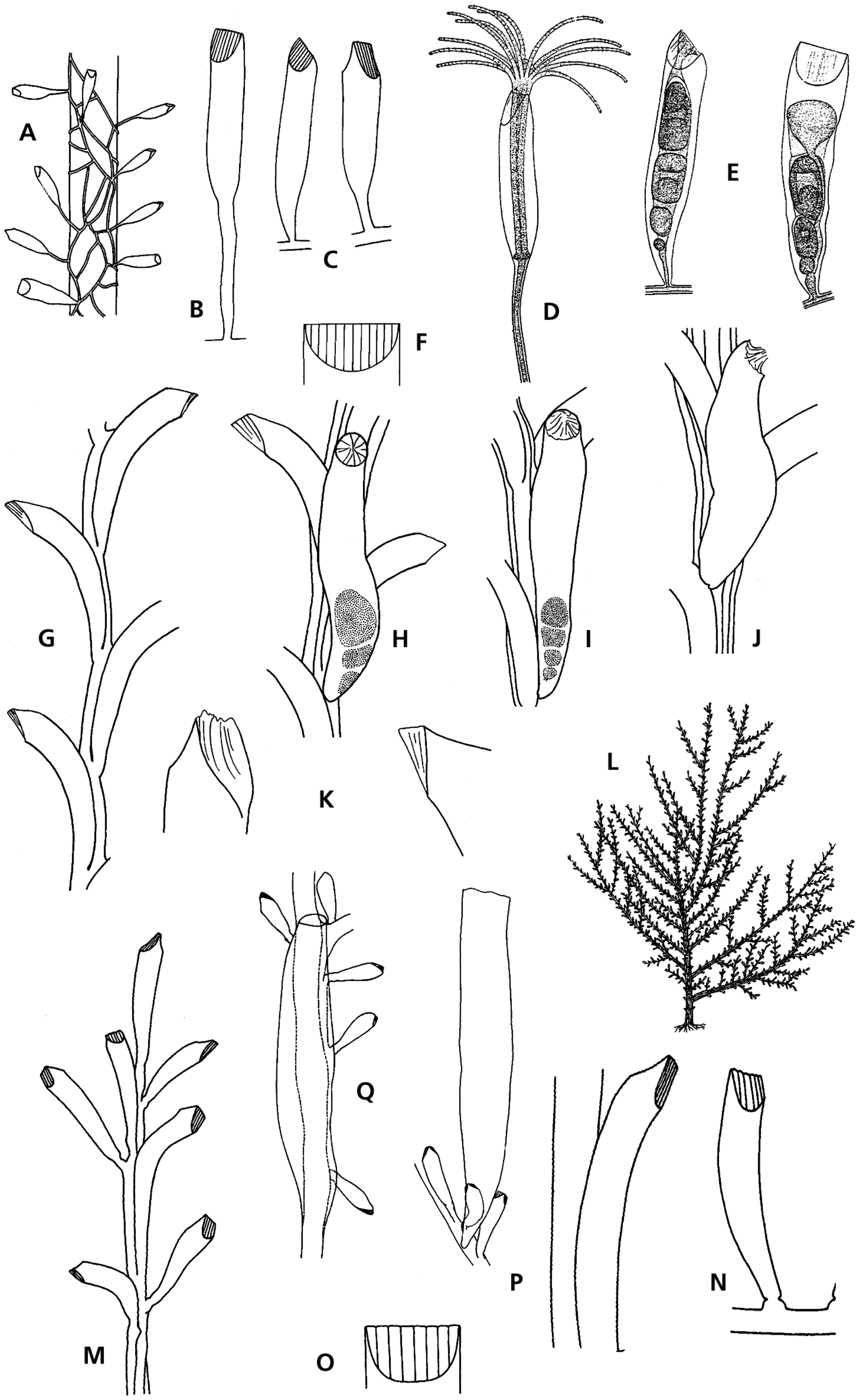
Recent references: Vervoort (1946a); Ramil & Vervoort (1992a); Hirohito (1995); Calder & Vervoort (1998); Watson & Vervoort (2001).

Stegolaria geniculata (Allman, 1888)
Stegolaria irregularis Totton, 1930

Genus *STEGOPOMA* Levinsen, 1893

Figs 6O, 189L-P

Hydroid: colony erect, branching, polysiphonic, flabelliform, with tendency to ramification in one plan; hydrothecae on stem and branches, all pedicellate or pedicellate and sessile, adnate, in the same colony, in two alternate rows in the same plan as ramifications; hydrothecae tubular, curved outwards gradually narrowing downwards, ending in a gable-shaped operculum; of two types, sessile ones without diaphragm, pedicellate ones with thin diaphragm; gonophore development poorly known or unknown, sometimes as fixed sporosacs (i.e. *S. gilberti*), sometimes medusiform buds (i.e. *S. medusiforme*); gonothecae resembling either to pedicellate hydrothecae but larger, or elongated, completely adnate with branches and axis, variously reported with or without operculum.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Remarks: all species with a *Stegopoma* hydroid and with medusa buds, like for instance *Stegopoma fastigiatum* (Alder, 1860), are referable to the genus *Modeeria*; the genus *Stegopoma* is here kept for the species with fixed sporosacs; all the species with unknown gonophores should be considered as Tiarannidae *incertae sedis*.

Recent references: Gili *et al.* (1989); Ramil & Vervoort (1992a); Blanco *et al.* (2000); Schuchert (2001a).

Stegopoma bathyale Vervoort, 1966
Stegopoma dimorphum Nutting, 1927
Stegopoma giganteum Ramil & Vervoort, 1992a
Stegopoma gilberti Nutting, 1905
Stegopoma gracile Nutting, 1905
Stegopoma medusiforme Hargitt, 1924
Stegopoma plicatile (Sars, 1863)
Stegopoma plumicolum Nutting, 1905

Family TIAROPSIDAE Boero, Bouillon & Danovaro, 1987

Hydroid: colony "*Cuspidella*"-like; hydrotheca tubular, sessile or with reduced pedicel; operculum of numerous flaps demarcated or not from the rest of hydrotheca by a crease line; gonophores as free medusae, gonotheca tubular or rounded, laterally compressed, operculate or not, with short peduncle, growing singly from hydrorhiza.

Medusa: 4 or 8 radial canals (exceptionally up to 16); one or two types of marginal tentacles (long and rudimentary, both with marginal bulbs); sense organs compound, comprising an ecto-endodermal ocellus and an open velar statocyst.

Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

KEY TO HYDROIDS

1. operculum formed by several flaps not demarcated from the rest of hydrotheca by a crease line .... *Tiaropsis*
– operculum formed by several flaps sharply demarcated from the hydrothecal margin by a crease line .... *tiaropsidium*

KEY TO MEDUSAE

1. numerous (50-60) compound sense organs; mouth with 8 lips .... *Octogonade*
– 8 or 16 (exceptionally 48) compound sense organs; mouth with 4 lips 2
2. two kinds of marginal tentacles .... *Tiaropsidium*
– one kind of tentacle .... *Tiaropsis*

FIG. 189. Leptomedusae, Tiarannidae. A-F, *Modeeria rotunda*: A, hydroid colony; B, hydrothecae with long peduncle; C, two hydrothecae, not stalked (left), shortly stalked (right); D, fully grown hydranth; E, gonothecae bearing medusa buds; F, diagrammatic representation of operculum. G-K, *Stegolaria geniculata*: G, part of stem from distal end; H-J, parts of stem with completely adnate gonothecae; K, distal ends of hydrothecae showing opercula. L-P, *Stegopoma plicatile*: L, general view of a colony; M, hydrocladium, note stalked and non stalked hydrothecae; N, detail of adnate and shortly stalked hydrothecae; O, diagrammatic view of operculum; P, part of colony with empty gonothecae. Q, *Stegopoma bathyale*, adnate gonotheca (A, D-E after Edwards, 1973; B-C, F, L-O after Cornelius, 1995; G-K after Millard, 1977b; P after Gili *et al.*, 1989; Q after Ramil & Vervoort, 1992a).

FIG. 189. *Leptomedusae, Tiarannidae. A-F,* Modeeria rotunda : *A, portion d'une colonie d'hydroïdes ; B, hydrothèque avec long pédoncule ; C, deux hydrothèques, non pédonculée (à gauche), faiblement pédonculée (à droite) ; D, hydranthe adulte ; E, gonothèque contenant des bourgeons médusaires ; F, représentation diagrammatique de l'opercule. G-K,* Stegolaria geniculata : *G, partie distale d'une branche ; H-J, parties de branches avec des gonothèques complètement adnées ; K, extrémités distales d'hydrothèques montrant les opercules. L-P,* Stegopoma plicatile : *L, vue générale d'une colonie ; M, hydroclade, notez les hydrothèques pédonculées et sessiles ; N, détails d'une hydrothèque complètement adnées et d'une hydrothèque à court pédoncule ; O, vue diagrammatique de l'opercule ; P, portion de colonie avec une gonohèque vide. Q,* Stegopoma bathyale, *gonothèque adnée (A, D-E d'après Edwards, 1973 ; B-C, F, L-O d'après Cornelius, 1995 ; G-K, d'après Millard, 1977b ; P d'après Gili* et al., *1989 ; Q d'après Ramil & Vervoort, 1992a).*

Genus ***OCTOGONADE*** Zoja, 1896

Fig. 190A-C

Hydroid: unknown.
Medusa: 8 radial canals; mouth with 8 lips; numerous compound statocysts; two kinds of tentacles.

Octogonade mediterranea Zoja, 1896

Genus ***TIAROPSIDIUM*** Torrey, 1909

Fig. 190D-E

Hydroid: colony of "*Cuspidella*" type; operculum formed by several flaps sharply demarcated from hydrothecal margin by a crease line; gonotheca ellipsoid, without operculum.
Medusa: 4 or more (up to 16) simple radial canals; mouth with 4 lips; 8 or 16 (rarely 48) compound sense organs; two kinds of tentacles.

Tiaropsidium atlanticum Russell, 1956b
Tiaropsidium japonicum Kramp, 1932c
Tiaropsidium kelseyi Torrey, 1909
Tiaropsidium mediterraneum (Metschnikoff, 1886)
Tiaropsidium polyradiatum Kramp, 1965a
Tiaropsidium roseum (Maas, 1905)

Genus ***TIAROPSIS*** Agassiz, 1849

Figs 26J, 35E, 190F-H

Hydroid: colony of "*Cuspidella*" type; operculum formed by several flaps not demarcated from the rest of hydrotheca by a crease line; gonothecae tubular, smooth, operculate.
Medusa: 4 radial canals; 8 compound sense organs; marginal tentacles of one kind.

Tiaropsis multicirrata (Sars, 1835)

Order PROBOSCOIDEA Broch, 1910

Hydroid: hydranths with a complex, flared to globose, more or less peduncled 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.

KEY TO HYDROIDS

1. hypostome conical; hypostomial preoral or buccal cavity delimited by the base of tentacles projecting in the lumen of gastric cavity........ Bonneviellidae
– Hypostome not conical, buccal cavity delimited by a constriction of the hydranth walls........ 2
2. hypostome flared to globose........ Campanulariidae
– hypostome rounded........ Phialuciidae

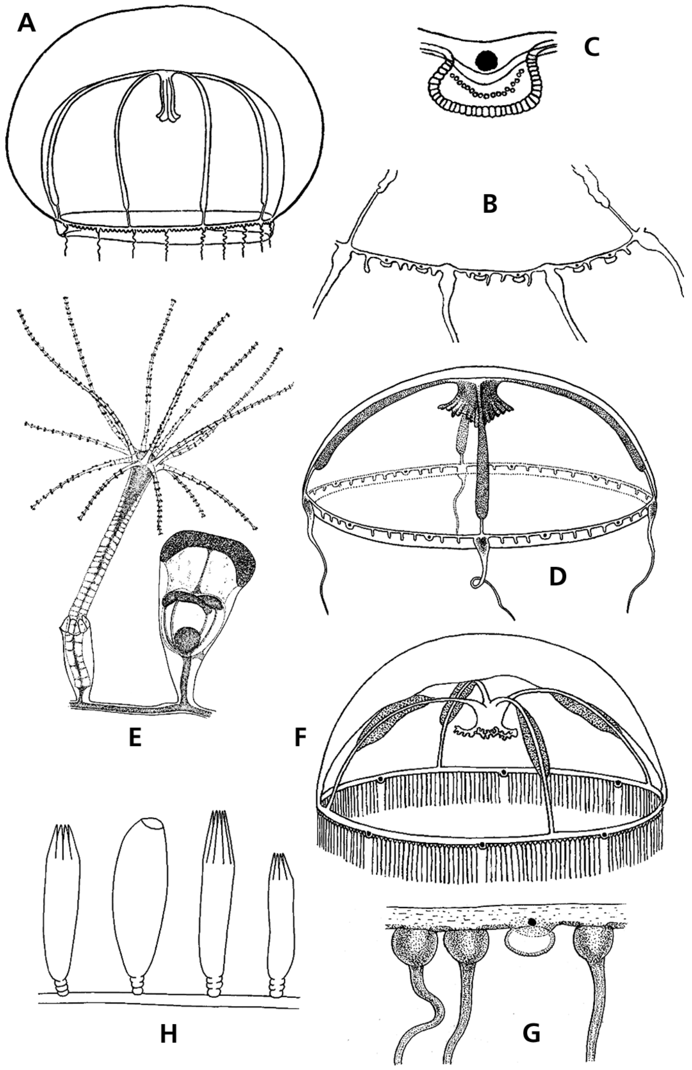


FIG. 190. Leptomedusae, Tiaropsidae. A-C, *Octogonade mediterranea*: A, adult medusa; B, portion of umbrella margin; C, complex ecto-endodermal open marginal sense organs. D-E, *Tiaropsidium roseum*: D, fully grown medusa; E, fragment of colony showing a hydrotheca with operculum sharply demarcated by a crease line from hydrothecal margin, with an extended hydranth and a gonotheca with a medusa bud. F-H, *Tiaropsis multicirrata*: F, fully grown medusa; G, detail of umbrella margin showing marginal tentacles and one of the eight ecto-endodermal open marginal sense organs, note absence of marginal cirri; H, fragment of colony with hydrothecae with opeculum not demarcated by a crease line and a gonotheca (A after Mayer, 1910; B after Pell, 1918; C after Trégouboff, 1957: pl. 67, fig. 7 B; D after Pagès *et al*., 1992; E after Boero *et al*., 1987; F-G after Russell, 1953; H after Rees, 1941b).

FIG. 190. *Leptomedusae, Tiaropsidae. A-C,* Octogonade mediterranea : *1 méduse adulte ; B, portion du bord exombrellaire ; C, organe des sens marginal complexe et ouvert ecto-endodermique. D-E,* Tiaropsidium roseum : *D, méduse adulte ; E, fragment de colonie montrant une hydrothèque possédant un opercule séparé du reste de la thèque par une nette ligne de démarcation et contenant un hydranthe en extension ainsi qu'une gonothèque avec un bourgeon médusaire. F-H,* Tiaropsis multicirrata *: F, méduse adulte ; G, détail du bord exombrellaire montrant des tentacules marginaux et un des huit organes des sens ouvert ecto-endodermique, notez l'absence de cirres marginaux ; H, fragment de colonies montrant des hydrothèques avec des opercules non demarqués de leur thèques et une gonothèque (A d'après Mayer, 1910 ; B d'après Pell, 1918 ; C d'après Trégouboff, 1957 : pl. 67, fig. 7 B ; D d'après Pagès* et al.*, 1992 ; E d'après Boero* et al.*, 1987 ; F-G d'après Russell, 1953 ; H d'après Rees, 1941b).*

KEY TO MEDUSAE

1. no permanent tenon-like rudimentary marginal bulbs .... Campanulariidae
– triangular, tenon-like permanent rudimentary marginal bulbs .... Phialuciidae

Family BONNEVIELLIDAE Broch, 1909

Hydroid: colony stolonal or erect, often polysiphonic; hydrothecae very large, bell-shaped, borne on smooth or segmented stalks, without diaphragm; hydranth with conical hypostome, base of tentacles projecting into gastric cavity, fused together forming a supporting ring dividing the cavity into oral and gastric regions; gonophores as fixed sporosacs, gonothecae bottle-shaped with annular or longitudinal ribs, sometimes arranged in groups resembling coppinia.

Remarks: this family presents affinities with both the Campanulariidae and the Lafœidae.

Genus *BONNEVIELLA* Broch, 1909

Figs 7E, 191A-D

See family characters.

Recent references: Schuchert (2001a); Calder *et al.* (2003).

Bonneviella enterovillosa Naumov, 1952
Bonneviella extensa Naumov, 1960
Bonneviella gracilis Fraser, 1939
Bonneviella grandis (Allman, 1876a)
Bonneviella ingens Nutting, 1915
Bonneviella laevigata Naumov, 1960
Bonneviella naumovi Antsulevich & Regel, 1986
Bonneviella regia (Nutting, 1901a)
Bonneviella superba Nutting, 1915
Bonneviella uschakovi Naumov, 1952

Family CAMPANULARIIDAE Johnston, 1836

Hydroid: colony erect or stolonal; hydrothecae bell-shaped or campanulate, radially or, secondarily, bilaterally symmetrical; generally pedicellate, rim cusped or not, with basal diaphragm or inward annular projection of perisarc; hydranth generally tubular, with flared or globose hypostome delimiting a "buccal cavity", gastric endoderm of uniform structure; hydrothecal spherules present or not; gonophores as free medusae, eumedusoids or sporosacs, in gonothecae.

Medusa: manubrium short; no gastric peduncle; 4 radial canals (except in *Gastroblasta* and *Pseudoclytia*); with or without velum (without in *Obelia*); "gonads" completely surrounding radial canals, separated from manubrium; tentacles hollow (except in *Obelia* where they are solid and with a short prolongation of endoderm into bell mesoglea); with or without tenon-like rudimentary bulbs; no cirri, excretory papillae or pores; numerous (16-200) closed, velar, marginal statocysts (8 in *Obelia*, each situated on underside of the basal bulb of some marginal tentacle); no ocelli. (Fig. 194E)

Recent references: Calder (1991); Pagès *et al.* (1992); Cornelius (1995); Hirohito (1995); Boero *et al.* (1996); Migotto (1996); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000); Medel & Vervoort (2000); Schuchert (2001a).

KEY TO HYDROIDS

1. colony usually stolonal 2
– colony with erect stems, bearing alternate hydrothecae 6

2. hydrotheca with true diaphragm, with free medusae .... *Clytia*
– hydrotheca without true diaphragm, with annular perisarcal thickening near base, free sporosacs or eumedusoids 3

3. hydranth completely retractable into hydrotheca; hydrotheca usually radially symmetrical, occasionally thickened and with bilateral tendency 4
– hydranth not completely retractable into hydrotheca; hydrotheca always bilaterally symmetrical and thickened .... *Silicularia*

4. hydrotheca large and deep, tulip-shaped .... *Tulpa*
– hydrotheca of normal size, campanulate or funnel shaped.......... 5

5. hydrothecal walls with unthickened perisarc; gonophores as fixed sporosac .... *Campanularia*
– hydrothecal walls with perisarc variably thickened; gonophores as eumedusoids .... *Orthopyxis*

6. gonophores released as free medusae.......... 7
– gonophores not released as free medusae.......... 8

7. medusa with more than one manubrium .... *Gastroblasta*
– medusa with only one manubrium; with solid marginal tentacles; no velum (see key below) . . *Obelia*

8. gonophores forming vestigial retained medusoids or meconidia .... *Gonothyraea*
– gonophores as fixed sporosacs 9

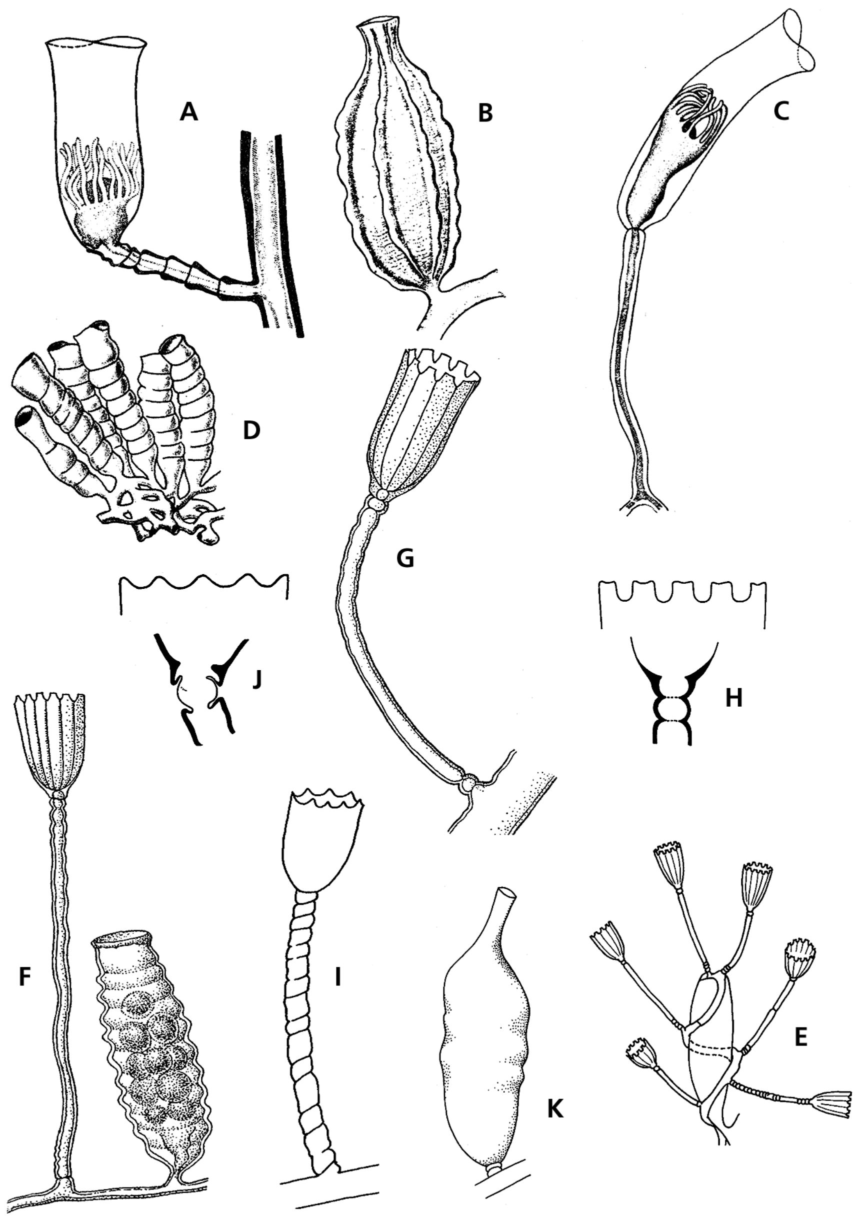


FIG. 191. Leptomedusae, Bonneviellidae. A-D, *Bonneviella*: A-B, *Bonneviella grandis*: A, hydrotheca; B, gonotheca; C-D, *Bonneviella superba*: C, hydrotheca; D, group of gonothecae. E-K, Campanulariidae, *Campanularia*: E-H, *Campanularia hincksii*: F, detail of colony showing the hydrotheca, pedicel and gonotheca; G, detail of hydrotheca and pedicel; H, hydrothecal rim (above), diagram of the basal chamber of the hydrotheca with a sub-hydrothecal spherule (below); I-K, *Campanularia volubilis*: I, single hydrotheca and pedicel; J, hydrothecal rim (above), diagram of the basal chamber of the hydrotheca with a sub-hydrothecal spherule (below); K, gonotheca (A-D after Naumov, 1969; E after Vervoort, 1946; F after Hincks, 1868; G after Leloup, 1952; H-K after Cornelius, 1995).

FIG. 191. *Leptomedusae, Bonneviellidae. A-D,* Bonneviella : *A-B,* Bonneviella grandis : *A, hydrothèque ; B, gonothèque ; C-D,* Bonneviella superba : *C, hydrothèque ; D, groupe de gonothèques. E-K, Campanulariidae,* Campanularia : *E-H,* Campanularia hincksii : *F, détail d'une colonie montrant l'hydrothèque, le pédicelle et une gonothèque ; G, détail d'une hydrothèque et de son pédicelle ; H, bord marginal de l'hydrothèque (au-dessus), diagramme de la chambre basale de l'hydrothèque avec le sphérule sub-hydrothèqual (au-dessous) ; I-K,* Campanularia volubilis : *I, hydrothèque et son pédicelle ; J, bord marginal de l'hydrothèque (au-dessus), diagramme de la chambre basale de l'hydrothèque avec le sphérule sub-hydrothèqual (au-dessous) ; K, gonothèque (A-D d'après Naumov, 1969 ; E d'après Vervoort, 1946 ; F d'après Hincks, 1868 ; G d'après Leloup, 1952 ; H-K d'après Cornelius, 1995).*

9. stem monosiphonic .... *Laomedea*
– stem polysiphonic already early in life 10

10. hydrothecae alternate, without sub-hydrothecal spherule .... *Hartlaubella*
– hydrothecal pedicels in loosely defined whorls, with sub-hydrothecal spherule .... *Rhizocaulus*

Remarks: the classification of the Campanulariidae is unsatisfactory; generic divisions, as in many other families of Leptomedusae hydroids, are not well defined, and vary even in modern works (see: Calder 1991; Cornelius 1982; 1995; Hirohito 1995). Hirohito (1995), for instance, taking into account characters such as presence/absence of diaphragm and sub-hydrothecal spherules, treated *Orthopyxis* and *Rhizocaulus* as synonyms of *Campanularia*, and *Laomedea* and *Gonothyraea* as synonyms of *Obelia*, so simplifying greatly the generic contents of the family. But *Obelia* is very different from all other campanulariid genera at the medusa level. Furthermore the reduction of free medusae to fixed gonophores may have occurred several times independently during the evolution of the Campanulariidae and so it is impossible to refer presently the taxa with fixed sporosacs to any presently known medusa genus. Nevertheless many genera are very close to each other, for instance, *Hartlaubella* and *Laomedea*, *Rhizocaulus* and *Campanularia*, *Tulpa* and *Campanularia* and could be treated as synonyms without great difficulty.

KEY TO MEDUSAE

1. more than 4 radial canals 2
– normally 4 radial canals 3
2. up to 20 radial and centripetal canals; numerous manubria, with 4 lips .... *Gastroblasta*
– up to 7 radial canals; one manubrium and as many lips as radial canals .... *Pseudoclytia*
3. reduced medusae; no manubrium; no tentacles .... *Orthopyxis*
– normally developed medusae; one manubrium with 4 lips; with tentacles 4
4. marginal tentacles hollow; velum .... *Clytia*
– solid marginal tentacles; no velum .... *Obelia*

Genus ***CAMPANULARIA*** Lamarck, 1816

Figs 5O, 9A, 191E-K

Synonyms: *Eucalix* Stechow, 1921; *Paracalix* Stechow, 1923.
Hydroid: colony stolonal, seldom erect and branched; hydrorhiza not anastomosing; hydrothecal pedicel unbranched; hydrothecae campanulate or bell-shaped, with entire or cusped margin; demarcated from pedicel basally by a variably developed annular perisarcal thickening; hydrothecal walls with unthickened perisarc, not abruptly everted distally; true diaphragm absent, sub-hydrothecal spherule present; gonophores as fixed sporosacs, gonothecae on hydrorhiza.
Remarks: genus *Paracalix* Stechow, 1923 is characterized by two opposing folds in the hydrothecal walls, this genus is considered by most authors as identical with *Campanularia* Lamarck, 1816. Watson (1997) maintains it nevertheless as a separate genus for *Campanularia ambiplica* Mulder & Trebilcock, 1914a.
Recent references: Calder (1991); Cornelius (1995); Schuchert (2001); Calder *et al.* (2003).

Campanularia abyssa Fraser, 1940b
Campanularia africana Stechow, 1923a
Campanularia agas Cornelius, 1982
Campanularia ambiplica Mulder & Trebilcock, 1914b
Campanularia antarctica Stechow, 1922
Campanularia brevicaulis Nutting, 1915
Campanularia breviscyphia Sars, 1857
Campanularia carduella Allman, 1885
Campanularia castellata Fraser, 1925 [invalid name]
Campanularia certidens Fraser, 1947
Campanularia compressima Kubota & Yamada, 1992
Campanularia clytioides (Lamouroux, 1824a)
Campanularia corrugata Jarvis, 1922 [doubtful status]
Campanularia costata (Gravier-Bonnet, 1979)
Campanularia crenata Allman, 1876
Campanularia denticulata Clark, 1876b

Campanularia diversa Fraser, 1948
Campanularia erythraea Thornely, 1908
Campanularia eurycalyx Hartlaub, 1905
Campanularia fasciculata Fraser, 1941
Campanularia fusiformis Clarke, 1876a
Campanularia gigantea Hincks, 1866
Campanularia groenlandica Levinsen, 1893b
Campanularia hincksii Alder, 1856a
Campanularia indopacifica Stechow, 1919a
Campanularia laminacarpa Millard, 1966
Campanularia longitheca Stechow, 1924
Campanularia macroscypha Allman, 1877
Campanularia morgansi Millard, 1957
Campanularia nodosa Stechow, 1923b
Campanularia pecten Gow & Millard, 1975
Campanularia pumila Bale, 1914a
Campanularia pygmaea Clark, 1875
Campanularia roberti Gow & Millard, 1975
Campanularia sinuosa (Leloup, 1935)
Campanularia speciosa Clark, 1876a
Campanularia subantarctica Millard, 1971
Campanularia sulcata Jäderholm, 1896
Campanularia tincta Hincks, 1861b
Campanularia volubilis (Linnaeus, 1758)

Genus ***CLYTIA*** Lamouroux, 1812

Figs 5P, 9C, 25J, 26I, T, 192A-G

Hydroid: colony reptant, unbranched stolonal or erect branched, usually minute, monosiphonic or polysiphonic; hydrorhiza branched but not anastomosing; hydrothecae deep, campanulate, hydrothecal rim sinuous or deeply indented, with clefts between round to sharply-pointed cusps; true hydrothecal diaphragm; subhydrothecal spherule absent (present in *C. hummelincki*); gonophores as free medusae, gonotheca conical.
Medusa: manubrium short; velum normal; marginal tentacles hollow; no tenon-like permanent rudimentary bulbs; numerous statocysts.
Remarks: very few species of *Clytia* medusae are clearly identified, most morphological characters used to distinguish them possibly falling in the range of variation that can be expected in a single species and having little or no taxonomic value. Most of the *Clytia* species have been described either from hydroids or from medusae only. The genus needs a revision, with careful elucidation of life cycles and molecular work.
Recent references: Pagliara *et al.* (2000); Lindner and Migotto (2002); Calder *et al.* (2003); Schuchert (2003).

Clytia ambigua (Agassiz & Mayer, 1899)
Clytia arborescens Pictet, 1893
Clytia attenuata Calkins, 1899 [probably a syn. of *C. hemisphaerica*]
Clytia bakeri Torrey, 1904
Clytia brevicyatha Mammen, 1965
Clytia brunescens (Bigelow, 1904)
Clytia colombiana Wedler, 1976
Clytia crenata Mammen, 1965
Clytia cruciferum (Annandale, 1915) [doubtful status]
Clytia delicatula (Thornely, 1900) [only medusa buds known]
Clytia discoida (Mayer, 1900a)
Clytia edentula Gibbons & Ryland, 1989
Clytia elongata Marktanner-Turneretscher, 1890
Clytia exilis Fraser, 1948
Clytia fascicularis Fraser, 1948
Clytia folleata (McCrady, 1859a)
Clytia gardineri (Browne, 1905b)
Clytia gelatinosa (Mayer, 1900a)
Clytia globosa (Mayer, 1900a) [as *Oceania*]
Clytia gracilicaulis (Fraser, 1938a) [as *Campanularia*]
Clytia gracilis (M. Sars, 1850) [syn. *C. elsaeoswaldae* Stechow, 1914]
Clytia gregaria (L. Agassiz, 1862a)
Clytia hemisphaerica (Linnaeus, 1767) [syn. *C. bicophora* L. Agassiz, 1862a; *C. coronata* (Clarke, 1879); *C. minuta* (Nutting, 1901b); *C. similis* Fraser, 1947]
Clytia hesperia (Torrey, 1904)
Clytia hexacanalis Xu, Huang & Chen Xu, 1991 [doubtful status]
Clytia hummelincki (Leloup, 1935) [only immature medusa known]
Clytia iridescens (Maas, 1906)
Clytia irregularis Fraser, 1938a
Clytia islandica (Kramp, 1919)
Clytia kincaidi (Nutting, 1899)
Clytia languida (L. Agassiz, 1862a)
Clytia latitheca Millard & Bouillon, 1973 [only immature medusa known]
Clytia liguiliformis Mammen, 1965
Clytia linearis (Thornely, 1900) [syn. *C. gravieri* (Billard, 1904)]
Clytia lomae (Torrey, 1909)
Clytia macrocarpa Fraser, 1938b
Clytia macrogonia Bouillon, 1984b [perhaps a syn. of *C. linearis*]
Clytia macrotheca (Perkins, 1908)
Clytia malayense (Kramp, 1961)
Clytia mccradyi (Brooks, 1888)
Clytia multiannulata Hirohito, 1995
Clytia multidentata Fraser, 1938
Clytia noliformis (McCrady, 1859a)

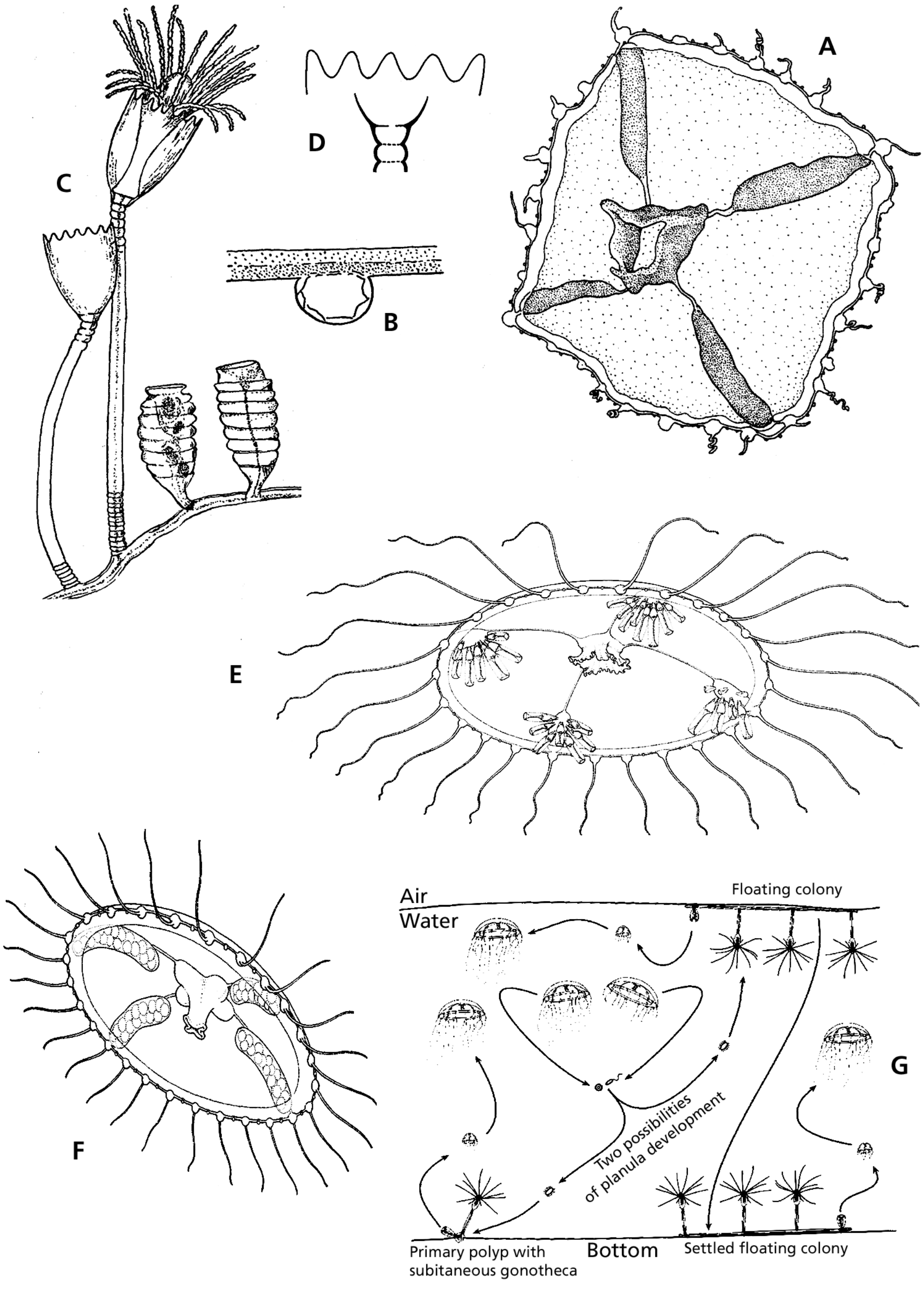


FIG. 192. Leptomedusae, Campanulariidae. A-G, *Clytia*: A-D, *Clytia hemisphaerica*: A, adult medusa; B, detail of statocyst without concretion; C, part of a hydroid colony; D, detail of hydrotheca, hydrothecal rim (above), diagram of the basal chamber (below); E, *Clytia macradyi*, with hydroid ''blastostyles'' on radial canals giving rise to medusa buds; F, *Clytia macrogonia*, adult medusa; G, *Clytia viridicans*, alternative life cycle pathways involving planula settlement either on the bottom or on air-water surface (A & D after Russell, 1953; B after Cornelius, 1995; C after Pagès *et al*., 1992; E-F after Bouillon, 1984b; G after Pagliara *et al*., 2000).

FIG. 192. *Leptomedusae, Campanulariidae. A-G,* Clytia : *A-D,* Clytia hemiphaerica : *A, méduse adulte ; B, détail d'un statocyste, les concrétions ne sont pas représentées ; C, portion d'une colonie d'hydroïdes ; D, détail d'une l'hydrothèque, bord hydrothèqual (au-dessus), diagramme de la chambre basale (au-dessous) ; E,* Clytia macradyi*, méduse avec des ''blastostyles'' d'hydroïdes sur les canaux radiaires donnant naissance à des bourgeons médusaires ; F,* Clytia macrogonia*, méduse adulte ; G,* Clytia viridicans*, voies alternatives du cycle biologique où la planula se développe soit sur le fond de la mer soit au niveau de la surface air-eau (A & D d'après Russell, 1953 ; B d'après Cornelius, 1995 ; C d'après Pagès* et al.*, 1992 ; E-F d'après Bouillon, 1984b ; G d'après Pagliara* et al.*, 2000).*

Clytia pacifica (Agassiz & Mayer, 1899)
Clytia paradoxa (Stechow, 1923a)
Clytia paulensis (Vanhöffen, 1910)
Clytia pearsonensis Watson, 1973
Clytia phosphorica (Péron & Lesueur, 1810) [name covering the medusae of several species of *Clytia*]
Clytia rangiroae (Agassiz & Mayer, 1902)
Clytia seriata Fraser, 1938a
Clytia sibogae Billard, 1917
Clytia simplex (Browne, 1902)
Clytia singularis (Mayer, 1900b)
Clytia stechowi Hargitt, 1927
Clytia trigona Pictet, 1893
Clytia tubitheca Hargitt, 1924
Clytia universitatis Torrey, 1904
Clytia uchidai (Kramp, 1961)
Clytia viridicans (Leuckart, 1856)
Clytia warreni (Warren, 1908) [only medusa buds known]

Genus ***GASTROBLASTA*** Keller, 1883

Fig. 193A-B

Hydroid: *Clytia*-like, living embedded in sponges.
Medusa: several urn-shaped manubria (up to 16); up to 20 radial and centripetal canals; velum normal; marginal tentacles hollow; numerous statocysts, gonads developing near the middle of radial canals.

Gastroblasta ovale (Mayer, 1900a)
Gastroblasta raffaelei Lang, 1886
Gastroblasta timida Keller, 1883

Genus ***GONOTHYRAEA*** Allman, 1864

Figs 5Q, 10A, 193C-D

Hydroid: colony erect, branched or unbranched, monosiphonic or polysiphonic; stem divided into regular internodes bearing alternate hydrothecae; hydrothecae campanulate to bell-shaped, radially symmetrical; hydrothecal rim cusped; with true diaphragm; gonophores forming degenerate medusae (meconidia), extruded from gonotheca but remaining attached while planula develops in a sac-like meconidium with marginal tentacles, but no mouth or sense organs; gonotheca urn-shaped, pedicellate axillary on stem.
Recent references: Östman (1982); Cornelius (1995); Schuchert (2001a).

Gonothyraea clarki (Marktanner-Turneretscher, 1890)
Gonothyraea inornata Nutting, 1901a
Gonothyraea loveni (Allman, 1859)
Gonothyraea nodosa Stechow, 1914

Genus ***HARTLAUBELLA*** Poche, 1914

Figs 5R, 193E-H

Hydroid: colony erect, polysiphonic, branched or unbranched, growing on branched but not anastomosing hydrorhiza; hydrocauli divided in regular internodes bearing alternate hydrothecae; hydrothecae campanulate with castellated, often abraded rim, radially symmetrical, on pedicels, with true diaphragm; gonophores as fixed sporosacs with large embryos, gonothecae axillary, inverted conical.
Recent reference: Cornelius (1995).

Hartlaubella gelatinosa (Pallas, 1766)

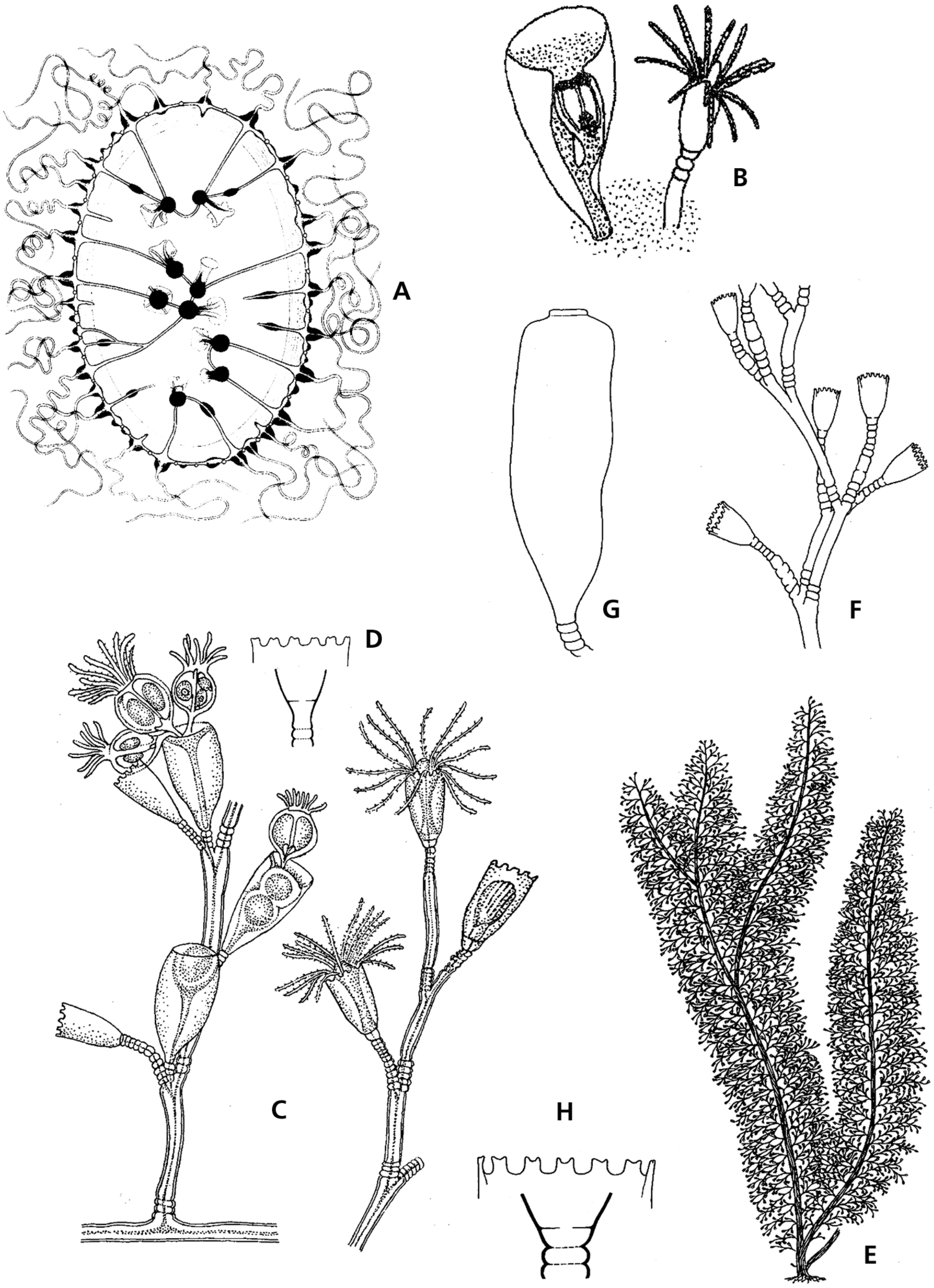


FIG. 193. Leptomedusae, Campanulariidae. A-B, *Gastroblasta raffaelei*: A, adult medusa; B, polyp and gonotheca. C-D, *Gonothyraea loveni*: C, detail of colonies with and without gonothecae and gonophores; D, diagrams of hydrothecal rim and basal chamber. E-H, *Hartlaubella gelatinosa*: E, colony; F, detail of a branch; G, gonotheca; H, diagram of hydrothecal rim and basal chamber (A after Lang, 1886; B after Boero, 1980; C-H after Cornelius, 1995).

