



An introduction to Hydrozoa

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PUBLICATIONS SCIENTIFIQUES DU MUSÉUM

An introduction to Hydrozoa

**Mémoires du Muséum national d'Histoire naturelle
Tome 194**

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**Publications Scientifiques du Muséum
Paris**

2006

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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 currently 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.

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 sibogae Lens & van Riemsdijk, 1908

Bathyphysa japonica Kawamura, 1943 [invalid species, see Pagès 2002]

Genus *RHIZOPHYSA* Périon & 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 eysenhardtii 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.

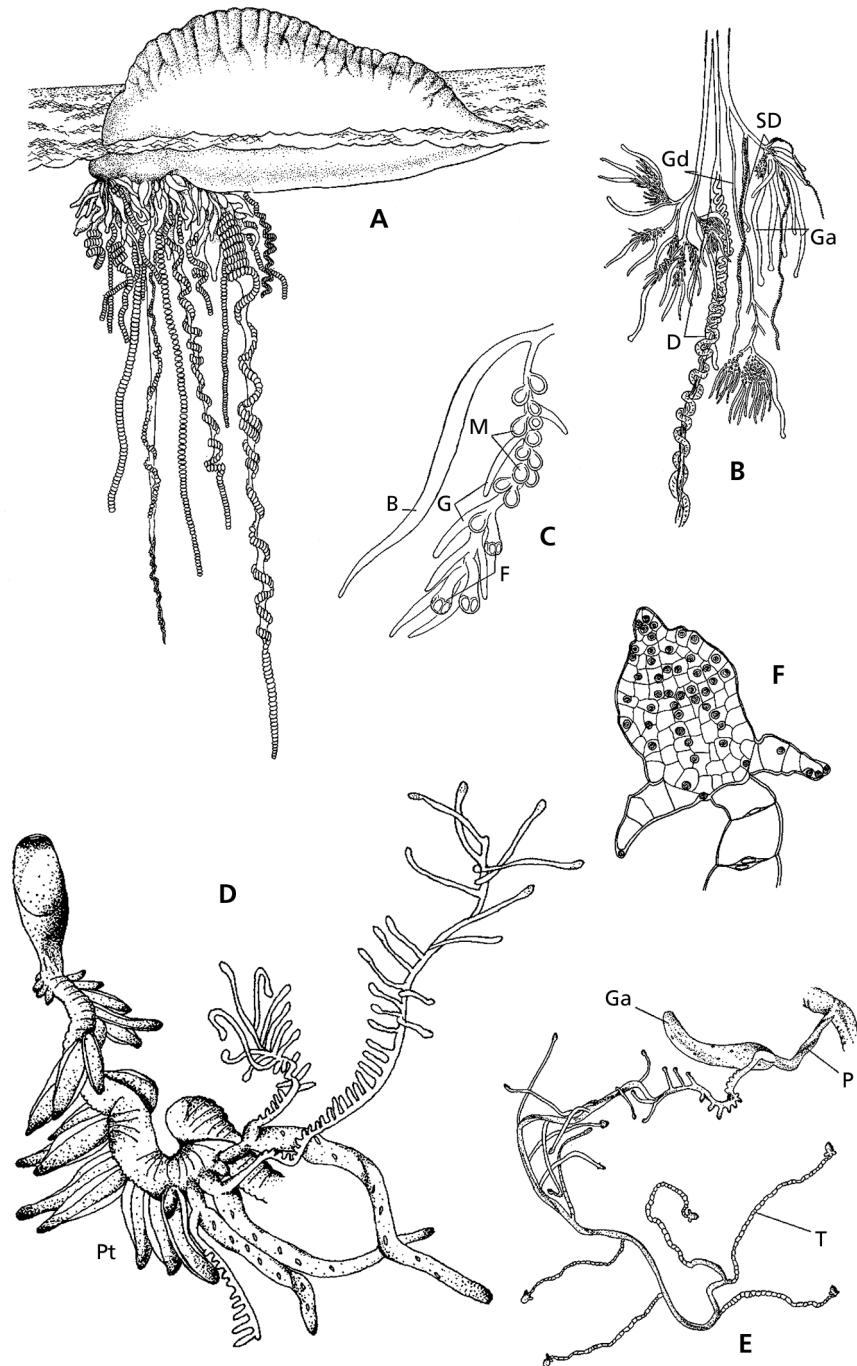


FIG. 207. Siphonophorae, Cystonectae, Physaliidae. A-C, *Physalia physalis*: A, general view; B, detail of a cormus; C, detail of a small part of a gonodendron. D-F, *Bathypysa sibogae*: D, polygastric stage; E, old gastrozooid; F, trifid tentilla (A after Pagès & Gili, 1992; B-C after Hyman, 1940; D-F 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, *Bathypysa 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 aniso-

rhizae; 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

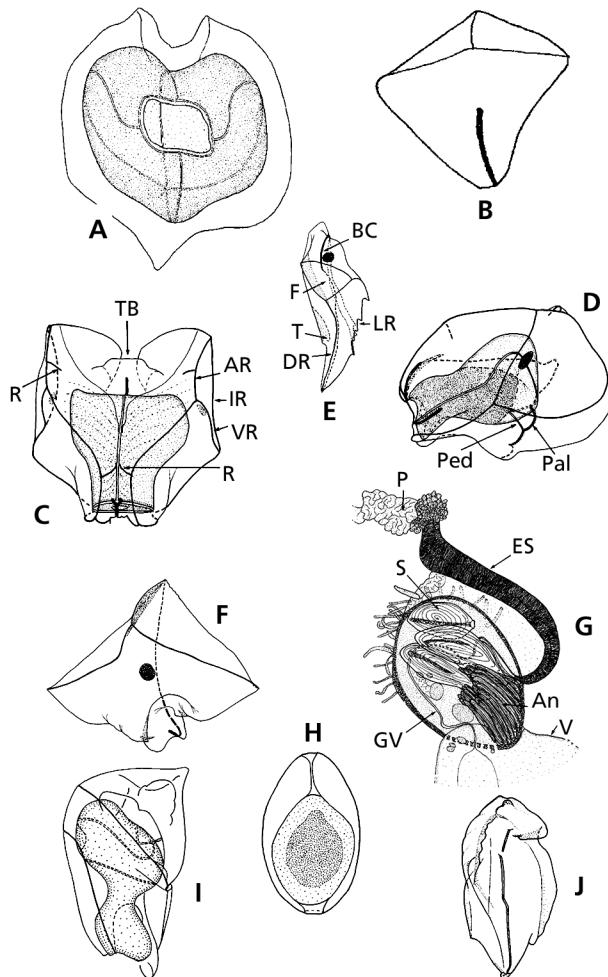


FIG. 208. Siphonophorae, Physonectae, Agalmatidae. A-B, *Cordalgama*, *Cordalgama cordiformis*: A, nectophore (ostial view); B, bract. C-H, *Frillaglma vityazi*: C-D, upper and lateral view of a mature nectophore; E, ventral bract (dorsal view); F, right-hand side of lateral bract; G, detail of the proximal 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, *Frillaglma 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 tonon élastique plissé et ainsi que la capsule du cnidocyte; 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 = tonon élastique; F = facette dorsale; GV = canal gastro-vasculaire; IR = crête infra-latérale; LR = crête longitudinale; P = pélicelle; Pal = canal pallial; Ped = canal pédiculaire; R = petite crête; S = stenoteles; 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).

Frillaglma 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).