FIG. 193. *Leptomedusae, Campanulariidae. A-B,* Gastroblasta raffaelei : *A, méduse adulte ; B, polype et gonothèque. C-D,* Gonothyraea loveni *: C, détails de colonies avec ou sans gonothèques et gonophores ; D, diagramme du bord hydrothèqual et de la chambre basale. E-H,* Hartlaubella gelatinosa : *E, vue d'une colonie ; F, détail d'une branche ; G, gonothèque ; H, diagramme du bord hydrothèqual et de la chambre basale (A d'après Lang, 1886 ; B d'après Boero, 1980 ; C-H d'après Cornelius, 1995).*

Genus *LAOMEDEA* Lamouroux, 1812

Figs 7C, 9D, 17, 47B, 194A-C

Hydroid: colony erect, monosiphonic, branched or unbranched, growing on branched but not anastomosing hydrorhiza; hydrocauli divided in regular internodes bearing alternate hydrothecae; hydrothecae campanulate, rim even or cusped, radially symmetrical, on pedicels, with true diaphragm; gonophores as fixed sporosacs, gonothecae sessile or shortly pedicellate stolonal or axillary.

Recent references: Östman (1982); Cornelius (1995).

Laomedea amphora A. Agassiz, 1862
Laomedea angulata Hincks, 1861a
Laomedea austrogeorgiae Jäderholm, 1905
Laomedea calceolifera (Hincks, 1871)
Laomedea exigua M. Sars, 1857
Laomedea flexuosa Alder, 1857
Laomedea neglecta Alder, 1856b
Laomedea pseudodichotoma Vervoort, 1959
Laomedea tottoni Leloup, 1935

Genus *OBELIA* Péron & Lesueur, 1810

Figs 2A, 9E, 25F, 57A, 194D-H

Hydroid: colony erect, branched or unbranched, monosiphonic or polysiphonic, variably flexuose; stolons not anastomosing; internodes annulated proximally, supporting distally a pedicellate hydrotheca on apophysis; hydrotheca bell-shaped to campanulate, radially symmetrical, margin cusped or even, true hydrothecal diaphragm, no sub-hydrothecal spherule; hydranth with globose hypostome forming a "buccal cavity"; gonophores as free medusae, gonothecae inverted conical, usually with raised terminal aperture but sometimes simply truncated.

Medusa: manubrium short, quadrangular; no velum; tentacles numerous, solid, stiff, not extensile, with short endodermal roots extending into bell mesoglea; 8 statocysts on underside of basal bulbs of some marginal tentacles.

Recent references: Östman (1982); Cornelius (1995), Boero *et al.* (1996); Calder *et al.* (2003).

Obelia bidentata Clarke, 1875
Obelia castellata Clarke, 1894
Obelia dichotoma (Linnaeus, 1758)
Obelia fimbriata (Dalyell, 1848)
Obelia geniculata (Linnaeus, 1758)
Obelia longissima (Pallas, 1766)

Genus *ORTHOPYXIS* L. Agassiz, 1862

Figs 56C, 195A-F

Synonym: *Agastra* Hartlaub, 1897.

Hydroid: colony stolonal or with short unbranched uprights; hydrorhiza branched and anastomosing; hydrotheca campanulate, fundamentally radially symmetrical but sometimes biradially symmetrical with walls laterally compressed and oval in cross section; perisarc wall variably thickened; rim even or toothed; without true diaphragm but variably developed perisarcal thickening, sub-hydrothecal spherule; gonophores as eumedusoids either free, facultatively retained, or never released; no manubrium and tentacles but with 8 statocysts, gonothecae on hydrorhiza.

Remarks: Sometimes considered as congeneric with *Campanularia*.

Recent references: Calder (1991); Cornelius (1995); Vervoort & Watson (2003).

Orthopyxis affabilis Vervoort & Watson, 2003
Orthopyxix asymmetrica Stechow, 1919 [probably a syn. of *O. integra*]
Orthopyxis bilateralis Antsulevich & Tchernova, 1997
Orthopyxis caliculata Hincks 1853
Orthopyxis compressa (Clark, 1876b)
Orthopyxis crenata (Hartlaub, 1901b)
Orthopyxis everta Clark, 1876a [probably a syn. of *O. crenata*]
Orthopyxis fujianensis Huang & Xu, 1994
Orthopyxis integra (MacGillivray, 1842)
Orthopyxis platycarpa Bale, 1914c
Orthopyxis sargassicola (Nutting, 1915)
Orthopyxis tincta (Hincks, 1861b)

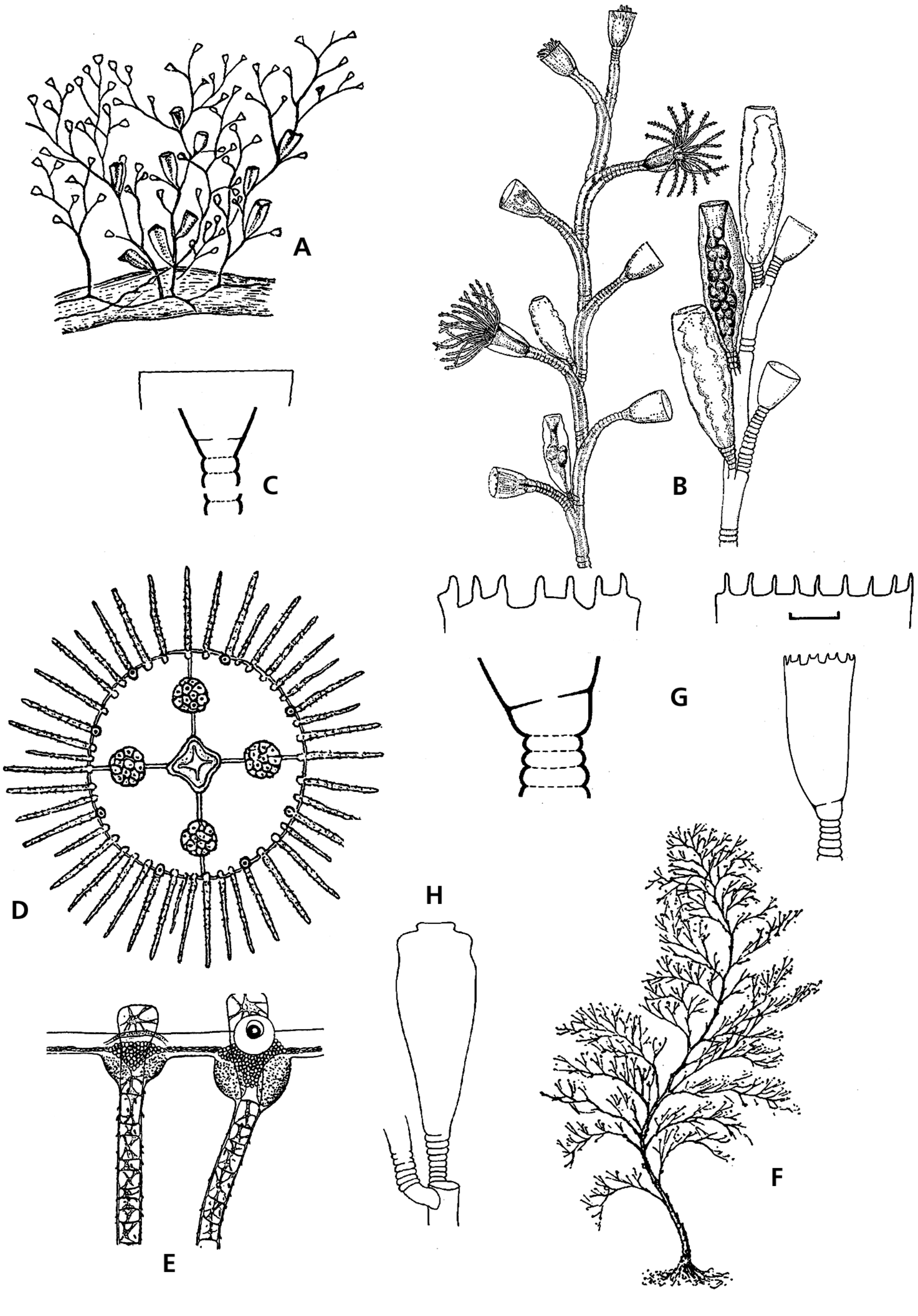


FIG. 194. Leptomedusae, Campanulariidae. A-C, *Laomedea flexuosa*: A, colony; B, detail of branches showing hydrothecae and gonothecae; C, diagram of hydrothecal rim and basal chamber. D-H, *Obelia*: D, *Obelia* sp., adult medusa; E, *Obelia* sp., portion of the umbrella margins showing the position of the statocyst at the base of the tentacular bulb; F-H, *Obelia bidentata*: F, hydroid colony; G, detail of the hydrotheca, the bicuspidate and uniform hydrothecal rim and the basal chamber; H, gonotheca (A-B after Hincks, 1868; C, G-H after Cornelius, 1995; D-E after Kramp, 1933; F after Leloup, 1952).

FIG. 194. *Leptomedusae, Campanulariidae. A-C,* Laomedea flexuosa : *A, vue d'une colonie ; B, détail de branches montrant les hydrothèques et les gonothèques ; C, diagramme du bord hydrothèqual et de la chambre basale. D-H,* Obelia : *D,* Obelia *sp., méduse adulte ; E,* Obelia *sp., portion du bord marginal exombrellaire montrant la position du statocyste à la base du bulbe tentaculaire ; F-H,* Obelia bidentata *: F, colonie d'hydroïdes ; G, détails d'hydrothèques montrant le bord hydrothèqual soit bicuspidé ou uniformément denté ainsi que la chambre basale ; H, gonothèque (A-B d'après Hincks, 1868 ; C, G-H d'après Cornelius, 1995 ; D-E d'après Kramp, 1933 ; F d'après Leloup, 1952).*

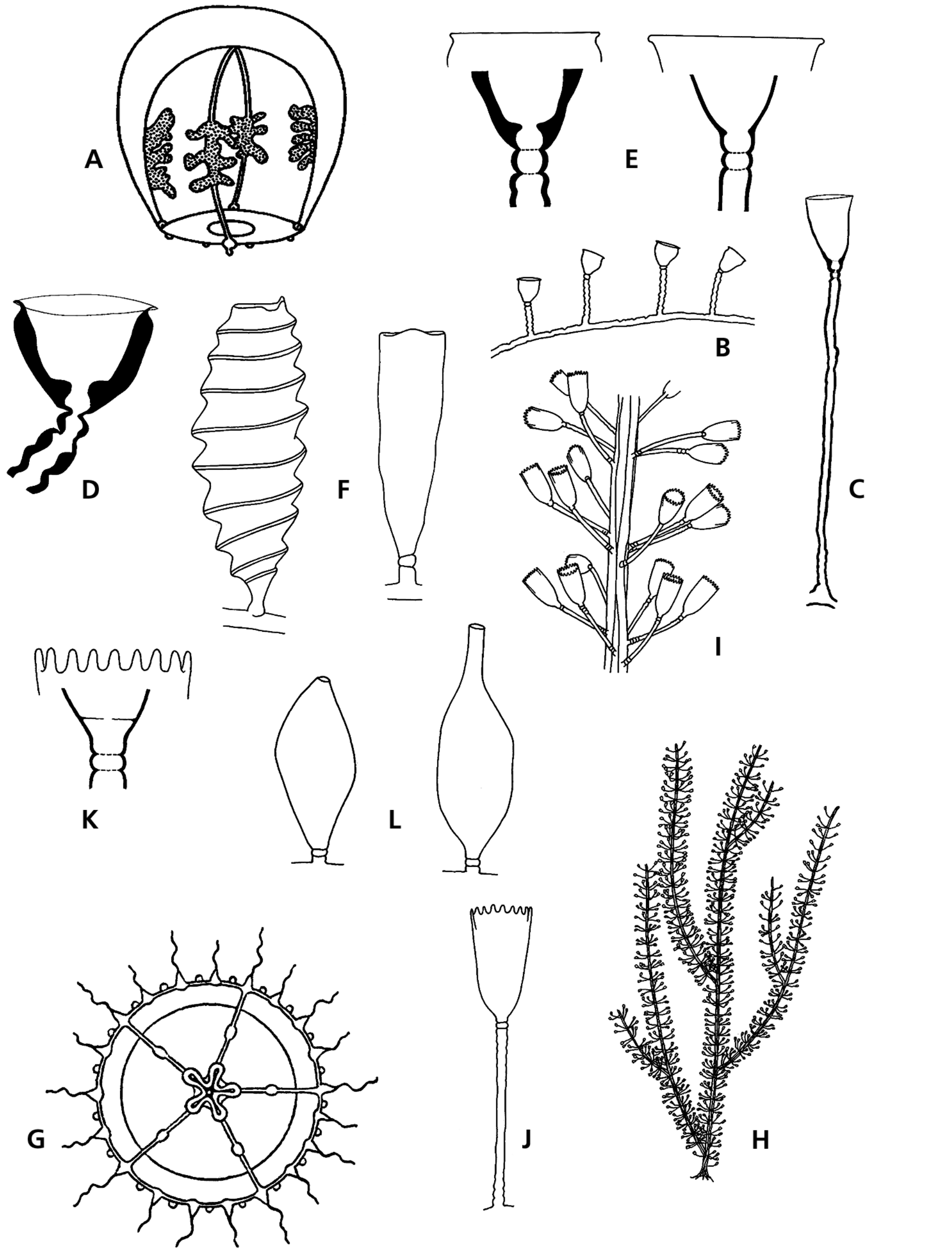


FIG. 195. Leptomedusae, Campanulariidae. A-F, *Orthopyxis integra*: A, eumedusoid after release; B, part of hydroid colony; C, hydrotheca and pedicel; D, detail of hydrotheca showing sub-hydrothecal spherule; E, diagram of hydrothecal rim and basal chamber of unthickened and thickened hydrotheca; F, grooved and smooth-walled gonothecae. G, *Pseudoclytia pentata*, medusa. H-L, *Rhizocaulus verticillatus*: H, hydroid colony; I, detail of a part of colony; J, hydrotheca and pedicel; K, diagram of the hydrothecal rim and basal chamber; L, gonothecae with short and long necks (A after Russell, 1953; B , E, H-K after Cornelius, 1995; C-D & L after Cornelius,1982; F left after Hincks, 1868, F right after Vervoort, 1946; G after Kramp, 1959b).

***FIG. 195.** Leptomedusae, Campanulariidae. A-F,* Orthopyxis integra *: A, eumedusoïde après sa libération ; B, partie de colonie d'hydroïdes ; C, hydrothèque et son pédicelle ; D, détail d'une hydrothèque montrant le sphérule sub-hydrothèqual ; E, diagrammes de bords d'hydrothèques et de chambres basales appartenant à des hydrothèques épaissies ou non ; F, gonothèques à parois cannelées ou lisses. G,* Pseudoclytia pentata*, méduse. H-L,* Rhizocaulus verticillatus *: H, colonie d'hydroïdes ; I, détail d'une partie de colonie ; J, hydrothèque et son pédicelle ; K, diagramme du bord hydrothéqual et de la chambre basale ; L, gonothèques avec un col court ou long (A d'après Russell, 1953 ; B, E, H-K d'après Cornelius, 1995 ; C-D & L d'après Cornelius,1982 ; F gauche d'après Hincks, 1868, F droite d'après after Vervoort, 1946 ; G d'après Kramp, 1959b).*

Genus *PSEUDOCLYTIA* Mayer, 1900

Fig. 195G

Hydroid: unknown.
Medusa: more than 4 radial canals and a corresponding number of manubrial lips.

Pseudoclytia pentata (Mayer, 1900a)

Genus *RHIZOCAULUS* Stechow, 1919

Fig. 195H-L

Hydroid: colony strongly ramified, erect, rhizocaulic; hydrotheca bell-shaped, rim with blunt cusp, pedicels smooth or spirally twisted; arising from hydrocauli and hydrocladia in form of loosely defined whorls; no true diaphragm, sub-hydrothecal spherule present; gonophores as fixed sporosacs, gonothecae on hydrocaulus and hydrocladia, bottle-shaped.
Recent references: Vervoort (1987); Cornelius (1995).

Rhizocaulus chinensis (Marktanner-Turneretscher, 1890)
Rhizocaulus verticillatus (Linnaeus, 1758)

Genus *SILICULARIA* Meyen, 1834

Fig. 196A-G

Hydroid: colony stolonal; hydrotheca with greatly thickened walls, asymmetrical or bilaterally symmetrical, no diaphragm, annular thickening; hydrothecal margin sloping; hydrothecal wall so thick that hydranths are no more longer completely retractable; gonophores giving rise to eumedusoids, gonothecae borne on hydrorhiza.
Recent references: Stepanjants (1979); Vervoort (1987).

Silicularia bilabiata (Coughtrey, 1875)
Silicularia rosea Meyen, 1834
Silicularia undulata (Mulder & Trebilcock, 1914b)

Genus *TULPA* Stechow, 1921

Fig. 196H-J

Hydroid: colony stolonal or erect, branched; hydrotheca very deep and large, tulip-shaped, with flared margin, narrowing under, usually longitudinally ridged or lined, without true diaphragm but with annular thickening; hydranth with distinct trumpet-shaped hypostome; gonophores as fixed sporosacs, gonothecae pedicellate, borne on hydrorhiza, annulated, planula developing inside gonothecae.
Recent reference: Vervoort (1987).

Tulpa diverticulata Totton, 1930
Tulpa tulipifera (Allman, 1888)

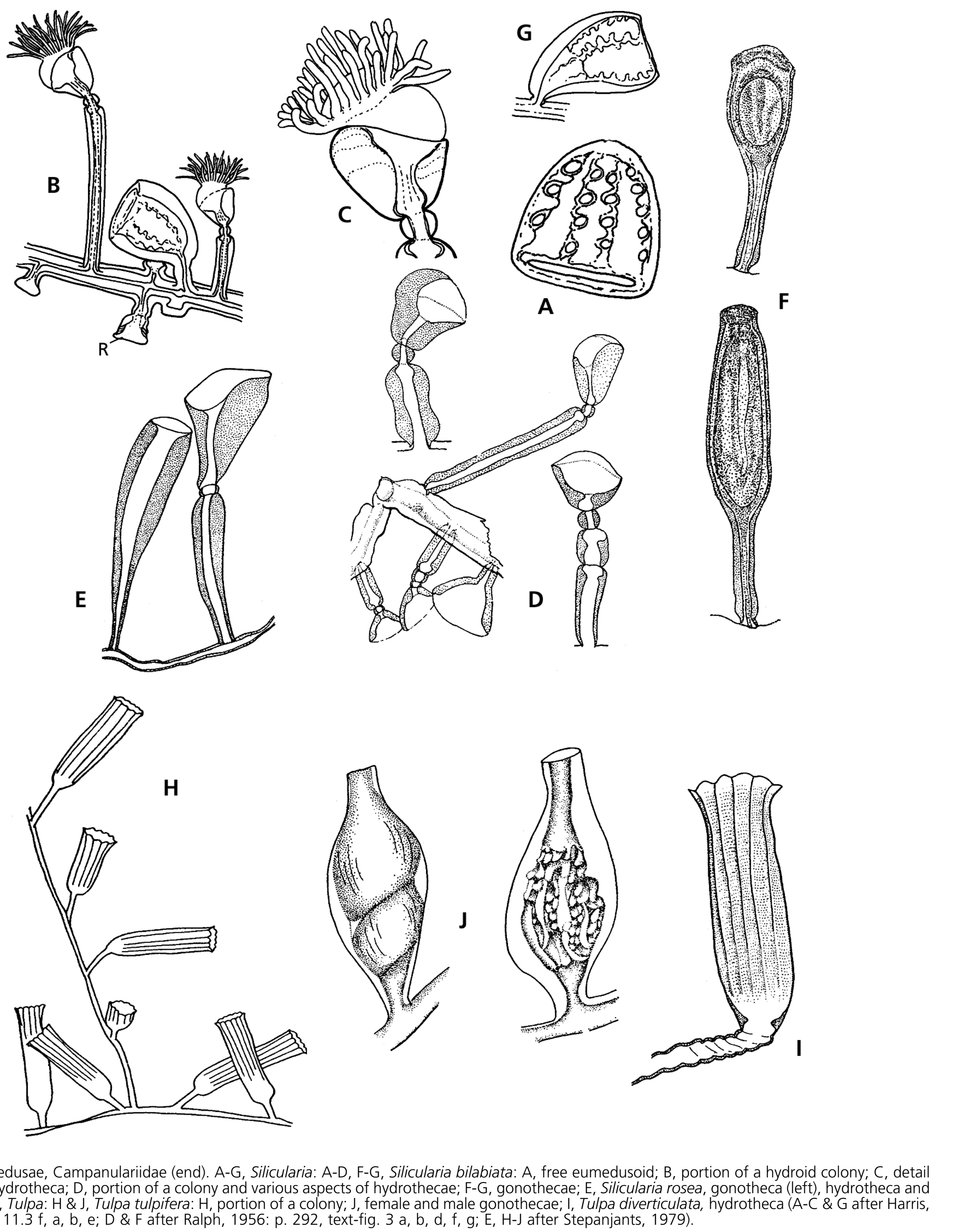


FIG. 196. Leptomedusae, Campanulariidae (end). A-G, *Silicularia*: A-D, F-G, *Silicularia bilabiata*: A, free eumedusoid; B, portion of a hydroid colony; C, detail of hydranth and hydrotheca; D, portion of a colony and various aspects of hydrothecae; F-G, gonothecae; E, *Silicularia rosea*, gonotheca (left), hydrotheca and pedicel (right). H-J, *Tulpa*: H & J, *Tulpa tulpifera*: H, portion of a colony; J, female and male gonothecae; I, *Tulpa diverticulata,* hydrotheca (A-C & G after Harris, 1990: p. 228, fig. 11.3 f, a, b, e; D & F after Ralph, 1956: p. 292, text-fig. 3 a, b, d, f, g; E, H-J after Stepanjants, 1979).

FIG. 196. *Leptomedusae, Campanulariidae (fin). A-G,* Silicularia *: A-D, F-G,* Silicularia bilabiata *: A, eumédusoïde libre ; B, portion d'une colonie d'hydroïdes ; C, détail d'un hydranthe et de son hydrothèque ; D, portions de colonies montrant différents aspects d'hydrothèques ; F-G, gonothèques ; E,* Silicularia rosea*, gonothèque (à gauche), hydrothèque et son pédicelle (à droite). H-J,* Tulpa *: H & J,* Tulpa tulpifera *: H, portion d'une colonie ; J, gonothèques femelle et mâle ; I,* Tulpa diverticulata*, hydrothèque (A-C & G d'après Harris, 1990 : p. 228, fig. 11.3 f, a, b, e ; D & F d'après Ralph, 1956 : p. 292, text-fig. 3 a, b, d, f, g ; E, H-J d'après Stepanjants, 1979).*

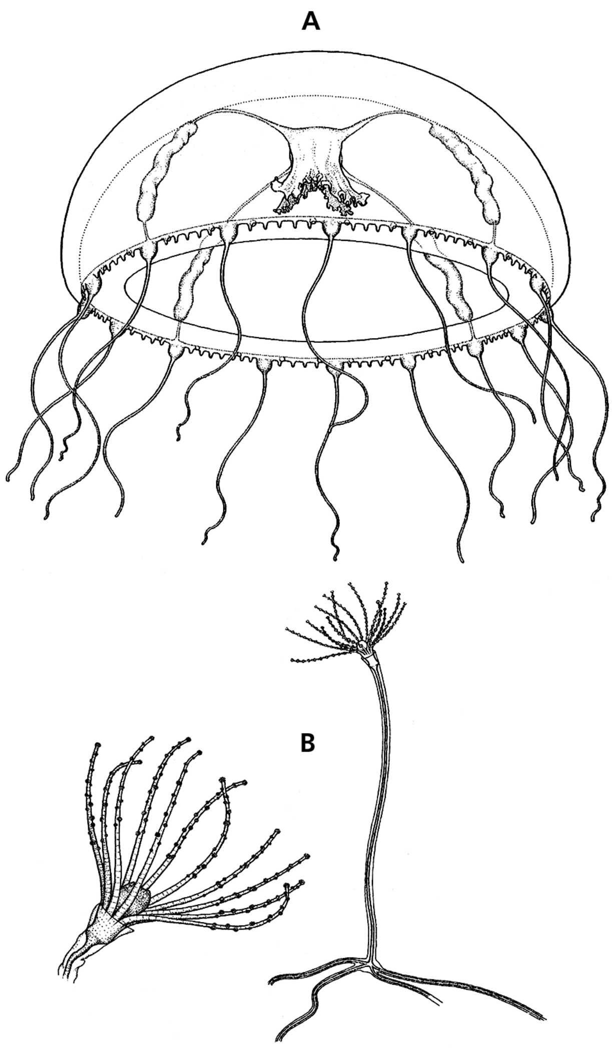
Campanulariidae *nomen nudum*:

Genus *ZELOUNIES*

Zelounies estrambordi Gravier-Bonnet, 1992: life cycle described from rearing but species diagnosis or formal description never given by the author: unavailable name.

Family PHIALUCIIDAE Kramp, 1955

Hydroid: "Campanulariid" type; hypostome peduncled; stem long, not annulated.
Medusa: manubrium small; no peduncle; 4 simple radial canals; "gonads" on radial canals, completely surrounding them and separated from manubrium; marginal tentacles hollow; triangular tenon-like permanent marginal rudimentary bulbs; closed statocysts.



Genus *PHIALUCIUM* Maas, 1905

Fig. 197A-B
See family characters.

Phialucium mbenga (Agassiz & Mayer, 1899)

Subclass LIMNOMEDUSAE Kramp, 1938

Hydroid: very simple, solitary or colonial; small, sessile; with or without tentacles; often close to planula structure and budding planula-like structures or frustules; body plans range from: forms without mouth and permanent gastric cavity = feeding planula: Microhydrulidae, to forms with mouth and hypostome, but without tentacles, forming transitory colonies or definitive colonies with a limited number of individuals: *Craspedacusta*, *Limnocnida*, *Olindias*; to forms with hypostome and tentacles: *Calpasoma, Gonionemus, Scolionema, Vallentinia*; no perisarcal thecae, but cysts and stolons covered by chitin.
Medusa: usually without marginal cnidocyst ring (except *Craspedacusta* and *Limnocnida*); "gonads" along radial canals or exceptionally on manubrium (*Armorhydra* and *Limnocnida*); marginal tentacles peripheral, hollow, without true basal bulb, tentacle base usually with a parenchymatic endodermal core embedded in umbrellar

FIG. 197. Leptomedusae, Phialuciidae. A-B, *Phialucium mbenga*: A, adult medusa; B, hydroid (both after Bouillon, 1984c).

FIG. 197. *Leptomedusae, Phialuciidae. A-B,* Phialucium mbenga : *A, méduse adulte ; B, hydroïdes (d'après Bouillon, 1984c).*

mesoglea; marginal sense organs as internal enclosed ecto-endodermal statocysts embedded in the mesoglea near ring canal or in the velum (only in *Craspedacusta*); no ocelli; exceptionally reduced medusoids (*Monobrachium*); planulae with cnidoblasts but without embryonic glandular cells.
Remarks: the Limnomedusae is a small group of Hydroidomedusa with a dimorphic benthic-pelagic cycle; hydroids are small, poorly developed, rarely really modular; medusa production is comparatively much reduced; many of the present-day Limnomedusae inhabit fresh- or brackish-waters, the hydroids and resting stages are perennial, resisting adverse conditions: *Craspedacusta* cysts can survive 40 years while completely desiccated.

Key to hydroids

1. hydroid reduced to a spherical or irregular body (20 to 480 μm), without tentacles, mouth and gastric cavity . . . . Microhydrulidae
– hydroid with permanent mouth and gastric cavity . . . . Olindiidae

Key to medusae

1. reduced medusa, creeping, burrowed in coarse sand sediments; no radial canals, statocysts and nerve system . . . . Armorhydridae
– free swimming medusa, with radial canals, statocysts and nerve system . . . . Olindiidae

Family ARMORHYDRIDAE Swedmark & Teissier, 1958

Hydroid: polyp small, solitary, mesopsammic, attached to sand grains by mucous periderm; about 10 short but extensible capitate-like tentacles, small hypostome, mouth inconspicuous; tentacular frustules and podocysts; gonophores as free medusae, borne on body (Lacassagne 1968; 1973).
Medusa: reduced, creeping within the interstices in coarse sand sediments; umbrella margin with a whorl of two kind of solid tentacles, filiform and adhesive; manubrium voluminous, linked to subumbrella by longitudinal septa containing endodermal tubes; "gonads" on manubrium; velar opening narrow; no radial canals, nerve system, statocysts or any other visible sense organ; sexes separate.
Recent reference: Thiel (1988).

Genus *ARMORHYDRA* Swedmark & Teissier, 1958

Fig. 198A-B

See family diagnosis.

Armorhydra janowiczi Swedmark & Teissier, 1958c

Family MICROHYDRULIDAE Bouillon & Deroux, 1967

Hydroid: reduced to a spherical or irregular body ranging from 20 to 480 μm, included in the superficial biological layer covering immersed objects in the sea or epibiotic on bivalve shells; didermic but very simple, without tentacles and mouth, gastric cavity becomes temporarily visible only when food is engulfed; body covered by mucus, with a basal lamella of periderm; sexual reproduction unknown, asexual reproduction by mobile frustules.
Recent references: Thiel (1988); Jarms & Tiemann (1996).

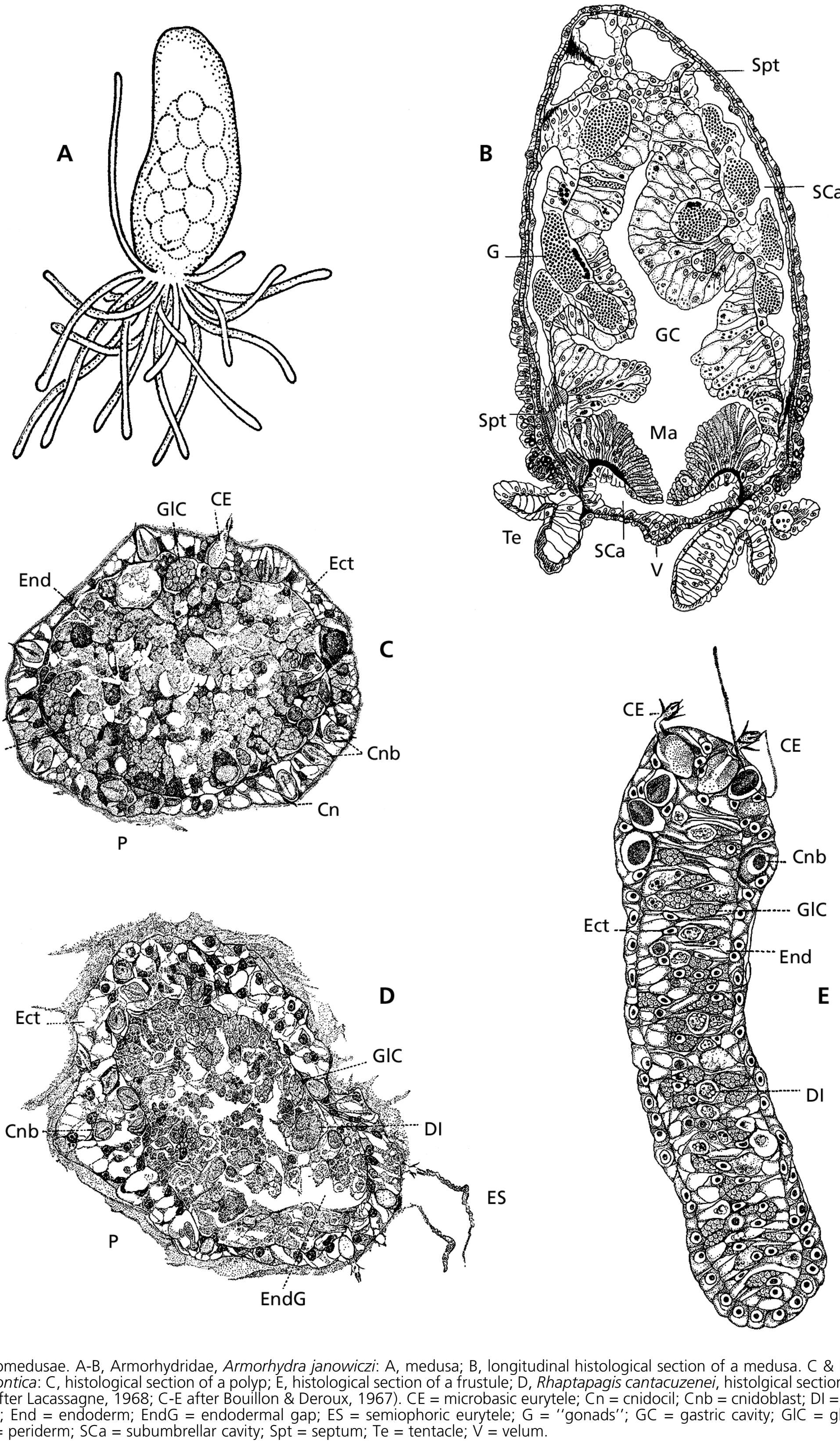


FIG. 198. Limnomedusae. A-B, Armorhydridae, *Armorhydra janowiczi*: A, medusa; B, longitudinal histological section of a medusa. C & E, Microhydrulidae, *Microhydrula pontica*: C, histological section of a polyp; E, histological section of a frustule; D, *Rhaptapagis cantacuzenei*, histolgical section of a polyp (A after Thiel, 1988; B after Lacassagne, 1968; C-E after Bouillon & Deroux, 1967). CE = microbasic eurytele; Cn = cnidocil; Cnb = cnidoblast; DI = digestive inclusion; Ect = ectoderm; End = endoderm; EndG = endodermal gap; ES = semiophoric eurytele; G = ''gonads''; GC = gastric cavity; GlC = glandular cell, Ma = manubrium; P = periderm; SCa = subumbrellar cavity; Spt = septum; Te = tentacle; V = velum.

FIG. 198. *Limnomedusae. A-B, Armorhydridae,* Armorhydra janowiczi : *A, méduse ; B, section histologique longitudinale d'une méduse. C & E, Microhydrulidae,* Microhydrula pontica : *C, section histologique d'un polype ; E, section histologique d'une frustule ; D,* Rhaptapagis cantacuzenei*, section histologique d'un polype (A d'après Thiel, 1988 ; B d'après Lacassagne, 1968 ; C-E d'après Bouillon & Deroux, 1967). CE = eurytèle microbasique ; Cn = cnidocil ; Cnb = cnidoblaste ; DI = inclusion digestive ; Ect = ectoderme ; End = endoderme ; EndG = discontuinité endodermique ; ES = eurytèle semiophore ; G = ''gonades'' ; GC = cavité gastrique ; GlC = cellule glandulaire ; Ma = manubrium ; P = périderme ; SCa = cavité sous-ombrellaire ; Spt = septum ; Te = tentacule ; V = velum.*

KEY TO HYDROIDS

1. cnidocysts: microbasic euryteles .... *Microhydrula*
– cnidocysts: microbasic semiophoric euryteles .... *Rhaptapagis*

Genus ***MICROHYDRULA*** Valkanov, 1965

Figs 198C, E, 199

Hydroid: body rounded or elongated, terminal end either hemispherical or cauliflower-like in shape and armed with cnidocysts pending the species, ectoderm in a well defined unistratified layer, basal layer of periderm thin; frustules formed by a great number of small cells; cnidome: microbasic euryteles.

Microhydrula limopsicola Jarms & Tiemann, 1996
Microhydrula pontica Valkanov, 1965

Genus ***RHAPTAPAGIS*** Bouillon & Deroux, 1967

Fig. 198D

Hydroid: body irregular; ectoderm not very regularly organised; peridermal basal lamella thick; frustules formed by a reduced number of large cells; cnidome: microbasic semiophoric euryteles.

Rhaptapagis cantacuzenei Bouillon & Deroux, 1967

Family OLINDIIDAE Haeckel, 1879

Hydroid: usually solitary, seldom colonial; generally reduced, minute, either without tentacles or with one tentacle, or with a few tentacles in a single ring, sometimes with dactylozooids; no theca; active asexual reproduction by buds or frustules; usually with free medusae, exceptionally with free or fixed eumedusoids.

Medusa: with or without centripetal canals; internal ecto-endodermal statocysts; simple, unbranched radial canals; "gonads" on radial canals or exceptionally on manubrium (*Limnocnida*); no ocelli.

Recent references: Pagès *et al.* (1992); Bouillon (1999); Bouillon & Barnett (1999); Bouillon & Boero (2000).

FIG. 199. Limnomedusae, Microhydrulidae: *Microhydrula pontica* eating a nematode (after Bouillon & Deroux, 1967).

FIG. 199. *Limnomedusae, Microhydrulidae :* Microhydrula pontica *mangeant un nématode (d'après Bouillon & Deroux, 1967).*

KEY TO HYDROIDS

1. with tentacles 4
– without tentacles 2

2. enclosed in a long perisarcal tube, solitary, marine .... *Olindias*
– not enclosed in perisarc 3

3. fresh-water; solitary but often forming small colonies.......... *Craspedacusta* and *Limnocnida*, hydroids identical
– sea water; only primary polyps known, inconspicuous (almost 0.1 mm) atentaculate, gross morphology similar to those of *Craspedacusta* .... *Aglauropsis* and *Maeotias*

4. colonial, hydranth with one tentacle 5
– solitary, hydranth with more than one tentacle.......... 6

5. reticulate hydrorhiza; gonophores on hydrorhiza as fixed or free eumedusoids.......... *Monobrachium*
– creeping hydrorhiza not forming a network; gonophores on hydranths as free medusae .... *Eperetmus*

6. solitary, small, flat, discoidal; not well defined hypostomial region .... *Scolionema*
– Solitary, small, with a conspicuous conical hypostome.......... *Gonionemus* and *Vallentinia*

KEY TO MEDUSAE

1. statocysts in elongated vesicles enclosed in velum; “gonads” on radial canals .... *Craspedacusta*
– statocysts spherical, enclosed in mesoglea of umbrellar margin 2

2. centripetal canals.......... 3
– no centripetal canals 5

3. tentacles of one kind 4
– primary tentacles projecting above umbrellar margin, with terminal adhesive pads, secondary tentacles on umbrellar margin, without adhesive pads .... *Olindias*

4. tentacles on exumbrella at different height above bell margin; no adhesive pads.......... *Eperetmus*
– all tentacles on umbrellar margin, no adhesive pads .... *Maeotias*

5. tentacles in groups on bell margin .... *Gossea*
– tentacles not in groups 6

6. 6 radial canals .... *Nuarchus*
– 4 radial canals.......... 7

7. “gonads” on manubrium .... *Limnocnida*
– “gonads” on radial canals 8

8. all tentacles without adhesive pads .... *Aglauropsis*
– some or all tentacles with adhesive pads 9

9. one type of tentacle, with terminal adhesive pad 10
– two kinds of tentacles, with and without adhesive pads.......... 11

10. numerous statocysts .... *Gonionemus*
– not more than 16 statocysts .... *Scolionema*

11. adhesive pads terminal .... *Vallentinia*
– adhesive pads at some distance from outer end of tentacles .... *Cubaia*

Remarks: see also *incertae sedis*.

Genus *AGLAUROPSIS* F. Müller, 1865

Fig. 200A

Hydroid: only primary polyps known from rearing, without tentacles.
Medusa: 4 radial canals; no centripetal canals; numerous tentacles of one kind on bell margin, not arranged in groups, no adhesive pads; "gonads" on radial canals; numerous statocysts.
Recent reference: Pagès *et al.* (1991).

Aglauropsis aeora Mills, Rees & Hand, 1976
Aglauropsis agassizi F. Müller, 1865
Aglauropsis conanti Browne, 1902
Aglauropsis edwardsi Pagès, Bouillon & Gili, 1991
Aglauropsis jarli Kramp, 1955
Aglauropsis kawari Moreira & Yamashita, 1972
Aglauropsis vannuccii Thomas & Chapgar, 1975

Genus *CRASPEDACUSTA* Lankester, 1880

Figs 5G, 26K, 200B-F

Hydroid: fresh-water, 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 colony to substrate; medusa buds lateral, on the middle or lower part of body column, often becoming terminal by hydranth reduction; asexual reproduction by frustules, transversal division and resting stages (cysts).
Medusa: well developed marginal cnidocyst ring, no gastric peduncle; 4 simple radial canals; no centripetal canals; "gonads" only on radial canals, hanging, pouch-like; evenly distributed marginal tentacles all of one kind, no adhesion organs; closed ecto-endodermal statocysts in the velum and forming centripetal tubes.
Remarks: Several species of *Craspedacusta* have been described, mainly from China, and it is not unlikely that they represent nothing more than variations of a single species. The same remark can be applied to the species of *Limnocnida* from India.
Recent reference: Jankowski (2001).

Craspedacusta chuxiongensis He *et al.,* 2000
Craspedacusta iseanum (Oka & Hara, 1922)
Craspedacusta kuoi Shieh & Wang, 1959
Craspedacusta sichuanensis He & Kou, 1984
Craspedacusta sinensis Gaw & Kung, 1939
Craspedacusta sowerbyi Lankester, 1880
Craspedacusta vovasi Naumov & Stepanjants, 1971
Craspedacusta ziguinensis He & Xu, 1985a

Genus *CUBAIA* Mayer, 1894

Fig. 201A

Hydroid: unknown.
Medusa: 4 simple radial canals; no centripetal canals; 2 series of tentacles: one (20) issuing from exumbrella above bell margin, with terminal adhesive disks and about 8 cnidocyst rings, other series (50-60) without adhesive disks, with 25-30 cnidocyst rings arising from bell margin; "gonads" on radial canals; numerous statocysts.

Cubaia aphrodite Mayer, 1894

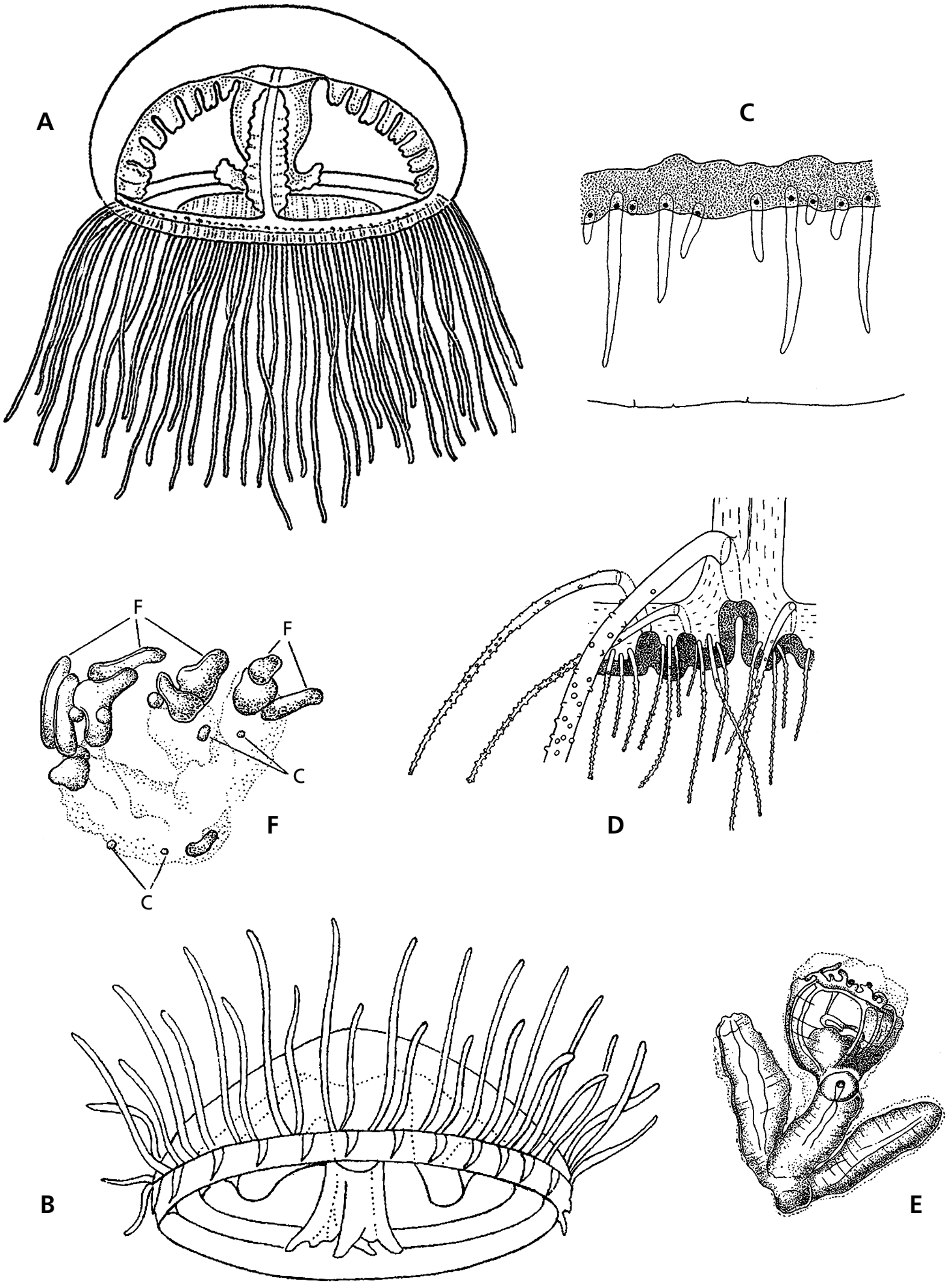


FIG. 200. Limnomedusae, Olindiidae. A, *Aglauropsis conanti*, adult medusa. B-F, *Craspedacusta sowerbyi*: B, adult medusa; C, portion of the velum with the centripetal tubes of the statocysts; D, portion of the umbrella margin showing the marginal cnidocyst ring and the endodermal tentacular roots; E, a polyp colony; F, a colony reducing itself in frustules and resting stages or cysts (A after Kramp, 1959b; B after Tardent, 1978; C-D after Russell, 1953; E-F after Damas, 1939). C = cyst; F = frustule.