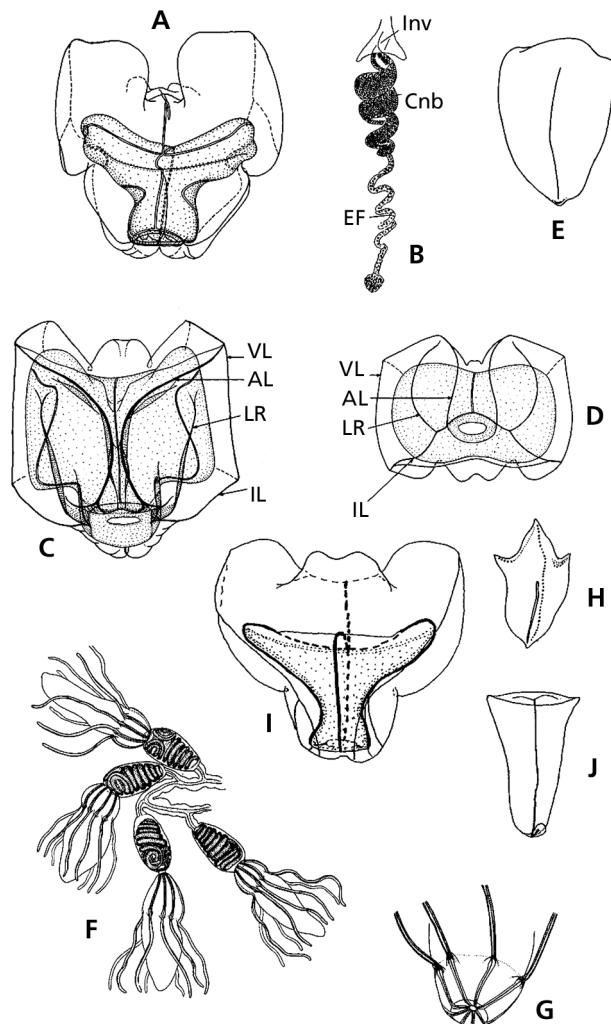


FIG. 209. Siphonophorae, Physonectae, Agalmatidae. A-B, *Halistemma rubrum*: A, nectophore (vue ventrale); B, tentille. C-H, *Lychnagalma*: C-G, *Lychnagalma utricularia*: C, nectophore (vue dorsale); D, nectophore (vue ostiale); E, bractée; F, vue générale de quatre tentilles, notez la cnido-bande spiralee incluse dans l'involucrum et la vésicule terminale; G, détail de la base détachée d'une vésicule terminale montrant les filaments octo-radiales; H, *Lychnagalma vesicularia*, bractée. I-J, *Marrus antarcticus*: I, vue apicale d'un nectophore; J, bractée (A 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 tentillium; IL = crête infra-latérale; Inv = involucrum; LR = crête latérale; VL = crête verticale-latérale.

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 cnido-bande spiralee incluse dans l'involucrum et la vésicule terminale; G, détail de la base détachée d'une vésicule terminale montrant les filaments octo-radiales; H, *Lychnagalma vesicularia*, bractée. I-J, *Marrus antarcticus*: I, vue apicale d'un nectophore; J, bractée (A 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 tentillium; IL = crête infra-latérale; Inv = involucrum; LR = crête latérale; VL = crête verticale-latérale.

Halistemma amphytidis (Lesueur & Petit, 1807)
Halistemma cupulifera Lens & Van Riemsdijk, 1908
Halistemma rubrum (Vogt, 1852)

Halistemma striata Totton, 1965
Halistemma transliratum Pugh & Youngbluth, 1988

Genus **LYNCHAGALMA** 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).

Lynchagalma 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 Margulies, 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** Margulies, 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 Margulies, 1976 [doubtful status]

Genus **RUDJAKOVIA** Margulies, 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; gastrozoids devoid of tentacles.

Rudjakovia plicata Margulies, 1982 [doubtful status]