FIG. 200. *Limnomedusae, Olindiidae. A,* Aglauropsis conanti*, méduse adulte. B-F,* Craspedacusta sowerbyi : *B, méduse adulte ; C, portion du velum avec les tubes centripètes des statocystes ; D, portion du bord exombrellaire montrant l'anneau marginal de cnidocystes et les racines endodermiques tentaculaires ; E, colonie de polypes ; F, colonie réduite à des frustules et à des stades de résistance ou cystes (A d'après Kramp, 1959 ; B d'après Tardent, 1978 ; C-D d'après Russell, 1953 ; E-F d'après Damas, 1939). C = cyste ; F = frustule.*

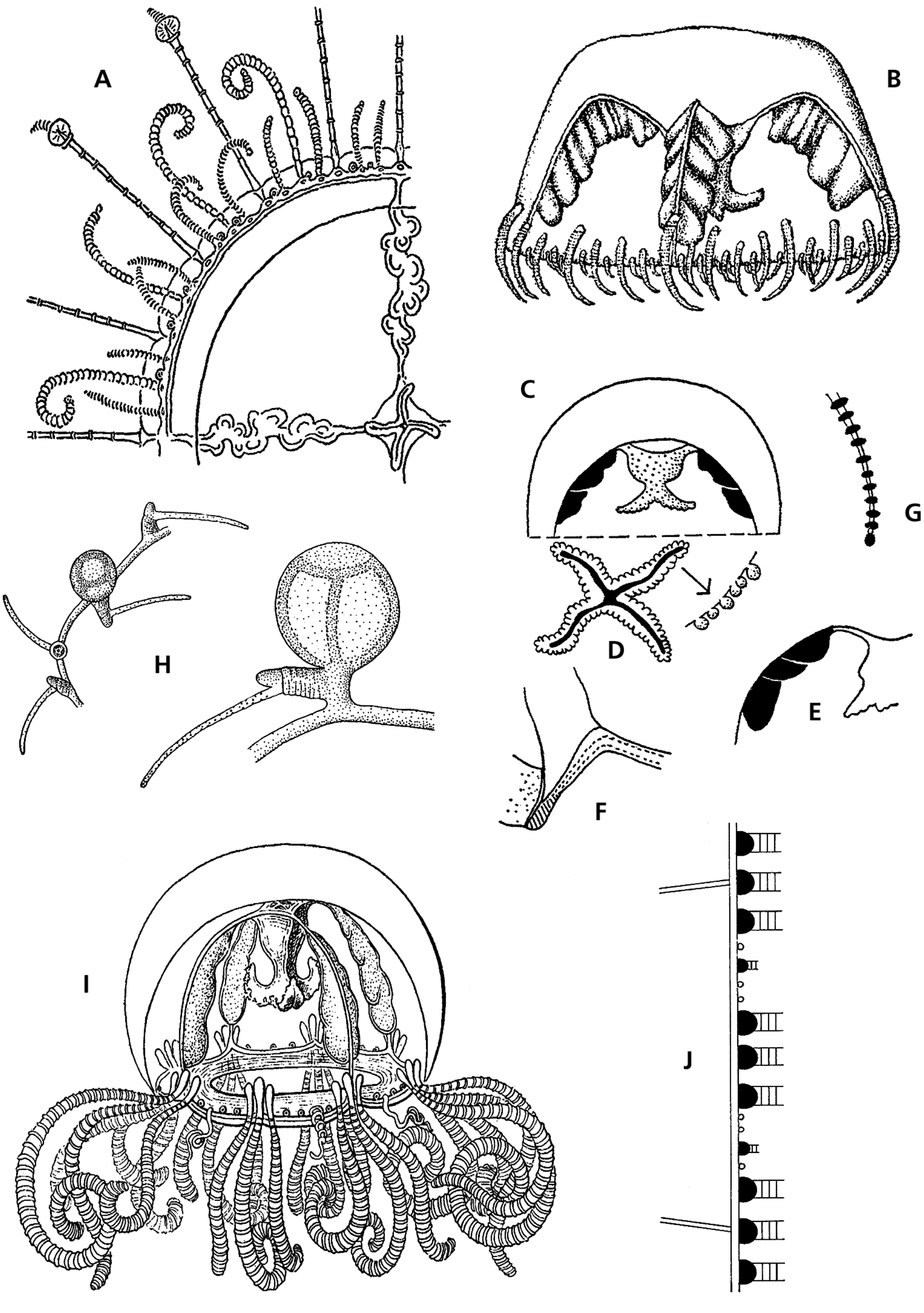


FIG. 201. Limnomedusae, Olindiidae. A, *Cubaia aphrodite*, quadrant of a medusa. B-H, *Eperetmus typicus*: B, adult medusa; C-G, details of medusa parts: C, umbrella; D, oral lips; E, gonad; F, tentacle base; G, tentacle; H, parts of polyp colonies with medusa buds. I-J *Gossea corynetes*, I, mature medusa; J, schematic view of a portion of the umbrella margin sowing the disposition of the two types of tentacles and of the statocysts (A & I after Mayer, 1910; B after Uchida, 1940; C-H after Nagao, 1969 & 1973; J after Bouillon, 1978a).

***FIG. 201.** Limnomedusae, Olindiidae. A,* Cubaia aphrodite, *quadrant d'une méduse. B-H,* Eperetmus typicus : *B, méduse adulte ; C-G, détails de parties de méduses : C, ombrelle ; D, lèvres orales ; E, ''gonade'' ; F, base tentaculaire ; G, tentacule ; H, fragments de colonies de polypes avec des bourgeons médusaires. I-J,* Gossea corynetes : *I, méduse mature ; J, vue schématique d'une portion du bord exombrellaire montrant la disposition des deux types de tentacules et des statocystes (A & I d'après Mayer, 1910 ; B d'après Uchida, 1940 ; C-H d'après Nagao, 1969 & 1973 ; J d'après Bouillon, 1978a).*

Genus ***EPERETMUS*** Bigelow, 1915

Fig. 201B-H

Hydroid: colony stolonal; small hydranths arising at intervals from creeping, rather thick stolon, never forming a network, hydranths with a single elongated filiform tentacle below hypostome, stem below tentacle covered by thin membranous sheath often wrinkled by hydranth contraction, usually encrusted by mud particles; gonophores as medusa buds borne singly at the base of hydroid on a short peduncle.
Medusa: 4 radial canals and several blind centripetal canals, cnidocyst knobs on oral lips; numerous tentacles of one kind, not in-groups, at different heights above umbrella margin, with cnidocyst rings; "gonads" on radial canals; numerous statocysts.

Eperetmus typus Bigelow, 1915

Genus ***GONIONEMUS*** A. Agassiz, 1862

Fig. 202A-F

Hydroid: small, solitary, conical, devoid of hydrorhiza, with conspicuous conical hypostome and a circlet of 4-6 long tentacles; medusa buds, frustules, cysts formed by intense asexual budding.
Medusa: peduncle slight or absent; 4 simple radial canals; no centripetal canals; folded "gonads" on radial canals only; evenly distributed marginal tentacles all of one kind, with adhesion organs; numerous statocysts enclosed in mesoglea.

Gonionemus chekiangensis Kao, Li, Chang & Li, 1958
Gonionemus depressus Goto, 1903
Gonionemus hamatus Kramp, 1965b
Gonionemus hornelli Browne, 1905a
Gonionemus vertens A. Agassiz, 1862 [syn. *G. murbachii* Mayer, 1901; *G. agassizii* Murbach & Shearer, 1902]
Gonionemus vindobonensis Joseph, 1918 [juvenile, indeterminate]

Genus ***GOSSEA*** L. Agassiz, 1862

Figs 26, 201I-J

Hydroid: unknown.
Medusa: 4 simple radial canals; with or without gastric peduncle; no centripetal canals; "gonads", folded, ribbon-like on radial canals; one kind of tentacles, some arranged in groups; no adhesive pads; statocysts enclosed in exumbrellar mesoglea.

Gossea brachymera Bigelow, 1909
Gossea corynetes (Gosse, 1853)
Gossea faureae Picard, 1952
Gossea indica Bouillon, 1978a

Genus ***LIMNOCNIDA*** Günther, 1893

Figs 31, 32, 39, 53, 54, 57C-D, 203A-B

Hydroid: fresh-water, similar to *Craspedacusta*.
Medusa: well developed marginal cnidocyst ring; manubrium circular, flat; mouth large, simple, circular; 4 simple radial canals; "gonads" on manubrium only, enclosed marginal statocysts embedded in mesoglea between circular canal and umbrella margin.
Remarks: see under *Craspedacusta*.
Recent reference: Jankowski (2001).

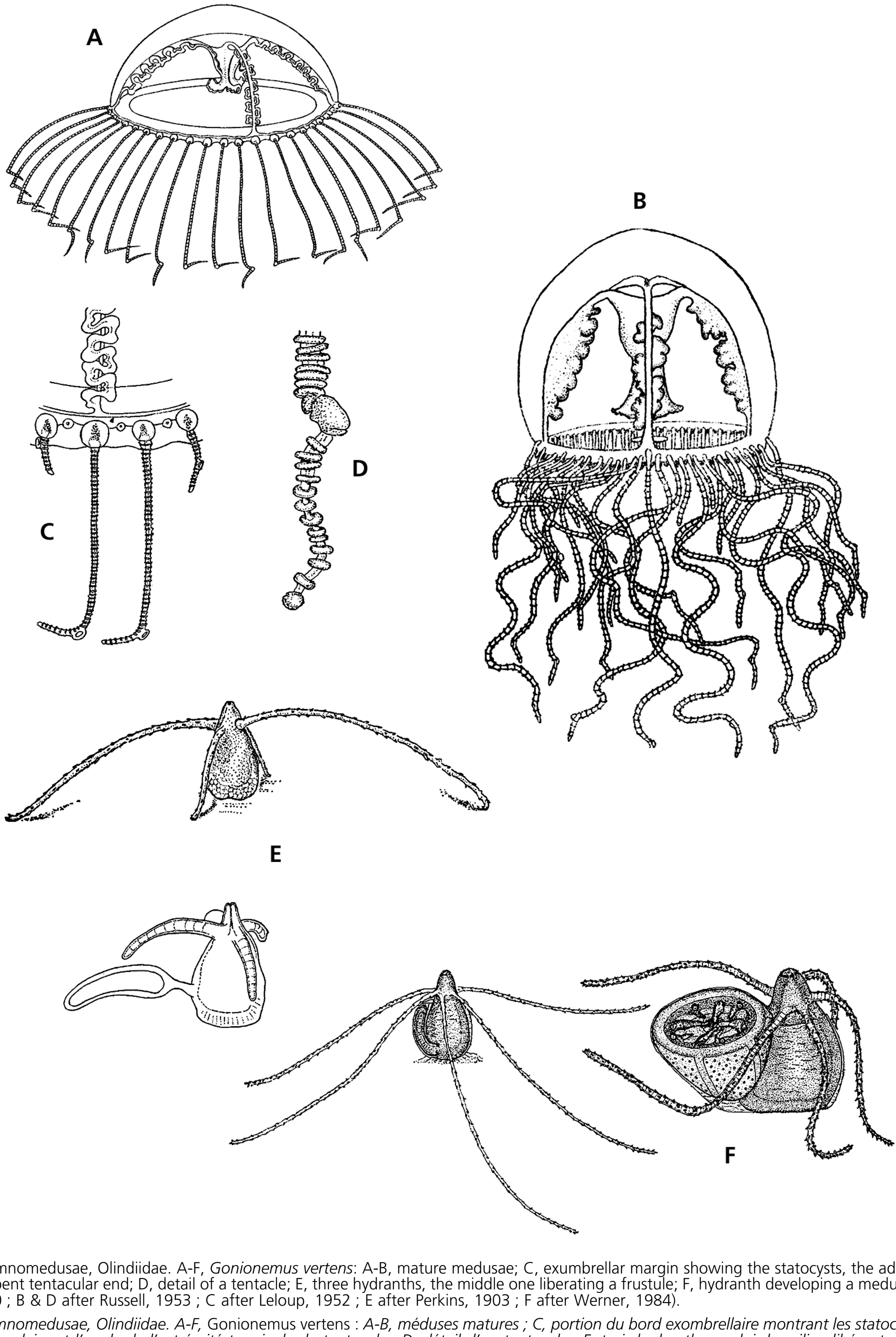


FIG. 202. Limnomedusae, Olindiidae. A-F, *Gonionemus vertens*: A-B, mature medusae; C, exumbrellar margin showing the statocysts, the adhesive pad and the sharply bent tentacular end; D, detail of a tentacle; E, three hydranths, the middle one liberating a frustule; F, hydranth developing a medusa bud (A after Mayer, 1910 ; B & D after Russell, 1953 ; C after Leloup, 1952 ; E after Perkins, 1903 ; F after Werner, 1984).

***FIG. 202.** Limnomedusae, Olindiidae. A-F,* Gonionemus vertens : *A-B, méduses matures ; C, portion du bord exombrellaire montrant les statocystes, le disque adhésif tentaculaire et l'angle de l'extrémité terminale du tentacule ; D, détail d'un tentacule ; E, trois hydranthes, celui du milieu libérant une frustule ; F, hydranthe développant un bourgeon médusaire (A d'après Mayer, 1910 ; B & D d'après Russell, 1953 ; C d'après Leloup, 1952 ; E d'après Perkins, 1903 ; F d'après Werner, 1984).*

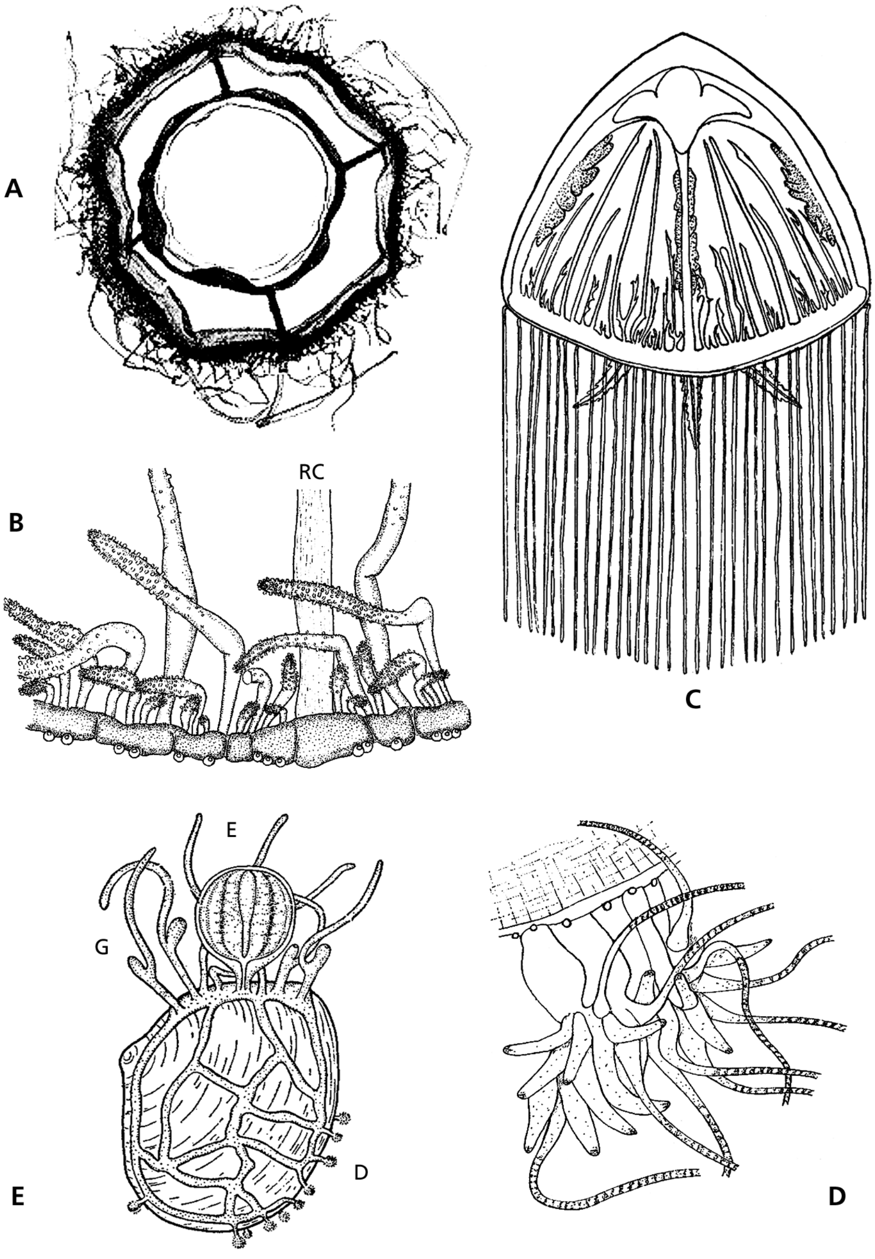


FIG. 203. Limnomedusae, Olindiidae. A-B, *Limnocnida*: A, *Limnocnida congoensis*, adult medusa ; B, *Limnocnida tanganyicae*, part of umbrella margin showing the different sizes of marginal tentacles, the statocysts and the folded cnidocyst ring. C-D, *Maeotias marginata* (= *inexpectata*): C, whole medusa; D, portion of the umbrella margin showing the base of the oldest tentacles of which the tips have been shed. E, *Monobrachium parasiticum*, view of a colony developing a medusa bud (A after Bouillon, 1957; B after Kramp, 1954; C after Borcea, 1928; D after Denayer, 1973; E after Hand, 1957). D = dactylozooid; E = eumedusoid; G = gastrozooid; RC = radial canal.

FIG. 203. *Limnomedusae, Olindiidae. A-B,* Limnocnida : *A,* Limnocnida congoensis*, méduse adulte ; B,* Limnocnida tanganyicae*, partie du bord exombrellaire montrant la différence de taille existant entre les tentacules marginaux, les statocystes et l'anneau urticant plissé. C-D,* Maeotias marginata *(=* inexpectata*) : C, méduse adulte ; D, portion du bord exombrellaire montrant la base des tentacules dont les extémités des plus âgés se sont autotomisés. E,* Monobrachium parasiticum*, colonies développant un bourgeon médusaire (A d'après Bouillon, 1957 ; B d'après Kramp, 1954 ; C d'après Borcea, 1928 ; D d'après Denayer, 1973 ; E d'après Hand, 1957). D = dactylozoïde ; E = eumédusoïde ; G = gastérozoïde ; RC = canal radiaire.*

Limnocnida biharensis Firoz-Ahmad, Sen, Mishra & Bharti, 1986 [probably a syn. of *L. indica*]
Limnocnida congoensis Bouillon, 1958
Limnocnida cymodocea Jordaan, 1934 [probably a syn. of *L. tanganyicae*]
Limnocnida indica Annandale, 1912
Limnocnida nepalensis Dumont, 1976 [probably a syn. of *L. indica*]
Limnocnida rhodesiae Boulenger, 1912 [probably a syn. of *L. tanganyicae*]
Limnocnida tanganyicae Günther, 1893

Genus ***MAEOTIAS*** Ostroumoff, 1896

Fig. 203C-D

Hydroid: only primary polyps known, inconspicuous (almost 0.1 mm) atentaculate, gross morphology similar to that of *Craspedacusta* (Rees & Gershwin 2000)
Medusa: centripetal canals; numerous tentacles with tightly packed cnidocyst rings, all on umbrellar margin and without adhesive pads; "gonads" on radial canals.
Recent references: Mills & Sommer (1995); Mills (2001); Mills & Rees (2000).

Maeotias marginata (Modeer, 1791) [syn. *M. inexpectata* Ostroumov, 1896]

Genus ***MONOBRACHIUM*** Mereshkovsky, 1877

Figs 5F, 203E

Hydroid: colony creeping, living on bivalve shells; hydrorhiza reticulated or incrusting or both reticulated and incrusting; hydranth sessile, claviform, only one oral filiform tentacle; hypostome large, club-shaped; sometimes dactylozooids in form of peduncled cnidocyst knobs; gonophores peduncled on hydrorhiza giving fixed or free eumedusoids, sexual cells borne in hydrorhizal coenosarc and migrating in eumedusoid radial canals after eumedusoid formation; with or without statocysts.
Recent references: Ramil (1988); Besteiro *et al.* (1991); Schuchert (2001a).

Monobrachium antarcticum Robins, 1972
Monobrachium drachi Marche-Marchad, 1963
Monobrachium parasiticum Mereshkovsky, 1877

Genus ***NUARCHUS*** Bigelow, 1912

Hydroid: unknown.
Medusa: 6 radial canals, no centripetal canals, mouth simple, circular; "gonads" leaf-like, on radial canals; statocysts at base of tentacles.

Nuarchus halius Bigelow, 1912

Genus ***OLINDIAS*** Müller, 1861

Fig. 204A-D

Hydroid: not yet found in field; Weill (1936) described from laboratory observations a small solitary hydranth without tentacles enclosed in a cylindrical or irregularly curved hydrotheca covering more than half its length, and much longer than the polyp itself; mouth distal surrounded by large cnidocysts.

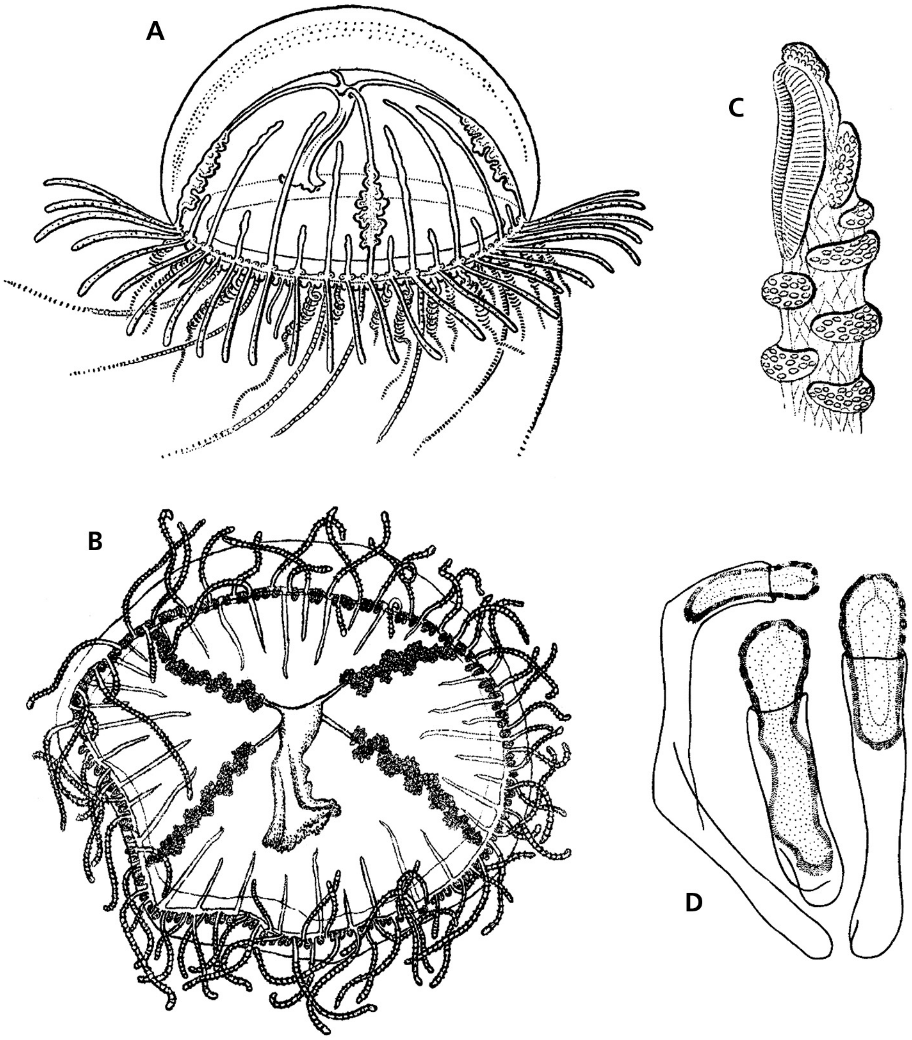


FIG. 204. Limnomedusae, Olindiidae. A-D, *Olindias phosphorica*: A-B, adult medusae; C, adhesive pad on the aboral side of a primary tentacles; D, some hydroids (A after Kramp, 1959b; B after Trégouboff, 1957: pl. 70, fig. 3; C after Mayer, 1910; D after Weill, 1936).

FIG. 204. *Limnomedusae, Olindiidae. A-D,* Olindias phosphorica *: A-B, méduses adultes ; C, coussinet adhésif aboral d'un tentacule primaire ; D, divers hydroïdes (A d'après Kramp, 1959b ; B d'après Trégouboff, 1957 : pl. 70, fig. 3 ; C d'après Mayer, 1910 ; D d'après Weill, 1936).*

Medusa: 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, no adhesive pads, cnidocysts in rings; "gonads" with papilliform processes, on radial canals; numerous marginal clubs which may transform into tentacles, statocysts usually in pairs at base of primary tentacles.

Olindias formosa (Goto, 1903)
Olindias malayensis Maas, 1905
Olindias muelleri Graeffe, 1884
Olindias phosphorica (Delle Chiaje, 1841)
Olindias sambaquiensis F. Müller, 1861
Olindias singularis Browne, 1905b
Olindias tenuis (Fewkes, 1882b)

Genus ***SCOLIONEMA*** Kishinouye, 1910

Fig. 205A-C

Hydroid: solitary, small, flat, discoidal; with not well defined hypostomial region, up to 5 tentacles; varied and intensive lateral asexual budding: medusa buds, frustules, cysts.
Medusa: without or with slight peduncle; 4 simple radial canals; no centripetal canals; folded "gonads" extending along 1/3 to 1/2 of distal part of radial canals only; evenly distributed marginal tentacles all of one kind, with rudimentary organs of adhesion; never more than 16 statocysts enclosed in mesoglea.

Scolionema suvaense (A. Agassiz & Mayer, 1899) [syn. *S. gemmifera* Kishinouye, 1910]

Genus ***VALLENTINIA*** Browne, 1902

Fig. 205D-E

Hydroid: solitary, small, conical, with one apical ring of tentacles, asexual reproduction by frustules.
Medusa: 4 radial canals, no centripetal canals; 4 to 8 hollow tentacles with terminal adhesive pads, and numerous tentacles without adhesive pads but with numerous rings of cnidocysts; "gonads" on radial canals; 16 or more statocysts.

Vallentinia adherens Hyman, 1947
Vallentinia falklandica Browne, 1902
Vallentinia gabriellae Vannucci-Mendes, 1948

Olindiidae *incertae sedis*; with eumedusoids; or only known by juvenile medusae; or insufficiently described:

Genus ***ANTHOHYDRA*** Salvini-Plawen & Rao 1973

Hydroid: mesopsammic, with filiform tentacles and adhesive disc, treated here as *incertae sedis,* considered by some authors as an eirenid polyp of the genus *Eugymnanthea* (*E. psammobionta*)?

Anthohydra psammobionta Salvini-Plawen & Rao, 1973

Genus ***ASTROHYDRA*** Hashimoto, 1981

Fig. 206A-B

Hydroid: solitary, barrel-shaped, with 10-30 very fine, filiform tentacles, irregularly strewn over hydranth; frustules and medusa buds on hydranth body.
Medusa: only juvenile known; up to 29 hollow marginal tentacles without marginal bulbs, each bearing many unicellular long and straight bristle-like expansions with one to three cnidocysts on apices; manubrium quadrangular; mouth with 4 small lips; radial canals usually 4; up to 15 spherical statocysts, no "gonads" formed (Hashimoto 1985).
Recent reference: Jankowski (2001).

Astrohydra japonica Hashimoto, 1981

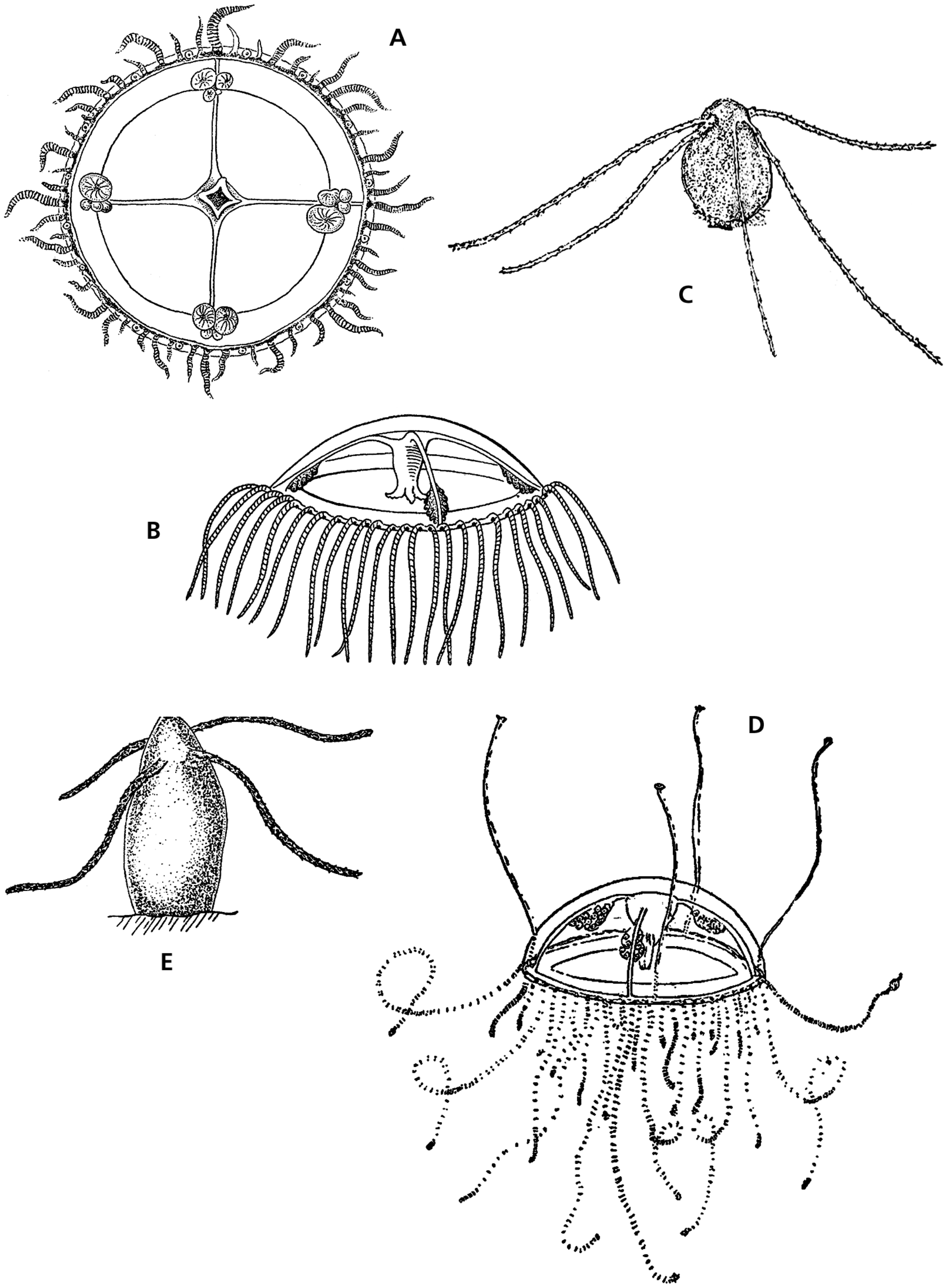


FIG. 205. Limnomedusae, Olindiidae. A-C, *Scolionema suvaense*: A-B, adult medusae; C, polyp. D-E, *Vallentina gabriellae*: D, medusa; E, polyp (A & D after Kramp, 1959b; B after Mayer, 1910; C reconstruction after Goy, 1973; E after Mendes, 1948).

FIG. 205. *Limnomedusae, Olindiidae. A-C,* Scolionema suvaense *: A-B, méduses adultes ; C, polype. D-E,* Vallentina gabriellae *: D, méduse adulte ; E, polype (A & D d'après Kramp, 1959b ; B d'après Mayer, 1910 ; C reconstruction d'après Goy, 1973 ; E d'après Mendes, 1948).*

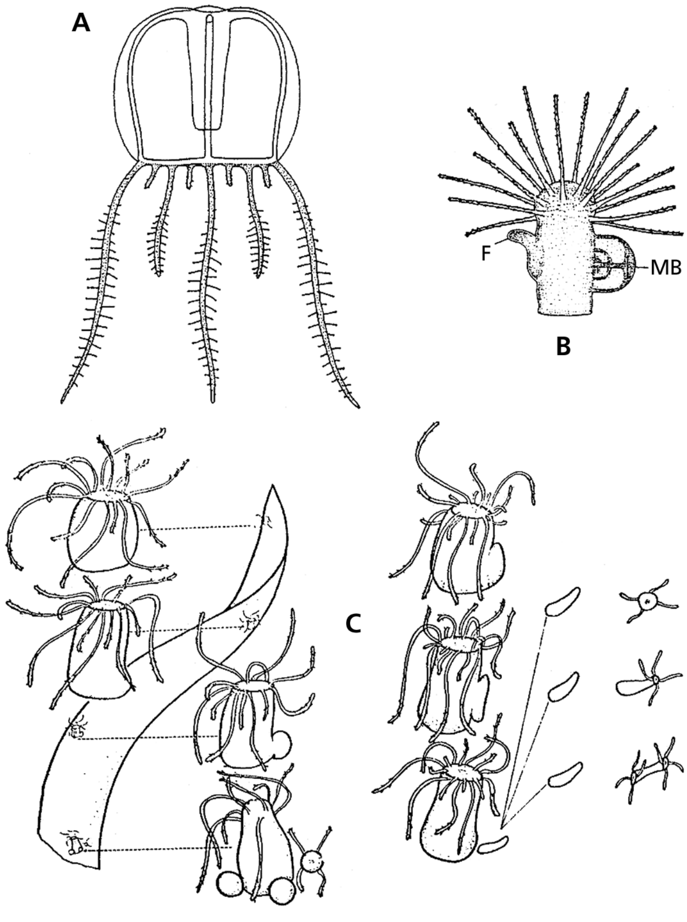


FIG. 206. Limnomedusae, Incertae sedis. A-B, *Astrohydra japonica*: A, young medusa; B, hydranth with a medusa bud and a frustule; C, *Calpasoma dactyloptera*, hydranths showing different stages of asexual reproduction (A-B after Hashimoto, 1985; C after Matthews, 1966). F = frustule; MB = medusa bud.

FIG. 206. *Limnomedusae, Incertae sedis. A-B,* Astrohydra japonica : *A, jeune méduse ; B, hydranthe avec un bourgeon médusaire et une frustule ; C,* Calpasoma dactyloptera*, hydranthes montrant différents stades de reproduction asexuée (A-B d'après Hashimoto, 1985 ; C d'après Matthews, 1966). F = frustule ; MB = bourgeon médusaire.*

Genus ***CALPASOMA*** Fuhrmann, 1939

Fig. 206C

Hydroid: freshwater, of small size (100-600 μ); solitary but sometimes bi- or tripolar; 2 irregular whorls of tentacles at oral end, each tentacle consisting of a process of a single ectodermal cell (tentaculocyte) scattered with a few cnidocysts; hydranth reproducing only asexually, forming new polyps of their own type or frustules, never producing medusae; erroneously considered as a tentaculate form of *Craspedacusta* but no inter-conversion has been observed between the two forms, presently considered or as two distinct species or at least as two stable forms of the same species.
Recent references: Rahat & Campbell (1974a; b); Jankowski (2001).

Calpasoma dactyloptera Fuhrmann, 1939

Genus ***KERALICA*** Khatri, 1984

Hydroid: unknown.
Medusa: 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 (?).

Keralica idukkensis Khatri, 1984

Genus ***MANSARIELLA*** Malhotra, Duda & Jyoti, 1976

Hydroid: unknown.
Medusa: about 160 marginal tentacles; one statocyst per tentacle; manubrium short, mouth circular; "gonads" unknown; with medusa buds.
Recent reference: Jankowski (2001).

Mansariella lacustris Malhotra, Duda & Jyoti, 1976

Subclass SIPHONOPHORAE Eschscholtz, 1829

Pelagic, pleustonic or epibenthic Hydrozoa, forming highly polymorphic modular colonies of polypoid and medusoid zooids attached to a stem or stolon supported by a floating and/or swimming system.
Polypoid zooids of several sorts: pneumatophore, gastrozooids, dactylozooids, and bracts. All of them usually associated with the gonophores in repetitive groups, or cormidia, along the stolon. All polypoid structures without oral tentacles. The part of the stem below the floating system, bearing the cormidia, is the siphosome, usually representing most of animal's length. Floating system composed by pneumatophores and/or nectophores (swimming bells) together forming the nectosome. The complete and fully developed animal is referred as the polygastric stage. The Siphonophorae have a global cnidome of nine cnidocyst types depending on the suborders: acrophores, anacrophores, desmonemes, stenoteles, homotrichous anisorhizae, atrichous isorhizae, microbasic mastigophores and birhopaloids, 4 of them being exclusive to the group but not common to all species: acrophores, anacrophores, homotrichous isorhizae and birhopaloids.
On the basis of the presence or absence of either an apical pneumatophore, or of nectophores grouped in a nectosome three orders of Siphonophorae may be distinguished: the Cystonectae possessing only a pneumatophore; the Physonectae possessing both a pneumatophore and a nectosome; the Calycophorae with only a nectosome.
Recent general references: Mackie & Boag (1963); Kirkpatrick & Pugh (1984); Purcell (1984); Mackie *et al.* (1987); Carré & Carré (1995); Pugh (1999a).

Order CYSTONECTAE Haeckel, 1887

Siphonophores with a relatively large pneumatophore and without nectosome; pneumatophore with apical pore; cormidia with gastrozooid, tentacle and gonodendron, without bracts; gonodendron with gonopalpons, gonophores and asexual swimming bells.

KEY TO FAMILIES

1. pneumatophore horizontal .... Physaliidae
– pneumatophore oval rounded .... Rhizophysidae

Family PHYSALIIDAE Brandt, 1835

This family is monotypic for *Physalia physalis*, the Portuguese Man O'War.

Genus ***PHYSALIA*** Lamarck, 1801

Fig. 207A-C

Physalids with huge, asymmetric pneumatophore, purplish blue in colour, up to 30 cm in length; top of the pneumatophore formed by an erectile "sail" running diagonally; cormidia attached to one side of the float, tentacles can stretch down many metres.

Recent references: Totton (1960); Shannon & Chapman (1983); Pagès & Gili (1992).

Physalia physalis (Linnaeus, 1758)

Family RHIZOPHYSIDAE Brandt, 1835

With oval-rounded pneumatophore with hypocystic villi at its base.

Genus ***BATHYPHYSA*** Studer, 1878

Fig. 207D-F

Rhizophysids with wing-like processes in young gastrozooids.

Recent references: Biggs & Harbison (1976); Pagès *in press.*

Bathyphysa conifera (Studer, 1878b)
Bathyphysa japonica Kawamura, 1943 [invalid species, see Pagès 2002]
Bathyphysa sibogae Lens & van Riemsdijk, 1908

Genus ***RHIZOPHYSA*** Péron & Lesueur, 1807

Figs 37B, 38G

Synonym: *Epibulia* Haeckel, 1888.
Rhizophysids with no wing-like processes in young gastrozooids.

Recent references: Purcell (1981a); Pagès & Gili (1992); Mills *et al.* (1996).

Rhizophysa eysenhardti Gegenbaur, 1859
Rhizophysa filiformis (Forskål, 1775)

Order PHYSONECTAE Haeckel, 1888

Siphonophorae with an apical pneumatophore and, beneath it, a series of nectophores, except in the Athorybiidae which lack nectophores or with a reduced nectophore. Nectophores arranged in two opposite rows or circular chains forming the nectosomal region around the stem. Most of the Physonects present two budding zones, one under the pneumatophore giving nectophores and the other at the basal end of the nectosome, giving the cormidia that form the siphosome. Cormidia with bracts, with dactylozooids. Without asexual medusoids on the siphosome. When known with siphonula larvae.

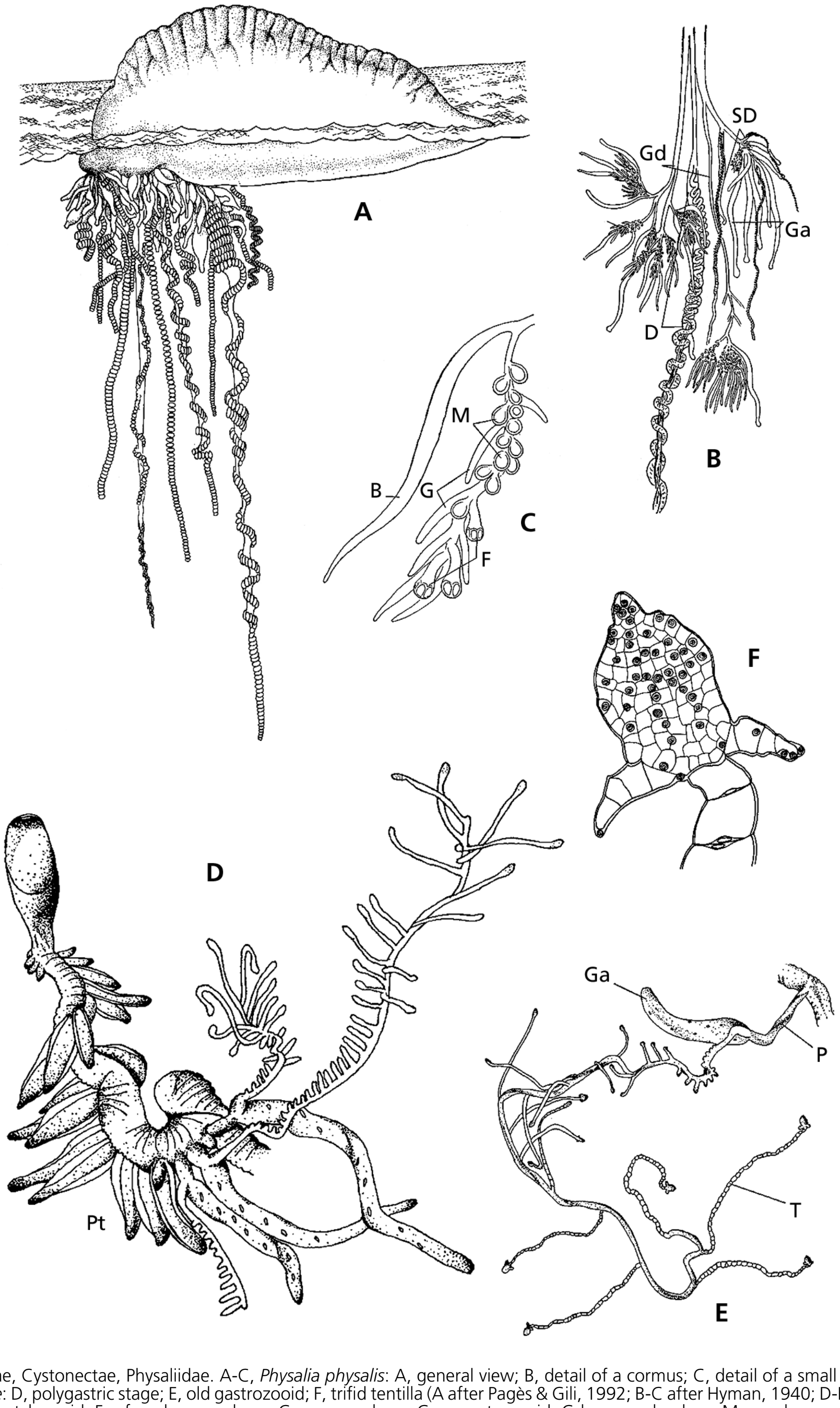


FIG. 207. Siphonophorae, Cystonectae, Physaliidae. A-C, *Physalia physalis*: A, general view; B, detail of a cormus; C, detail of a small part of a gonodendron. D-F, *Bathyphysa sibogae*: D, polygastric stage; E, old gastrozooid; F, trifid tentilla (A after Pagès & Gili, 1992; B-C after Hyman, 1940; D-F after Biggs & Harbison, 1976). B = bract; D = dactylozooid; F = female gonophore; G = gonopalpon; Ga = gastrozooid, Gd = gonodendron; M = male gonophore; P = palpon; Pt = ptera; SD = small dactylozooid; T = tentilla.

FIG. 207. *Siphonophorae, Cystonectae, Physaliidae. A-C,* Physalia physalis *: A, vue générale ; B, détail d'un cormus ; C, détail d'un fragment de gonodendron. D-F,* Bathyphysa sibogae *: D, stade polygastrique ; E, vieux gastérozoïde ; F, tentille trifide (A d'après Pagès & Gili, 1992 ; B-C d'après Hyman, 1940 ; D-F d'après Biggs & Harbison, 1976). B = bractée ; D = dactylozoïde ; F = gonophore femelle ; G = gonopalpon ; Ga = gastérozoïde ; Gd = gonodendron ; M = gonophore mâle ; P = palpon ; Pt = ptera ; SD = petit dactylozoïde ; T = tentille.*

KEY TO FAMILIES
(mostly after Pugh 1999a)

1. nectophores present 2
– nectophores absent 7

2. nectophores deeply hollowed axially and with tentacles between them; small delicate bracts. . . . . Apolemiidae
– nectophores not hollowed axially, nectosomal tentacles absent 3

3. nectosome and siphosome elongate, with a narrow stem 4
– nectosome and/or siphosome contracted or reduced 7

4. nectophores bilaterally symmetrical, arranged biserially 5
– nectophores dorso-ventrally flattened, usually asymmetric in shape, arranged in spiral . . Forskaliidae

5. nectophores with straight dorsal radial canal 6
– nectophores with sinuous dorsal radial canal . . . . Pyrostephidae

6. tentilla uncoiled; cnidoband hypertrophied; no cnidocyst on terminal process . . . . Erennidae
– tentilla coiled; cnidoband normal . . . . Agalmatidae

7. Nectosome reduced or absent; siphosome reduced to solid body or corm . . . . Athorybiidae
– nectosome normal 8

8. nectosome elongated; siphosome shortened into laterally expanded spiral sac bearing enlarged palpons; bracts absent. . . . . Physophoridae
– nectosome and siphosome contracted to form a solid corm; with a pneumatophore and an aurophore . . . . Rhodaliidae

Family AGALMATIDAE Brandt, 1835

Physonect siphonophores with a biserial arrangement of nectophores in the nectosome and a long usually contractile siphosome. For many agalmatids four type of cnidocysts are present on the tentillum: homotrichous anisorhizae; either microbasic mastigophores or stenoteles; desmonemes and acrophores.
Remarks: This is rather a catch-all family.