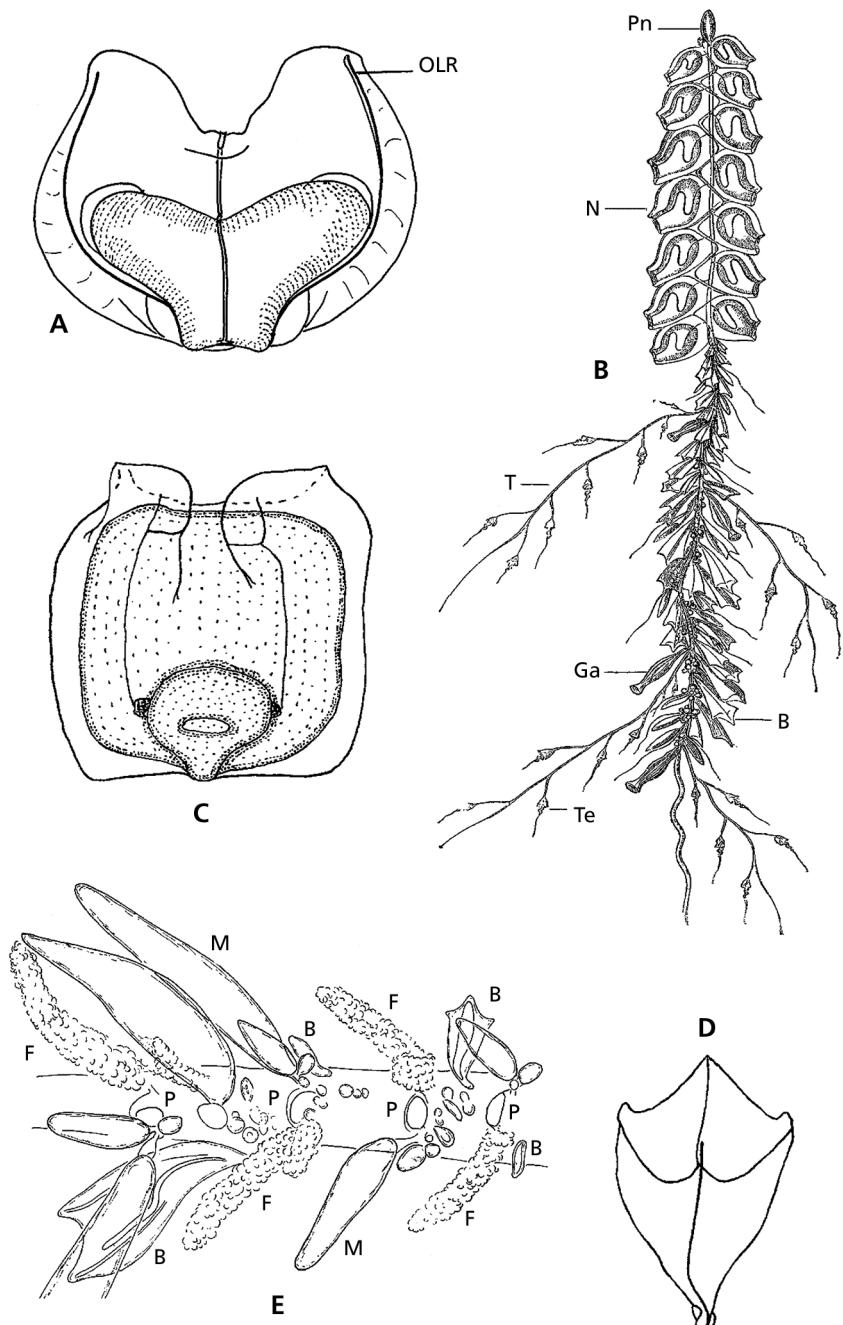


FIG. 210. Siphonophorae, Physonectae, Agalmatidae. A, *Moseria convoluta*, upper view of a young nectophore. B-E, *Nanomia bijuga*: B, view of a polygastric stage; C, upper view of a nectophore; D, bract; E, part of an internode of the stem showing alternating male and female gonodendra arising from 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 polygastrique ; 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 = gastérozoïde ; M = gonophore mâle ; N = nectophore ; Pn = pneumatophore ; OLR = crête oro-latérale ; P = palpon ; T = tentacule ; Te = tentille.

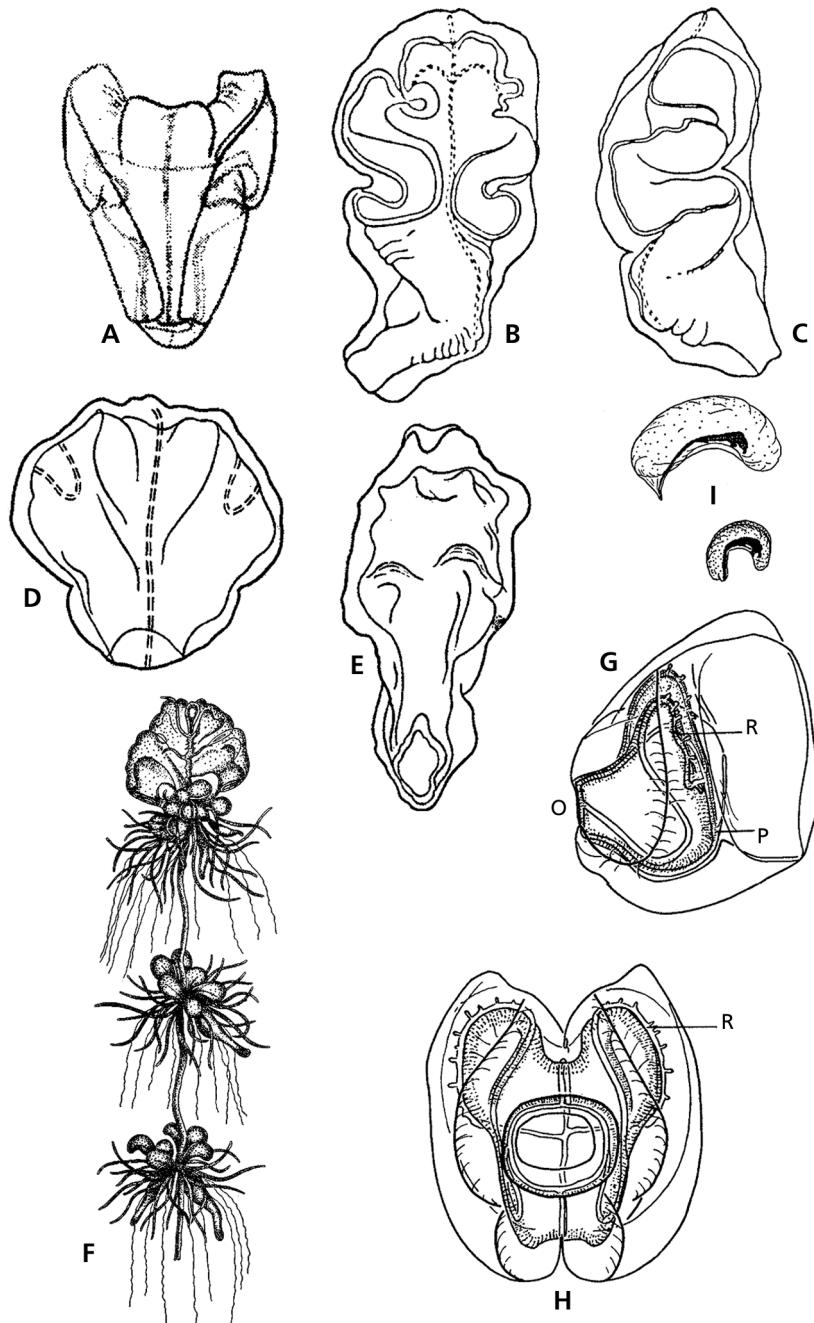


FIG. 211. Siphonophorae, Physonectae, Agalmatidae. A, *Paragalma birsteini*, nectophore. B-C, *Rudjakovia plicata*: B, nectophore (ventral side); C, nectophore (side view). D-E, *Stepanyantsia polymorpha*: D, nectophore (dorsal view); E, nectophore (lateral view). F-I, Apolemiidae, *Apolemia uvaria*: 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 vitiazii 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]