Genus ***AGALMA*** Eschscholtz, 1825

Figs 36A-C, 38A-B

Agalmatids with tricornuate tentilla consisting of a central swelling and two contractile lateral filaments.
Recent references: Pagès & Gili (1992); Mills *et al.* (1996).

Agalma clausi (Bedot, 1888)
Agalma elegans (Sars, 1846)
Agalma haeckeli Bigelow, 1911a [doubtful status]
Agalma okeni Eschscholtz, 1825

Genus ***CORDAGALMA*** Totton, 1932

Fig. 208A-B

Agalmatids with unicornuate tentilla; with heart-shaped nectophores devoid of lateral or vertical lateral ridges.
Recent references: Carré (1968b); Pagès & Gili (1992); Margulis (1993); Mills *et al.* (1996).

Cordagalma cordiformis Totton, 1932
Cordagalma tottoni Margulis, 1993

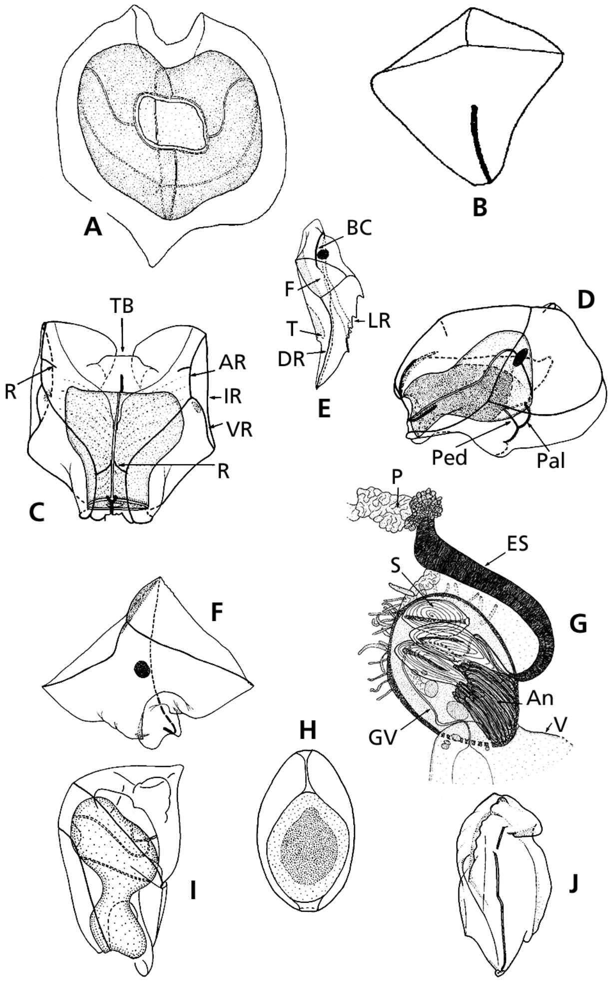


FIG. 208. Siphonophorae, Physonectae, Agalmatidae. A-B, *Cordalgama*, *Cordalgama cordiformis*: A, nectophore (ostial view); B, bract. C-H, *Frillagalma vityazi*: C-D, upper and lateral view of a mature nectophore; E, ventral bract (dorsal view); F, right-hand side of lateral bract; G, detail of the proximal region of a tentillum showing the folded elastic strand and the cnidocyst capsule; H, female gonophore. I-J, *Halistemma rubrum*: I, nectophore, lateral view; J, bract (A after Pagès & Gili, 1992; B after Pugh, 1999a; C-H after Pugh, 1998; I-J after Kirkpatrick & Pugh, 1984). An = anisorhiza; AR = apico-lateral ridge; BC = bracteal canal; DR = dorsal ridge; ES = elastic strand; F = dorsal facet; GV = gastro-vascular canal; IR = infra-lateral ridge; LR = longitudinal ridge; P = pedicel; Pal = pallial canal; Ped = pedicular canal; R = ridgelet; S = stenoteles; T = tooth; TB = thrust block; V = vesicle; VR = vertical lateral ridge.

***FIG. 208.** Siphonophorae, Physonectae, Agalmatidae. A-B,* Cordalgama, Cordalgama cordiformis *: A, nectophore (vue ostiale) ; B, bractée. C-H,* Frillagalma vityazi *: C-D, vues dorsale et latérale d'un nectophore mature ; E, bractée ventrale (vue dorsale) ; F, bractée latérale (vue de droite) ; G, détail de la région proximale d'un tentille montrant le toron élastique plissé et ainsi que la capsule du cnidocyste ; H, gonophore femelle. I-J,* Halistemma rubrum *: I, nectophore, vue latérale ; J, bractée (A d'après Pagès & Gili, 1992 ; B d'après Pugh, 1999a ; C-H d'après Pugh, 1998 ; I-J d'après Kirkpatrick & Pugh, 1984). An = anisorhize ; AR = crête apico-latérale ; BC = canal bractéal ; DR = crête dorsale ; ES = toron élastique ; F = facette dorsale ; GV = canal gastro-vasculaire ; IR = crête infra-latérale ; LR = crête longitudinale ; P = pédicelle ; Pal = canal pallial ; Ped = canal pédiculaire ; R = petite crête ; S = stenotèles ; T = dents ; TB = échancrure entre les deux lobes supérieurs du nectophore ; V = vésicule ; VR = crête verticale latérale.*

Genus ***FRILLAGALMA*** Daniel, 1966

Fig. 208C-H

Agalmatids with rigid stem, with nectophores arranged biserially on nectophore, nectophores with pairs of lateral and vertical ridges

Recent reference: Pugh (1998).

Frillagalma vityazi Daniel, 1966

Genus ***HALISTEMMA*** Huxley, 1859

Figs 208I-J, 209A-B

Agalmatids whose tentilla have a single terminal filament (unicornuate) and only a vestigial involucrum. Characteristic sigmoid courses for radial canals on the nectosac of the nectophore that begins with a downward sweep.

Recent references: Pugh & Youngbluth (1988); Pagès & Gili (1992).

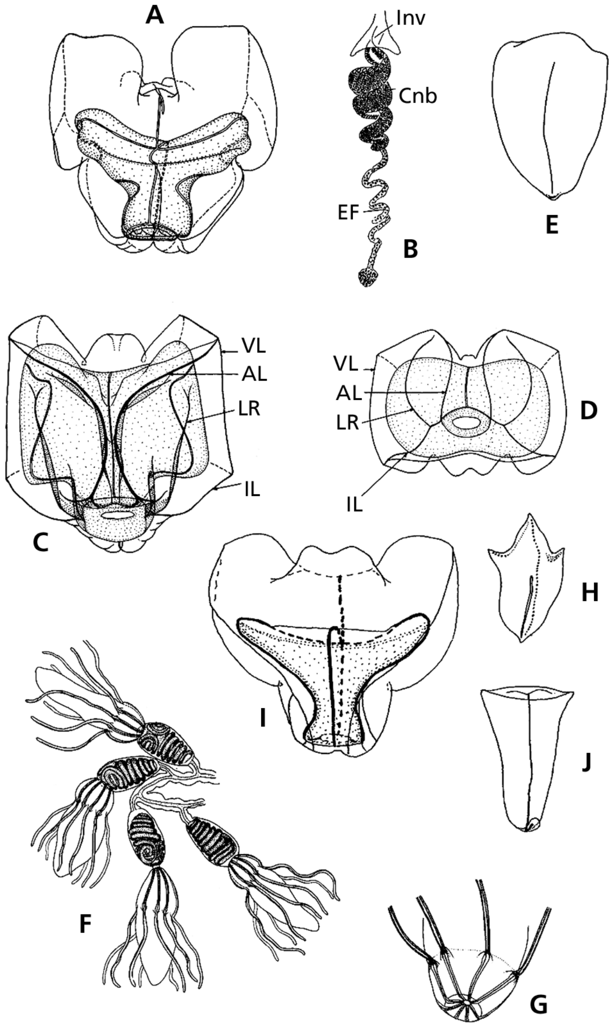


FIG. 209. Siphonophorae, Physonectae, Agalmatidae. A-B, *Halistemma rubrum*: A, nectophore (seen from below); B, tentillium. C-H, *Lychnagalma*: C-G, *Lychnagalma utricularia*: C, nectophore (upper dorsal view); D, nectophore (ostial view); E, bract; F, general view of four tentilla, note the coiled cnidoband enclosed within the involucrum and the terminal vesicle; G, detail of the base of a detached terminal vesicle showing the octoradial filaments; H, *Lychnagalma vesicularia*, bract. I-J, *Marrus antarcticus*: I, upper view of a nectophore; J, bract (A after Kirkpatrick & Pugh, 1984; B after Hyman, 1940; C-H after Pugh & Harbison, 1986; I-J after Pugh, 1999). AL = apico-lateral ridge; Cnb = cnidoband; EF = end of the tentillium filament; IL = infra-lateral ridge; Inv = involucrum; LR = lateral ridge; VL = vertical lateral ridge.

FIG. 209. *Siphonophorae, Physonectae, Agalmatidae. A-B,* Halistemma rubrum : *A, nectophore (vue ventrale) ; B, tentille. C-H,* Lychnagalma : *C-G,* Lychnagalma utricularia : *C, nectophore (vue dorsale) ; D, nectophore (vue ostiale) ; E, bractée ; F, vue générale de quatre tentilles, notez la cnidobande spiralée incluse dans l'involucre et la vésicule terminale ; G, détail de la base détachée d'une vésicule terminale montrant les filaments octoradiares ; H,* Lychnagalma vesicularia*, bractée. I-J,* Marrus antarcticus : *I, vue apicale d'un nectophore ; J, bractée (A d'après Kirkpatrick & Pugh, 1984 ; B d'après Hyman, 1940 ; C-H d'après Pugh & Harbison, 1986 ; I-J d'après Pugh, 1999). AL = crête apico-latérale ; Cnb = cnidobande ; EF = extrémité du filament d'un tentillille ; IL = crête infra-latérale ; Inv = involucre ; LR = crête latérale ; VL = crête verticale-latérale.*

Halistemma amphytridis (Lesueur & Petit, 1807)
Halistemma cupulifera Lens & Van Riemsdijk, 1908
Halistemma rubrum (Vogt, 1852)
Halistemma striata Totton, 1965
Halistemma transliratum Pugh & Youngbluth, 1988

Genus ***LYNCHNAGALMA*** Haeckel, 1888

Fig. 209C-H

Agalmatids whose nectophores have a prominent pair of apico-lateral ridges on the dorsal surface that divide close to the base, with the inner pair of branches running directly to the ostium while the outer pair curve out laterally. Large tentilla composed by involucrum and terminal vesicle; involucrum completely enclosing a cnidoband with apical and distal coils arranged perpendicularly; terminal vesicle with octaradial filaments attached in the apical part and free for most of its length.
Recent references: Pugh & Harbison (1986); Mills *et al.* (1996).

Lynchnagalma utricularia (Claus, 1879)

Genus ***MARRUS*** Totton, 1954

Fig. 209I-J

Agalmatids with nectophores truncated apically, with nectosacs with straight, unlooped radial canals; with unicornuate tentilla.

Recent reference: Andersen (1981).

Marrus antarcticus Totton, 1954
Marrus orthocanna (Kramp, 1942)
Marrus orthocannoides Totton, 1954

Genus ***MOSERIA*** Totton, 1965

Fig. 210A

Agalmatids with very thin, flimsy nectophores with straight radial canals. Involucrum covers cnidoband of unicornuate tentilla.

Moseria convoluta (Moser, 1925)
Moseria similis Margulis, 1977 [doubtful status]

Genus ***NANOMIA*** Agassiz, 1865

Fig. 210B-E

Agalmatids whose unicornuate tentillum has a basal involucrum. Characteristic arrangement of the gonodendra in that male and female ones, attached at the base of palpons, alternate on either side.

Recent reference: Pagès & Gili (1989)

Nanomia bijuga (Delle Chiaje, 1841)
Nanomia cara Agassiz, 1865

Genus ***PARAGALMA*** Margulis, 1976

Fig. 211A

Agalmatids with slender, elongate, nectophores; with small axial wings; with large thrust bloc; with lateral radial canals forming loops; with lateral ridges.

Paragalma birnsteini Margulis, 1976 [doubtful status]

Genus ***RUDJAKOVIA*** Margulis, 1982

Fig. 211B-C

Agalmatids with flat and branched stem; nectophore oval; nectosac folded, ventral folds irregularly shaped, number of folds increasing with age; aperture of nectosome displaced to dorsal side; gastrozooids devoid of tentacles.

Rudjakovia plicata Margulis, 1982 [doubtful status]

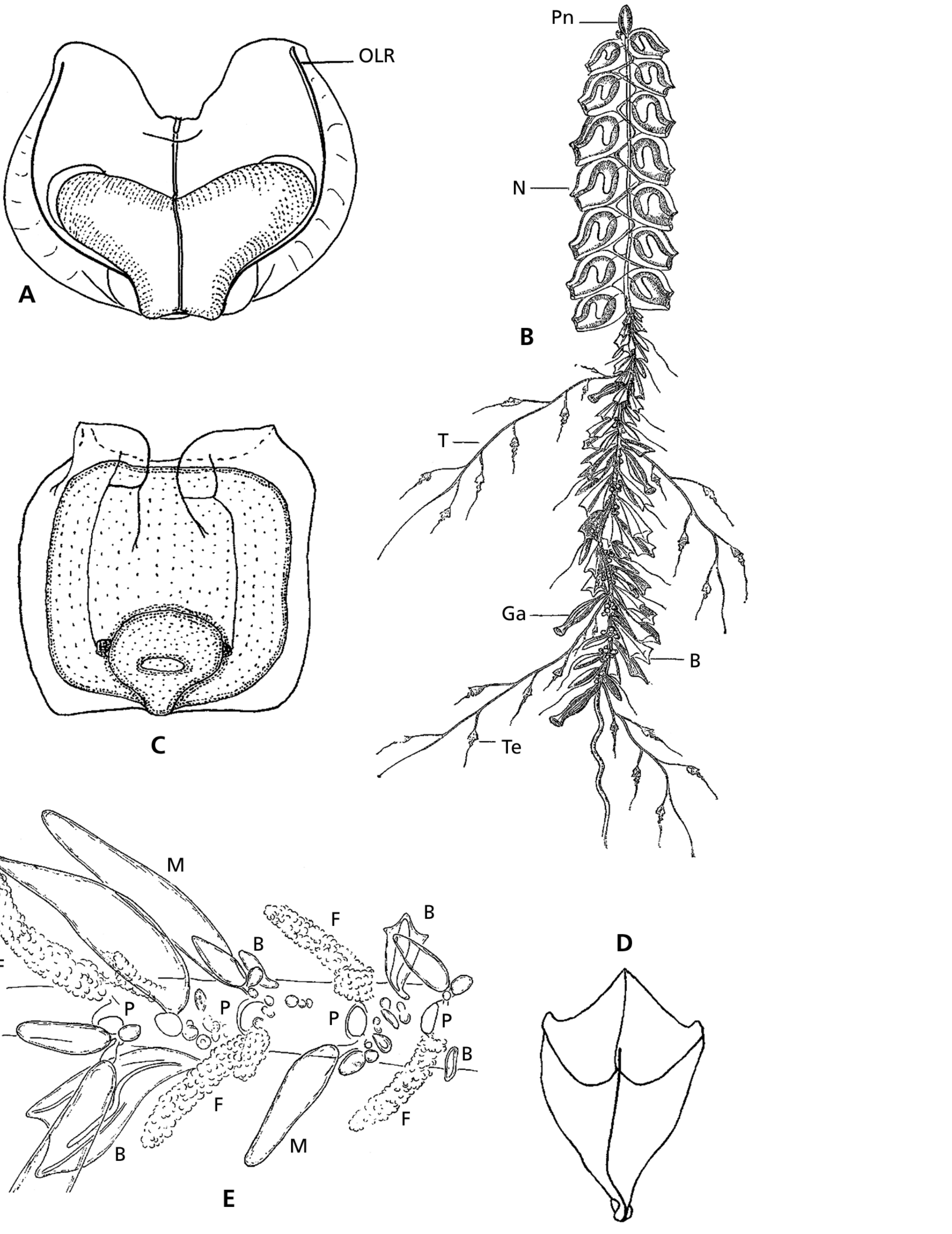


FIG. 210. Siphonophorae, Physonectae, Agalmatidae. A, *Moseria convoluta*, upper view of a young nectophore. B-E, *Nanomia bijuga*: B, view of a polygastric stage; C, upper view of a nectophore; D, bract; E, part of an internode of the stem showing alternating male and female gonodendra arising from the base of a series of palpons (A-B & E after Totton, 1965: p. 67, fig. 31; p. 71, fig. 36; pl. X, fig. 1; C-D after Pugh, 1999). B = bract; F = female gonophore; Ga = gastrozooid; M = male gonophore; N = nectophore; Pn = pneumatophore; OLR = oro-lateral ridge; P = palpon; T = tentacle; Te = tentillum.

FIG. 210. *Siphonophorae, Physonectae, Agalmatidae. A,* Moseria convoluta*, vue dorsale d'un jeune nectophore. B-E,* Nanomia bijuga *: B, vue d'un stade polygastique ; C, vue dorsale d'un nectophore ; D, bractée ; E, partie d'un internode du stolon montrant les gonodendrons mâles et femelles alternants et issus de la base d'une série de palpons (A-B & E d'après Totton, 1965 : p. 67, fig. 31 ; p. 71, fig. 36 ; pl. X, fig. 1 ; C-D d'après Pugh, 1999). B = bractée ; F = gonophore femelle ; Ga = gastérozooide ; M = gonophore mâle ; N = nectophore ; Pn = pneumatophore ; OLR = crête oro-latérale ; P = palpon ; T = tentacule ; Te = tentille.*

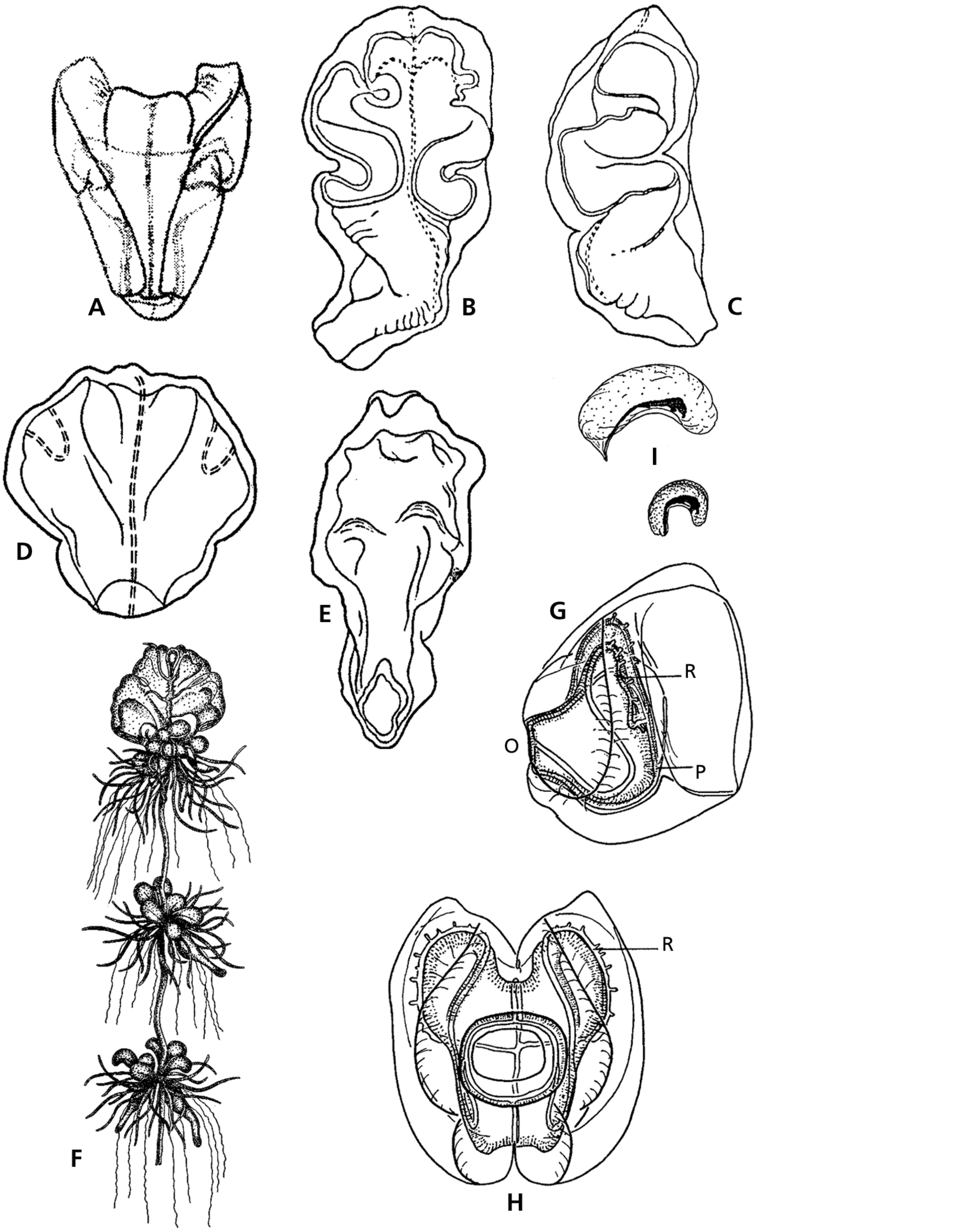


FIG. 211. Siphonophorae, Physonectae, Agalmatidae. A, *Paragalma birsteini*, nectophore. B-C, *Rudjakovia plicata*: B, nectophore (ventral side); C, nectophore (side view). D-E, *Stepanyantsia polymorpha*: D, nectophore (dorsal view); E, nectophore (lateral view). F-I, Apolemiidae, *Apolemia uvaria*: F, polygastric stage; G, nectophore (lateral view); H, nectophore (ostial view); I, bracts (A after Margulis, 1976; B-C after Margulis, 1982a; D-E after Margulis, 1982b; F-I after Totton, 1965: p. 46, fig. 13; p. 48, fig. 14 A, B, C). O = ostium; P = peduncle; R = lateral radial canal.

FIG. 211. *Siphonophorae, Physonectae, Agalmatidae. A,* Paragalma birsteini, *nectophore. B-C,* Rudjakovia plicata *: B, nectophore (vue ventrale) ; C, nectophore (vue latérale). D-E,* Stepanyantsia polymorpha *: D, nectophore (vue dorsale) ; E, nectophore (vue latérale). F-I, Apolemiidae,* Apolemia uvaria *: F, stade polygastrique ; G, nectophore (vue latérale) ; H, nectophore (vue ostiale) ; I, bractées (A d'après Margulis, 1976 ; B-C d'après Margulis, 1982a ; D-E d'après Margulis, 1982b ; F-I d'après Totton, 1965 : p. 46, fig. 13 ; p. 48, fig. 14 A, B, C). O = ostium ; P = pédoncule ; R = canal latéral radiaire.*

Genus *SPHAERALGALMA* Margulis, 1982

Invalid name.

Genus *STEPANJANTSIA* Margulis, 1976
Fig. 211D-E

Agalmatids with minute nectophores, very variable in shape; nectosac occupying most of nectophore; with looped lateral radial canals; tentacles filiform? Doubtful genus.

Stepanjantsia polymorpha Margulis, 1982 [doubtful status]

Family APOLEMIIDAE Huxley, 1859

Unique, amongst the physonects, there is a tentacle or clump of tentacles between each pair of nectophores. Nectophore deeply hollowed axially, forming a pair of large axial wings. Nectosac extensive, lateral radial canals follow an S-shape course of varying complexity. Bracts small and flimsy. This family requires a thorough review.

Genus *APOLEMIA* Eschscholtz, 1829
Fig. 211F-I

Apolemiids with 5-6 tentacles between each pair of nectophores.
Recent references: Pagès & Gili (1992); Båmsted *et al.* (1998).

Apolemia uvaria (Lesueur, 1811)*
* The author of A. uvaria is cited as Lesueur (1811) by Totton (1965).

Genus *RAMOSIA* Stepanjants, 1967
Fig. 212A-C

Apolemiids with a single and large tentacle between each pair of nectophores.

Ramosia vitiazi Stepanjants, 1967

Genus *TOTTONIA* Margulis, 1976
Fig. 212D-G

Apolemiids with oval pneumatophore, without apical canal; nectophores oval, elongate; opening of nectosac displaced onto dorsal side; with lanceolate wings directed upwards; with lateral straight radial canals; some tentacles between each pair of nectophores, never disposed in bundles.
Recent reference: Margulis (1980).

Tottonia contorta Margulis, 1976 [doubtful status]

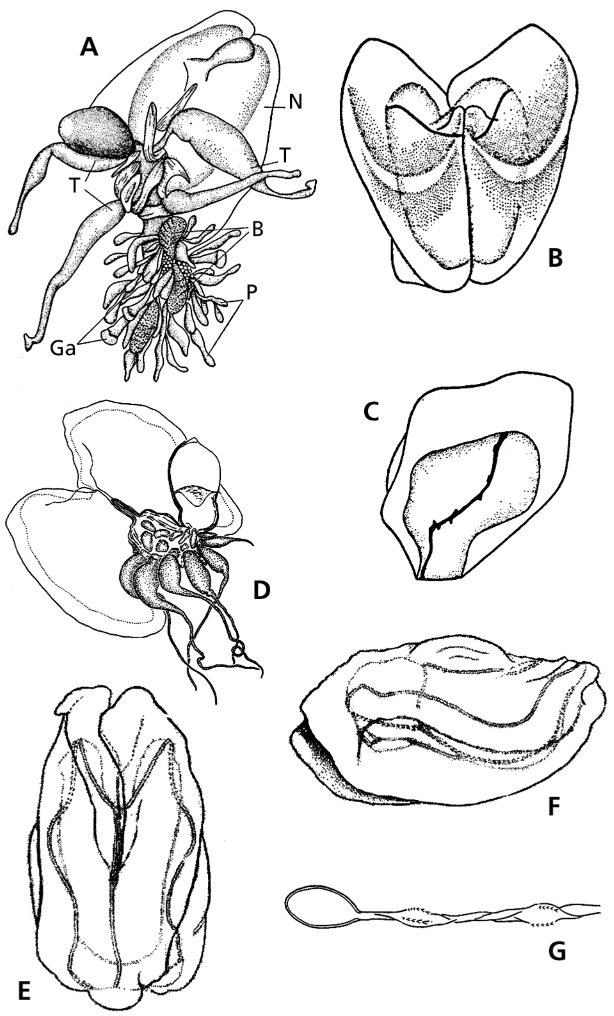


FIG. 212. Siphonophorae, Physonectae, Apolemiidae. A-C, *Ramosia vitiazi*: A, part of polygastric stage; B-C, nectophores. D-G, *Tottonia contorta*: D, nectosome and cormidial group, note the two chambered pneumatophore and the tentacles arranged in a single row; E, nectophore (upper view); F, nectophore (lateral view); G, birhopaloid cnidocyst (A-C after Stepanjants, 1967; D & G after Margulis, 1980; E-F after Margulis, 1976). B = bract; Ga = gastrozooid; N = nectophore; P = palpon; T = tentacle.

FIG. 212. *Siphonophorae, Physonectae, Apolemiidae. A-C,* Ramosia vitiazi : *A, partie d'un stade polygastrique ; B-C, nectophores. D-G,* Tottonia contorta : *D, nectosome et groupe cormidial, notez le pneumatophore à deux chambres et les tentacules disposés en une simple rangée ; E, nectophore (vue dorsale) ; F, nectophore (vue latérale) ; G, cnidocyste birhopaloide (A-C d'après Stepanjants, 1967 ; D & G d'après Margulis, 1980 ; E-F d'après Margulis, 1976). B = bractée ; Ga = gastérozoïde ; N = nectophore ; P = palpon ; T = tentacule.*

Family ATHORYBIIDAE Huxley, 1859

Physonects with relatively large pneumatophore. Nectosome greatly reduced or absent. Siphosome reduced to a dense corm on which the cormidia are arranged in a spiral.

Genus ***ATHORYBIA*** Eschscholtz, 1829

Figs 38H, 213A-C

Athorybiids without nectosome; pneumatophore large; bracts flimsy with inconspicuous rows of cnidocysts.

Athorybia lucida Biggs, 1978
Athorybia longifolia Kawamura, 1954 [invalid species, see Pagès 2002]
Athorybia rosacea (Forskål, 1775)

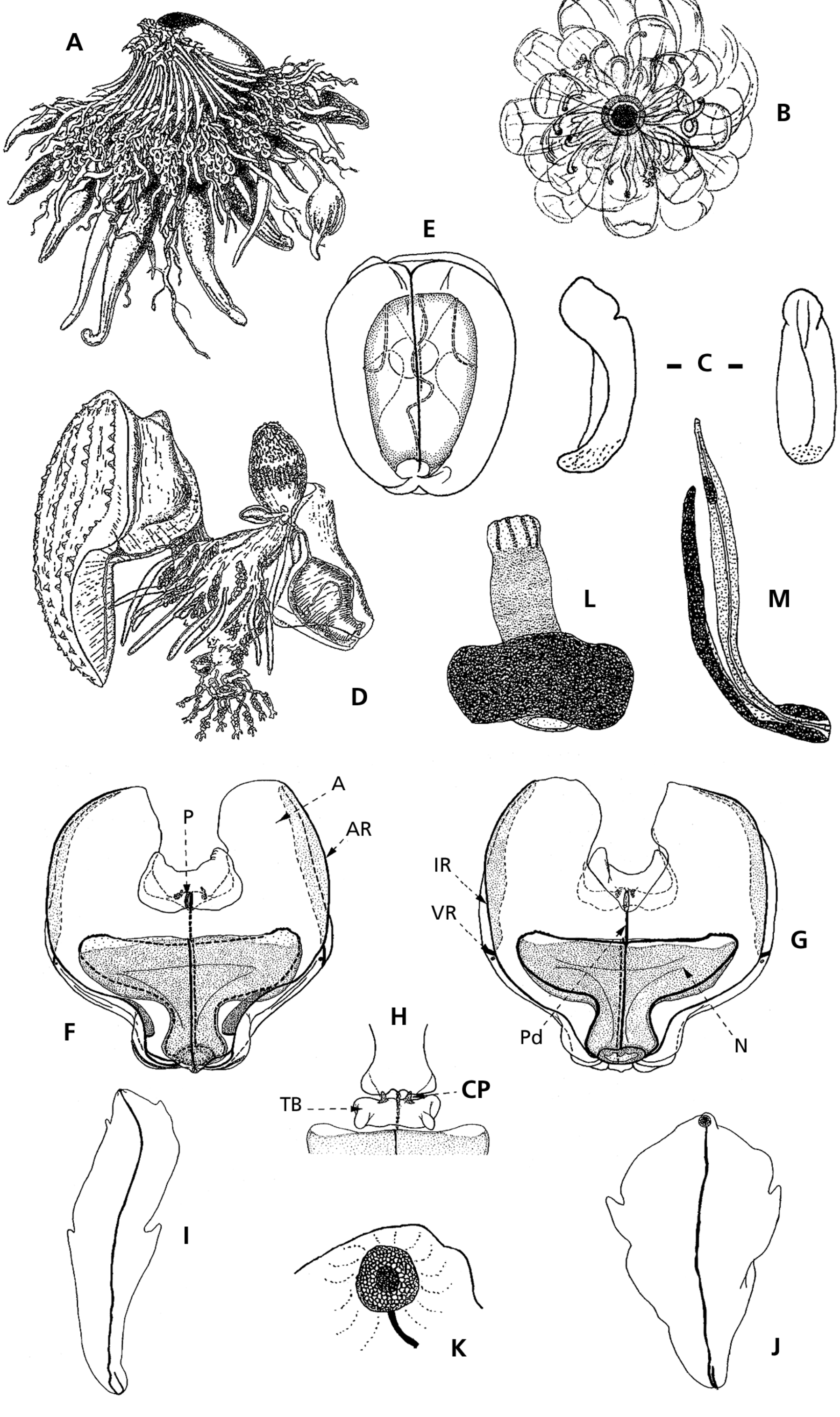
Genus ***MELOPHYSA*** Haeckel, 1888

Fig. 213D-E

Athorybiids with reduced nectosome bearing a maximum of 5 boot-shaped nectophores with nectosac occupying most of the foot; long, thick pedicular canal running from its apex up through the heel; flattened base with two facets separated

FIG. 213. Siphonophorae, Physonectae, Athorybiidae. A-C, *Athorybia rosacea*: A, polygastric stage (lateral view); B, polygastric stage (dorsal view); C, bracts. D-E, *Melophysa melo*: D, polygastric stage with only one bract retained; E, nectophore (upper view). F-L, Erennidae, *Erenna richardi*: F, nectophore (upper view); G, nectophore (lower view); H, detail of folded back thrust block; I, first type of bract; J, second type of bract; K, detail of a distal end of a bract showing the ectodermal patch including cnidocysts; L, gastrozooid with large basigaster and without pedicel. M, *Erenna laciniata*, hypertrophied mature tentillium with uncoiled cnidoband (A, C-D after Pugh, 1999a; B after Trégouboff, 1957: pl. 77, fig. 1; E after Totton, 1965: p. 91, fig. 50 C; F-M after Pugh, *in press*). A = axial wing; AR = apico-lateral ridge; CP = conical protuberance; IR = infra-lateral ridge; N = nectosac; P = pallial canal; Pd = peduncular canal; TB = thust block; VR = vertical lateral ridge.

FIG. 213. *Siphonophorae, Physonectae, Athorybiidae. A-C,* Athorybia rosacea : *A, stade polygastrique (vue latérale) ; B, stade polygastrique (vue dorsale) ; C, bractées. D-E,* Melophysa melo : *D, stade polygastrique avec une seule bractée retenue ; E, nectophore (vue dorsale). F-L, Erennidae,* Erenna richardi : *F, nectophore (vue dorsale) ; G, nectophore (vue ventrale) ; H, détail de l'arrière d'une échancrure plissée entre les deux lobes postérieurs du nectophore ; I, bractée du premier type ; J, bractée du second type ; K, détail de l'extrémité distale d'une bactée montrant la tache ectodermale de cnidocystes ; L, gastérozoïde avec un large bourrelet cilié ou basigaster et sans pédoncule ; M,* Erenna laciniata*, tentille hypertrophié mature avec une cnidobande non spiralée (A, C-D d'après Pugh, 1999a; B d'après Trégouboff, 1957: pl. 77, fig. 1; E d'après Totton, 1965: p. 91, fig. 50 C; F-M after Pugh,* in press*). A = aile axiale ; AR = crête apico-latérale ; CP = protubérance conique ; IR = crête infra-latérale ; N = nectosac ; P = canal pallial ; Pd = canal pédunculaire ; TB = échancrure entre les deux lobes supérieurs du nectophore ; VR = crête verticale latérale.*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by a central protuberance; dorsal canal straight, ventral one with several curves; lateral canals looped; large gelatinous bracts have a proximal keel for attachment; dorsal surface of bracts have several rows of prominent papillae.

Melophysa melo (Quoy & Gaimard, 1827)

Family ERENNIDAE Pugh, 2001

Physonects characterised by uncoiled tentilla bearing a hypertrophied cnidoband with cnidocysts of three types; large homotrichous anisorhizae; microbasic mastigophores and atrichous isorhizas? Terminal process devoid of cnidocysts. Nectophores with basic ridge pattern of apico-, infra- and vertical laterals; with apical muscle-free zone on nectosac; radial canals straight or slightly curved. Ostium, without mouth plate, opens basally. Pneumatophore without apical pore. Gastrozooids without pedicle. Dioecious.

Genus ***ERENNA*** Bedot, 1904

Fig. 213F-M

Erennids with dorso-ventrally flattened nectophores, with tapering axial wings; apico- and infra-lateral ridges respectively form upper and lower margins of lateral surface, with short, perpendicular, vertical lateral ridge connecting them. Lateral radial canals straight, thickened on apico-lateral margins of nectosac; with or without additional small protuberances, spikes, or 'horn' canals. Bracts of two types, both with patches of ectodermal cells, including nematocysts, on dorsal swelling at distal extremity. Tentillum large, with hypertrophied, uncoiled cnidoband. Gastrozooid with large swollen basigaster, but no obvious pedicle.
Recent references: Margulis (1990); Pugh (2001).

Erenna cornuta Pugh, 2001
Erenna laciniata Pugh, 2001
Erenna richardi Bedot, 1904

Genus ***PARERENNA*** Pugh, 2001

Fig. 214A-F

Erennids with nectophores not dorso-ventrally compressed; with muscle-free zone on nectosac mainly in lower surface adaxially. Vertical lateral and incomplete infra-lateral ridges very indistinct: the latter not forming the lower margin of lateral surface. Apico-laterals peter out well above ostial level. Gastrozooid with minute basigaster. Tentillum with long pedicle: with cnidoband extending beyond terminal process, which has a small spherical distal swelling.

Parerenna emilya Pugh, 2001

Family FORSKALIIDAE Haeckel, 1888

Physonects with cylindrical or cone-shape nectosome, whose numerous nectophores have a multiserial, spiral arrangement. Nectophores flattened dorso-ventrally, often asymmetrical in shape. Nectosac restricted to basal half, with straight radial canals. Siphosome also coiled, with gastrozooids borne on long stalks. Bracts of variable shape.

Genus ***FORSKALIA*** Kölliker, 1853

Fig. 214G-J

See family characters.
Recent references: Pagès & Gili (1992); Pugh, 2003.

Forskalia asymmetrica Pugh, 2003
Forskalia contorta (Milne Edwards, 1841)
Forskalia cuneata Chun, 1888
Forskalia edwardsi Kölliker, 1853b
Forskalia formosa Keferstein & Ehlers, 1860 [doubtful status]
Forskalia leuckarti Bedot, 1893 [syn. *Forskalia contorta* Pugh, 2003]
Forskalia misakiensis Kawamura, 1954 [invalid species, see Pagès 2002]
Forskalia saccula Pugh, in press
Forskalia tholoides Haeckel, 1888

Family PHYSOPHORIDAE Eschscholtz, 1829

Physonects with a flimsy, apparently ridgeless nectophores each with an extensive nectosac, which has characteristic, looped lateral radial canals. Both dorsal and ventral canals are sinuous. Siphosome compact sac on which the simple, bractless cormidia are borne in spiral. Each cormidium has a single, greatly enlarged palpon. Monotypic family for the species *Physophora hydrostatica*

Genus ***PHYSOPHORA*** Forskål, 1775

Fig. 215A-C

See family characters.
Recent reference: Pagès & Gili (1992).

Physophora hydrostatica Forskål, 1775

Family PYROSTEPHIDAE Moser, 1925

Long-stemmed physonect. Nectophores with large triangular thrust block, with lateral wedge-shaped processes reduced or absent. With apico-, infra and vertical (meso-) lateral ridges; apico-laterals divided above ostial level. Adaxial wall of nectosac lacking musculature; deeply hollowed: long pallial canal; short pedicular canal, giving rise on nectosac, to only dorsal and ventral radial canals; lateral radial canals arise separately from dorsal. Dorsal and lateral radial canals either looped or straight. Tentillum with straight (or twisted, but not tightly coiled) cnidoband; lacking an involucrum; with terminal filament. Dactylozooids either absent or modified to form peculiar palpacle-less oleocysts.

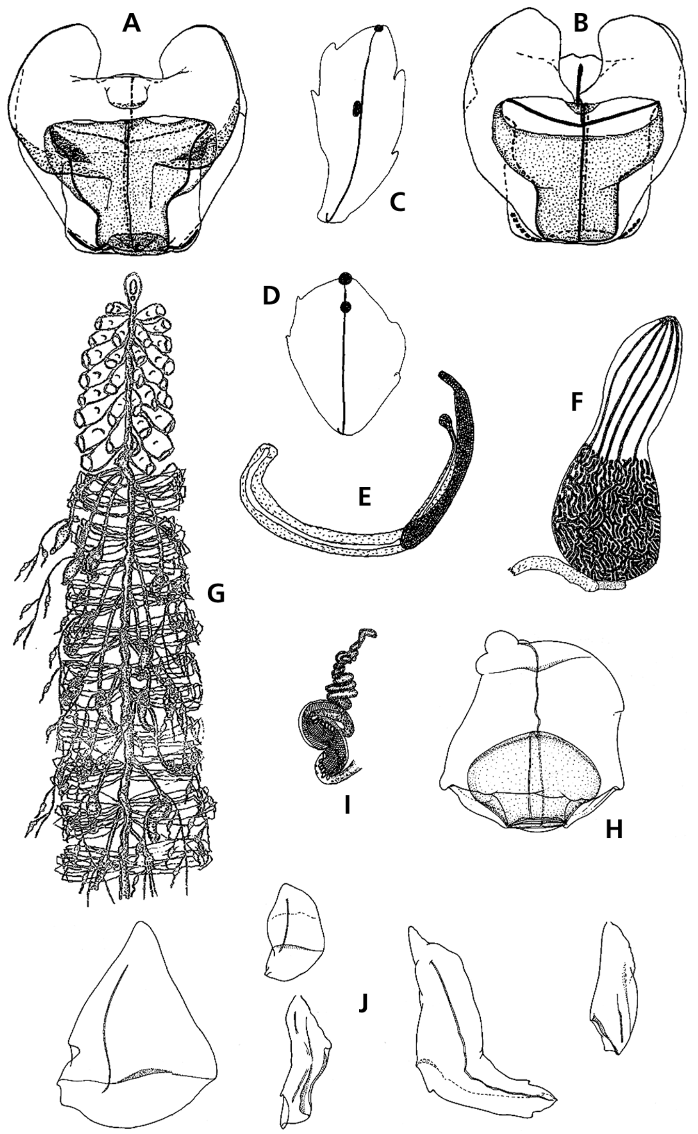


FIG. 214. Siphonophorae, Physonectae. A-F, Erennidae, *Parerenna emilya*: A, nectophore (upper view); B, nectophore (lower view); C, bract of the first type; D, bract of the second type; E, tentillum with long pedicle and cnidoband extending beyond terminal process; F, gastrozooid with small basigaster and peduncle. G-J, Forskaliidae, *Forskalia*: G & I, *Forskalia contorta*: G, epigastric stage; I, tentillum; H & J, *Forskalia edwardsi*: H, nectophore (upper view); J, various type of bracts (A-F after Pugh, *in press*; G & I after Trégouboff, 1957: pl. 79, figs. 7 & 9; H & J after Kirkpatrick & Pugh, 1984).

FIG. 214. *Siphonophorae, Physonectae. A-F, Erennidae,* Parerenna emilya : *A, nectophore (vue dorsale) ; B, nectophore (vue ventrale) ; C, bractée du premier type ; D, bractée du second type ; E, tentille avec long pédoncule et une cnidobande s'étendant au-délas du processus terminal ; F, gastérozoïde avec un petit basigaster et un pédoncule. G-J, Forskaliidae,* Forskalia : *G & I,* Forskalia contorta : *G, stade polygastrique ; I, tentille ; H & J,* Forskalia edwardsi *: H, nectophore (vue dorsale) ; J, bractées de plusieurs types (A-F d'après Pugh,* in press *; G & I d'après Trégouboff, 1957: pl. 79, figs. 7 & 9; H & J d'après Kirkpatrick & Pugh, 1984).*

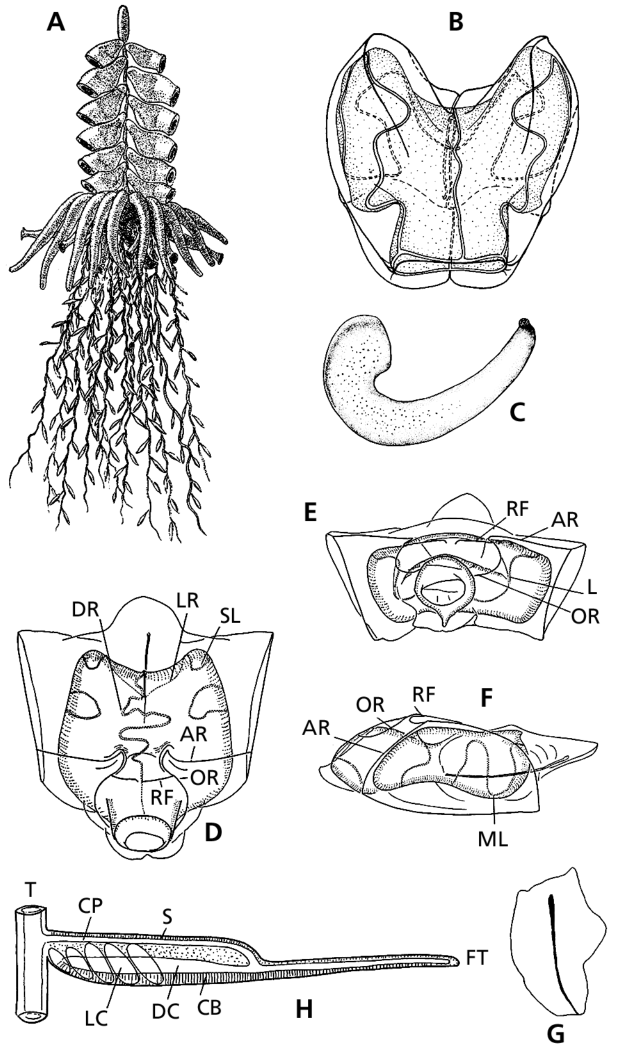


FIG. 215. Siphonophorae, Physonectae. A-C, Physophoridae, *Physophora hydrostatica*: A, polygastric stage; B, nectophore (upper view); C, palpon. D-H, Pyrostephidae, *Pyrostephos vanhoeffeni*: D, nectophore (from above); E, nectophore (ostial view); F, nectophore (lateral view); G, bract; H, schematic sketch of an early growth stage of a tentillium showing the straight cnidoband, the diverticular canal and the terminal filament (A after Brien, 1963; B after Kirkpatrick & Pugh, 1984; C after Pagès & Gili, 1992; D-F & H after Totton, 1965: p. 77, fig. 40 A, B, C; p. 81, fig. 44; G after Pugh, 1999a). AR = apico-lateral ridge; CB = cnidoband; CP = pedicular canal; DC = diverticular canal; DR = dorsal radial canal; FT = terminal filament; L = final downward lateral loop; LC = lateral cnidocyst; LR = lateral radial canal; ML = main downward lateral loop; OR = oro-lateral ridge; RF = frontal ridge; S = saccus; SL = small downward lateral loop; T = tentacle.