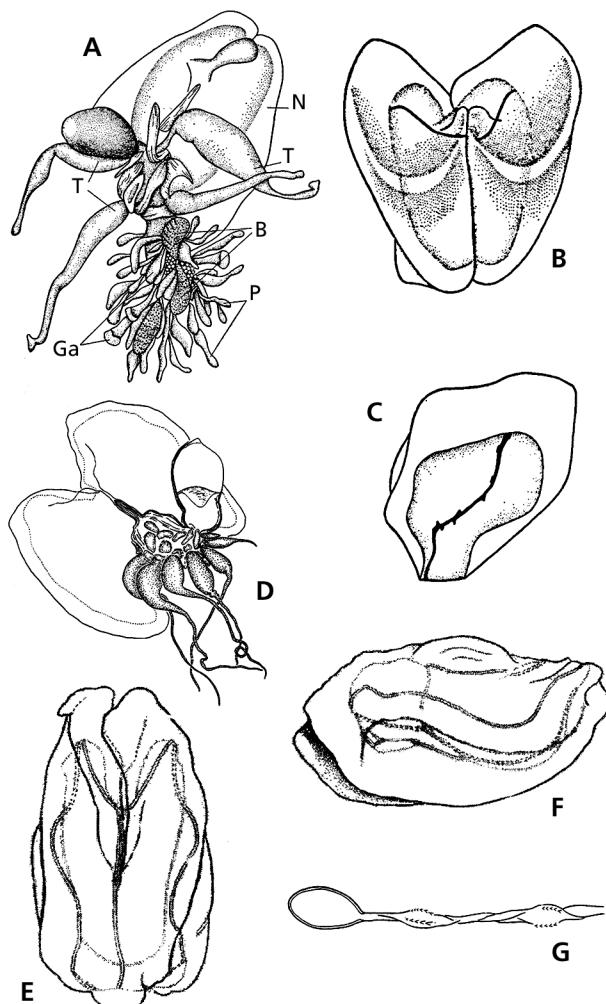


FIG. 212. Siphonophorae, Physonectae, Apolemidae. A-C, *Ramosia vitiazi*: A, partie d'un stade polygastrique ; B-C, nectophores. D-G, *Tottonia contorta*: D, nectosome et groupe cormidal, notez le pneumatophore à deux chambres et les tentacules disposés en une simple rangée ; E, nectophore (vue dorsale) ; F, nectophore (vue latérale) ; G, cnidocyste birhopaloïde (A-C après Stepanjants, 1967 ; D & G après Margulis, 1980 ; E-F après Margulis, 1976). B = bracte ; Ga = gasterozoïde ; N = nectophore ; P = palpon ; T = tentacule.

FIG. 212. Siphonophorae, Physonectae, Apolemidae. A-C, *Ramosia vitiazi* : A, partie d'un stade polygastrique ; B-C, nectophores. D-G, *Tottonia contorta* : D, nectosome et groupe cormidal, notez le pneumatophore à deux chambres et les tentacules disposés en une simple rangée ; E, nectophore (vue dorsale) ; F, nectophore (vue latérale) ; G, cnidocyste birhopaloïde (A-C 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)