***FIG. 215.** Siphonophorae, Physonectae. A-C, Physophoridae,* Physophora hydrostatica : *A, stade polygastrique ; B, nectophore (vue dorsale) ; C, palpon. D-H, Pyrostephidae,* Pyrostephos vanhoeffeni : *D, nectophore (vue dorsale) ; E, nectophore (vue ostiale) ; F, nectophore (vue latérale) ; G, bractée ; H, croquis schématique d'un jeune stade de croissance d'un tentille montrant la cnidobande rectiligne, le canal diverticulaire et le filament terminal (A d'après Brien, 1963 ; B d'après Kirkpatrick & Pugh, 1984 ; C d'après Pagès & Gili, 1992 ; D-F & H d'après Totton, 1965 : p. 77, fig. 40 A, B, C ; p. 81, fig. 44 ; G d'après Pugh, 1999a). AR = crête apico-latérale ; CB = cnidobande ; CP = canal pédiculaire ; DC = canal diverticulaire ; DR = canal dorsal radial ; FT = filament terminal ; L = boucle latérale descendante terminale ; LC = cnidocyste latéral ; LR = canal radiaire latéral ; ML = boucle latérale descendante principale ; OR = crête oro-latérale ; RF = crête frontale ridge ; S = saccus ; SL = petite boucle latérale descendante ; T = tentacule.*

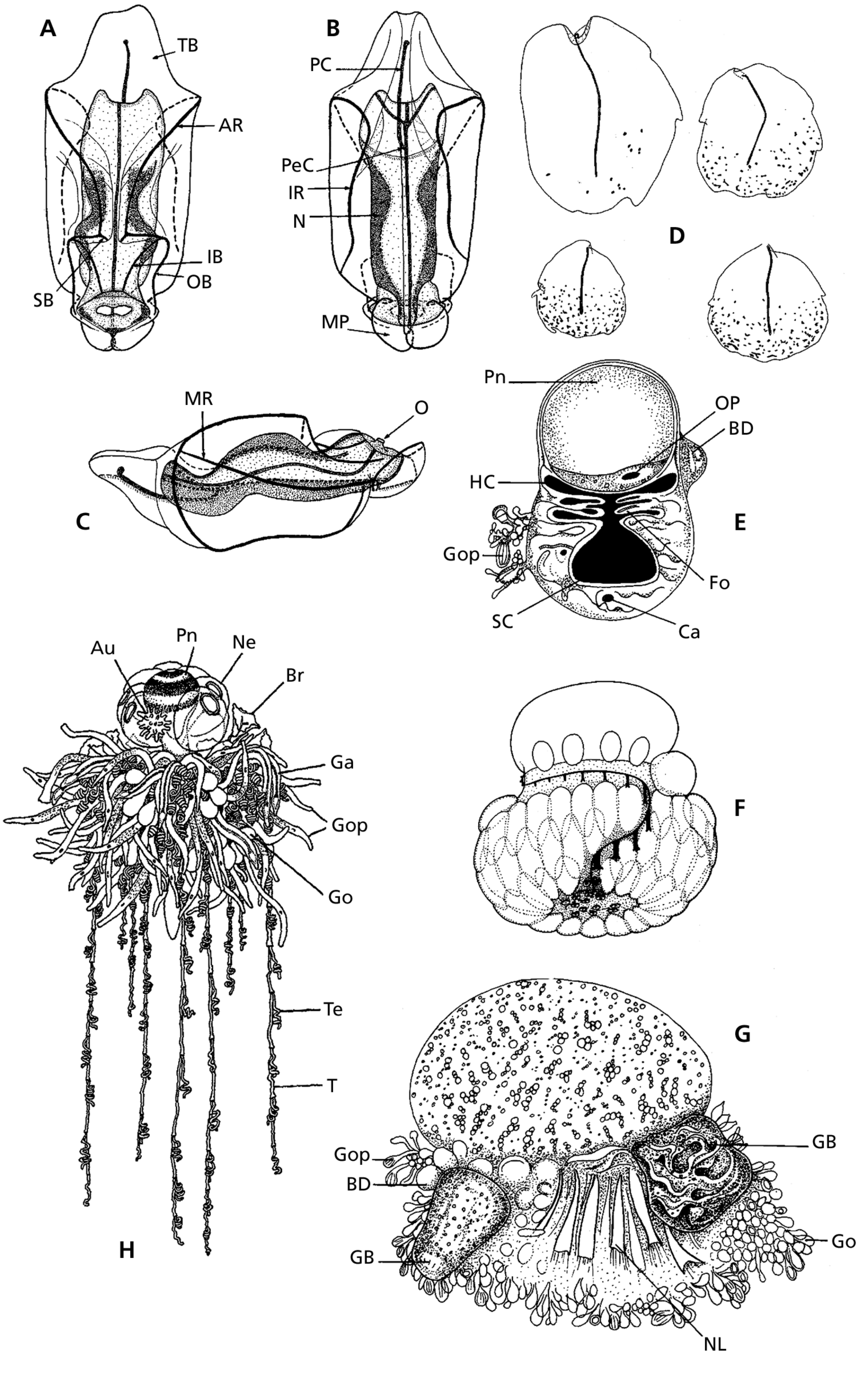
Genus ***BARGMANNIA*** Totton, 1954

Fig. 216A-D

Pyrostephids with distinctive elongate nectophores. Mature nectophores with large, triangular thrust block; without apical wedge-shaped processes; with extensive ventro-lateral wings. Basic ridge pattern may be augmented by additional ridges branching from apico-laterals. Nectosac cylindrical; dorsal and ventral radial canals straight; lateral radial canals arise separately but in close proximity. Pneumatophore without apical pore. Siphosome diffuse, devoid of fully formed dactylozooids. Bracts

FIG. 216. Siphonophorae, Physonectae. A-D, Pyrostyphidae, *Bargmannia elongata*: A, upper view of a nectophore; B, lower view of a nectophore; C, lateral view of a nectophore; D, bracts. E-H, Rhodaliidae, *Angelopsis*: E-F, *Angelopsis globosa*: E, median section through the corm showing the arrangement of the cavities, note that the hypogastric cavity (HC) is in direct communication with the siphosomal cavity (SC) although partially separated by some folds (Fo) of a cartilaginous plate. The thickened walls of the siphosome are penetrated by a ramifying network of canals (Ca); F, diagram showing the arrangement of the series of young cormidial units on the side of the specimen from their origin in the zone of proliferation to the point where they connect up with the biserial arrangement of scars at the base of the corm; G, side view of a specimen, note the globular bodies (GB = aurophores?), some young buds (BD), the nectophoran lamellae (NL), the gonophores (GO) and the gonopalpons (Gop); H, *Archangelopsis jagoa*, view of a living polygastric stage (A-D after Pugh, 1999b; E-G after Pugh, 1984; H after Hissmann *et al*., 1995: p. 672, fig. 1). AR = apico-lateral ridge; Au = aurophore; BD = young buds; Br = bract; Ca = canals; FO = folds; Ga = gastrozooid; GB = globular bodies (aurophores)?; Go = gonophore; Gop = gonopalpon; HC = hypogastric cavity; IB = inner branch; IR = infra-lateral ridge; OB = outer branch of apico-lateral ridge; MP = mouth fig.; MR = meso-lateral ridge; N = nectosac; Ne = nectophore; NL = nectophoran lamellae; O = ostium; Op = opening in the pneumatophoral cavity; PC pallial canal; PeC = pedicular canal; Pn = pneumatophore; SB = side branch of apico-lateral ridge; SC = siphosomal cavity; T = tentacle; TB = thrust block; Te = tentillum.

***FIG. 216.** Siphonophorae, Physonectae. A-D, Pyrostyphidae,* Bargmannia elegans : *A, nectophore (vue dorsale) ; B, nectophore (vue ventrale) ; C, nectophore (vue latérale) ; D, bractées. E-H, Rhodaliidae,* Angelopsis : *E-F,* Angelopsis globosa : *E, section médiane d'une cormidie montrant l'arrangement des cavités, notez que la cavité hypogastrique (HC) est en communication directe avec la cavité siphosomale (SC) bien que partiellement séparée par les plis (Fo) d'une plaque cartilagineuse. Les parois épaissies du siphosome sont pénétrées par un réseau ramifié de canaux (Ca) ; F, diagramme montrant l'arrangement des séries de jeunes unités cormidiales le long du spécimen depuis leur origine dans la zone de prolifération jusqu'au point où elles se connectent avec les cicatrices bisérielles à la base de la cormidie ; G, vue latérale d'un spécimen, notez les corps globulaires (GB = aurophores?), les jeunes bourgeons (BD), les lamelles nectophorales (NL), les gonophores (GO) et les gonopalpons (Gop) ; H,* Archangelopsis jagoa*, vue d'un stade polygastrique vivant (A-D d'après Pugh, 1999b ; E-G d'après Pugh, 1984 ; F d'après Hissmann* et al.*, 1995 : p. 672, fig. 1). AR = crête apico-latérale ; Au = aurophore ; BD = jeunes bourgeons ; Br = bractée ; Ca = canal ; FO = plis ; Ga = gastérozoïde ; GB = corps globulaires (aurophores?); Go = gonophore ; Gop = gonopalpon ; HC = cavité hypogastrique ; IB = branche interne de la crête apico-latérale ; IR = crête infra-latérale ; OB = branche externe de la crête apico-latérale ; MP = plaque buccale ; MR = crête meso-latérale ; N = nectosac ; Ne = nectophore ; NL = lamelles nectophorales; O = ostium ; Op = ouverture dans la cavité pneumatophorale ; PC = canal pallial ; PeC = canal pédiculaire ; Pn = pneumatophore ; SB = branche latérale de la crête apico-latérale ; SC = cavité siphosomale; T = tentacule ; TB =section aborale d'un nectophore Physonecte ; Te = tentille.*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E
Gop
Fo
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Ca
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Au
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Br
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NL

specifically variable in shape. Each cormidium with simple tentacle-like structure attached to the stem midway between successive gastrozooids; with single gonodendron. Siphosomal tentacles present.
Recent references: Pagès & Gili (1989); Pugh (1999a; b).

Bargmannia amoena Pugh, 1999b
Bargmannia elongata Totton, 1954
Bargmannia gigas Pugh, 1999b
Bargmannia lata Mapstone, 1998

Genus ***PYROSTEPHOS*** Moser, 1925

Fig. 215D-H

Pyrostephids with distinctive butterfly-shaped nectophores; triangular thrust block is best seen in smaller nectophores, on larger preserved ones it is bent up dorsally; with reduced apical wedge-shaped processes. Looping of the lateral radial canal on the nectosac, and three to four marked bends of the dorsal canal. Dactylozooids modified to form peculiar palpacle-less oleocysts.

Pyrostephos vanhoeffeni Moser, 1925

Family RHODALIIDAE Haeckel, 1888

Physonect with nectosome and siphosome contracted to form a globular corm below the enlarged pneumatophore. The gas-secreting area is developed greatly to form a characteristic structure the aurophore, extending from the baso-dorsal surface of the pneumatophore. Benthic, attached to the seabed by their tentacles.

Genus ***ANGELOPSIS*** Fewkes, 1886

Fig. 215E-G

Rhodaliids with smooth-walled aurophore and pneumatophore; with an extensive cavity in the siphosome, the thickened walls of which are penetrated by a network of canals, although this network may be restricted to the peripheral regions.
Recent reference: Pugh (1983)

Angelopsis euryale Pugh, 1983
Angelopsis globosa Fewkes, 1886

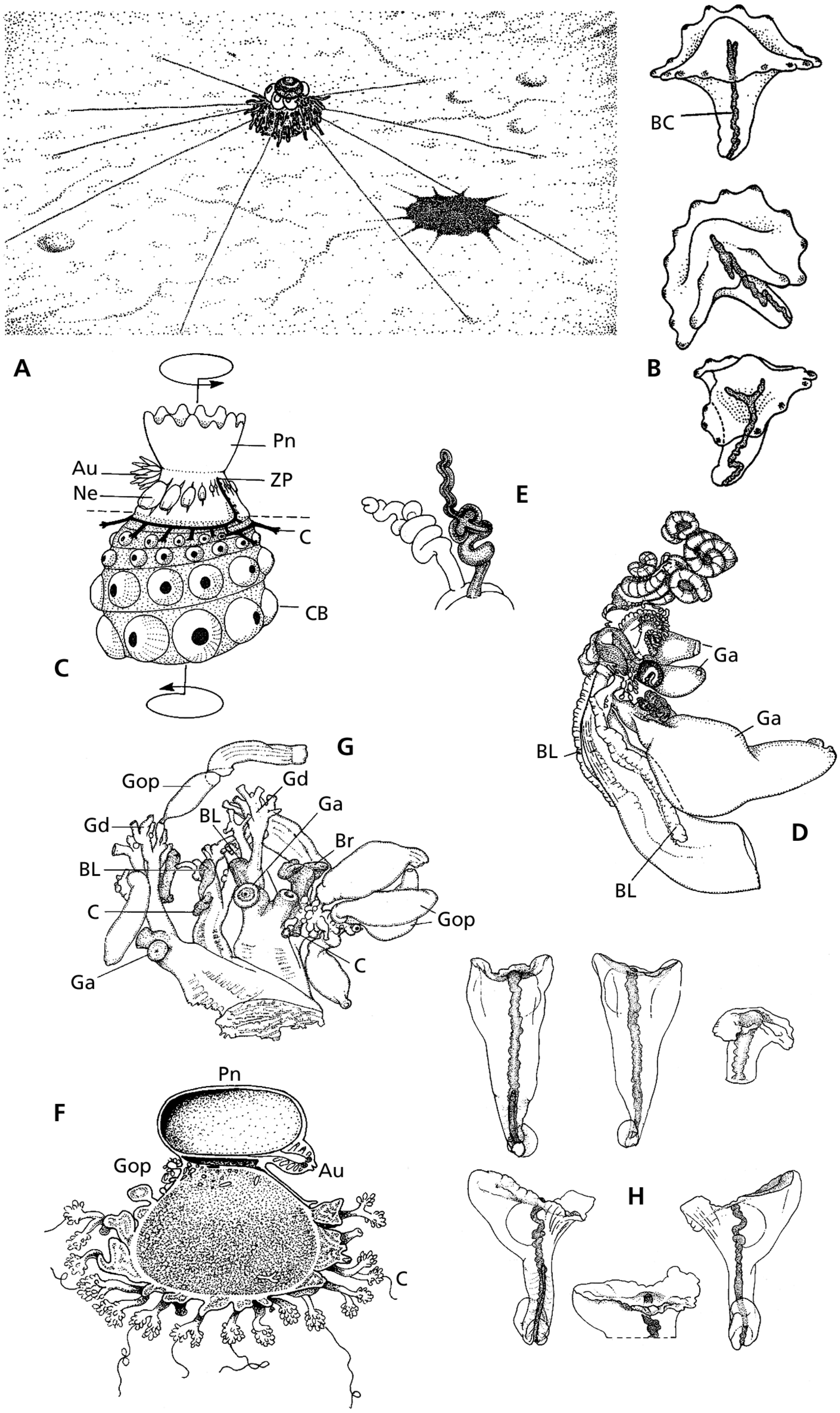
Genus ***ARCHANGELOPSIS*** Lens & van Riemsdijk, 1908

Figs 216H, 217A-B

Rhodaliids with smooth-walled pneumatophore. Aurophore with numerous papilliform processes on its external surface. The corm is a voluminous, thin-walled sac, on the siphosomal region of which are (?) spirally arranged cormidia. The walls

FIG. 217. Siphonophorae, Physonectae, Rhodaliidae. A-B, *Archangelopsis jagoa*: A, view of a live specimen attached to sediment with its long tentacles, and with the main corm at a distance of approximately 10-15 cm from sea bed; B, various aspects of mature bracts. C-E, *Dromalia alexandri*: C, developing of a corm, note the series of developing cormidial units on the apical siphosomal whorls. Their presence indicates the possibility that the nectosomal and siphosomal regions are twisting relative to each other in the plane marked by the dotted line and in the direction indicated; D, a cormidial unit with three gastrozooids attached; E, detail of an individual tricornuate tentillum. F-H, *Rhodalia miranda*: F, sagittal section throuh the entire corm; G, two developing cormidial units; H, bracts (A-B after Hissmann *et al*., 1995: p. 677, figs 7-6; C-H after Pugh, 1984). Au = aurophore; BC= bracteal canal; BL = bracteal lamella; Br = bract; C = cormidium; CB = cormidal attachment base; Ga = gastrozooid; Gd = gonodendron; Gop = gonopalpon; Ne = nectophore; Pn = pneumatophore; ZP = zone of proliferation.

FIG. 217. *Siphonophorae, Physonectae, Rhodaliidae. A-B,* Archangelopsis jagoa : *A, vue d'un spécimen vivant attaché au sédiment par ses longs tentacules, la cormidie principale étant à une distance d'environ 10-15 cm du fond de la mer ; B, aspects différents de bractées matures. C-E,* Dromalia alexandri : *C, développement des cormidies, notez la série d'unités cormidiales en développement au niveau des anneaux apicaux siphosomaux. Leur présence indique la possibilité que les régions nectosomale et siphosomale se tordent l'une par rapport à l'autre dans le plan marqué en pointillé et dans la direction indiquée par les flèches ; D, unité cormidiale avec trois gastérozoïdes ; E, détail d'un tentille trifides. F-H,* Rhodalia miranda : *F, section sagittale au travers d'une cormidie ; G, deux unités cormidiales en développement ; H, bractées (A-B d'après Hissmann* et al*., 1995 : p. 677, figs 7-6 ; C-H d'après Pugh, 1984). Au = aurophore ; BC= canal bractéal ; BL = lamelle bractéale ; Br = bractée ; C = cormidie ; CB = base d'attache cormidial ; Ga = gastérozoïde ; Gd = gonodendron ; Gop = gonopalpon ; Ne = nectophore ; Pn = pneumatophore ; ZP = zone de prolifération.*


A
B
BC
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Au
ZP
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H

of the siphosomal cavity do not possess a network of gastrovascular canals. The monogastric cormidia are borne on stout stalks at the base of which a bract is developed. Secondary, (?) reduced cormidia also may bud from the base of these stalks.
Recent references: Pugh (1983); Hissmann *et al.* (1995).

Archangelopsis jagoa Hissmann, Schauer & Pugh, 1995
Archangelopsis typica Lens & van Riemsdijk, 1908

Genus *DROMALIA* Bigelow, 1911

Fig. 217C-E

Rhodaliids whose pneumatophore is flattened apically and bears several gelatinous protuberances around its outer rim. The aurophore bears papilliform appendages. The hypocystic cavity is very reduced or absent and the remainder of the corm is solid. A sparse system of gastrovascular canals penetrates through the translucent mesogleal ground substance of the corm and an anastomosing network of canals is present peripherally, just below the surface of the corm. The cormidia are arranged into distinct dexiotropic spirals around the surface of the siphosome and a developmental series can be discerned on the most apical (youngest) whorl. The mature cormidia are borne on thickened bases, which are distinct one from another. Bracts, with a many branched bracteal canal system, are present. The tentilla are tricornuate and may possess a basal involucrum.
Recent reference: Pugh (1983).

Dromalia alexandri Bigelow, 1911a

Genus *RHODALIA* Haeckel, 1888

Fig. 217F-H

Rhodaliids with a smooth-walled aurophore and pneumatophore. The nectosomal region bears a large number of nectophores, usually between 50 and 80, which may, by their mutual compression, arrange themselves into a double or a multiple corona. The siphosome bears numerous, crowded cormidial units which possess characteristically shaped bracts. Internally, the hypocystic cavity is restricted to a very shallow, but broad, zone immediately below the pneumatophore. The remainder of the corm is composed of a spongy, cartilaginous ground substance, which is penetrated throughout by a network of innumerable small canals. No major canal system is present.
Recent reference: Pugh (1983).

Rhodalia miranda Haeckel, 1888

Genus *SAGAMALIA* Kawamura, 1954

Fig. 218A-C

Rhodaliids with smooth-walled aurophore and pneumatophore. The aurophore is very small and has an indistinct external pore. Approximately 12 or 13 nectophores are present. The siphosome is not a bulbous corm, but maybe a narrow stem on which the cormidia are spirally arranged, or it may contain a large thin-walled cavity. Bracts of a characteristic shape are present.
Recent reference: Pugh (1983).

Sagamalia hinomaru Kawamura, 1954

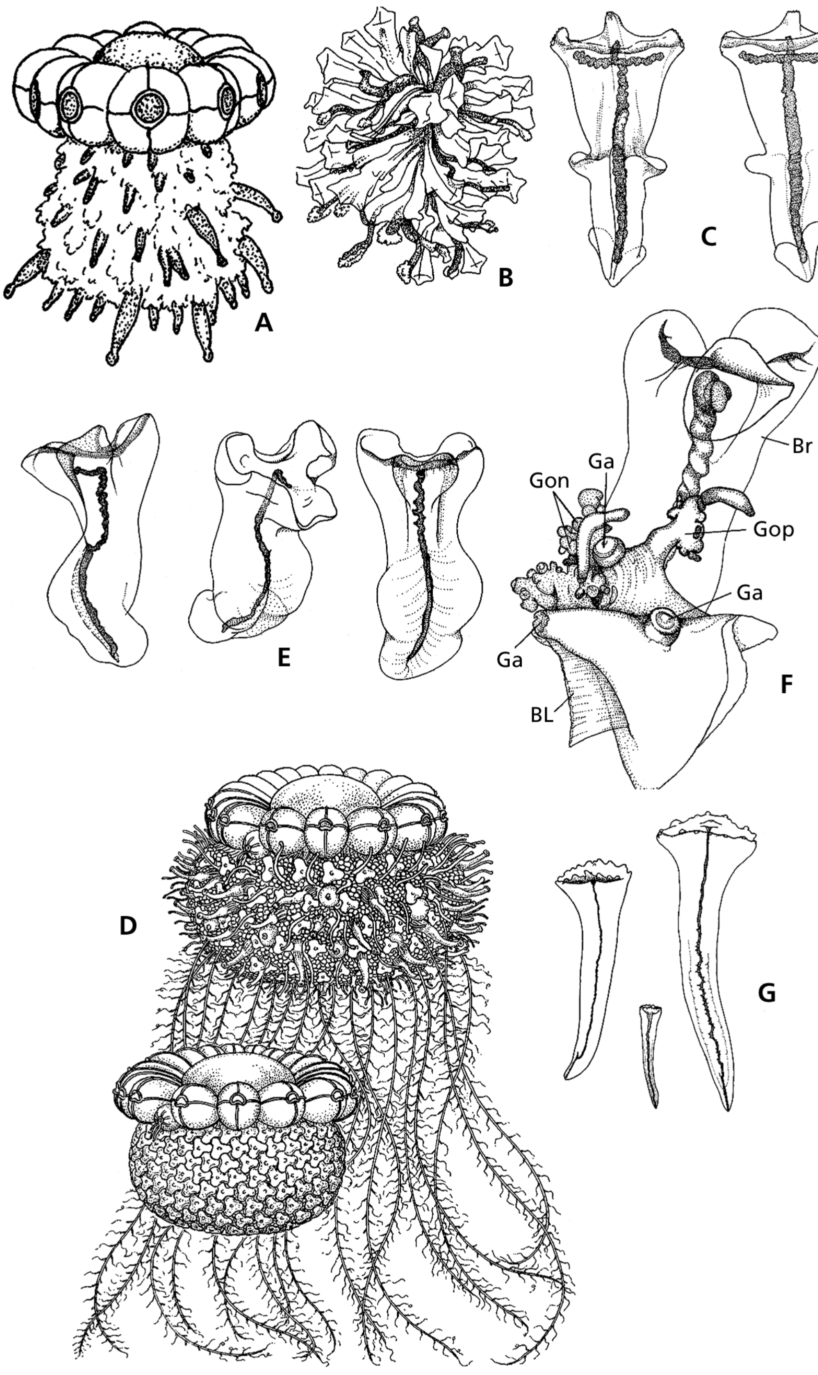

FIG. 218. Siphonophorae, Physonectae. A-C, Rhodaliidae, *Sagamalia hinomaru*: A, sketch of an entire animal before preservation; B, aboral view of the siphosome; C, bracts. D-F, *Stephalia corona*: D, reconstruction of the whole animal, expanded and contracted; E, various aspects of mature bracts; F, aspect of a cormidial base. G, *Thermopalia taraxaca*, bracts (A-C, E-G after Pugh, 1984; D after Totton, 1965: p. 93, fig. 51). BL = bracteal lamella; Br = bract; Ga = gastrozooid; Gon = gonophore; Gop = gonopalpon.

FIG. 218. *Siphonophorae, Physonectae. A-C, Rhodaliidae,* Sagamalia hinomaru : *A, croquis d'animaux complets, avant fixation ; B, vue aborale du siphosome ; C, bractées ; D-F,* Stephalia corona : *D, reconstruction d'un animal complet, au-dessus en extension, en-dessous contracté ; E, différents aspects de bractées matures ; F, aspect de la base d'une cormidie. G,* Thermopalia taraxaca, *bractées (A-C, E-G d'après Pugh, 1984 ; D d'après Totton, 1965 : p. 93, fig. 51). BL = lamelle bractéale ; Br = bractée ; Ga = gastérozoïde ; Gon = gonophore ; Gop = gonopalpon.*

Genus ***STEPHALIA*** Haeckel, 1888

Figs 37D, 218D-F

Rhodaliids with smooth-walled aurophore and pneumatophore; with the hypocystic cavity occupying the majority of the nectosomal region; with a solid siphosome traversed by a network of canals, which includes a major branching stem.
Recent reference: Pugh (1983).

Stephalia bathyphysa (Haeckel, 1888)
Stephalia corona Haeckel, 1888
Stephalia dilata (Bigelow, 1911b)

Genus ***THERMOPALIA*** Pugh, 1983

Fig. 218G (Photos in Pugh 1983)

Rhodaliids with smooth-walled pneumatophore and aurophore. The aurophore has a large basal attachment with the nectosomal region. There is a narrow, axial cavity within the siphosome. The cormidia, in the younger specimens, are arranged into obvious spiral whorls and are not borne on distinct, gelatinous bases. The gonodendra of the cormidia bear long-stalked gonophores, but gonopalpons are absent.
Recent reference: Pugh (1983).

Thermopalia taraxaca Pugh, 1983

Order CALYCOPHORAE Leuckart, 1854

Highly polymorphic Siphonophorae without pneumatophore, with a reduced nectosome typically formed by one or two but sometimes more nectophores. Usually with a single bract per cormidia (except the Hippopodiidae without bracts), without dactylozooids (except in *Stephanophyes*), in some cases with asexual medusoid structures on siphosome. Generally the cormidial units are detached successively from the stem and become eudoxid or sexual stage. Usually a calyconula larvae.

KEY TO FAMILIES
(after Pugh 1999a)

1. nectophores dorso-ventrally flattened 2
– nectophores not dorso-ventrally flattened, bracts present.......... 3

2. up to 15+ similar, closely applied, dorso-ventrally fattened nectophores bearing protuberances or spines; large but shallow nectosac; bracts absent .... Hippopodiidae
– small, flattened nectophores, with vestigial nectosac and reduced somatocyst.......... Prayidae, subfamily Amphicaryoninae

3. nectophores and bracts rounded, smooth-walled, with thick mesoglea.......... 4
– nectophores and bracts pointed, toothed or of irregular shape.......... 6

4. usually 2 nectophores 5
– single, fragile, larval nectophore, with a simple somatocyst and narrow hydroecium. Small, fragile bract with a single canal .... Sphaeronectidae

5. two nectophores of approximately equal size, forming an apposed pair; somatocyst simple or branched. Bracts with 5 or 6 branches to the canal system.......... Prayidae, subfamily Prayinae
– two nectophores of unequal size, with reduced somatocysts; nectosac of smaller nectophore usually reduced or obsolent. Bracts with two branches to canal system . . Prayidae, subfamily Amphicaryoninae

6. two morphologically different nectophores; one (anterior) superimposed over the other (posterior). 8
– with usually a single nectophore 7

7. single, usually large nectophore bearing simple or toothed ridges; somatocyst usually branched. Large bract without neck shield and extensively branched canal system . . . . Prayidae, subfamily Nectopyramidinae
– single, usually small, apically pointed nectophore, with simple caecal somatocyst. Bract conical or angular 9

8. posterior nectophore with a somatocyst; anterior nectophore with extensive opening of hydroecium onto ventral surface. Small bract with phyllocyst and 2 canals extending into neck shield. . . . Clausophyidae
– posterior nectophore without somatocyst; hydroecium of anterior nectophore usually opens basally. Bracts conical or angular, with phyllocyst and, at most, one canal 9

9. conical streamlined anterior nectophore, usually with shallow hydroecium; posterior nectophore, when present, usually apically truncated and of similar size or smaller than anterior one. Conical bracts. . . . . Diphyidae
– anterior nectophore angular, with inflated somatocyst and deep hydroecium; posterior nectophore, when present, larger than anterior one. Rigid angular bracts . . . . Abylidae

Family ABYLIDAE Agassiz, 1862

Calycophorans with rigid, angular nectophores, the posterior one, without a somatocyst, usually being much larger, and bearing serrated ridges and teeth. In all but one species, the somatocyst of the anterior nectophore has curved over to occupy a ventral position. The hydroecium of the anterior nectophore is an enclosed tube opening basally. During development a temporary larval bract is formed before the larval nectophore. The latter is retained in the polygastric stage as the anterior nectophore.

Subfamily ABYLINAE L. Agassiz, 1862

Genus ***ABYLA*** Quoy & Gaimard, 1827

Fig. 219A-E

Abylines with anterior nectophores with 10 or 11 facets. The apical facet is divided by a transverse ridge, and many ridges are serrated, particularly basally. Dorsal nectosac and median hydroecium are long tubes extending almost to apex of nectophore. The large oval somatocyst lies ventrally. Posterior nectophore with long, tapering apical apophysis, has only 4 ridges. The ventral ridges define the hydroecial wings and are heavily serrated basally. The left hydroecial wing bears a toothed comb or flap. Five, usually serrated, ostial teeth. Prismatic bracts with 6 facets, the dorsal one being rectangular. Very large phyllocyts, with 2 canals running down toward the ventro-lateral corners of the apical facet. The bracts cannot, at present, be identified specifically.

Recent reference: Pagès & Gili (1992).

Abyla bicarinata Moser, 1925
Abyla carina Haeckel, 1888
Abyla haeckeli Lens & Van Riemsdijk, 1908
Abyla ingeborgae Lens & Van Riemsdijk, 1908 [perhaps a syn. of *A. haeckeli*]
Abyla peruana Sears, 1953
Abyla schmidti Sears, 1953
Abyla tottoni Sears, 1953
Abyla trigona Quoy & Gaimard, 1827

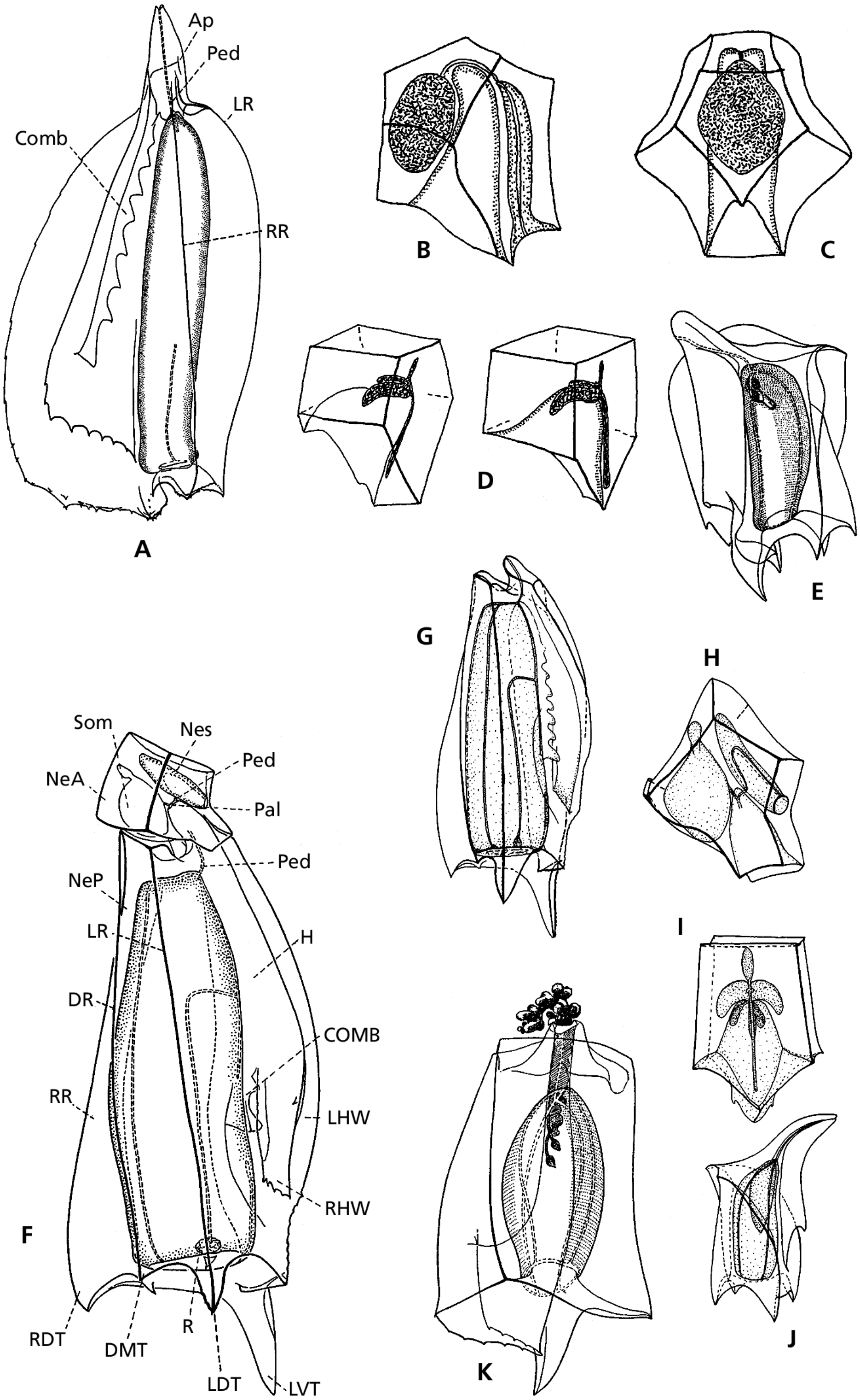

FIG. 219. Siphonophorae, Calycophorae, Abyliidae. A-E, *Abyla*: A, *Abyla trigona*, polygastric stage; B-C, anterior nectophore of *Abyla haeckeli*: B, ventral view; C, lateral view; D, bract of *Abyla eschschotzi* (left), bract of *Abyla tetragona* (right); E, eudoxid of *Abyla haeckeli*. F-J, *Abylopsis teragona*: F, polygastric stage; G, posterior nectophore; H, anterior nectophore; I, eudoxid bract; J, gonophore. K, *Bassia bassensis*, polygastic stage (dorsal view) (A, E & K after Totton, 1965: p. 209, fig. 142 A; p. 211, fig. 143; p. 220, fig. 152; B-D after Pugh, 1999a; F-J after Kirckpatrick & Pugh, 1984). Ap = apophysis; COMB = comb; DMT = dorso median tooth; DR = dorsal ridge; H = hydroecium; Nes = nectosac; LDT = left dorsal tooth; LHW = left hydroecial wing; LR = left ridge; LVT = left ventral tooth; NeA = anterior nectophore; NeP = posterior nectophore; Pal = pallial canal; Ped = pedicular canal; R = rete; RDT = right dorsal tooth; RHW = right hydroecial wing; RR = right ridge; Som = somatocyst.

FIG. 219. *Siphonophorae, Calycophorae, Abyliidae. A-E,* Abyla : *A,* Abyla trigona*, stade polygastrique ; B-C, nectophore antérieur d'*Abyla haeckeli : *B, vue ventrale ; C, vue latérale ; D, bractée d'*Abyla eschschotzi *(à gauche), bractée d'*Abyla tetragona *(à droite) ; E, eudoxie d'*Abyla haeckeli. *F-J,* Abylopsis teragona *: F, stade polygastrique ; G, nectophore posterieur ; H, nectophore antérieur ; I, bractée de l'eudoxie ; J, gonophore. K,* Bassia bassensis*, stade polygastrique (vue dorsale) (A, E & K d'après Totton, 1965 : p. 209, fig. 142 A ; p. 211, fig. 143 ; p. 220, fig. 152 ; B-D d'après Pugh, 1999a ; F-J d'après Kirckpatrick & Pugh, 1984). Ap = apophyse ; C = cormidie ; COMB = peigne ; DMT = dent dorsomediane ; DR = crête dorsale ; H = hydroécie; Nes = nectosac ; LDT = dent dorsale gauche ; LHW = aile hydroéciale gauche ; LR = crête gauche ; LVT = dent ventrale gauche ; NeA = nectophore anterieur ; NeP = nectophore postérieur ; Pa = canal pallial ; Ped = canal pédiculaire ; R = rete ; RDT = dent dorsale droite ; RHW = aile hydroeciale droite wing ; RR = crête droite ; Som = somatocyste.*

Genus ***CERATOCYMBA*** Chun, 1888

Fig. 220D-H

Abylines with characteristically shaped bract, called a cymba. Anterior nectophore with 7 facets. Apical facet not divided by a transverse ridge. Posterior nectophore long and narrow, without wing-like expansions. Short dorsal ridge ends on the dorsal tooth. Bracts with a median dorsal ridge. Left lateral facet divided by another ridge. Bracts roughly triangular with a concave apical facet and prominent lateral horns. Phyllocyst with 2 thin ventro-lateral branches. Its distal end bends dorsal to form a blind sac.
Recent reference: Pagès & Gili (1992).

Ceratocymba dentata (Bigelow, 1918)
Ceratocymba intermedia Sears, 1953
Ceratocymba leuckarti (Huxley, 1859)
Ceratocymba sagittata (Quoy & Gaimard, 1827)

Subfamily ABYLOPSINAE Totton 1954

Genus ***ABYLOPSIS*** Chun, 1888

Fig. 219F-J

Abylines with anterior nectophore with a pentagonal dorsal facet without a median ridge. Seven-facet anterior nectophore, but without an apical facet, and pentagonal dorsal and ventral facets. The somatocyst has an apical diverticulum. Posterior nectophore has prominent basal teeth and with 5 ridges and a short curved apical apophysis. The left lateral ridge bifurcates close to the apex. Flaps on both wings of hydroecium. Bracts with 7 facets. Phyllocyst with swollen apico-lateral branches and apical diverticulum, while distally is a narrow tube.
Recent reference: Pagès & Gili (1992).

Abylopsis eschscholtzi (Huxley, 1859)
Abylopsis tetragona (Otto, 1823)

Genus ***BASSIA*** Agassiz, 1862

Figs 219K, 220A-C

Abylines with anterior nectophore without an apical diverticulum to the somatocyst, and with the hydroecium not extending below the basal facet. Somatocyst large and globular. Posterior nectophore with 4 ridges ending in short basal teeth. Bract with median apical ridge has a quadrilateral dorsal facet. Phyllocyst is a long tube, swollen apically, without apico-lateral branches. Gonophore has four longitudinal ridges which end basally in minute teeth.

Bassia bassensis (Quoy & Gaimard, 1833)

Genus ***ENNEAGONUM*** Quoy & Gaimard, 1827

Fig. 220I-J

Abylines where the large, pyramidal anterior nectophore is the only one developed. The conical somatocyst is situated above the hydroecium, and extends to a greater height than the nectosac. The bract is cubical, with slightly concave facets. Swollen somatocyst with 2 lateral and apical processes.
Recent reference: Pagès & Gili (1992).

Enneagonum hyalinum Quoy & Gaimard, 1827

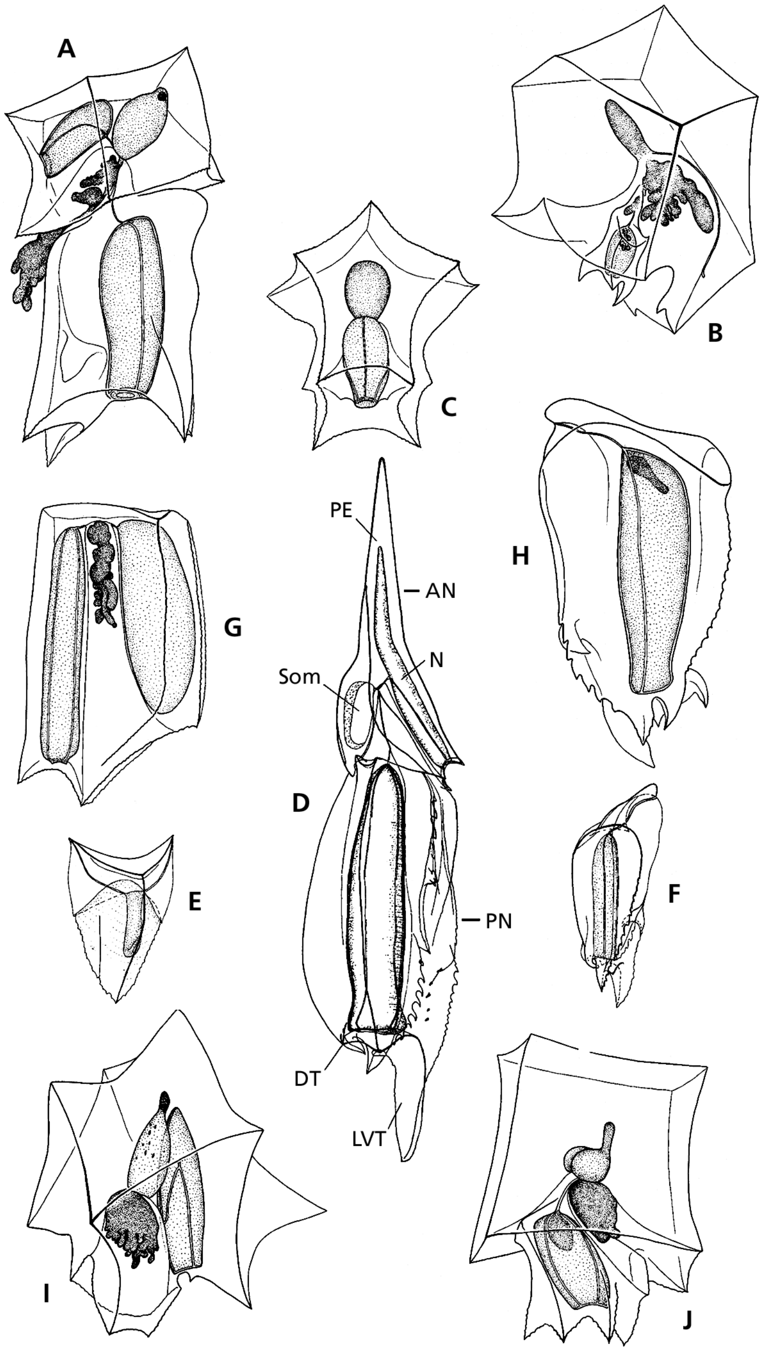

FIG. 220. Siphonophorae, Calycophorae, Abyliidae. A-C, *Bassia bassensis*: A, polygastric stage (lateral view); B, eudoxid (latero-ventral view); C, anterior nectophore (dorsal view). D-H, *Ceratocymbia*: D-F, *Ceratocymba sagittata*: D, polygastric stage; E, eudoxid bract; F, gonophore; G, *Ceratocymba leuckarti*, anterior nectophore; H, *Ceratocymba dentata*, gonophore. I-J, *Enneagonum hyalinum*: I, polygastric stage (lateral view); J, eudoxid (lateral view) (A-C, G-J after Pagès & Gili, 1992; D after Totton, 1965: p. 206, fig. 140; E-F after Kirckpatrick & Pugh, 1984). AN = anterior nectophore; DT = dorsal tooth; LVT = left ventral tooth; N = nectosac; PE = pyramydal extension; PN = posterior nectophore; Som = somatocyst.

FIG. 220. *Siphonophorae, Calycophorae, Abyliidae. A-C,* Bassia bassensis : *A, stade polygastrique (vue latérale) ; B, eudoxie (vue latéro-ventrale) ; C, nectophore antérieur (vue dorsale). D-H,* Ceratocymbia : *D-F,* Ceratocymba sagittata : *D, stade polygastrique ; E, bractée de l'eudoxie ; F, gonophore ; G,* Ceratocymba leuckarti, *nectophore antérieur ; H,* Ceratocymba dentata, *gonophore. I-J,* Enneagonum hyalinum : *I, stade polygastrique (vue latérale) ; J, eudoxie (vue latérale) (A-C, G-J d'après Pagès & Gili, 1992 ; D d'après Totton, 1965 : p. 206, fig. 140 ; E-F d'après Kirckpatrick & Pugh, 1984). AN = nectophore antérieur ; DT = dent dorsale ; LVT = dent ventrale gauche ; N = nectosac ; PE = extension pyramydale ; PN = nectophore postérieur ; Som = somatocyste.*

Family CLAUSOPHYIDAE Totton, 1965

Both anterior and posterior nectophores possess a somatocyst. The nectophores are stream-lined, although the hydroecium is more prominent than in the diphyids. The phyllocyst of the eudoxid bracts characteristically bears two fine basal branches extending down into the neck shield.

Genus *CHUNIPHYES* Lens & van Riemsdijk, 1908

Fig. 221A-C

Clausophyids with nectophores with ridges that end in distinct basal teeth. Anterior nectophores with 4 ridges (dorsal, ventral, and a pair of laterals) at the pointed apex. Each of these ridges bifurcates below the apex, the ventral ones forming the margins of the hydroecium, so that there are 8 ridges at the base. Posterior nectophore with 3 ridges (dorsal and pair of laterals) reaching apex, all of which bifurcate further down. Hydroecium extends for virtually the whole length of the nectophore and has 2 large, symmetrical flaps in its upper half. Bract flattened; phyllocyst asymmetrical with an apical and 2 lateral horns in addition to the canals running down into the neck shield.

Chuniphyes moserae Totton, 1954
Chuniphyes multidentata Lens & Van Riemsdijk, 1908

Genus *CLAUSOPHYES* Lens & van Riemsdijk, 1908

Fig. 221D-F

Clausophyids with smooth, unridged, laterally flattened nectophores. Anterior nectophore with deep hydroecium in basal half and is open at the ostial level. Posterior nectophore has a large, notched mouth plate. Lateral radial canals of both nectophores are looped. Somatocyst long tube of varying thickness, part of which is swollen. Bracts are conical with a rounded apex and an extensive neck-shield. The phyllocyst, slightly swollen basally, reaches the apex. For most species the eudoxid stage is unknown.
Recent references: Pugh & Pagès (1993); Pugh (1995).

Clausophyes galeata Lens & Van Riemsdijk, 1908
Clausophyes laetmata Pugh & Pagès, 1993
Clausophyes moserae Margulis, 1988
Clausophyes ovata (Keferstein & Ehlers, 1861) [syn. *C. massiliana* Patriti, 1969]
Clausophyes tropica Pugh, 1995

Genus *CRYSTALLOPHYES* Moser, 1925

Fig. 221G-I

Clausophyids with slender anterior nectophore with 5 ridges, dorso-lateral ridges sharply recurved ventrally at their bases; nectosac up to 3/4 nectophore height, hydroecium deep in the central third extending along all the ventral side; somatocyst swollen in the basal third and tapering towards the nectosac apex, with some short side branches. Posterior nectophore with five ridges, lateral and ventral ones join near the apex. Lateral ridges end basally in distinct teeth; hydroecium extends along the whole length of the nectophore, with lateral flaps, somatocyst long, simple.
Recent references: Zhang & Lin (1997); Pagès & Pugh (2002).

Crystallophyes amygdalina Moser, 1925

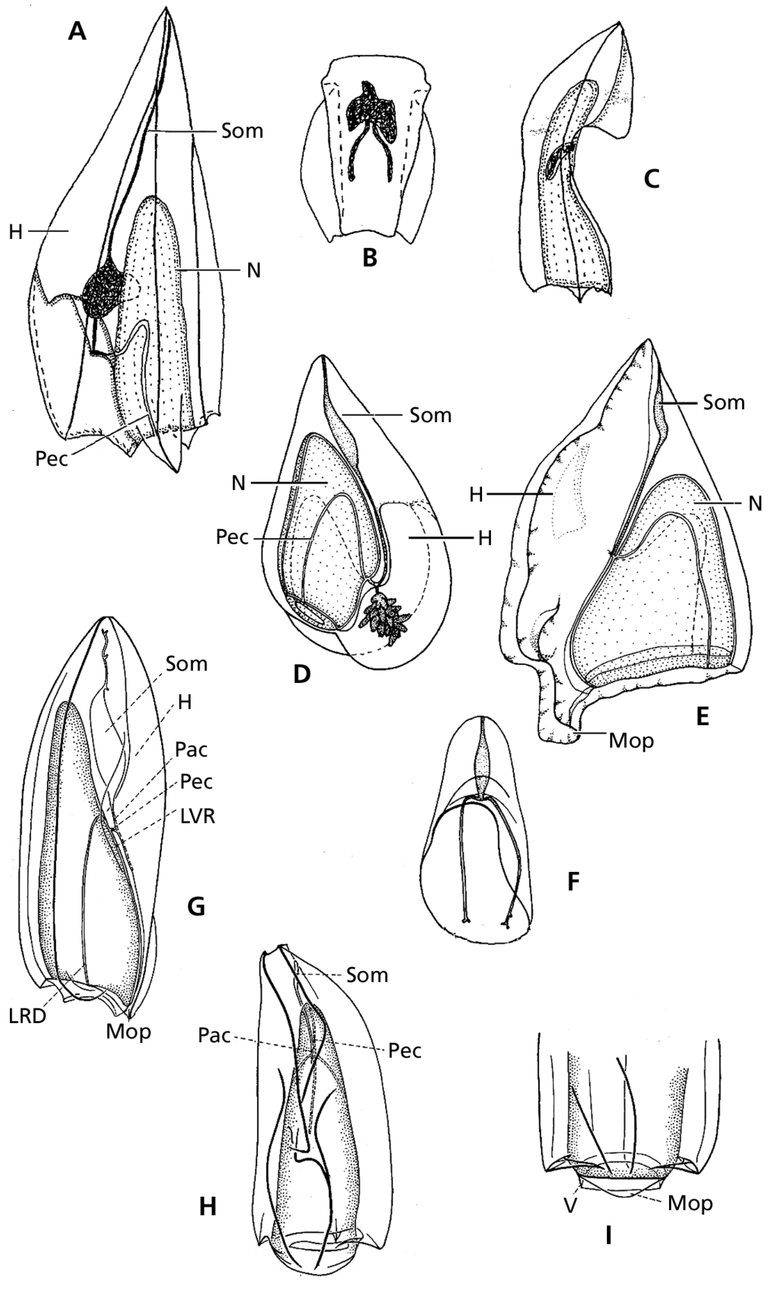

FIG. 221. Siphonophorae, Calycophorae, Clausophyidae. A-C, *Chuniphyes multidentata*: A, lateral view of the anterior nectophore; B, bract; C, gonophore. D-F, *Clausophyes ovata*: D, anterior nectophore (lateral view); E, posterior nectophore (lateral view); F, eudoxid bract (ventral view). G-I, *Crystallophyes amagdalina*: G, lateral view of the anterior nectophore; H, ventral view of the posterior nectophore; I, detail of the mouth plate. (A-C after Pugh, 1999; E-F after Kirckpatrick & Pugh, 1984; D, G-I after Totton, 1965: pl. XXXV, fig. 1; p. 197, fig. 133 A, B, C). H = hydroecium; Mop = mouth-plate; N = nectosac; Pac = pallial canal; Pec = pedicular canal; LRD = lateral dorsal radial canal; LVR= lateral ventral radial canal; Som = somatocyst; V = velum.

FIG. 221. *Siphonophorae, Calycophorae, Clausophyidae. A-C,* Chuniphyes multidentata : *A, nectophore antérieur (vue latérale) ; B, bractées ; C, gonophore. D-F,* Clausophyes ovata : *D, nectophore antérieur (vue latérale) ; E, nectophore postérieur (vue latérale) ; F, bractée de l'eudoxie (vue ventrale). G-I,* Crystallophyes amagdalina : *G, nectophore antérieur (vue latérale) ; H, nectophore postérieur (vue ventrale) ; I, détail de la plaque buccale (A-C d'après Pugh, 1999 ; E-F d'après Kirckpatrick & Pugh, 1984 ; D, G-I d'après Totton, 1965 : pl. XXXV, fig. 1 ; p. 197, fig. 133 A, B, C). H = hydroécie ; Mop = plaque buccale ; N = nectosac ; Pac = canal pallial ; Pec = canal pédiculaire ; LRD = canal radiaire latéro-dorsal ; LVR= canal radiaire latéro-ventral ; Som = somatocyste ; V = velum.*

Genus ***HETEROPYRAMIS*** Moser, 1925

Fig. 222A-C

Clausophyids with anterior nectophore with 5 straight, complete longitudinal ridges; nectosac small, hydroecium located in the ventral medium third; sausage-shaped somatocyst above of the nectosac, tapering towards the nectophore apex. Posterior nectophore not developed. Pyramidal bract, phyllocyst similar to somatocyst.
Recent reference: Pagès & Pugh (2002).

Heteropyramis crystallina (Moser, 1925)
Heteropyramis maculata Moser, 1925

Family DIPHYIDAE Quoy & Gaimard, 1827

Calycophora with polygastric stage with two dissimilar streamlined definitive nectophores arranged serially. Anterior nectophore with somatocyst, posterior not, somatocyst often with oil droplets; hydroecium generally reduced in anterior nectophore; a nectosac occupies most of the nectophore.

Subfamily DIPHYINAE Quoy & Gaimard, 1827

Genus ***CHELOPHYES*** Totton, 1932

Fig. 222D-H

Diphyids with rigid anterior nectophores with 5 ridges, dorsal one extends only a short distance up from the ostium. Claw-shaped hydroecium. Posterior nectophore apically pointed, mouth-plate divided with two strong asymmetric teeth. Conical eudoxid bracts, small rounded neck-shield, relatively deep hydroecium; cylindrical hydroecium that almost stretches the apex.
Recent reference: Pagès & Gili (1992).

Chelophyes appendiculata (Eschscholtz, 1829)
Chelophyes contorta (Lens & Van Riemsdijk, 1908)

Genus ***DIMOPHYES*** (Chun, 1897)

Fig. 222I-K

Diphyids with anterior nectophore without ridges, mouth plate undivided, hydroecium largely opened on its ventral side, carrot-shape somatocyst reaching to about two-thirds the height of the nectophore. Posterior nectophore reduced, with the opening of the nectosac lying dorso-basally. Conical bract with extensive neck-shield that is run by a median canal from the phyllocyst; the latter with apical and lateral horns.
Recent references: Pagès & Gili (1989; 1992).

Dimophyes arctica (Chun, 1897)

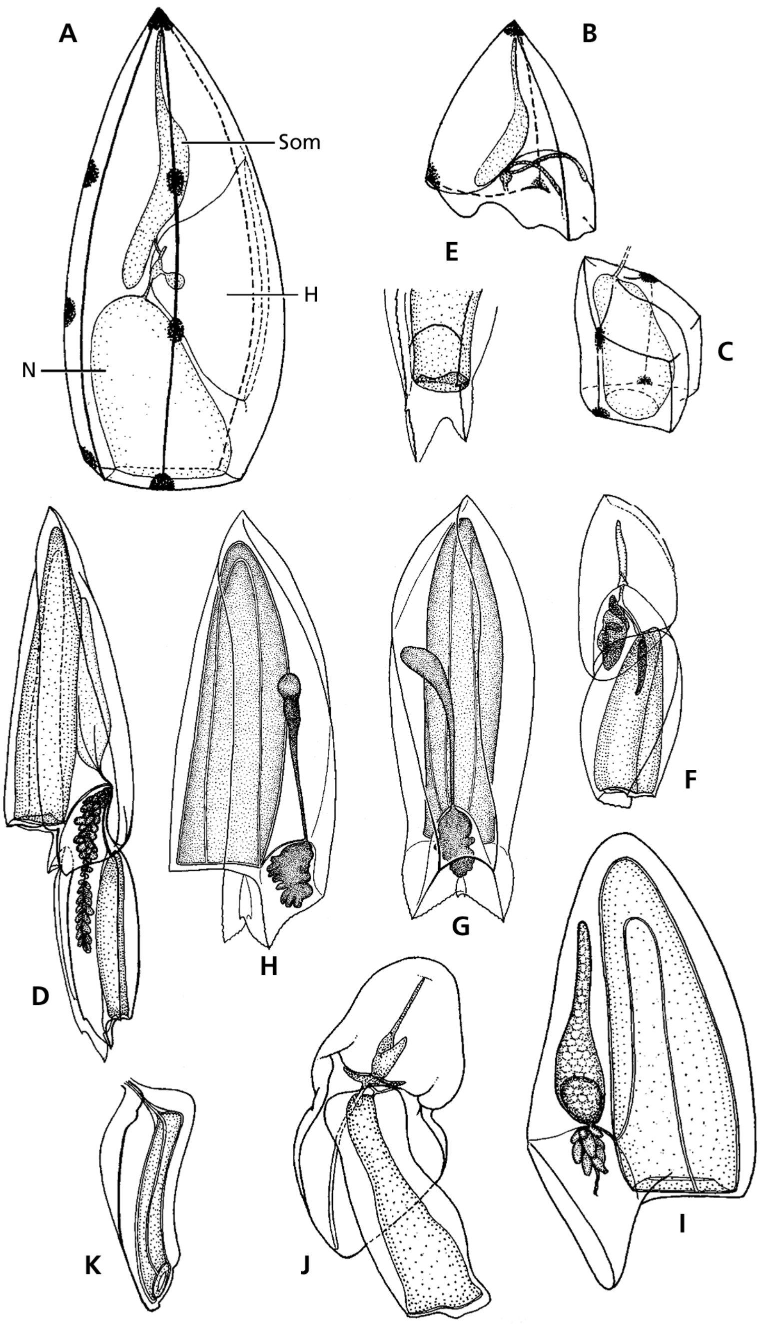

FIG. 222. Siphonophorae, Calycophorae, Clausophyidae. A-C, *Heteropyramis maculata*: A, anterior nectophore (lateral view); B, eudoxid bract; C, gonophore. Diphyidae. D-H, *Chelophyes*. D-F, *Chelophyes appendiculata*: D, polygastric stage; E, detail of mouth-plate of posterior nectophore; F, eudoxid stage; G-H, *Chelophyes contorta*: G, anterior nectophore; H, posterior nectophore. I-K, *Dimophyes arctica*: I, anterior nectophore; J, eudoxid stage; K, posterior nectophore (A-F, I-K after Kirkpatrick & Pugh, 1984; G-H after Pagès & Gili, 1992). H = hydroecium; N = nectosac; Som = somatocyst.

FIG. 222. *Siphonophorae, Calycophorae, Clausophyidae. A-C,* Heteropyramis maculata : *A, nectophore antérieur (vue latérale) ; B, bractée de l'eudoxie ; C, gonophore. Diphyidae. D-H,* Chelophyes. *D-F,* Chelophyes appendiculata : *D, stade polygastrique ; E, détail de la plaque buccale du nectophore postérieur ; F, stade eudoxie ; G-H,* Chelophyes contorta : *G, nectophore antérieur ; H, nectophore postérieur. I-K,* Dimophyes arctica : *I, nectophore antérieur ; J, stade eudoxie ; K, nectophore postérieur (A-F, I-K d'après Kirkpatrick & Pugh, 1984 ; G-H d'après Pagès & Gili, 1992). H = hydroécie ; N = nectosac ; Som = somatocyste.*

Genus *DIPHYES* Cuvier, 1817

Fig. 223A-C

Diphyids with anterior nectophores with 5 complete longitudinal ridges, 3 prominent dorsal teeth in general. Deep hydroecium. Posterior nectophores, when developed, also with 3 ostial teeth in general. Long apical process (apophysis). Bracts generally helmet-shaped.
Recent reference: Pagès & Gili (1992).

Diphyes antarctica Moser, 1925
Diphyes bojani (Eschscholtz, 1829)
Diphyes chamissonis Huxley, 1859
Diphyes dispar Chamisso & Eysenhardt, 1821
Diphyes indica Daniel, 1985 [doubtful status]

Genus *EUDOXIA* Totton, 1954

Fig. 223D-F

This genus includes only singular diphyid sexual stages or eudoxids whose polygastric stage has not been identified yet.

Eudoxia macra Totton, 1954

Genus *EUDOXOIDES* Huxley, 1859

Fig. 223G-K

Diphyids with small, rigid anterior nectophores, spirally twisted or not, with 5 serrated ridges, the dorsal one being complete. Mouth plate divided; no conspicuous ostial teeth. Posterior nectophore, when developed, with curved furrow between apex and pedicel
Recent references: Pagès & Gili (1989; 1992).

Eudoxoides mitra (Huxley, 1859)
Eudoxoides spiralis (Bigelow, 1911a)

Genus *LENSIA* Totton, 1932

Fig. 224C-E

Diphyids with pyramidal anterior nectophores, generally ridged, number and disposition of the ridges being variable, from 5 to many. Small, divided mouth plate, with shallow hydroecium, rarely extending above ostial level. No ostial teeth. Posterior nectophore, when developed, truncated apically with a rounded mouth plate. Bracts helmet-shaped. Shape of phylloyst generally resembling that of somatocyst of anterior nectophore. (need of review).
Recent references: Carré (1968a); Pagès & Gili (1989; 1992).

Lensia achilles Totton, 1941
Lensia ajax Totton, 1941
Lensia asymmetrica Stepanjants, 1970
Lensia baryi Totton, 1965
Lensia beklemishevi Margulis & Alekseev, 1986 [doubtful status]
Lensia campanella (Moser, 1925)
Lensia canopusi Stepanjants, 1977 [doubtful status]
Lensia challengeri Totton, 1954
Lensia conoidea (Keferstein & Ehlers, 1860)
Lensia cordata Totton, 1965
Lensia cossack Totton, 1941
Lensia eltanin Alvariño & Wojtan, 1984 [doubtful status]
Lensia eugenioi Alvariño & Wojtan, 1984 [doubtful status]
Lensia exeter Totton, 1941
Lensia fowleri (Bigelow, 1911b)
Lensia gnanamuthui Daniel & Daniel, 1964 [doubtful status]
Lensia grimaldi Leloup, 1933
Lensia hardy Totton, 1941

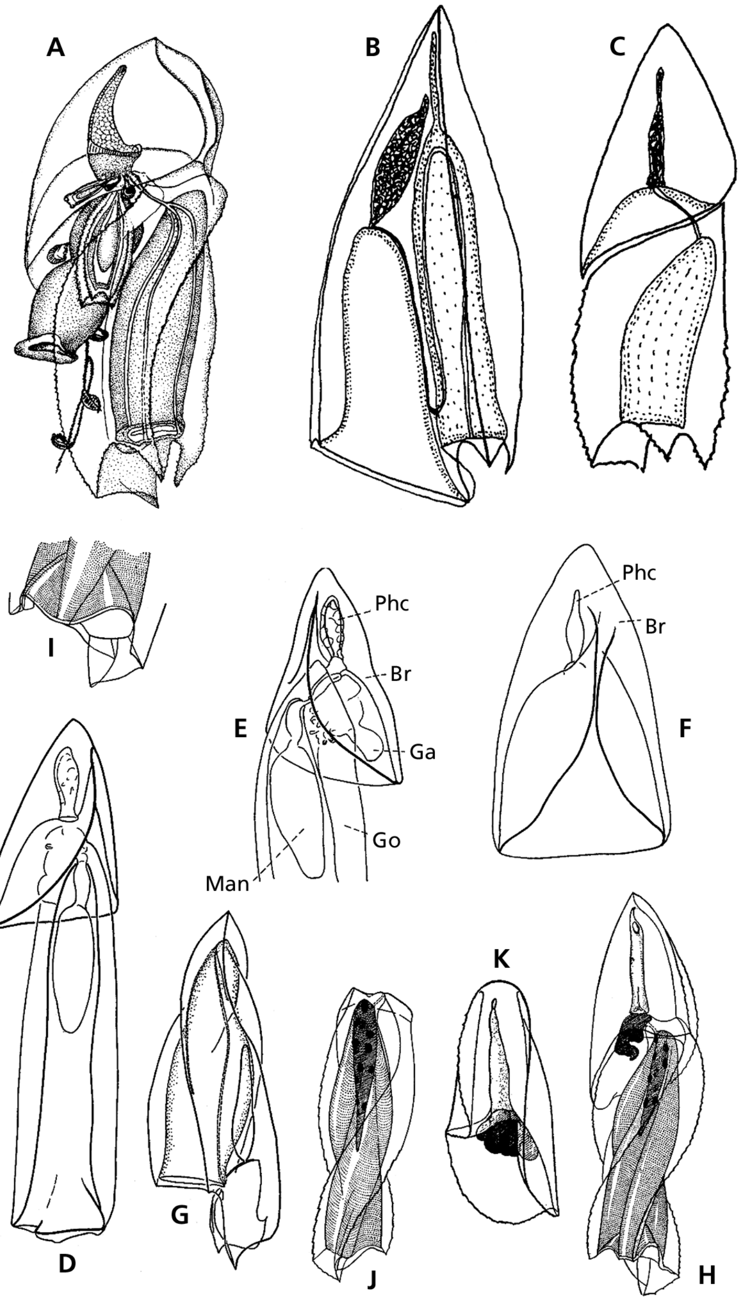

FIG. 223. Siphonophorae, Calycophorae, Diphyidae. A-C, *Diphyes dispar*: A, polygastric phase; B, anterior nectophore (lateral view); C, bract and gonophore. D-F, *Eudoxia macra*: D, whole eudoxid stage; E, detail of the eudoxial bract and of the apical part of the gonophore; F, eudoxid bract. G-K, *Eudoxoides spiralis*: G, polygastric stage; H, lateral view of a whole animal; I, enlarged view of the base of figure H; J, lateral view of a detached femelle gonophore; K, ventral view of the bract (A after Trégouboff, 1957: pl. 83, fig. 8; B-C after Pugh, 1999a; D-K after Totton, 1965: p. 190, figs 128-129; p. 191, fig. 130 A, B, C). Br = bract; Ga = gastrozooid; Go = gonophore; Man = manubrium; Phc= phyllocyst.

***FIG. 223.** Siphonophorae, Calycophorae, Diphyidae. A-C,* Diphyes dispar : *A, stade polygastrique ; B, nectophore antérieur (vue latérale) ; C, bractée et gonophore. D-F,* Eudoxia macra : *D, stade eudoxie complet ; E, détail de la bractée de l'eudoxie et de la partie apicale du gonophore ; F, bractée de l'eudoxie. G-K,* Eudoxoides spiralis : *G, stade polygastrique ; H, vue latérale d'un animal complet ; I, vue élargie de la base de la figure H ; J, vue latérale d'un gonophore femelle détaché ; K, vue ventrale d'une bractée (A d'après Trégouboff, 1957 : pl. 83, fig. 8 ; B-C d'après Pugh, 1999a ; D-K d'après Totton, 1965 : p. 190, fig. 128-129 ; p. 191, fig. 130 A, B, C). Br = bractée ; Ga = gastérozoïde ; Go = gonophore ; Man = manubrium ; Phc = phyllocyste.*

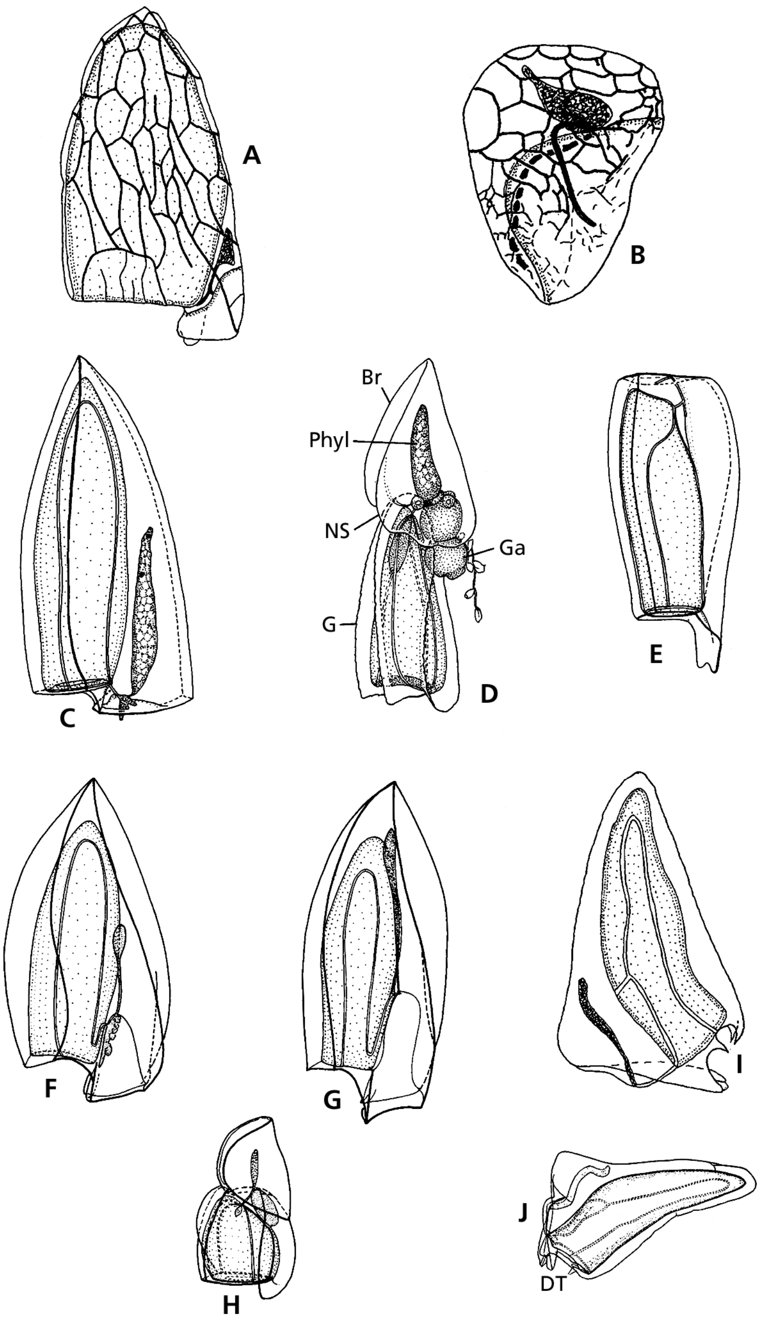

FIG. 224. Siphonophorae, Calycophorae, Diphyidae. A-B, *Gilia reticulata*: A, lateral view of an anterior nectophore; B, bract with gonophore. C-E, *Lensia conoidea*: C, anterior nectophore; D, eudoxid stage; E, posterior nectophore. F-H, *Muggiaea*: F, *Muggiaea kochi*, anterior nectophore (lateral view); G, *Muggiaea atlantica,* anterior nectophore (lateral view); H, *Muggiaea* sp., eudoxid stage (lateral view). I-J, *Sulculeolaria quadrivalvis*: I, lateral view of an anterior nectophore; J, lateral view of an anterior nectophore in the position of horizontal progression (A-B & I after Pugh, 1999a; C-H after Kirkpatrick & Pugh, 1984; J after Totton, 1965: p. 144, fig. 82 C). Br = bract; DT = dorsal teeth; G = gonophore; Ga = gastrozooid; NS = neck-shield; Phyl = phyllocyst.

FIG. 224. *Siphonophorae, Calycophorae, Diphyidae. A-B,* Gilia reticulata *: A, nectophore antérieur (vue latérale) ; B, bractée et gonophore. C-E,* Lensia conoidea *: C, nectophore antérieur ; D, stade eudoxie ; E, nectophore postérieur. F-H,* Muggiaea *: F,* Muggiaea kochi*, nectophore antérieur (vue latérale) ; G,* Muggiaea atlantica*, nectophore antérieur (vue latérale) ; H,* Muggiaea *sp., stade eudoxie (vue latérale). I-J,* Sulculeolaria quadrivalvis *: I, nectophore antérieur (vue latérale) ; J, vue latérale d'un nectophore antérieur en position de progression horizontale (A-B & I d'après Pugh, 1999a ; C-H d'après Kirkpatrick & Pugh, 1984 ; J d'après Totton, 1965 : p. 144, fig. 82 C). Br = bractée ; DT = dent dorsale ; G = gonophore ; Ga = gastérozoïde ; NS = extention de la bractée de l'eudoxie ; Phyl = phyllocyste.*

Lensia havock Totton, 1941
Lensia hostile Totton, 1941
Lensia hotspur Totton, 1941
Lensia hunter Totton, 1941
Lensia landrumae Alvariño & Wojtan, 1984
Lensia lebedevi Alekseyev, 1984 [doubtful status]
Lensia leloupi Totton, 1954
Lensia lelouveteau Totton, 1941
Lensia meteori (Leloup, 1934b)
Lensia minuta Patriti, 1970 [doubtful status]
Lensia multicristata (Moser, 1925)
Lensia multicristoides Zhang & Ling 1988 [doubtful status]
Lensia nagabhushanami Daniel, 1970 [doubtful status]
Lensia pannikari Daniel, 1970 [doubtful status]
Lensia patriti Alekseyev, 1984[doubtful status]
Lensia roonwali Daniel, 1970 [doubtful status]
Lensia subtilis (Chun, 1886)
Lensia subtiloides (Lens & Van Riemsdijk, 1908)
Lensia tiwari Daniel, 1971 [doubtful status]
Lensia tottoni Daniel & Daniel, 1963 [doubtful status]
Lensia zenkevitchi Margulis, 1970

Genus ***MUGGIAEA*** Bush, 1851

Figs 37A, 224F-H

Diphyids with posterior nectophore not developed. Pyramidal anterior nectophore with 5 ridges. Deep hydroecium not open ventrally, divided mouth plate may be oblique. Somatocyst lies very close to wall of nectosac.
Recent references: Russell (1938); Pagès & Gili (1989; 1992).

Muggiaea atlantica Cunningham, 1892
Muggiaea bargmannae Totton, 1954
Muggiaea delsmani Totton, 1954
Muggiaea kochi (Will, 1844)

Subfamily GILIINAE Pugh & Pagès, 1995

Monotypic subfamily for genus *Gilia*.

Genus ***GILIA*** Totton, 1954

Fig. 224A-B

Diphyids with anterior nectophore reticulated, mouth plate divided, hydroecium extending above ostial level, small ovoid somatocyst. Bract reticulated; phyllocyst with two canals running down into the neck shield.
Recent reference: Pugh & Pagès (1995).

Gilia reticulata (Totton, 1941) [as *Lensia*]

Subfamily SULCULEOLARIINAE Totton, 1954.

Monotypic subfamily for the genus *Sulculeolaria*.

Genus ***SULCULEOLARIA*** Blainville, 1834

Figs 38C, 224I-J

Diphyids with anterior nectophore with rounded apex, and without ridges; posterior nectophore of similar size with extensively looped lateral radial canals. Replacement nectophores of both types frequently produced with different characters. Small leaf-like bracts that may not be released as eudoxids.
Recent references: Carré (1979); Pagès & Gili (1992).

Sulculeolaria angusta Totton, 1954
Sulculeolaria bigelowi (Sears, 1950) [doubtful status]
Sulculeolaria biloba (M. Sars, 1846)
Sulculeolaria chuni (Lens & Van Riemsdijk, 1908)
Sulculeolaria monoica (Chun, 1888)
Sulculeolaria pacifica (Stepanjants, 1973) [doubtful status]
Sulculeolaria quadrivalvis de Blainville, 1834
Sulculeolaria turgida (Gegenbaur, 1853) [syn. *S. tropica* Zhang Jinbiao, 1980]
Sulculeolaria xihaensis Hong & Zhang, 1981[perhaps a syn. of *S. chuni*]

Family HIPPOPODIIDAE Kölliker, 1853

Calycophora with biserial arrangement of up to 16 or more flattened definitive nectophores in varying stages of development, the youngest being apical, nectophores fitting tightly together around a thin stem which can be retracted between them; without bracts, somatocyst curving smoothly over mid-dorsal surface of hydroecium.
Remarks: all the species of this family may well be congeneric (Totton, 1965; Kirkpatrick & Pugh, 1984)

Genus ***HIPPOPODIUS*** Quoy & Gaimard, 1827

Fig. 225A-D

Hippopodiids with horseshoe shaped definitive nectophores with 4 rounded dorsal protuberances of variable size forming an arc above ostium of nectosac; larval nectosac of nectophore with only two radial canals.
Recent reference: Pagès & Gili (1992).

Hippopodius hippopus (Forskål, 1776)

Genus ***VOGTIA*** Kölliker, 1853

Fig. 225E-G

Hippopodiids with distinctive protuberances, or spines, or ridges; larval nectosac of nectophore with 4 radial canals.
Recent references: Pagès & Gili (1992); Pugh (1999a).

Vogtia glabra Bigelow, 1918
Vogtia kurvae Alvariño, 1967 [doubtful status]
Vogtia microsticella Zhang & Lin, 1991 [doubtful status]
Vogtia pentacantha Kölliker, 1853b
Vogtia serrata (Moser, 1925)
Vogtia spinosa Keferstein & Ehlers, 1861

Family PRAYIDAE Kölliker, 1853

Nectophores relatively large and usually rounded, mesoglea abundant; larval nectophore sometimes retained during polygastric stage or replaced by one to four definitive nectophores, whose somatocysts are often complexly branched; the eudoxid bracts are rounded and unridged.
Recent reference: Pugh (1992c).

Subfamily AMPHICARYONINAE Chun, 1888

Two nectophores differing in size. The larger, rounded one is believed to be the retained larval nectophore. The first definitive one smaller or vestigial. The bracteal canals are reduced to 2 long hydroecials. Bracts undistinguishable at present.

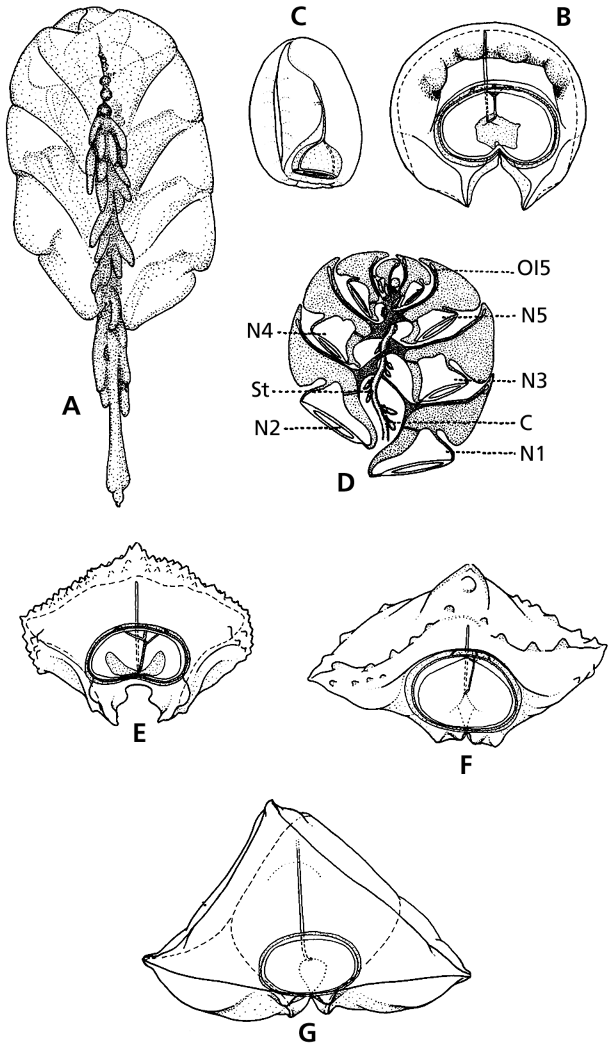

FIG. 225. Siphonophorae, Calycophorae, Hippopodiidae. A-D, *Hippopodius hippopus*: A, polygastric stage; B, definitive nectophore; C, larval nectophore; D, schema of the disposition of the nectophores in a colony. E-G, *Vogtia*, definitive nectophores (dorsal views): E, *Vogtia spinosa*; F, *Vogtia pentacantha*; G, *Vogtia serrata* (A-C, E-G after Kirkpatrick & Pugh, 1984; D after Trégouboff, 1957: pl. 80, fig. 1). C = cormidia; N1, N2, N3, N4, N5 = nectophores; Ol5 = oleocyte of nectophore n° 5; St = stolon.

***FIG. 225.** Siphonophorae, Calycophorae, Hippopodiidae. A-D,* Hippopodius hippopus *: A, stade polygastrique ; B, nectophore définitif ; C, nectophore larvaire ; D, schéma de la disposition des nectophores dans une colonie. E-G,* Vogtia*, nectophores définitifs (vue dorsale) : E,* Vogtia spinosa *; F,* Vogtia pentacantha *; G,* Vogtia serrata *(A-C, E-G d'après Kirkpatrick & Pugh, 1984 ; D d'après Trégouboff, 1957 : pl. 80, fig. 1). C = cormidie ; N1, N2, N3, N4, N5 = nectophores ; Ol5 = oleocyte du nectophore n° 5 ; St = stolon.*

Genus ***AMPHICARYON*** Chun, 1888

Fig. 226A-B

Prayids with two dissimilar nectophores; the larger, which is possibly the retained larval nectophore, partly encloses the reduced or vestigial definitive nectophore. The nectosac of the latter does not have an ostium. The eudoxid bract has a pair of lateral hydroecial canals.

Recent reference: Pagès & Gili (1992).

Amphicaryon acaule Chun, 1888
Amphicaryon ernesti Totton, 1954
Amphicaryon intermedia Daniel, 1974
Amphicaryon peltifera (Haeckel, 1888)

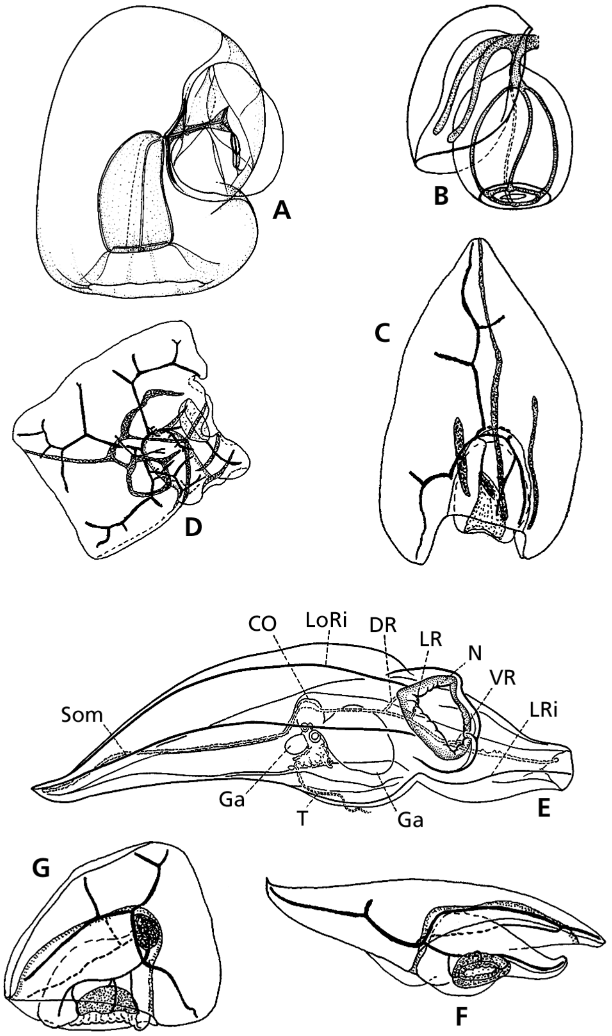

FIG. 226. Siphonophorae, Calycophorae. A-B, Prayidae, Amphicaryoninae, *Amphicaryon acaule*: A, nectophore of polygastric stage; B, eudoxid stage. C-D, Prayidae, Nectopyramidinae, *Nectadamus diomedeae*: C, eudoxid stage; D, definitive nectophore (lateral view). E-G, *Nectopyramis*: E-F, *Nectopyramis natans*: E, polygastric stage; F, eudoxid stage; G, *Nectopyramis thetis*, eudoxid stage (A-B after Kirkpatrick & Pugh, 1984; C-D, F-G after Pugh, 1999a; E after Totton, 1965: p. 136, fig. 78). CO = central organ; DR = dorsal radial canal; Ga = gastrozooid; LoRi = longitudinal ridge; LR = lateral radial canal; LRi = lateral ridge; N = nectosac; Som = somatocyst; T = tentacle; VR = ventral radial canal.

***FIG. 226.** Siphonophorae, Calycophorae. A-B, Prayidae, Amphicaryoninae,* Amphicaryon acaule : *A, nectophore du stade polygastrique ; B, stade eudoxie. C-D, Prayidae, Nectopyramidinae,* Nectadamus diomedeae : *C, stade eudoxie ; D, nectophore définitif (vue latérale). E-G,* Nectopyramis : *E-F,* Nectopyramis natans : *E, stade polygastrique ; F, stade eudoxie ; G,* Nectopyramis thetis*, stade eudoxie (A-B d'après Kirkpatrick & Pugh, 1984 ; C-D, F-G d'après Pugh, 1999a ; E d'après Totton, 1965 : p. 136, fig. 78). CO = organe central ; DR = canal radiaire dorsal ; Ga = gastérozoïde ; LoRi = crête longitudinale ; LR = canal radiaire latéral ; LRi = crête latérale ; N = nectosac ; Som = somatocyste ; T = tentacule ; VR = canal radiaire ventral.*

Subfamily NECTOPYRAMIDINAE Bigelow, 1911

Only a single asymmetrical large definitive nectophore, which bears a vague pattern of ridges. Eudoxid stage resembles nectophore and a special nectophore may be present.

Genus ***NECTODAMAS*** Pugh, 1992

Fig. 226C-D

Prayids from which the definitive nectophore bears a complex pattern of lateral ridges and, in the apico-dorsal plane, a circumferential ridge that divides to circumvent the openings of the nectosac and hydroecium. Somatocyst short, from which branch three primary canals that run only in the apico-dorsal plane. The radial canals of the nectosac arise from, or close to, a single pedicular canal. Hydroecium small pocket-shaped, with a narrow ventral opening. Small rounded larval

nectophore appears to have circumferential and lateral ridges. The arrangement of the nectosac and hydroecium are similar to the definitive nectophore, although the latter is more extensive. Somatocyst simple, although small, median branches may be present. The bract is roughly triangular or a truncate ovoid in shape. It bears ridges, including a circumferential ridge. The canal system of basic prayid design, although the "spurs" to the longitudinal canals are much reduced or absent. Large gonophore with a pedicular canal from which the canals of the subumbrella arise together. Without special nectophore.
Recent reference: Pugh (1992a).

Nectodamas richardi Pugh, 1992a
Nectodamas diomedeae (Bigelow, 1911b)

Genus ***NECTOPYRAMIS*** Bigelow, 1911
Fig. 226E-G

Prayids with elongate or pyramidal definitive nectophore with longitudinal ridges. The hydroecium stretches the entire length of the ventral surface, but apically has little if any depth. Somatocyst short, which may have lateral branches and, basally, may be deflected to one side. The dorsal, lateral and ventral canals to the nectosac arise directly and separately from the pedicular canal; the laterals also may arise separately. Small larval nectophore with spinose ridges. Somatocyst simple and the radial canals to the nectosac arise directly from it. The somatocyst extends, basally, beyond the point of origin of the ventral radial canal. The free-living eudoxid consists of a bract, a special nectophore, some small gonophores, gastrozooid and tentacle. The bract bears an apico-ventral and pairs of dorso-lateral and hydroecial ridges. Canal system of basic prayid design. A branch from the dorsal canal to the dorsal surface usually is present. The large special nectophore has the dorsal, lateral and ventral canals to the sub-umbrella arising separately, as in the definitive nectophore. Gonophores small.
Recent reference: Pugh (1992a).

Nectopyramis natans (Bigelow, 1911) [syn. *N. spinosa* Sears, 1953]
Nectopyramis thetis Bigelow, 1911b

Sub-family PRAYINAE Kölliker, 1853

Prayids with two, occasionally up to 4, rounded, smooth-walled nectophores of similar size. Bracts with 6 canals, occasionally reduced to 5.

Genus ***CRASEOA*** Pugh & Harbison, 1987
Fig. 227

Prayids with an apposed pair of cylindrical nectophores. Somatocyst simple, without either ascending or descending branch. The lateral radial canals on the small nectosac are S-shaped. The bracts are rounded and divided into two almost equal lobes by a deep fissure. Six bracteal canals are present. The gonophores are asymmetric in shape with wing-like expansions. The sub-umbrella cavity is relatively small, occupying only part of the lower half of the gonophore. The arrangement of the two mantle canals is slightly asymmetric. Special, asexual nectophores are absent.
Recent reference: Pugh & Harbison (1987).