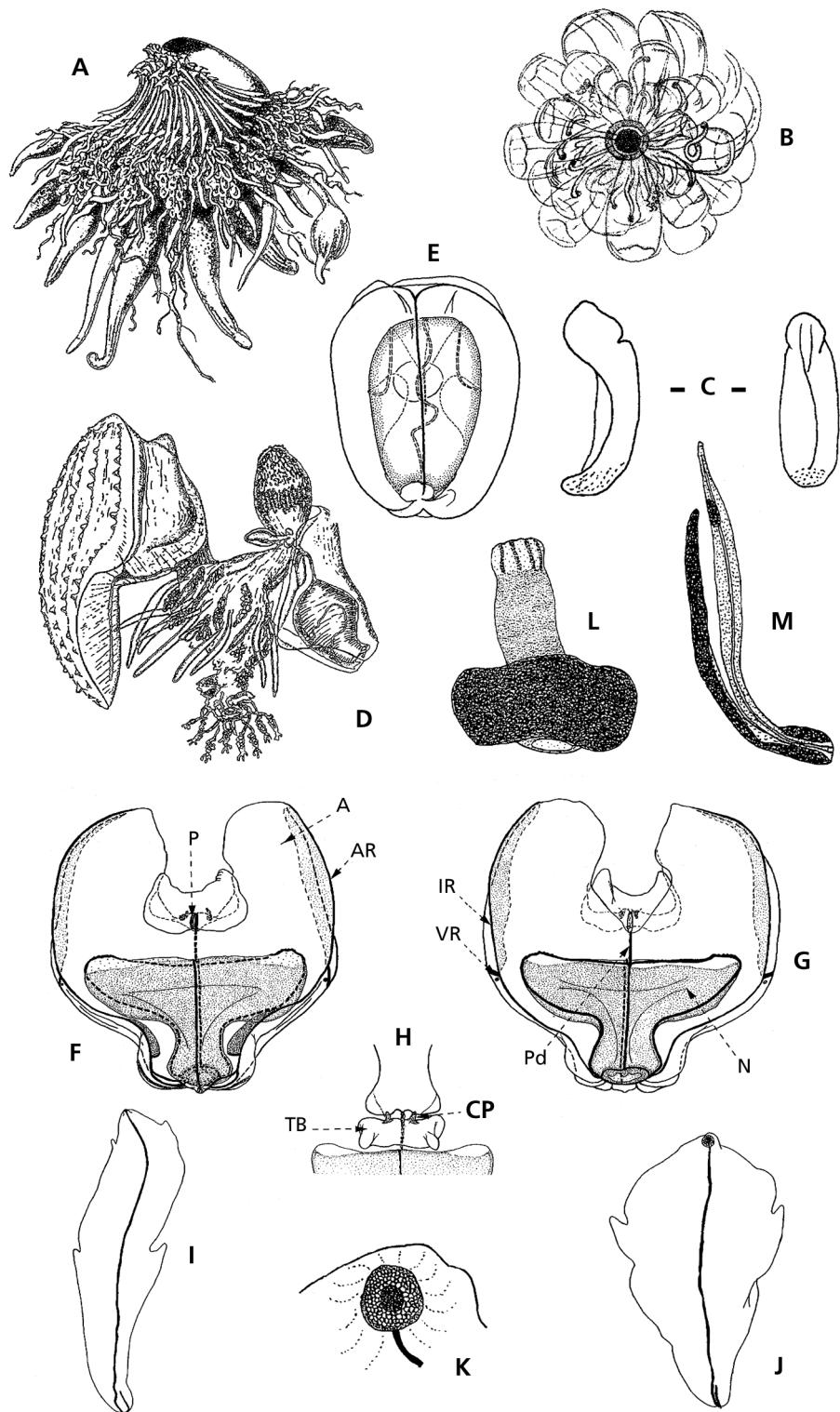
Genus **MELOPHYSA** Haeckel, 1888

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, gasterozooid 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 = thrust 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 ventrale). 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 spiralee (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 pédonculaire ; TB = échancrure entre les deux lobes supérieurs du nectophore ; VR = crête verticale latérale.



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 ectophores, 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: Margulies (1990); Pugh (2001).

Erenna cornuta Pugh, 2001

Erenna laciinata Pugh, 2001

Erenna richardi Bedot, 1904

Genus **PARERENNA** Pugh, 2001

Fig. 214A-F

Erennids with ectophores 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 emilia Pugh, 2001

Family FORSKALIIDAE Haeckel, 1888

Physonects with cylindrical or cone-shape nectosome, whose numerous ectophores have a multiserial, spiral arrangement. Ectophores 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.