Craseoa lathetica Pugh & Harbison, 1987

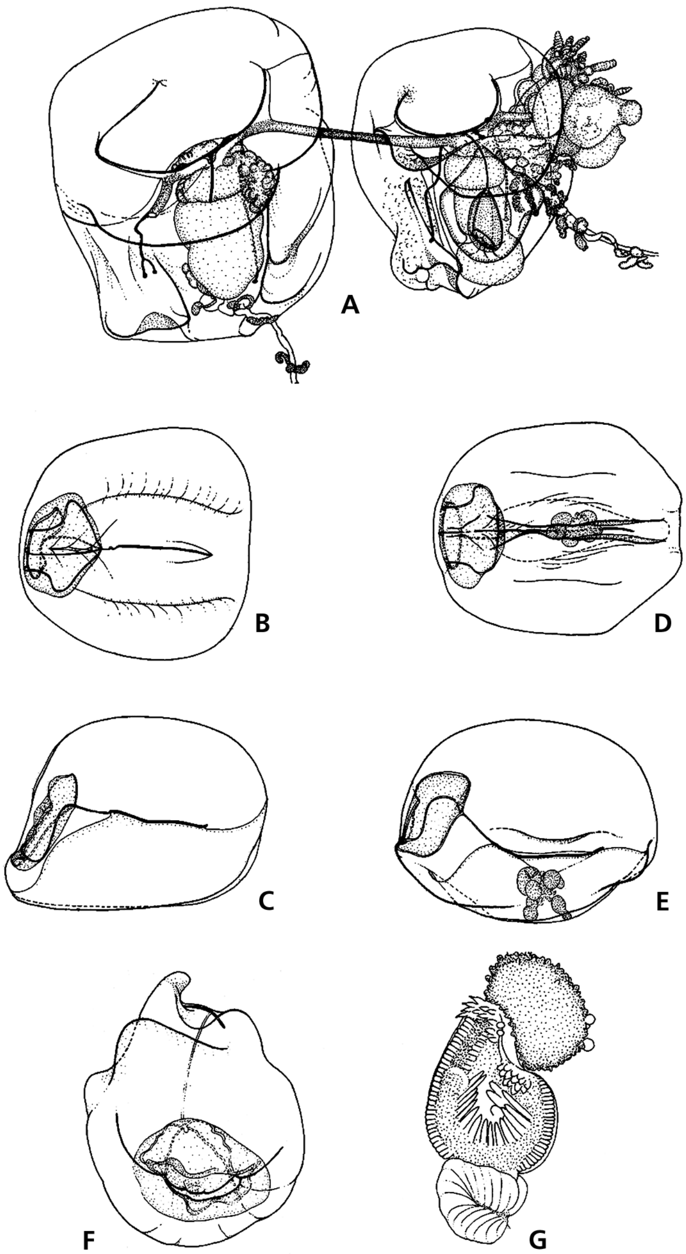

FIG. 227. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G, *Craseoa lathetica*: A, two attached stem groups viewed ventrally; B-C, nectophores n° 1: B, ventral view; C, lateral view; D-E, nectophore n° 2: D, ventral view; E, lateral view; F, gonophore; G, tentillum (all after Pugh & Harbison, 1987).

FIG. 227. *Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G,* Craseoa lathetica *: A, deux groupes cormidiaux attachés (vue ventrale) ; B-C, nectophores n° 1 : B, vue ventrale ; C, vue latérale ; D-E, nectophores n° 2 : D, vue ventrale ; E, vue latérale ; F, gonophore ; G, tentille (d'après Pugh & Harbison, 1987).*

Genus ***DESMOPHYES*** Haeckel, 1888

Fig. 228A-C

Prayids with usually two flimsy, ovoid nectophores but there can be up to 6 biserially arranged nectophores. Nectosac small and shallow, with four straight radial canals. Somatocyst unbranched and with a distinctive whitish swelling at the apex. Bracts small, compact and kidney-shaped, characterized by the presence of a large white spherical or ovoid central organ, giving rise to the thin bracteal canal. Gonophores fragile and reduced.
Recent references: Pugh (1992a, b; 1999b).

Desmophyes annectens Haeckel, 1888
Desmophyes haematogaster Pugh, 1992b
Desmophyes villafrancae (Carré, 1969a)

Genus ***LILYOPSIS*** Chun, 1885

Fig. 228D-F

Prayids with two, possibly more, very delicate nectophores with large nectosacs. Larval nectophore has a simple somatocyst, slightly swollen at its tip, and straight radial canals on the nectosac. Definitive nectophore has a bifurcated somatocyst and sinuous lateral canals on the nectosac. Bract like a cushion, with characteristically arranged canals.
Recent references: Carré (1969b); Pugh (1999a).

Lilyopsis rosea Chun, 1885

Genus ***MARESEARSIA*** Totton, 1954

Fig. 228G-I

Prayid with two rounded nectophores, both with a functional flask-shaped nectosac, fit together to form a ball-like structure. The larval nectophore has large, often swollen somatocyst, while that of the definitive one is minute. The radial canals on the nectosac of the larval nectophore are highly branched near their bases, and those of the definitive one also show some branching. Small, spherical bract with 2 recurved hydroecial canals.
Recent reference: Pugh (1999a).

Maresearsia praeclara Totton, 1954

Genus ***MISTOPRAYINA*** Pugh & Harbison, 1987

Fig. 229

Prayid with an apposed pair of conoid nectophores. The nectosac is extensive occupying the basal two-thirds of the nectophore, and has a wide dorso-basal opening. In one nectophore the lateral radial canals are straight, while in the other they are slightly curved. A descending branch to the somatocyst is present in both nectophores, while a simple ascending branch, penetrating dorsally into the mesoglea occurs only in one of them. The young bracts are saddle-shaped, but with age become flattened, with the stem attachment region raised on a mesogleal process. Six bracteal canals are present. The rounded gonophores possess a very extensive sub-umbrella cavity. The two mantle canals are of different lengths, the longer being distinctly recurved. No special, asexual nectophores are present.

Mistoprayina fragosa Pugh & Harbison, 1987

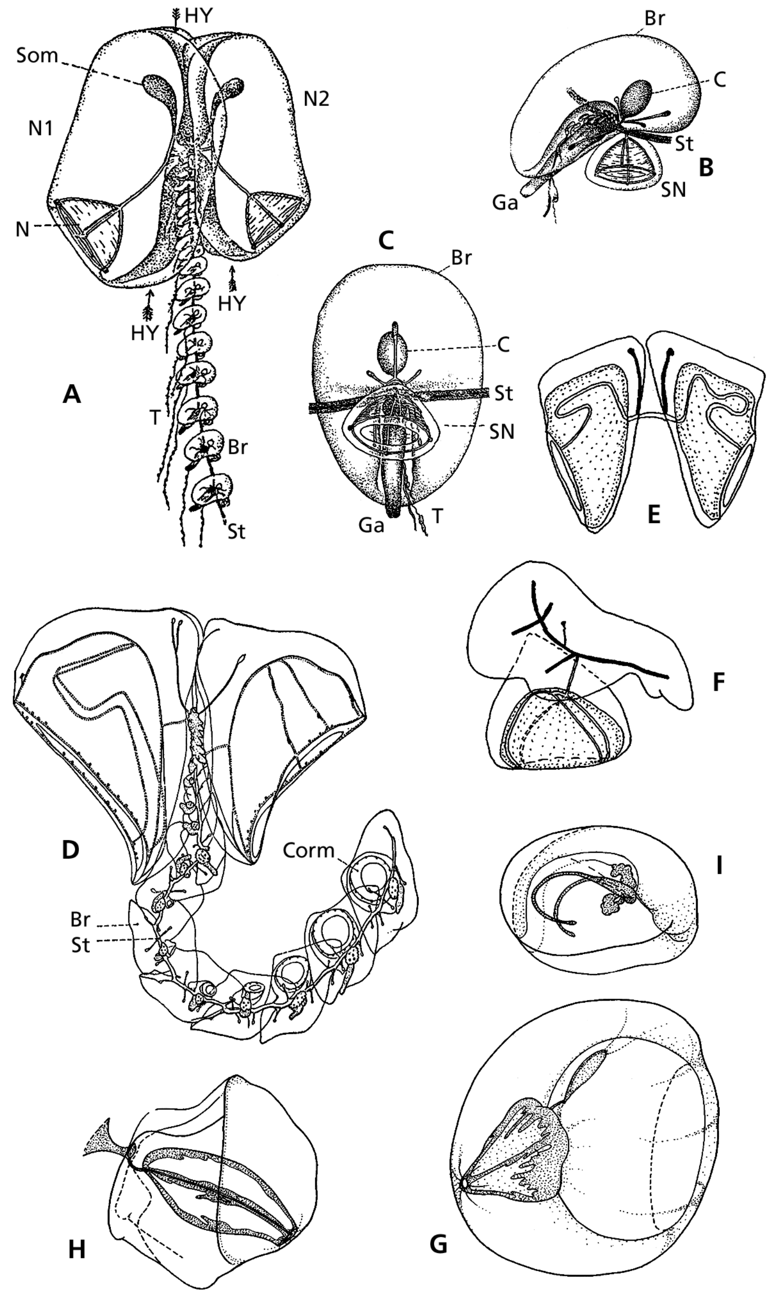

FIG. 228. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-C, *Desmophyes annectens*: A, polygastric stage; B, eudoxid phase (lateral view); C, eudoxid phase (dorsal view). D-F, *Lilyopsis rosea*: D, polygastric stage; E, nectophore (lateral view); F, bract. G-I, *Maresearsia praeclara*: G, larger nectophore; H, smaller nectophore; I, eudoxid bract (A-C after Totton, 1965: pl. XXII, figs 4, 5, 6; D after Carré & Carré, 1995: p. 571, fig. 192; E-F after Pugh, 1999a; G-I after Kirkpatrick & Pugh, 1984). Br = bract; C = central organ; Corm = cormidia; Ga = gastrozooid; HY = hydroecium; N = nectosac; N1, N2 = nectophore 1, nectophore 2; Som = somatocyst; SN = special nectophore; St = stolon; T = tentacle.

FIG. 228. *Siphonophorae, Calycophorae, Prayidae, Prayinae. A-C,* Desmophyes annectens : *A, stade polygastrique ; B, stade eudoxie (vue latérale) ; C, stade eudoxie (vue dorsale) ; D-F,* Lilyopsis rosea : *D, stade polygastrique ; E, nectophore (vue latérale) ; F, bractée. G-I,* Maresearsia praeclara : *G, grand nectophore ; H, petit nectophore ; I, bractée de l'eudoxie (A-C d'après Totton, 1965 : pl. XXII, figs 4, 5, 6 ; D d'après Carré & Carré, 1995 : p. 571, fig. 192 ; E-F d'après Pugh, 1999a ; G-I d'après Kirkpatrick & Pugh, 1984). Br = bractée ; C = organe central ; Corm = cormidie ; Ga = gastérozoïde ; HY = hydroécie ; N = nectosac ; N1, N2 = nectophore 1, nectophore 2 ; Som = somatocyste ; SN = nectophore spécial ; St = stolon ; T = tentacule.*

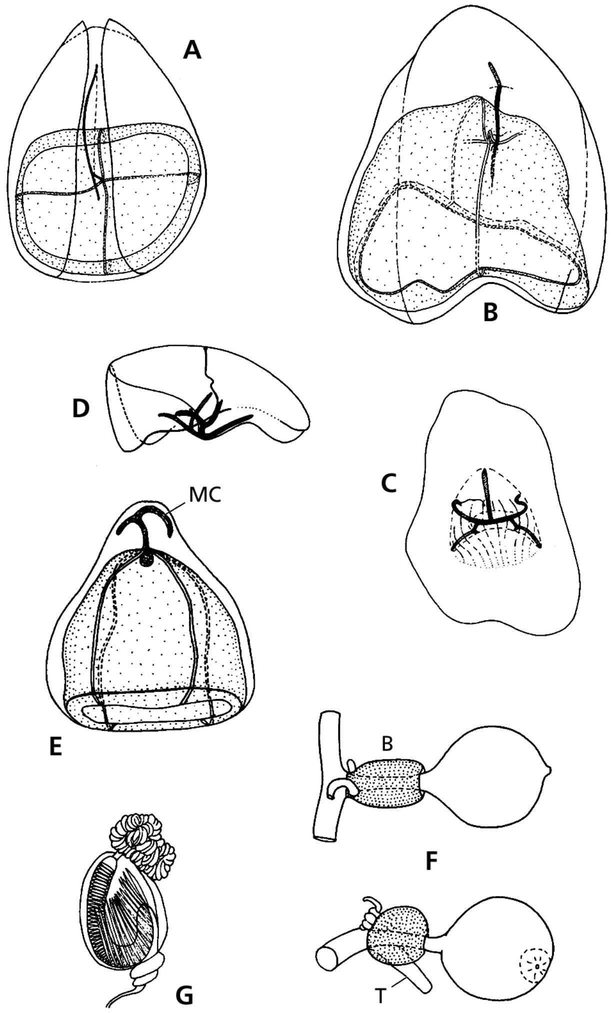

FIG. 229. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G, *Mistoprayina fragosa*: A, nectophore nº 1; B, ventro-lateral view of nectophore nº 2; C, ventral view of a large bract; D, lateral view of a large bract; E, gonophore; F, gastrozooids with basigasters; G, tentillum (all after Pugh & Harbison, 1987). B = basigaster; MC = mantle canal; T = tentacle.

***FIG. 229.** Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G,* Mistoprayina fragosa *: A, nectophore nº 1 ; B, vue ventro-latérale du nectophore nº 2 ; C, vue ventrale d'une grande bractée ; D, vue latérale d'une grande bractée ; E, gonophore ; F, gastérozoïdes avec basigasters ; G, tentille (d'après Pugh & Harbison, 1987). B = basigaster ; MC = canal du manteau ; T = tentacule.*

Genus ***PRAYA*** Quoy & Gaimard in Blainville, 1834

Fig. 230A-C

Synonym: *Prayoides* Leloup, 1934.

Prayids with two large, rounded nectophores (often with additional reserve bells) whose somatocysts can be complexly branched. Multibranched radial canals on nectosac. Bract laterally flattened with dorsal canal arising from end of spur-like right longitudinal canal. Gonophores with characteristically three-pronged mantle canal.

Recent references: Pagès & Gili (1992); Pugh (1992a; 1999a).

Praya dubia (Quoy & Gaimard, 1833)
Praya reticulata (Bigelow, 1911b)

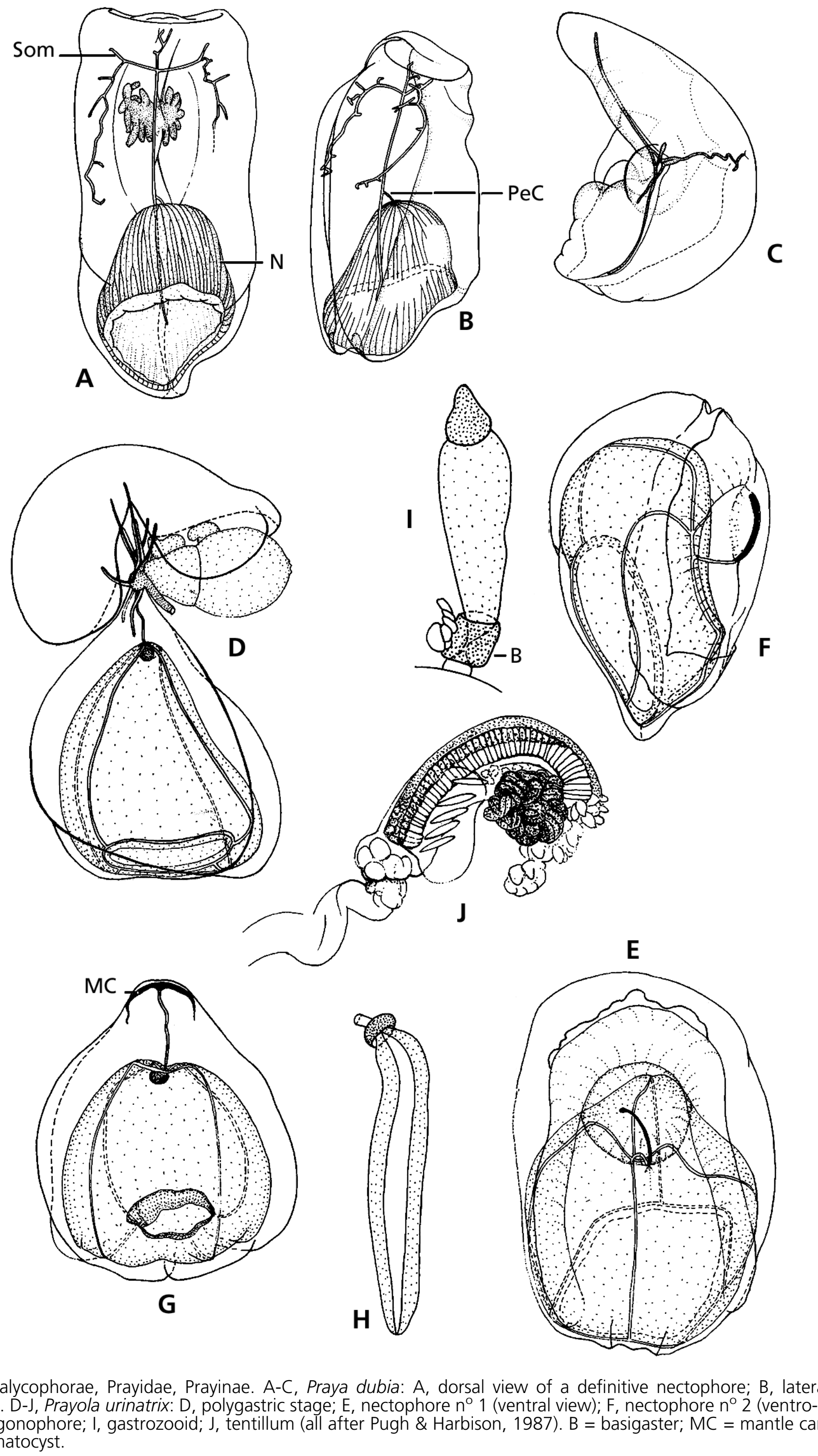

FIG. 230. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-C, *Praya dubia*: A, dorsal view of a definitive nectophore; B, lateral view of a definitive nectophore; C, eudoxid bract. D-J, *Prayola urinatrix*: D, polygastric stage; E, nectophore n° 1 (ventral view); F, nectophore n° 2 (ventro-lateral view); G, young gonophore; H, mature male gonophore; I, gastrozooid; J, tentillum (all after Pugh & Harbison, 1987). B = basigaster; MC = mantle canal; N = nectosac; PeC = pedicular canal; Som = somatocyst.

FIG. 230. *Siphonophorae, Calycophorae, Prayidae, Prayinae. A-C,* Praya dubia : *A, vue dorsale d'un nectophore définitif ; B, vue latérale d'un nectophore définitif ; C, bractée de l'eudoxie. D-J,* Prayola urinatrix : *D, stade polygastrique ; E, nectophore n° 1 (vue ventrale) ; F, nectophore n° 2 (vue ventro-latérale) ; G, jeune gonophore ; H, gonophore mâle mature ; I, gastérozoïde ; J, tentille (d'après Pugh & Harbison, 1987). B = basigaster ; MC = canal du manteau ; N = nectosac ; PeC = canal pédiculaire ; Som = somatocyste.*

Genus ***PRAYOLA*** Carré, 1969

Fig. 230D-J

Prayids with an apposed pair of conoid nectophores, whose extensive nectosacs (>half the height of the nectophore) open dorso-basally. The radial canals on the nectosac are slightly curved, suggesting an open S. The somatocyst possesses neither an ascending nor a descending branch. The bracts have only five bracteal canals, there being no dorsal one. The gonophores possess a hydroecial gutter and two mantle canals of equal length. No special, asexual nectophores are present.
Recent reference: Pugh & Harbison (1987).

Prayola tottoni Carré, 1969c
Prayola urinatrix Pugh & Harbison, 1987

Genus ***ROSACEA*** Quoy & Gaimard, 1827

Figs 37C, 231A-B

Prayids with two medium, rounded nectophores with simple somatocyst without side branches. Sinuous lateral radial canals on nectosac. Bracts kidney-shaped, but with characteristic arrangement of canals.
Recent references: Purcell (1981b); Pugh & Harbison (1987); Pagès & Gili (1992).

Rosacea arabiana Pugh, *in press*
Rosacea cymbiformis (Delle Chiaje, 1822)
Rosacea flaccida Biggs, Pugh & Carré, 1978
Rosacea limbata Pugh & Youngbluth, 1988
Rosacea plicata (Quoy & Gaimard, 1833)
Rosacea repanda Pugh & Youngbluth, 1988

Genus ***STEPHANOPHYES*** Chun, 1888

Fig. 231C-D

Prayid with four large nectophores forming a corona. Somatocyst with only one bifurcation in young stages of development, but in mature nectophores each of these branches may rebranch complexly about ten times, the tips of the branchlets being pigmented. When fully grown the nectosac ostium lies nearly parallel with the long axis. Unique amongst calycophorans, the stem groups bear in addition to the gastrozooids, nectophores, bracts, and gonophores some characteristic reduced palpons growing singly or two to three on a single pedicel. They bear heteromorphic tentacles. The lateral radial canals of the special swimming bells meander.

Stephanophyes superba Chun, 1888

Family SPHAERONECTIDAE Huxley, 1859

Calycophora with small, fragile spherical nectophore of larval origin, the only nectophore in the polygastric stage. Bract also small and spherical.

Genus ***SPHAERONECTES*** Huxley, 1859

Fig. 231E-F

See family characters.
Recent references: Carré (1968c); Purcell & Kremer (1983); Pagès & Gili (1992).

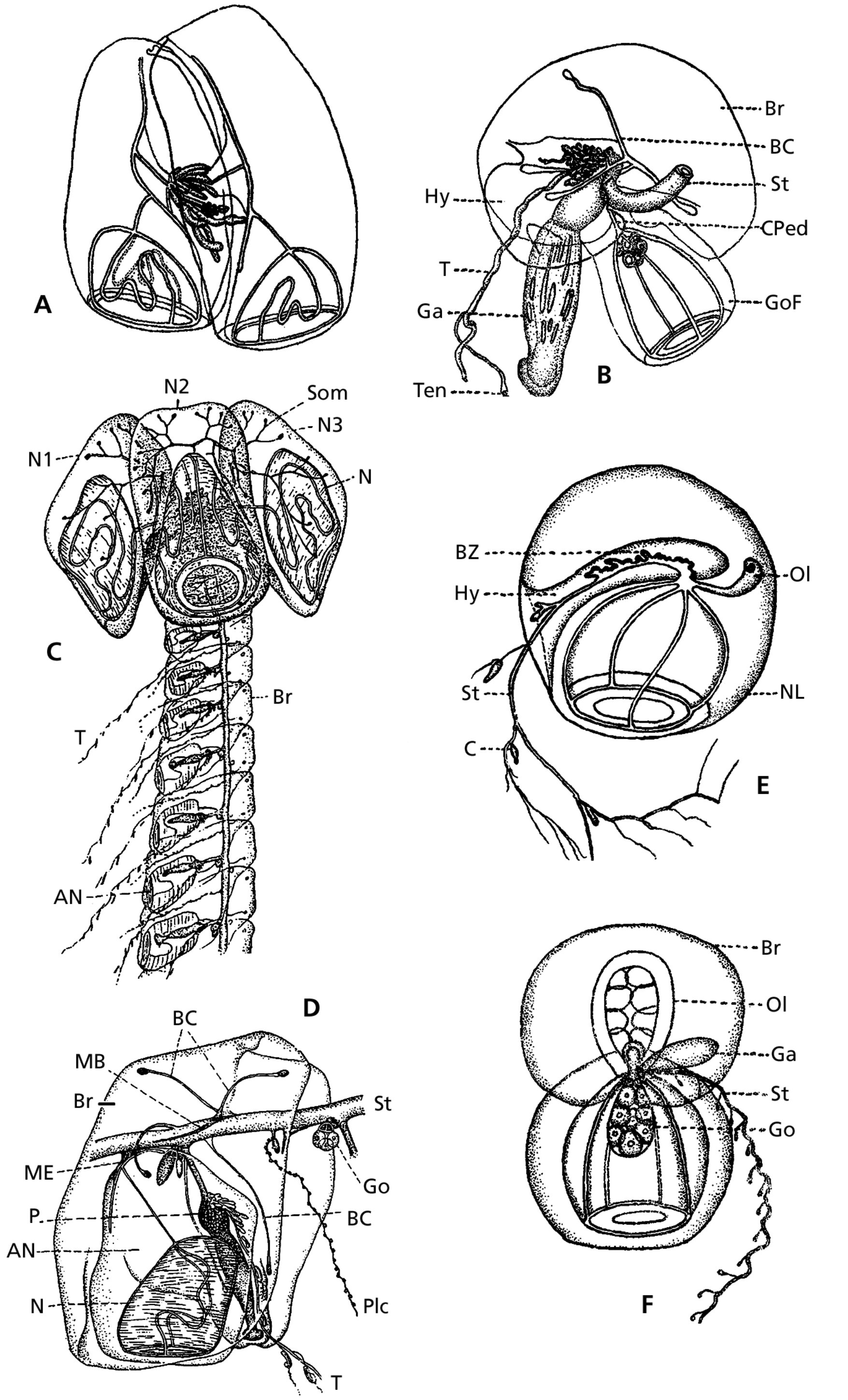

FIG. 231. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-B, *Rosacea cymbiformis*: A, two definitive nectophores; B, adult cormidia. C-D, *Stephanophyes superba*: C, polygastric phase; D, single stem group. E-F, Sphaeronectidae, *Sphaeronectes gracilis*: E, polygastric stage; F, eudoxid stage (A-B, E-F after Trégouboff, 1957: pl. 81. figs 2, 3; pl. 76, figs 9,10; C-D after Totton, 1965: pl. XXVI, figs 2, 3). AN = asexual nectophore; BC = bracteal canal; Br = bract; BZ = budding zone; C = cormidia; CPed = pedicular canal; Ga = gastrozooid; Go = gonophore; GoF = female gonophore; Hy = hydroecium; MB = muscular attachment of bract; ME = muscular attachment of asexual nectophore of eudoxid; N = nectosac; N1, N2, N3 = nectophores; NL = permanent larval nectophore; Ol = oleocyte; P = palpon; Plc = palpacle; Som = somatocyst; St = stolon; T = tentacle; Ten = tentillum.

FIG. 231. *Siphonophorae, Calycophorae, Prayidae, Prayinae. A-B,* Rosacea cymbiformis *: A, deux nectophores définitifs ; B, cormidie adulte. C-D,* Stephanophyes superba *: C, stade polygastrique ; D, groupe cormidial. E-F,* Sphaeronectidae, Sphaeronectes gracilis *: E, stade polygastrique ; F, stade eudoxie (A-B, E-F d'après Trégouboff, 1957 : pl. 81. figs 2, 3 ; pl. 76, figs 9,10 ; C-D, d'après Totton, 1965 : pl. XXVI, figs 2, 3). AN = nectophore asexuel ; BC = canal bractéal ; Br = bractée ; BZ = zone bourgeonnante ; C = cormidie ; CPed = canal pédiculaire ; Ga = gastérozoïde ; Go = gonophore ; GoF = gonophore femelle ; Hy = hydroécie ; MB = attachement musculaire de la bractée ; ME = attachement musculaire du nectophore asexuel de l'eudoxie ; N = nectosac ; N1, N2, N3 = nectophores ; NL = nectophore permanent larvaire ; Ol = oleocyte ; P = palpon ; Plc = palpacle ; Som = somatocyste ; St = stolon ; T = tentacule ; Ten = tentille.*

Sphaeronectes bougisi Carré, 1968c
Sphaeronectes fragilis Carré, 1968c
Sphaeronectes gamulini Carré, 1968c
Sphaeronectes gracilis (Claus, 1873)
Sphaeronectes irregularis (Claus, 1873)
Sphaeronectes japonica Stepanjants, 1967

Class POLYPODIOZOA Raikova, 1988

Life cycle as a succession of a free-living stage and of a stage parasitizing the eggs of some Acipenseridae and Polyodontidae [Pisces]. The earliest known stage is a binucleate cell, parasitizing previtellogenetic fish oocytes. Further development may last several years, leading to a convoluted didermic stolonal structure, with inverted germ layers, forming numerous inverted buds. Before fish spawning, eversion takes place and the germ layers take their normal position (ectoderm outside, endoderm inside). The stolon becomes free and fragments into individual buds, each giving rise to a free creeping globular stage that multiplies by longitudinal fission. Globular stages can move and feed, having an oral mouth-cone and 24, 12 or 6 tentacles, according to season. Germ cells are endodermal. So-called females with two kinds of “gonads”, each with a gonoduct opening in the gastral cavity. So-called males deprived of gonoducts, their “gonads” forming gametophores carrying cnidocysts.

Remarks: It is not known how the parasites get into young previtellogenic fish oocytes. The free-living stages are presumably homologous to sexual medusae, the parasitic stages to polyps. By their stolonal parasitic budding stage and their cnidome, the Polypodiozoa seem to present some affinities with the Narcomedusae, to which they were previously assigned. This class comprises only *Polypodium hydriforme* Ussov, 1885, which was until recently the only known metazoan adapted to an intracellular parasitic life.

The taxonomic status of *Polypodium* is still controversial and we tentatively include it in the Polypodiozoa. (see Siddall *et al.*, 1995; Monteiro, Okamura & Holland, 2002; Okamura, Curry, Wood, & Canning, 2002; Zrzavy, 2001; Zrzavy Hypsa, 2003)

Family POLYPODIIDAE Poche, 1914

See characters of the class.

Genus ***POLYPODIUM*** Ussov, 1887

Fig. 52

See characters of the class.

Polypodium hydriforme Ussov, 1885

COLLECTION OF MATERIAL

Hydroids

Benthic hydroids have been traditionally collected with dredges and grabs, from ordinary boats or research vessels. This practice has led to the collection of a host of large colonies of Sertulariidae, Aglaopheniidae, Syntheciidae, Plumulariidae, these being evident during sorting. The identification of inconspicuous hydroids, either alive or preserved, necessitates careful sorting of material, by inspecting each substrate fragment while in liquid. Many hydroids are commonly associated with algae, sea grasses, sponges, other hydroids, anthozoans, bryozoans, molluscs (bivalve, gastropods, pteropods), annelids, crustaceans, ascidians, fishes, and must be searched for under a stereomicroscope. Hydroids are common inhabitants of shaded hard substrates. Intertidal specimens can be collected easily at low tides, whereas subtidal specimens are best collected by SCUBA diving, since the crevices and small cavities they prefer are difficult to sample from the surface. While collecting, it is important to be aware of the substrates that are possibly conducive to hydroid settlement. These must be collected even if no specimens are evident. Kept in the laboratory, in calm water, these substrates might reveal fruitful catches.

Deep and soft-bottom species must be collected from boats, with either dredges or grabs. In shallow water, however, soft bottom hydroids can be seen while SCUBA diving, since some species are rather conspicuous. Interstitial species are collected by the standard techniques of meiobenthic research.

Many hydroids are not recognisable if not fertile, and information on complete life cycle is necessary for an accurate identification. It is advisable, for instance, to collect under a periodic basis, until fertile colonies are found, then bring them to the laboratory to observe gonophoral content in living specimens and, eventually, to rear medusae to maturity, so to produce complete descriptions. Even groups that are usually thought to be completely paedomorphic, and so deprived of medusae, have recently been found to produce swimming gonophores. Far too many species and genera have unknown hydroids or medusa stages, so that life cycle elucidation is still a priority for the study of this group.

Medusae

Gelatinous plankton is very fragile and easily torn and damaged when collected.

Hydromedusae can be caught by plankton nets that are very slowly towed (about 1 knot per hour) by a large or a small powered vessel, or even a row boat, for about ten to twenty minutes depending on plankton abundance. Mesh sizes of nets should be about 200-250 μm, larger meshes may allow small specimens to escape, while nets with smaller meshes may become clogged and the specimens damaged. In coastal waters, the opening of the net should be from 30 cm to 1 m, depending on the power of the vessel, much wider openings are used in the open sea and in deep waters, where the fauna is sparser. In areas very rich in plankton, a hand net or even a bucket may be used. The richest catches are generally obtained in the early morning, at dusk, and on rising tides. For qualitative horizontal subsurface sampling, the plankton net is towed by a rope of 50 m or more behind the vessel, to eliminate turbulence. For sampling in few meters below the surface, a buoy can be attached with a rope of known length to one side of the ring opening and a weight on the other side. Sampling between fixed depths requires closing nets. Quantitative sampling is possible with plankton nets fitted with a flow meter a little behind their front, after calibration water-meters give a measure of the quantity of filtered water.

If it is impossible to sort the medusae immediately, the catch should be fixed as quickly as possible with formaldehyde, so to obtain a final solution of 5% fixative (see fixation). If the material can be brought rapidly to the laboratory, the plankton samples, shielded from direct sunlight and kept as cool as possible, should be examined under a stereo-microscope and medusae individually removed with wide-mouthed pipettes and placed in finger bowls of clear sea water. After observation they can either be kept for rearing or they are anaesthetised and fixed as described below. This method the most rewarding, allowing both the observation of the characters of the living animals and a perfect fixation.

FIXATION AND PRESERVATION OF THE MATERIAL

HYDROIDS

Colonies are usually preserved directly either in formaldehyde or alcohol. This practice usually leads to specimens with poorly preserved coenosarc, skeletal parts being the only well preserved items. This is the reason why the material coming from "expeditions" is very rich in large thecate colonies, whereas athecate and delicate forms are apparently absent. In order to have properly preserved hydroid material, the same techniques employed for the medusae should be used. Modern molecular techniques require fixation in alcohol, since DNA extraction in formalin-preserved material is impossible. When possible, a batch of specimens should therefore be preserved in alcohol. Whole mounts, obtained by dehydration of specimens and mount on microscope slides, are very advisable. Mounted specimens can be studied also after centuries, whereas those preserved in liquid tend to disintegrate. This is very important for the preservation of type material.

MEDUSAE

Hydromedusae should be anaesthetised before fixation, since most fixatives cause shrinking and deformations. The animals should be allowed to extend in a vessel of water where the anaesthetic should be added slowly, crystal by crystal or drop by drop. The most common anaesthetic substances for marine medusae are menthol crystals, propylene phenoxetol and magnesium chloride (about 7.5% $Mg\ Cl_2$, $6H_20$ in fresh water), the last being the most recommended (Smaldon & Lee 1979). For general taxonomic purposes, hydromedusae can be fixed in 4% buffered 100% formaldehyde solution in seawater (commercial formaldehyde is only at 40% and then 10% should be used) and preserved for short periods in 2% pure formaldehyde (5% of commercial formaldehyde). The effects of formaldehyde preservation on size and weight of hydromedusae have been studied by de Lafontaine and Leggett (1989). Buffering with borax or calcium carbonate should be avoided since the medusae may adhere to any precipitate formed by those chemicals on the bottom of the containers, causing mesoglea destruction; the best buffer seems to be sodium glycerophosphate. Alcohol should not be used as a fixative because it leads to shrinkage, distortion and contraction of the specimens. Nevertheless, for long-term preservation, for instance in museum collections, formaldehyde is not adequate since it causes auto-maceration of the tissues and it should be replaced by 70% alcohol. The passage from formaldehyde to alcohol is to be gradual, going from formaldehyde to a very dilute alcoholic solution (less than 10%) and then, step by step (10% by 10%), in several days, to the final 70% solution (Petersen 1976). Polythene containers should be avoided; chemical precipitates being able to damage specimens. For histological studies, the best fixative is, after anaesthetisation, cold (5-8a C.) acidic Bouin's fixative (= 75% of a solution of saturated aqueous solution of picric acid + 25% formaldehyde from a commercial solution at 40%: just before use 5% glacial acetic acid should be added to this solution). The material can afterwards be preserved for a long time in 2% pure formaldehyde, the specimens being less affected after this treatment by formaldehyde auto-maceration.

A method of long-term storage has been developed by Van Impe (1992) where the medusae are suspended in a solid agar-agar gel coloured with serva-blue and from which extraction is easy when required. This method is particularly useful for transportation and for long-term conservation, all holotypes should be stored in such a gel which up to a certain point also avoids drying out and, furthermore, will nicely stain the tissues of the medusae in blue.

In most Museum collections hydromedusae specimens, including holotypes, have been destroyed because of the habit of museum keepers to put label cards into the storing jars containing the specimens. Such a custom should be totally avoided because after a few manipulations or a single material expedition to a specialist, only the label remains. Cotton or paper plugs should also be avoided, since the fibers tend to adhere to specimens, causing damage.

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GLOSSARY

A

ABAXIAL
Away from the main axis, or on a site remote from it; in a medusa marginal tentacle, the outer tentacular surface, in siphonophores the dorsal side.

ABCAULINE CAECUM, OR BLIND SAC, OR ABCAULINE DIVERTICULUM
A finger-shaped, blind expansion of the abcauline wall of the hydranth in many Sertulariidae and some Syntheciidae, mainly evident in contracted hydranths. Due in part to the attachment of the ectoderm of this region to the mantle and/or hydrothecal wall, preventing its complete withdrawal. It imparts a bilateral symmetry to the hydranth. In the Sertulariidae used in generic diagnoses, although the caecum is less evident when the hydranth expands. For instance, in the Sertulariidae present in *Abietinaria*, *Calamphora*, *Crateritheca*, *Hydrallmania*, *Parascyphus*, *Sertularella*, *Sertularia*, *Symplectoscyphus*, *Thuiaria*). In some genera of Sertulariidae, the hydranth is withdrawn symmetrically into the hydrotheca and there is no caecum, although a mantle may be present (for instance *Dictyocladium*, *Diphasia*, *Dynamena*, *Idiellana, Salacia*).

ABCAULINE
On the side away from the caulus, the opposite is adcauline.

ACANTHOZOOID
Polyp transformed into a protective spine.

ACNIDE TENTACLE
Tentacle deprived from cnidocysts, sensory tentacle in capitate hydroids.

ACRASPEDOTE
Medusae lacking velum.

ACROCYST
A gelatinous, apparently structureless body extending from the gonophore and held outside the gonothecal opening, where embryos develop (brood chamber).

ACROSPHERE
Conspicuous ectodermal knob at the end of a tentacle, laden with numerous cnidocysts = capitation.

ACTINULA
Creeping, post-embryonic, tentacled larval stage, characteristic of some Anthomedusae, resembling a small hydranth, usually with two or more circles of tentacles, developing directly into a hydroid stage. Not homologous to the tentaculated post-embryonic larvae of the Trachymedusae and Narcomedusae, inappropriately called "Actinulae", with only one aboral circle of tentacles, a different histological structure and giving rise directly to medusae.

ADAXIAL
Position opposite to abaxial, facing towards the main axis; in a medusa marginal tentacle, the inner tentacular surface, in siphonophores the ventral side.

ADCAULINE
Directed towards the caulus, see abcauline.

ADHESIVE PAD
Adhesive structure lacking cnidocysts, usually located near tentacle tip, sometimes along tentacle surface.

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 supporting stem).

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.

ALTERNATE
In hydroids, hydrocladia or hydrothecae arising alternately on the left and the right side of the stem.

AMPHICORONATE
Alternate up and down arrangement of a single row of oral tentacles.

AMPULLA
Superficial or internal rounded chamber from the outer surface (coenosteum) of calcareous hydrozoan colonies, containing the gonophores, usually forming blister-like convexities on the surface in the Stylasteridae, often with an efferent duct.

ANASTOMOSING
Branched structure in which some branches rejoin and fuse with others to form a network.

ANEURAL CONDUCTION
Type of conduction where the impulses are linked with electrical activities of cellular membranes other than neural (*e.g.*, epithelial cells, muscular cells, of both ectodermal and endodermal origin).

ANNULAR ECTODERMAL FOLD = RING FOLD
Folding of the mantle, linking the proximal part of the hydranth to the hydrotheca, evident in contracted hydranths (Thyroscyphidae).

ANNULAR PERISARCAL RING OR THICKENING
See diaphragm.

ANNULUS / ANNULATION
An encircling groove or any ring-shaped structure in a hydroid stem, usually with thinning of perisarc, allowing passive bending. One in a series of rings in perisarc, typically in groups directly below hydranths, demarcating the internodes, at nodes, or where stems branch.

APICAL KNOB OR CHAMBER
Small aboral chamber at the apex of the manubrium, protruding into the apical umbrellar mesoglea (*e.g.*, some *Coryne*; *Sarsia*; *Amphinema rubrum; Euphysora furcata, Plotocnide borealis,* etc.).

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.*, *Coryne* (= *Sarsia*) *producta*, *Corymorpha nutans*).

APICAL PROJECTION OR PROCESS
A rounded or pointed, usually roughly conical mesogleal extension of the top of the umbrella (*e.g.*, *Amphinema, Leuckartiara*).

APICAL WINGS
Apico-lateral processes of physonect nectophores, which extend around stem.

APICAL
Situated at the apex.

APOPHYSIS
Short process of the hydrocaulus that bears the hydrocladia, or of the hydrocladia bearing the hydrothecae (see hydrophore).

ARBORESCENT
Polyp colony with a stout hydrocaulus bearing many scattered branches at its distal end.

ATHECATE
Lacking a proper hydrotheca; the hydroids of the Anthomedusae.

ATHORYBIA STAGE
Larval stage in physonect development bearing a pneumatophore, primary gastrozooid, tentacles and a ring of larva bracts.

AUROPHORE
Gas-secreting portions of the pneumatophore, partially constricted off as bell-like bodies in the family Rhodaliidae.

B

BASAL FACET OF MOUTH PLATE
Ventral surface of mouth plate in calycophoran anterior nectophore, which may articulate with posterior nectophore.

BASAL LAMELLA
A thin extension of the nectophore below the ostium of the nectosac on its ventral side; one or more lamellae comprise the mouth plate.

BASAL WEB = INTERTENTACULAR WEB = UMBRELLULA

BASIGASTER
Basal part of the siphonophore gastrozooid.

BELL
See umbrella.

BICORONATE
Arrangement of oral tentacles in two whorls.

BICUSPIDATE
Having two cusps (said of hydrothecal cusps).

BIFID
Forked into two roughly equal parts.

BIMUCRONATE
With two sharp points (*e.g.*, the hydrothecal cusps of *Obelia bidentata*).

BINOMEN
(Binominal) comprising the two names which together form the

scientific name of a species, comprising the genus name followed by the species name.

BISERIATE
In two rows.

BLASTOSTYLE
Carrier of gonophores, 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 canal that does not join circular canal (*e.g.*, *Toxorchis*); centripetal canals that do not join radial canals or manubrium (*e.g.*, some *Calycopsis*).

BRACT
Protective or buoyant siphosomal element, usually containing much mesoglea and gastrovascular expansions.

BROOD CHAMBER
Protective chamber within which planulae develop (gonothecal acrocyst, marsupium, brood chamber of *Eleutheria* medusae etc.).

BUDDING
Asexual reproduction in which a new organism develops as an outgrowth or bud from the parent, either remaining attached (to form a colony) or becoming detached from the parent. Common in Cnidaria. Budded polyps and automedusae derive from simple buds; the medusae of Hydroidomedusa derive from special buds, containing the entocodon.

BUGLE
In haleciid an annular thickening of unknown function often present half way up the gastric column of the hydranths, perhaps the limit between two histologically distinct regions of the endoderm.

BULB
See tentacular or non-tentacular marginal bulb.

BUSHY
Polyp colony whose hydrocaulus bears many lateral branches throughout its length.

BUTT = SHAFT
Enlarged portion of cnidocyst tubule, it may bear stylets and/or spines, either of uniform or not uniform diameter.

C

CAMPANOPSID
Hydroids having hydrothecae reduced or absent of the form characteristic of the nominal genus *Campanopsis*, i. e., hydranths with an intertentacular web, each arising singly from a stolon; perisarc is thinning completely away below the hydranths, medusae buds formed on hydranth (see *Helgicirrha shulzei*; *Eirene viridula*).

CAMPANULATE OR CAMPANULIFORM
Bell-shaped.

CAMPANULINID
Hydroids having hydrothecae of the form characteristic of the nominal genus *Campanulina*, i.e., with campanulate, pedicellate hydrotheca with conical operculum formed by several triangular, convergent pleats or segments meeting centrally and which may be or may not be sharply demarcated from the hydrothecal margin, usually with diaphragm; such forms are not necessarily closely related.

CANALICULATED
Of a stem comprising several coenosarcal tubes in a common perisarc.

CAPITATE
Tentacle or nematophore with a distinct differentiated, large ectodermal knobbed end (acrosphere) richly armed with cnidocysts and often with sensory cells. Not to be confused with a simple accumulation of cnidocysts.

CAPSULE (CNIDOCYST CAPSULE)
Double-walled envelope of cnidocysts, containing the shaft, coiled tubule, intracapsular liquid and bearing a distal operculum.

CATENIFORM
Tentacle with cnidocysts in a distinct large terminal capitation and with numerous spirally arranged small cnidocyst clumps.

CATHAMNAL LAMELLA
Endodermal sheet connecting the radial canals through the umbrellar jelly and separating the outer from the inner mesoglea.

CAULUS
Main stem (hydrocaulus).

CENTRAL ORGAN
Swelling at junction of the canal system and stem in some Prayidae siphonophores.

CENTRIFUGAL CANAL
Canal issued from the manubrium and directed towards umbrellar margin.

CENTRIPETAL CANAL
Canal issued from the circular canal and directed to the manubrium (*e.g.*, *Calycopsis*).

CHEVAL-DE-FRISE
See ring palisade

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* medusae).

CIRCLET
Whorl or ring of tentacles whose bases are almost at the same level.

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 consists of a solid core of endodermal cells (*e.g.*, *Proboscidactyla*, Laingiomedusae). In the Narcomedusae, with umbrellar margin deeply cleft into broad flaps, the circular canal, when present, follows the edge of the margin of the exumbrellar flaps and is called "peripheral canal system", whose vertical parts are the peronial canals.
Cirri may be immediately 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*).

CIRRUS (CIRRI)
Small tentacular-like organ situated on the umbrellar margin between marginal tentacles, solid and devoid of swollen marginal tentacular bulbs. Two types are generally found: cirri immediately adjacent to marginal: lateral cirri (*e.g.*, *Eucheilota*); cirri along the umbrellar margin in the inter-spaces between marginal tentacles: marginal cirri (*e.g.*, *Cosmetira, Phialopsis*).

CLADIUM
A branchlet given off the main stem or caulus (hydrocladium).

CLASP
Part of a marginal bulb embracing the exumbrella (*e.g.*, *Leuckartiara*) (see exumbrellar spur).

CLEPTOCNIDAE (CNIDOSACS)
Cnidocysts deriving from cnidarian prey kept in specialised structures of nudibranchs, Nemertea, Turbellaria etc. Cleptocnidae may also occur in cnidarian that have preyed on other cnidarians.

CNIDAE
A general term for the stinging or adhesive cells characteristic and source of the name of the phylum Cnidaria: cnidocysts, spirocysts and ptychocysts.

CNIDOBAND
Structure on the tentillum bearing dense aggregations of various kinds of cnidocysts.

CNIDOBLASTS
Developing cnidocyte often used as synonym with cnidocyte.

CNIDOCIL
Bristle-shaped projection adjacent to operculum at the distal end of a cnidocyte; serves as trigger to discharge the cnidocyst.

CNIDOCYST (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 operculum, 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 cnidocyst are recognised, they are of great use in taxonomy. Cnidocyst are used for prey capture, defence, and attachment. They are known to be under nervous control.

CNIDOCYST MARGINAL RING = NETTLE RING
A dense band of cnidocytes and cnidocysts encircling the exumbrellar margin, characteristic of the Trachymedusae but present also in some species of other medusae.

CNIDOCYTE
Specialised cell type, usually located 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; characteristic of most of the Zancleida (see remarks in Weill 1934 p. 404; Bouillon 1974), not to be confused with branched capitate tentacles or with the special cnidocysts-bearing processes of *Eudendrium racemosum* and *E. armatum*.

CNIDOTHYLACIUM
Cluster of cnidocysts enclosed in an endodermal canal running along the umbrella.

COENOSARC
The living tissue of a hydroid colony, the living tubes connecting the various polyps of a colony, typically covered by perisarc.

COENOSTEUM
Calcareous exoskeleton in hydrozoan colonies (i.e. Milleporidae, Stylasteridae), bearing pores for the gastrozooids (gastropores), dactylozooids (dactylopores) and "nematophores" (nematopores). In Stylasteridae, the texture of the coenosteum is either a reticulate maze or a series of straight parallel, longitudinal bands of calcium carbonate (= linear coenosteal strips); these often covered by granules or bear imbricate scales or platelets. The coenosteum has mainly two types of texture: reticulate-granular and linear-imbricate. The two other combinations, i.e. reticulate-imbricate and linear-granular, are very rare.

COLONY
Asexually produced assemblage of zooids that have a common coenosarc, deriving from a single zygot or asexual reproduction.

COLUMN
The tubular part of a polyp, excluding the hypostome, the tentacles and, if any, the most basal region.

COMMISSURAL CANALS
Transverse connections of the nectosac between lateral radial and dorsal canals (in *Sulculeolaria* spp. only)

COMPOUND SENSE ORGAN
Marginal sense organ formed by an ecto-endodermal ocellus and an open ectodermal statocyst (in the Tiaropsidae).

CONGENERIC
Species referable to the same genus.

CONSPECIFIC
Referable to the same species.

COPPINIA
A close aggregation of numerous gonothecae together in a muff-like structure including also modified, elongate polyps (presumed defensive) (*e.g.*, in the Lafoeidae).

CORALLUM
The calcareous skeleton of a colony as a whole.

CORBULA (CORBULAE)
Protective basket-like group of modified hydrocladia (called corbulacostae or ribs) typically provided with nematothecae, loosely fused or lying closely parallel, bent around and protecting several gonangia in the space within (Aglaopheniidae) (see phylactocarps). The primary modified hydrocladium, rachis or axis of the corbula, is called gonocladium, it bears the first secondary hydrocladium, or gonohydrocladium, which support the accessory hydrocladia differentiated in corbulacostae.

CORBULACOSTA (CORBULACOSTAE)
One of the modified hydrocladia of a corbula; also called ribs, they are alternately inserted to the gonocladium.

CORDYLUS (CORDYLI)
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).

CORM
Contracted nectosome and siphosome of the Rhodaliidae forming a globular mass below the pneumatophore.

CORMIDIUM
In thecate hydroids, a repeated unit of the cladium comprising an internode, one hydrotheca and usually three nematothecae, delimited by annuli; in siphonophores, an organised group of siphosomal elements, usually including a gastrozooid, tentacle, palpons (in physonects), blastostyle and bracts.

CORMOID
Erect polyp-bearing elements of a colony that arise from a common hydrorhiza or hydrorhiza-like stem, e.g. one single feather-like structure of a *Halopteris* colony or a simple stem of *Antennella* species. A cormoid is a hydrocaulus, or its homologue, and all accessory structures.

CRASPEDOTE
Medusae with a velum.

CRENULATED
Having low rounded cusps or lobes separated by sharp but shallow notches (*e.g.*, of mouth lips).

CRUCIFORM
Cross-shaped.

CRUMPLING
See introversion.

CRYPTOMEDUSOID
Strongly reduced medusa; seldom with free pelagic life (swimming sporosacs, and gonophores); without radial canals but with an endodermal lamina lining the exumbrellar ectoderm: the umbrella endoderm (homologous to the cathamnal lamella); subumbrellar cavity reduced or represented only by an ectodermal layer: the internal ectoderm, germ cells on spadix (= manubrium), in eccentric position.

CUSP
Distal projection (often called tooth) from the rim of a hydrotheca or a gonotheca.

CUSPIDELLID
Hydroid morphologically referable to the nominal genus *Cuspidella*. Colony stolonal; hydrotheca tubular, usually sessile, without pedicel; operculum conical, made of several pleats or cusps meeting centrally, with or without crease-line at base; differing from "campanulid" in lacking pedicel and diaphragm.

CYCLOSYSTEM
An arrangement of pores in which several dactylopores surround central gastropore in calcareous Hydrozoa.

CYMBA
Angular and flattened eudoxid bract, characteristic of *Ceratocymba* spp.

CYMOSE
Colony not growing distally but from successive lateral branches.

CYST
Generally chitinous, protective structure containing eggs, embryos or even portion of an organism in an inactive stage. Cysts are resting stages, usually resistant to adverse environmental conditions. They can be either part of the normal life cycle or appear depending on circumstantial conditions.

D

DACTYLOPORE
A small pore in the coenosteum of calcareous Hydrozoa housing dactylozooids may be borne on projections

DACTYLOSTYLE
See style

DACTYLOTOME
The lateral slits which borders the gastropores tube in Stylasteridae.

DACTYLOZOOID (= MACHOZOOID)
Defensive polyp, usually highly extensible and mobile, richly armed with cnidocysts, 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 chemoreceptor.

DESMOCYTE
Minute chitinous rivet anchoring the skeleton (theca) to the mesoglea of the hydranth (= 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 by which the coenosarc passes.

DIASTEMA
A gap, a space between. In the Stylasteridae, when cyclosystems are aging, the dactylopores become obsolete and are filled with coenosteum. The section of cyclosystem missing dactylopores is called a diastema.

DIPLOBLASTIC
Being composed of two epithelia, i. e. 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) or where a hydroid will produce directly another hydroid (*e.g.*, *Hydra*).

DISTAL
At the far end, near the end (opposite = proximal).

E

ECTODERM
Outermost cellular layer (epidermis).

ECTODERMAL LAMELLA OR LINING = ECTODERMAL LAMINA
See mantle.

ECTODERMAL STATOCYST
Marginal sense organ of equilibrium 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.

ECTO-ENDODERMAL STATOCYST = TENTACULOCYST = SENSORY CLUB
Club-like, sense organ of equilibrium growing out of the umbrellar margin in the fashion of a tentacle; 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*).

ECTO-THECA
Ectodermal layer surrounding in some species medusa buds and more generally reduced gonophores.

EGESTION
The elimination of undigested food through the mouth opening.

EMBAYMENT
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, the latter 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.

ENTOCODON = GLOCKENKERN = MEDUSARY NODULE
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, Hydractinia minima*, *Rathkea octopunctata*), the entocodon developing both ectodermal and endodermal components of the buds.

EPIBOLIC
A type gastrulation with the smaller cells of the animal pole growing down over the vegetal pole cells and enclose them, the large cells becoming the endoderm and forming an archenteron.

EPILITHIC
Living on stones or inorganic hard substrates in general.

EPIPHYTIC
Living on plants, without parasitizing them.

EPIZOOTIC
Living on animals, without parasitizing them.

EUDOXID
Reproductive stage of calycophorans that usually becomes detached from polygastric stage.

EUMEDUSOID
Reduced medusa 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; the first step in medusa reduction.

EXCRETORY PAPILLAE
Papillae situated 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 absent and pores open at the surface of the supporting structures (see excretory papillae).

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 (Zancleoidea) or on exumbrellar margin between tentacles (*e.g.*, *Proboscidactyla*).

EXUMBRELLAR SPUR
Upward growth of marginal tentacular bulbs, clasping umbrellar margin (*e.g.*, *Leuckartiara*).

F

FASCICLED
Stem comprising two or more coenosarc tubes united in a composite single stem structure (= polysiphonic). Sometimes fascicled stems are due to coalescence of colonies deriving from several planulae that settled together on the same spot.

FILIFORM
A straight tentacle, lacking prominent cnidocyst clusters, the cnidocyst appearing more or less evenly distributed.
FLABELLATE: fan-shaped hydroid colony.

FLEXILE CIRRI
Straight, do not coil and have cnidocysts in rings (*e.g.*, *Cosmetira*).

FLEXUOSE
Hydroid with hydrocauli or hydrocladia with successive internodes directed alternately left and right, in a zigzag way. Flexuose colonies are usually biseriate, bearing hydranths in two opposite, often alternate rows.

FRUSTULE
Little didermic tissue portion formed asexually either by budding or by constriction, acting as dormant and/or dispersion stage. Generally formed by polyps, exceptionally by medusae; all develop into polyps.

FUNNEL
An expanded chamber at the bottom of the pneumatophore where the lining ectoderm is modified to form the gas gland.

G

GAS-GLAND
Specialised area of modified ectoderm that secretes gas to inflate pneumatophore (see funnel), the gas gland may be simple (*Agalma*) or branched (*Rhizophysa*).

GASTRIC CAVITY
In medusae see manubrial cavity; in the hydranth, simple undivided enlargement of the digestive part of the hydranth body.

GASTRIC PEDUNCLE = PEDUNCLE
A cone-shaped median extension from the subumbrellar mesoglea projecting downwards into the subumbrellar cavity, bearing the manubrium terminally; the radial canals run down along 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 POUCHES
See manubrial pouches.

GASTROPORE
Large pore housing a gastrozooid, in calcareous Hydrozoa.

GASTROSTOME
The mouth of the gastropore.

GASTROVASCULAR SYSTEM
The coelenteron or enteron, comprising the manubrium cavity and the gastrovascular canals (i. e. the radial and circular canals and their derivatives) of medusae and the hydranth cavity and the coenosarcal canals in the hydroid. It serves for the digestion and distribution of food, the circulation of oxygen, waste, cnidoblasts and even gametes.

GASTROZOOID
Feeding polyp with mouth and normally with tentacles, without reproductive organs.

GEMMULE
Asexual reproductive body, see cyst and frustule.

GLOMULUS
In certain Haleciidae, a grouping of several to numerous laterally contiguous gonothecae each with a tubular neck, jointly borne on an irregularly branched network of tubes.

GONAD
An organ such as an ovary or a testis which produces sex cells or gametes. 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, usually on manubrium walls or/and on the radial canals, where the sex cells become mature. 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 (GONANGIA)
In Leptomedusae colonial hydroids, a reproductive unit consisting of the outer gonotheca and enclosed blastostyle bearing one or many gonophores.

GONODENDRON
In siphonophores, an organised group of gonopalpons, gonophores and occasionally asexual nectophores, developed from the siphosome.

GONOPALPON
A specialised palpon, budded from the gonodendron.

GONOPHORAL POLYP
Polyp protruding from the gonothecal opening of some *Halecium* species, perhaps with defence and/or feeding function.

GONOPHORE
Asexual reproductive structure normally developing into medusa buds; in many Hydrozoa, however, the medusae are reduced to a varying degree and are not liberated anymore, remaining attached to the hydroid, or to the siphosome, in the gonophoral structures. They are then called fixed gonophores, or sporosacs, or fixed sporosacs since they are not released anymore. The gonophores give origin to the generative elements, ova or spermatozoa (see medusa reduction).

GONOSOME
The gonophores and their protective structures.

GONOTHECA
Chitinous structure with a distal opening, surrounding and protecting a gonophore.

GONOZOOID
Reproductive polyp bearing gonophores; usually a modified gastrozooid at various stages of morphological reduction and often with few or no tentacles.

H

HERMAPHRODITIC
A colony of hydroids is hermaphroditic when all its zooids are hermaphroditic; but a colony may functionally be hermaphroditic when composed of both male and female zooids.

HETEROMEDUSOID = SPOROSAC
Highly atrophied medusa devoid of radial canals, umbrellar endoderm, tentacles and sense organs; internal ectoderm remnant of subumbrellar cavity still present.

HETEROMEROUS SEGMENTATION
Segmentation of hydrocaulus or hydrocladia by alternate hydrothecate and non-hydrothecate segments, oblique and transverse nodes thus alternating.

HINGE JOINT
A joint consisting of diamond-shaped thickenings of the stem perisarc, set obliquely in the sagittal plane and connected by relatively thin perisarc; it allows some bending in certain directions but not in others. The function is to orientate the colony in a favourable position in respect to food-bearing currents.

HOLLOW TENTACLE
Tentacle either with a central cavity in continuation with the cavity of the tentacular bulbs or, when these are missing, of the circular canal, or without any lumen but with an endodermal core formed by several peripheral rows of cells (parenchymatic). 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.

HOMOMEROUS SEGMENTATION
Segmentation of hydrocaulus or hydrocladia through uniform segments, usually separated by oblique nodes.

HOMONYM
Identical names denoting different taxa (see International Code of Zoological Nomenclature for further explanation).

HYDRANTH
The feeding polyp of a hydroid colony.

HYDROCAULUS
Main stem of a fixed, erect hydroid colony, typically bearing branches, the final of which, or hydrocladia, bearing the hydranths.

HYDROCLADIA
Final lateral, hydranth-bearing branch of the main stem (or hydrocaulus) or of its branches, in an erect hydroid colony.

HYDROECIUM
Ventral cavity of calycophoran nectophore into which the siphosome may be wholly or partly retracted.

HYDROID
The polypoid stage, or prolonged post-planula larva, of the Hydroidomedusa.

HYDROPHORE
Perisarcal structure at the base of the hydranths in some members of the family Solanderiidae, often as two parallel triangular processes. In some Leptomedusae species each hydranth arise from a short process situated near the distal end of an internode termed hydrophore (= apophysis). In Haleciidea protrusion or pedicel carrying the hydrothecae.

HYDROPORE
A hole in the definite floor of hydrotheca, in Syntheciidae, Sertulariidae and Plumulariidae, trough which the coenosarc passes, connecting the hydranth with the rest of the gastrovascular system.

HYDRORHIZA (HYDRORHIZAE)
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 encrusting or forming other different structures.

HYDROTHECA (HYDROTHECAE)
Chitinous structure surrounding entirely or partially the hydranth in most Leptomedusae.

HYDROTHECA REDUCTION
In some Campanulinida families, for instance the Eirenidae and the Eucheilotidae, only the newly developed polyps have a completely developed hydrotheca, with age these become reduced, losing their operculum and apical part, and are no longer high enough to accommodate the hydranths (haleciid-like).

HYPOCYSTIC VILLUS (VILLI)
Ectodermal processes of the gas-gland or pneumadenia in some Cystonect siphonophores.

HYPOSTOME
Distal end of the hydranth, carrying the mouth at its end.

I-J

INTERNODE
A segment often dividing hydrocauli and hydrocladia by partitions or nodes, part between two nodes, often delimited above and below by perisarcal annuli.

INTERRADIAL
The radial axis lying in between two adjacent perradii; between the radial canals. In Narcomedusae the axis between gastric pouches.

INTERTENTACULAR WEB = BASAL WEB = UMBRELLULA
Thin, transparent sheet, often containing cnidocysts, connecting the base of the hydranth tentacles of some leptomedusan hydroids.

INTRATHECAL RIDGE
Small internal perisarc extension into cavity of hydrotheca, for structural reinforcement.

INTRATHECAL SEPTUM
Internal and transversal shelf or ridge of perisarc inside the hydrotheca.

INTROVERSION = CRUMPLING
The turning inwards of the exumbrellar margin and the tentacles into the subumbrellar cavity afterwards closed by the velum, often with distal part of manubrium hanging out. Answers to various excitations like stress, the presence of other medusae, chemicals, food, etc. It depends on excitation of the epithelial aneural conduction.

INVOLUCRUM
In siphonophores, a fold round the base, or the whole, of a tentillum.

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.

L

LAPPET
A lobe-like extension of the umbrellar margin (some Laingiomedusae, the Narcomedusae).

LARVA
In the post-embryonic development of an animal, an immature intermediate stage distinctly different in morphology and physiology from the sexual adult. A complex life cycle can have more than one larval stage. In the Hydrozoa, the planula is often referred to as larva, whereas it is more properly defined as a gastrula (either hollow, coelogastrula, or solid, stereogastrula). In a strict sense, the larva of the Hydrozoa with a complex cycle is the hydroid, even though, through paedomorphosis, many species perform sexual reproduction in the hydroid stage, due to medusa reduction or suppression.

LATERAL CIRRI
See cirri.

LATERAL NEMATOTHECAE
Nematothecae arranged one each side of hydrothecal aperture, to which they are lateral in position.

LATERAL RIDGES
Cross ridges, bordering the apical wings, present on some physonect nectophores; there may be apico-lateral, infra-lateral, and vertical-lateral ridges.

LIGULA
An extensile outgrowth armed with cnidocysts from the base of the adcauline side of hydranths in some *Salacia* and *Sertularia* (a nematophore? see mantle).

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, elongated, pointed, 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 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.

M

MAMELON
A minute mound or nipple-shaped perisarc protuberance found on the upper surface of a hydrocladia-bearing apophysis. A small aperture in the centre communicates with the coenosarc. Origin and function unclear: either associated with nematophores, Plumulariidae and Aglaopheniidae, or considered as an atrophied hydrotheca in the Halopterididae.

MANTLE CANAL
In siphonophores, upper and lower diverticula of the pedicular canal at the point of its entry into a nectophore or gonophore

MANTLE
In Porpitidae (Anthomedusae) an outfolding along the float edge of the hydroid stage, probably acting as stabilizer. In Leptomedusae hydroids (some Sertulariidae and the Thyroscyphidae), the mantle, or ectodermal supporting lamella or “haftlamelle”, is a thin layer of ectoderm lining the interior of the hydrotheca. Usually issued from the base of the hydranth, wrapping the hydranth completely when withdrawn, forming a roofing plate. Sometimes with specialised regions of attachment to the hydranth and to the hydrotheca. In some genera a medio-basal annular lamella, the annular ectodermal fold, may link, like a diaphragm, the mantle to the hydranth body, in other genera the abcauline caecum region is attached to mantle directly or by a peculiar extension. In some genera, the

distal part of the mantle may contain cnidocysts, often in large aggregations (= kind of nematophores?). The ligula is presumably a mantle differentiation. A mantle may also exist in some gonangia of paedomorphic Leptomedusae, enveloping temporarily the gonophores.

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, cnidoblastic, or sexual when the "gonads" develop on the manubrium. Rather uniform in structure 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.

MANUBRIAL OR GASTRIC POUCH OR POCKET
Lateral perradial or interradial extension of the manubrial cavity (*e.g.*, in Narcomedusae, Tiarannidae, *Gotoea*).

MANUBRIUM
Axial didermic projection of the subumbrella containing the gastric or stomacal cavity, distally bearing the mouth and proximally leading to the radial canals. Manubria are greatly varied in shape and size, ranging from tubular to cruciform, quadratic, fusiform, barrel-shaped, flask-shaped, short, long, narrow or very large, etc. Erroneously considered as synonym with stomach (see stomach).

MARGINAL BULBS
See tentacular or non-tentacular marginal bulbs.

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, or margin, of the umbrella.

MARGINAL VESICLE
See statocyst.

MARGINAL WART OR SWELLING
Small, wart-like swelling of the umbrellar margin, never destined to carry tentacles and not in connection with the circular canal (*e.g.*, *Eutima mira*).

MARSUPIUM
Brood chamber formed by longitudinal gonothecal ribs, spines or leaves in female gonophores of some species of sertulariids hydroids (see brood chamber).

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 hydrocladia or on specialised structures. Common also among hydromedusae; medusa buds are formed either on the manubrium, the radial canals, the marginal bulbs or the subumbrellar rim. Medusa buds, in the Hydroidomedusa, imply the presence of an entocodon (see entocodon).

MEDUSA REDUCTION
In many Hydroidomedusae, 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; Halopterididae; Plumulariidae; Sertulariidae; Syntheciidae. The small leptomedusan colonies are usually characterised by free medusae, the smallest hydroids often producing the biggest medusae!

MEDUSA
Free living, sexual, pelagic stage in the cnidarian life cycle.

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*)

MESIAL (= MEDIAN) NEMATOTHECAE
Nematothecae located in the vertical mid-line of the hydrotheca, one below, or median inferior, and one above hydrotheca, or median superior, more rarely on ahydrothecate stems, cauline nematothecae, or on internodes.

MESOGLEA
A non-cellular substance lying between the ectoderm and the endoderm; it forms the gelatinous bulk of the umbrella (the jelly of jellyfish) and a lamella-like layer (mesolamella) in polypoid forms. Synonym with extracellular matrix (ECM).

MODULAR
Consisting of a series of morphologically similar structural units.

MONILIFILIFORM
With dispersed small isolated clusters of cnidocysts on the adoral side of the tentacle and with a continuous band of cnidocysts along the aboral side.

MONILIFORM
A tentacle with a terminal capitation and rather regularly spaced conspicuous clumps or bands of tall epidermal cells bearing cnidocysts.

MONOPODIAL
Branching pattern of stems in which the oldest hydranth remains at the distal end.

MOUTH ARM
Expansion or dilatation of a perradial corner of the manubrial mouth rim armed with cnidocyts clusters, usually open, groove-shaped (*e.g.*, Hydractiniidae).

MOUTH PLATE
See basal lamella.

MOUTH
Opening of the gastric cavity to exterior; in hydranth, at the end of the hypostome; in medusae, at the end of the manubrium, simple and circular or with either simple or complicated lips (see lips). Serves for both ingestion and elimination (egestion).

N

NECK SHIELD
Thin extension of eudoxid bract, partly surrounding gonophores.

NECTOPHORE
One of the numerous asexual medusoid swimming bells, grouped together towards the apex of the animal to form a region called nectosome. Differ from hydromedusae by their bilateral symmetry. Velum, radial canals, ring canal, endodermal lamella, a double nerve ring, striated muscles present. Manubrium, tentacles, "gonads", sense organs absent; polymorphic, serving for propulsion. Absent in Cystonectae and in an aberrant physonect, *Athorybia*.

NECTOSAC
The central cavity of nectophore, opening to exterior via an ostium and having muscular walls with propulsive function (= subumbrella cavity).

NECTOSOME
Section of stem bearing the nectophores.

NEMATOCLADIUM (NEMATOCLADIA)
The upper fused part of a corbula rib.

NEMATODACTYL
Specialised tentacle with glandular base and bearing a strong cnidocyst armature (typical of *Nemalecium*).

NEMATOPHORE
Type of highly extensible dactylozooid, 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 nematotheca) or naked. In some Aglaopheniids, the nematophores have two recognised portions, the body of the structure also called "sarcostyle" (see sarcostyle) and the region bearing the cnidocysts or cnidostyle. In Stylasteridae, see nematopore. (See tentaculozooid).

NEMATOPORE
Small shallow pores in the coenosteum of Stylasteridae housing the "nematophores", dense concentrations of long slender cnidocysts perpendicular to the branch surface, common around cyclosystems especially on pseudosepta and lids.

NEMATOTHECA
Chitinous theca of varied structure surrounding a nematophore. In the Plumularioidea sessile, immovable and one-chambered (monothalamic), or pedicellate, mobile and two-chambered (bithalamic). Present also in some anthomedusan hydroids (*Merona*).

NEOTENY
A type of heterochrony due to retardation of somatic development, so that sexual maturity is attained by organisms retaining juvenile characters.

NERVE RING
Hydromedusae have two nerve rings around umbrella margin, usually on opposite sides of the velum, separated by a mesoglean lamella: a subumbrellar one, above velum attachment (inner or upper nerve ring) and an exumbrellar one, below velum attachment (outer or lower nerve ring). The two are connected by neurites.

NETTLE RING
See cnidocyst ring.

NODE
Externally visible constricted section of hydrocaulus or hydrocladium marking junction of two internodes (see internode).

NON-TENTACULAR MARGINAL BULB OR RUDIMENTARY BULB
Marginal bulb developed on the umbrella margin without bearing tentacles. Some bulbs never develop tentacles; others can be the result of tentacle reduction. It is necessary to distinguish between bulbs that are permanently without tentacles, permanent non-tentacular marginal bulbs or rudimentary marginal bulbs, as in *Cirrhitiara superba*, *Aequorea macrodactyla*, and bulbs on which a marginal tentacles will develop later on during medusan growth (developing tentacular marginal bulbs, as in *Clytia* and Malagazziidae).

O

OBLATE
Flattened at the two poles; in medusae, species which contract primarily near bell margin when swimming, producing a low-velocity jet (*e.g.*, *Aequorea*, *Clytia*).

OCELLUS (PL. OCELLI)
Multicellular photoreceptor, common in Anthomedusae, usually abaxial or adaxial on marginal bulbs. Round, oblong or elongated spots, black, brown, yellow or red, 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 eighth 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 embayments (prominent crease-line) of the hydrothecal margin; they may be cast away during hydranth growth or after medusa liberation. The term also refers to the lid covering the opening of cnidocysts.

OPPOSITE
In hydroids, two hydrocladia or hydrothecae that arise on the same level, one pointing to the right, the other to the left.

ORAL TENTACLE
Tentacle arising above the mouth rim of some medusae with 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. Tentacles located immediately below the hypostome of hydroids.

ORAL
Near the mouth, the opposite end being aboral.

OSTIUM
Nectosac opening, through which water is expelled for propulsion (= velar opening).

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.

P

PAEDOMORPHOSIS
Acceleration (progenesis) or retardation (neoteny) of somatic development, leading to adults retaining juvenile features

PAEDOPHORE
An asexual, larval nurse carrier of other polyps in siphonophores.

PALLIAL CANAL
Section of gastrovascular system which joins radial canals on nectosac or to somatocyst = pedicular canal?

PALMATE
A form like that of an open palm or hand; in hydroids, a hydrocaulus with largely ascending, long branches converging strictly or loosely in one plane = thuja-like.

PALPACLE
A small tentacle borne on a palpon in siphonophores.

PALPON
In siphonophores, a cormidial element, probably a reduced gastrozooid, which may have sensory or excretory functions.

PEDICEL
Stalk of a hydrotheca, a gonotheca or a hydranth (= stem, hydrocladium); in general, in animals any stalk like structures (= pedicle = peduncle).

PEDICLE
In zoology a small stalk (= pedicel = peduncle).

PEDICULAR CANAL
Section of gastrovascular system which joins the apical point of convergence of the radial canals to somatocyst in calycophoran siphonophores, may present descending, ascending expansions or even branches (see mantle canal).

PEDUNCLE
See gastric peduncle. In general in animals any stalk or stalk-like process (= pedicel = pedicle).

PERIDERM
Mucoproteinic coating (= glycocalyx) of the exposed surface of hydroids and medusae.

PERIPHERAL CANAL SYSTEM
See circular canal.

PERIPHERAL CANAL
In some hydroids, longitudinal peripheral canals of the hydrocaulus, in medusae, see circular canal.

PERISARC
The chitinous exoskeleton surrounding the coenosarc of most hydroids. In the Anthomedusae the polyps are usually never surrounded by perisarc, in the Leptomedusae they usually are (see hydrothecae, gonothecae and nematothecae).

PERONIA
Grooves invaded by tentacular ectoderm making up together an ectodermal strand rich in cnidocysts, muscles and nerves, formed by the fusion of subumbrellar and exumbrellar ectoderm without interposition of mesoglea, at the edges of clefts separating the marginal lappets in Narcomedusae and some Laingiomedusae, where the tentacles originate. 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 issues from the manubrium; during umbrella growth, the tentacles remain attached close to the manubrium and the tentacular ectoderm, maintaining their connection with the umbrella margin, 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. In Narcomedusae the axis opposite each gastric pouch.

PETRA
In siphonophores lateral aliform ridges on gastrozooids in some Rhizophysidae

PHAGOCYTOSIS
The process by which cells surround, and engulf, a food particle that is then digested. The feeding method employed in particular by some unicellular protozoans and Cnidaria.

PHYLACTOCARPS
In some Aglaopheniidae, modified hydrocladia or appendages to a hydrocladium, forming a protective structure typically armed with nematothecae around gonothecae, similar to corbula hydrocladia, but more widely spaced, not fused and less modified.

PHYLACTOGONIUM
In some mature Aglaopheniids, accessory branch of bifurcated hydrocladia bearing the gonangium and its defensive differentiations.

PHYLLOCYST
The reduced gastrovascular canal system in a eudoxid bract.

PHYLLOZOOID = bract

PINNATE
Hydroid colony with branches (alternate or opposite) on each side of hydrocaulus, usually nearly in one plane, 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). Improperly called larva since, from a developmental point of view, it is an embryo (see embryo and larva). Planula of Hydrozoa do not feed but live entirely off yolk, the planulae of some species have zooxanthellae.

PLATELETS
See coenosteum.

PLUMOSE
Hydroid colony with closely arranged lateral branches, usually in one plane (see pinnate).

PNEUMADENIA
Gas-gland at the base of the pneumatophore cavity.

PNEUMATOCODON
Outer ectodermal wall of the pneumatophore separated from the inner wall or pneumatosaccus by gastrovascular space lined by endoderm, containing muscle fibers.

PNEUMATOPHORE
Apical gas-filled float, present in Cystonectae and Physonectae; in the latter its function can be for orientation rather than buoyancy. Derived directly from the larval stage, probably represents a highly modified polyp. In some species, the gastrovascular cavity may be divided by vertical septa clothed with endoderm (*Anthophysa*).

PNEUMATOSACCUS
Inner ectodermal wall of the pneumatophore, typically lined by a chitinous layer (see pneumatocodon).

PODOCYST
Multicellular capsule from nipped-off portions of coenosarc, functioning as a cyst.

POLYGASTRIC STAGE
In siphonophores, the complete animal bearing both asexual and reproductive elements (nectosome and siphosome).

POLYMORPHIC
Bearing different morphs (in hydroids: gastrozooids, gonozooids, dactylozooids, etc.).

POLYP
Basic individual of the hydroids; may be isolated or form colonies; represented by different types, such as hydranths, gonozooids and dactylozooids.

POLYSIPHONIC = FASCICLED
A hydroid stem made of more than one coenosarc and perisarc tube.

PRIMARY POLYP
The hydranth formed by the development of a newly settled planula.

PROGENESIS
A type of paedomorphosis due to acceleration of the gonad development, so that sexual maturity is attained by organisms retaining juvenile characters.

PROLATE
Lengthened in the direction of the polar diameter; in medusae, species which contract over their entire length when swimming, producing a high velocity jet: i.e. *Aglantha*, *Sarsia*.

PROPAGULE
Any asexual or sexual morph leading to propagation.

PROXIMAL
At the near end, towards or at the base of attachment.

PSEUDOFILIFORM
Tentacles with scattered cnidocysts in a relatively low epidermis along the adoral side and a concentration of cnidocysts in tall epidermis on the aboral side.

PSEUDOHYDROTHECA
A film-like, often gelatinous, flexible coat covering partly or entirely the hydranth body of some Anthomedusae hydroids, it has little form and adheres closely to the hydranth ectoderm, not homologous to the perisarcal hydrothecae but apparently similar in function (e.g., some bougainvilliids and pandeids).

PSEUDOSEPTA
Radially arranged ridges between the dactylozooids of a cyclosystem.

Q-R

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 sometimes 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). Siphonophore nectosomes have four radial canal linked by the ring canal. They are unequally developed and their point of convergence is only exceptionally at the apex of the nectosome.

RAMIFIED CAPITATE
Branched tentacles with a capitation on each branch.

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.

RETE
In siphonophores a flattened, disc-shaped expansion on a canal; function unknown.

RHIZOCAULOMIC
Stolonal colonies with erect hydrorhiza formed by a bundle of parallel stolons.

RHIZOID
In hydroids, lateral root like structure attaching the stolon to the substratum.

RING CANAL
See circular canal.

RING FOLD
See annular ectodermal fold.

RING PALISADE = CHEVAL-DE-FRISE
In Stylasteridae ring of tiny, blunt spines projecting from the wall of the gastropore tube at the level of the gastrostyle tip. It constricts the gastropore tube in a lower gastrostyle chamber and an upper funnel-shaped part leading to the branch surface. When the gastrostyle is

absent, the ring palisade forms a solid ring constricting the gastropore tube in a small flat lower chamber, which contains the bulk of the gastrozooid and a larger spacious upper chamber into which the dactylozooids enter.

RUDIMENTARY BULB
See non-tentacular marginal bulb.

S

SAIL
Thin erect, sail-like structure extending across surface in *Velella*.

SARCOPORE
See sarcostyle.

SARCOSTYLE
Specialised type of nematophore found mainly in the Plumularioidea and exceptionally in a few other families, naked, emerging through a hole of the perisarc (sarcopore) 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. Body of the nematophores in some Aglaopheniids.

SARCOTHECA
See sarcostyle.

SCAPUS
A structure similar to coppinia but lacking the protective elongate polyps

SCUTUM
Plate or shield-like process.

SEMIFILIFORM
Tentacle with a capitation stretched towards the aboral side.

SEMIMONILIFORM
Tentacle with a large capitation and numerous small cnidocyst clusters on the adoral side.

SENSORY CLUB
See ecto-endodermal statocyst.

SEPTUM
An internal partition, for instance an inward projection of hydroid perisarc that may occur in the stolon, hydrocaulus, hydrocladium or hydrothecae.

SHAFT
See butt.

SIPHON
Unusual specialisation for attachment and strengthening, seen in *Hartlaubella gelatinosa* and some other hydroids, consisting of an unsegmented tubular outgrowth of hydrocaulus, resembling a stolon, running back from the distal end of each segment of the main hydrocaulus toward the base of the colony and closely pressed to the main stems; the siphon branch out basally into the substratum and end blindly.

SIPHOSOME
In siphonophores, section of the stem below nectosome, generally long, bearing cormidia.

SOLID TENTACLE
Tentacle without central cavity, with an endodermal core formed by a single row of disk-like or superimposed cylindrical vacuolated cells (see chordal).

SOMATOCYST
In calycophoran siphonophores, prominent extension of the stem in nectophore may contain an oil droplet at its apex.

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 either liberated as such or transferred to a female.

SPHERULE = LOCULE = BASAL SPACE
A globular region of pedicel directly beneath hydrotheca, formed by two adjacent annular constrictions.

SPHINCTER (ISTHMUS)
Cellular structure at the aboral end of hydranths that can be closed so to allow localised digestion of prey and to prevent the transfer of too large prey pieces from the gastric cavity to the lumen of the stolonal system; in campanulariids and eudendriids also to the constriction of the base of the hypostome.

SPINE
One of numerous chitinous spines projecting from perisarc-covered hydrorhizal network. Also one in the series of minute spines on tubule of cnidocysts.

SPIRAL CIRRUS (CIRRI)
Coiling spirally, with scattered cnidocysts and a terminal cluster of cnidocysts (*e.g.*, *Mitrocomella*).

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).

SPIRAL
Colony appearance due to spiral arrangement of hydrocladia around the main stem.

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).

SPUR CANAL
Reduced longitudinal canals in gastrovascular system of siphonophore prayid eudoxid bracts; in medusae, see exumbrellar spur.

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
In hydroids, a general term for any main erect structure that can bear hydrocladia or hydranths; in siphonophores, the stem or stolon is divided in two distinct regions (see stolon).

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 return. In siphonophores, the stolon or stem is a very extensile ecto-endodermic tube (coenosarc) along which the various types of zooids are borne, organised down such that two distinct regions can be recognised (only one in the Cystonect) the nectosome and the siphosome, both forming the polygastric stage. The stolon begins at the apex of the colony as somatocyst or is continuous with gastrovascular cavity of the float.

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 of the manubrium or of the hydranth in which food digestion is initiated. Often erroneously used instead of manubrium (see manubrium, manubrial or gastric cavity).

STRAIGHT
Hydroid colony with a non-flexuose main stem, either biseriate (with hydranths in two opposite rows) or uniseriate (with hydranths in a single row).

STRIATED MUSCLE
A muscle with striated fibers, present in the subumbrella of medusae.

STYLE
In some calcareous hydrozoans, upright spine at the base of gastropore, occasionally also in dactylopore.

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.

SUCKER
Adhesive structure in medusae, located either along or at the tip of the tentacles or at the tip of specialised stalk-like structures, usually lacking cnidocysts.

SWIMMING GONOPHORE
Pelagic stage derived from strongly reduced medusa stages (cryptomedusoids and perhaps heteromedusoids) developing as free gamete carriers; usually without radial canals and circular canal (present in *Anthohebella*); without tentacles; without sense organs; with sexual elements always on “manubrium” even in Leptomedusae, the manubrium or spadix in eccentric position. They can not be 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 exentric position of the manubrium. 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*).

SWIMMING SPOROSAC
Liberated sporosac with a non-medusoid swimming apparatus (*Dicoryne*).

SYNONYM
One, or two or more names applied to the same taxon. Synonymised species or genera are said conspecific or congeneric.

SYNONYMY
The list of synonyms applied to a taxon, other than the currently accepted name.

T

TABULAE
In Milleporidae, horizontal calcareous plates crossing the cavities of the gastropores and dactylopores, the most recent secreted tabula corresponds to the level of the alive part of the coenosteum.

TENTACLE
Usually highly contractile cnidocyst-bearing processes with sensory, defending, feeding and occasionally anchoring functions. In the medusae, the tentacles are usually on the umbrella margin = marginal tentacles, or on exumbrella. They may also occur around the mouth = oral tentacles; in hydroids, the tentacles may be located immediately below the hypostome= oral tentacles and/or in one or more distinct rings on the hydranth body = aboral tentacles or even scattered over the whole body. Tentacles types vary according to the distribution of cnidocyst armature; the most common types are capitate, cateniform, filiform, moniliform, pseudofiliform, ramified capitate.

TENTACULAE
Small solid marginal tentacles (usually without marginal bulbs, but in contact with the circular canal) located between normal hollow tentacles (*e.g.*, Amphinema *rugosum*).

TENTACULAR MARGINAL BULB
In most Antho- and Leptomedusae, a dilated portion of the proximal part of a marginal tentacle, next umbrellar margin, containing a cavity in communication with the circular canal and with the tentacular cavity of hollow tentacles. Of various shapes, mostly simple but in some medusae compound, originating several tentacles (*e.g.*, *Hybocodon*, *Bougainvillia*); they perform digestive activities; are centres of cnidoblast formation and, in some species, bear 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 *Eugotoea petalina* and *Rhabdoon singularis*.

TENTACULAR ROOT
Projection of the endodermal tentacular core into the umbrella mesoglea (*Blackfordia, Obelia*, some Limnomedusae, Trachymedusae and the Narcomedusae) (see peronia).

TENTACULIFORM STRUCTURE
Solid marginal structure resembling tentaculae, without marginal bulb and with no contact with circular canal (exclusive to Orchistomatidae).

TENTACULOCYST
See ecto-endodermal statocyst.

TENTACULOZOOID
Reduced dactylozooid similar to tentacle in structure, with a solid core of chordal endoderm and no mouth or gastric cavity, richly armed with cnidocysts and often with chemosensory receptors; very extensible and contractile.

TENTILLA
In siphonophores, side branches of tentacle, bearing expanded terminal aggregations of cnidocysts (see cnidoband).

THECA
Chitinous extension typically protecting any kind of polyp.

THECATE
Name for the hydroid stage of the Leptomedusae, usually with thecae protecting hydranths and gonophores.

THREAD
Hollow thin tube coiled inside cnidocyst capsule. Turned inside out when discharged. Discharged threads may be differentiated into a proximal dilated section, shaft or butt, and a thinner distal section, the thread or tubule.

THRUST BLOCK
In siphonophores, aboral section of a physonect nectophore, separating apical wings and abutting against nectosomal stem.

TRANSVERSE COMMISSURES = COMMISSURAL CANALS

TROPHOSOME
All structures of a colony except the gonothecae.

TUBULE
See thread.

U

UMBILICAL CANAL
See apical canal.

UMBRELLA
Main body of medusa, excluding manubrium and tentacles; generally resembling a bell or an umbrella. Shapes: bell-shaped, bowl-shaped, dome-shaped, flat, hemispherical, pointed, saucer-shaped, tall, turreted. The outer, generally convex, surface is the exumbrellar surface (exumbrella); the inner concave surface is the subumbrellar surface (subumbrella), the concavity being the subumbrellar cavity. The edge of the umbrella is the umbrellar margin.

UMBRELLULA
See intertentacular web.

V

VASIFORM
Vase-shaped, with broad base and slender top.

VELAR RIDGE
In siphonophores, cross ridge, parallel to ostium, on nectophores of some *Lensia* spp.

VELAR
Of the velum.

VELUM
Horizontal fold projecting inwards from umbrellar margin, leaving a central, circular hole, the velar opening. It consists of two layers of ectoderm separated by a thin mesoglean lamella; the inner ectoderm, of subumbrellar origin, possesses 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.

VERONICA
In siphonophores, a spiral movement that spreads the tentacles into a characteristic pattern.

VERTICILLATE
Arranged in a succession of whorls, whorled.

Z

ZOOID
In colonial hydroids, any of several types of individual polyps: dactylozooids, gastrozooids, gonozooids etc.

ZOOXANTHELLAE
Unicellular algae, living in symbiotic association in the tissues of many Cnidaria.

SYSTEMATICAL INDEX

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Hydrozoa occur in all aquatic habitats. They form part of the plankton, the hard- and soft-bottom macrobenthos, and the meiofauna. They can also be symbiotic with a wide variety of animals and plants, and some are parasitic. Some hydrozoans are famous experimental animals, such as *Hydra* and *Hydractinia*. The presence of polyp and medusa stages in the life cycle of many species led to a double taxonomy that is being unified through a research project that started in the first half of the last century and is still continuing.

The present monograph assembles the most relevant knowledge on the group, with a list of all the known species and diagnoses of all supraspecific taxa. This is an intermediate step towards the appreciation of the diversity of the Hydrozoa, the aim being to attract the curiosity of biodiversity students and to motivate them to fill the many gaps that remain in our knowledge of this fascinating group. The authors are all members of the Hydrozoan Society and this book is a product of the philosophy of the Society.

Jean Bouillon dedicated his life to the study of the Hydrozoa, starting with life cycles, histology, developmental biology and evolution, culminating his career with the description of more than 150 new taxa, from species to orders. He established the core of this book.

Cinzia Gravili studies life cycles and taxonomy of the Hydrozoa. She has assembled a monumental database on the literature of the group. She worked on the nomenclatural and bibliographic aspects of this book.

Francesc Pagés specializes in the taxonomy and ecology of planktonic hydrozoans, with particular focus on the Siphonophores: he is the main contributor for this group in this treatise.

Josep-Maria Gili works on both planktonic and benthic Hydrozoa. His interests range from taxonomy to ecology and he contributed to the monograph by taking care of these aspects.

Ferdinando Boero works on taxonomy, life cycles, ecology and evolution of the Hydrozoa and contributed to these themes the writing of this book.

Les Hydrozoaires peuplent tous les milieux aquatiques et constituent une partie du plancton, du benthos et de la méiofaune. Ils peuvent être symbiontes d'animaux ou de plantes, voire même parasites. Quelques uns sont des organismes modèles bien connus, comme Hydra *et* Hydractinia. *Malheureusement, la connaissance de ce groupe d'organismes a été desservie par la complexité de leurs cycles de vie et de leurs morphologies. Ainsi, une double taxonomie confuse a souvent résulté de la présence de stades polype ou méduse chez de nombreuses espèces. La révision de cette taxonomie a commencé depuis la première moitié du siècle dernier et continue encore aujourd'hui. À cet égard, les auteurs sont tous membres de l'Hydrozoan Society et ce livre reflète la philosophie de cette société savante.*

La présente monographie fait la synthèse des connaissances actuelles sur ce groupe, avec une liste de toutes les espèces et des diagnoses de tous les taxons supraspécifiques. C'est une étape vers une meilleure appréciation de la diversité des Hydrozoaires, le but des auteurs étant de motiver et de faciliter la tâche des scientifiques afin qu'ils comblent les lacunes existant dans la connaissance de ce groupe fascinant.

Jean Bouillon a dédié sa vie à l'étude des Hydrozoaires, en commençant par l'étude des cycles de vie, l'histologie, la biologie du développement, l'évolution et a couronné sa carrière par la description de plus de 150 nouveaux taxons de l'espèce à l'ordre. Dans l'ouvrage, il est l'auteur de la compilation des données.

Cinzia Gravili étudie les cycles de vie et la taxonomie des Hydrozoaires. Elle a constitué une base de données monumentale sur la littérature concernant ce groupe. Dans le présent travail, elle a été chargée des aspects nomenclaturaux et bibliographiques.

Francesc Pagés est un spécialiste de la taxonomie et de l'écologie des Hydrozoaires planctoniques et plus particulièrement des Siphonophores. Dans le volume, il est le principal auteur du travail sur ce groupe.

Josep-Maria Gili étudie les Hydrozoaires planctoniques et benthiques. Ses centres d'intérêt incluent la taxonomie et l'écologie pour lesquelles il a participé à la monographie.

Ferdinando Boero travaille sur la taxonomie, les cycles de vie, l'écologie et l'évolution des Hydrozoaires, sujets de sa contribution dans ce volume.

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