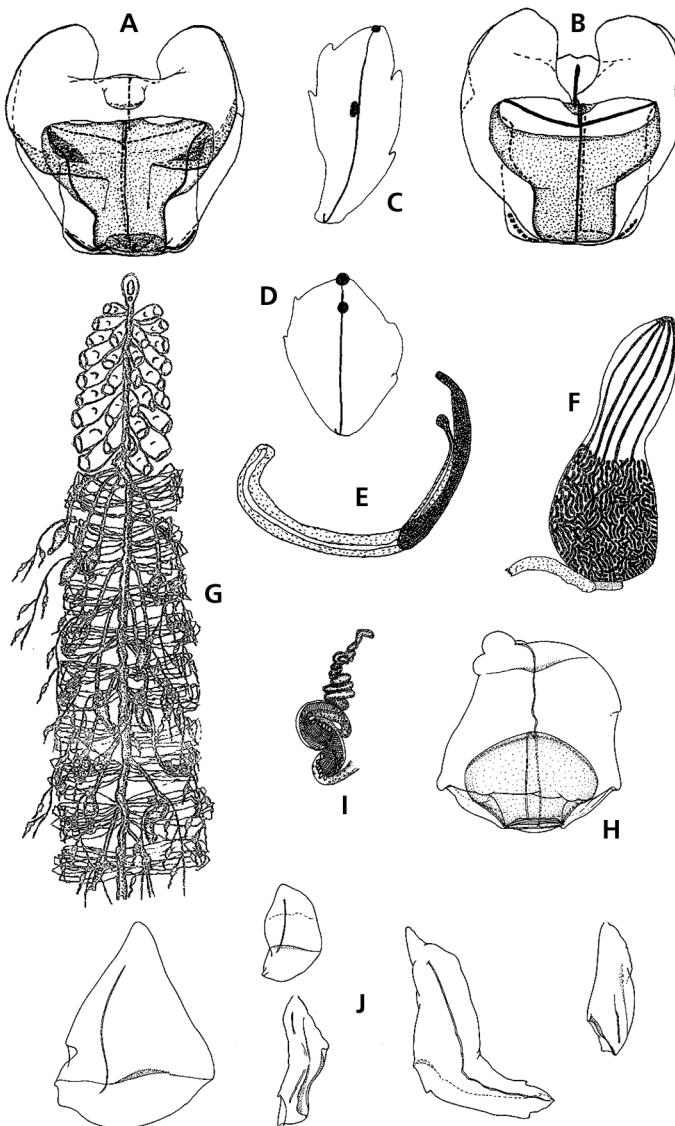


FIG. 214. Siphonophorae, Physonectae. A-F, Erennidae, *Parerenna emilia*: A, nectophore (upper view); B, nectophore (lower view); C, bract of the first type; D, bract of the second type; E, tentillum with long peduncle and cnidoband extending beyond terminal process; F, gastrozooid with small basigaster and peduncle. G-J, Forskalidiidae, *Forskalia*: G & I, *Forskalia contorta*: G, epigastric stage; I, tentillum; H & J, *Forskalia edwardsi*: H, nectophore (upper view); J, various types of bracts (A-F after Pugh, in press; G & I after Tréguer, 1957: pl. 79, figs. 7 & 9; H & J after Kirkpatrick & Pugh, 1984).

FIG. 214. Siphonophorae, Physonectae. A-F, Erennidae, *Parerenna emilia*: 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 cridobande s'étendant au-delà du processus terminal; F, gastérozoïde avec un petit basigaster et un pédoncule. G-J, Forskalidiidae, *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 Tréguer, 1957: pl. 79, figs. 7 & 9; H & J d'après Kirkpatrick & Pugh, 1984).

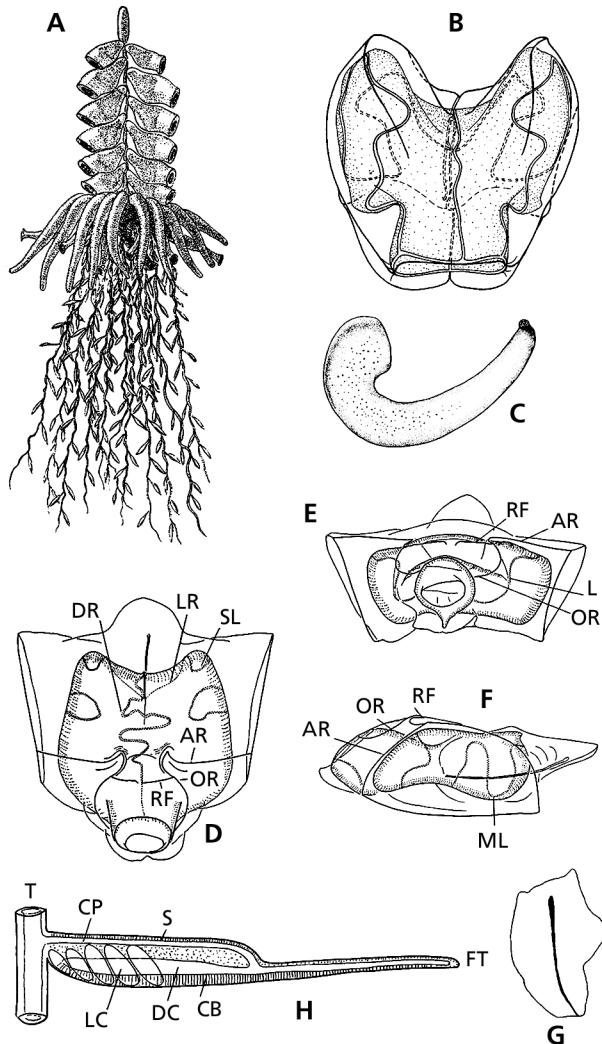


FIG. 215. Siphonophorae, Physonectae. A-C, Physophoridae, *Physophora hydrostatica*: A, stade polygastrique; B, nectophore (vue dorsale); C, palpon. D-H, Pyrostephidae, *Pyrostephos vanhoeffeni*: D, nectophore (vue dorsale); E, nectophore (vue ostiale); F, nectophore (vue latérale); G, bractée; H, croquis 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 Pages & 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.

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 Pages & 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.

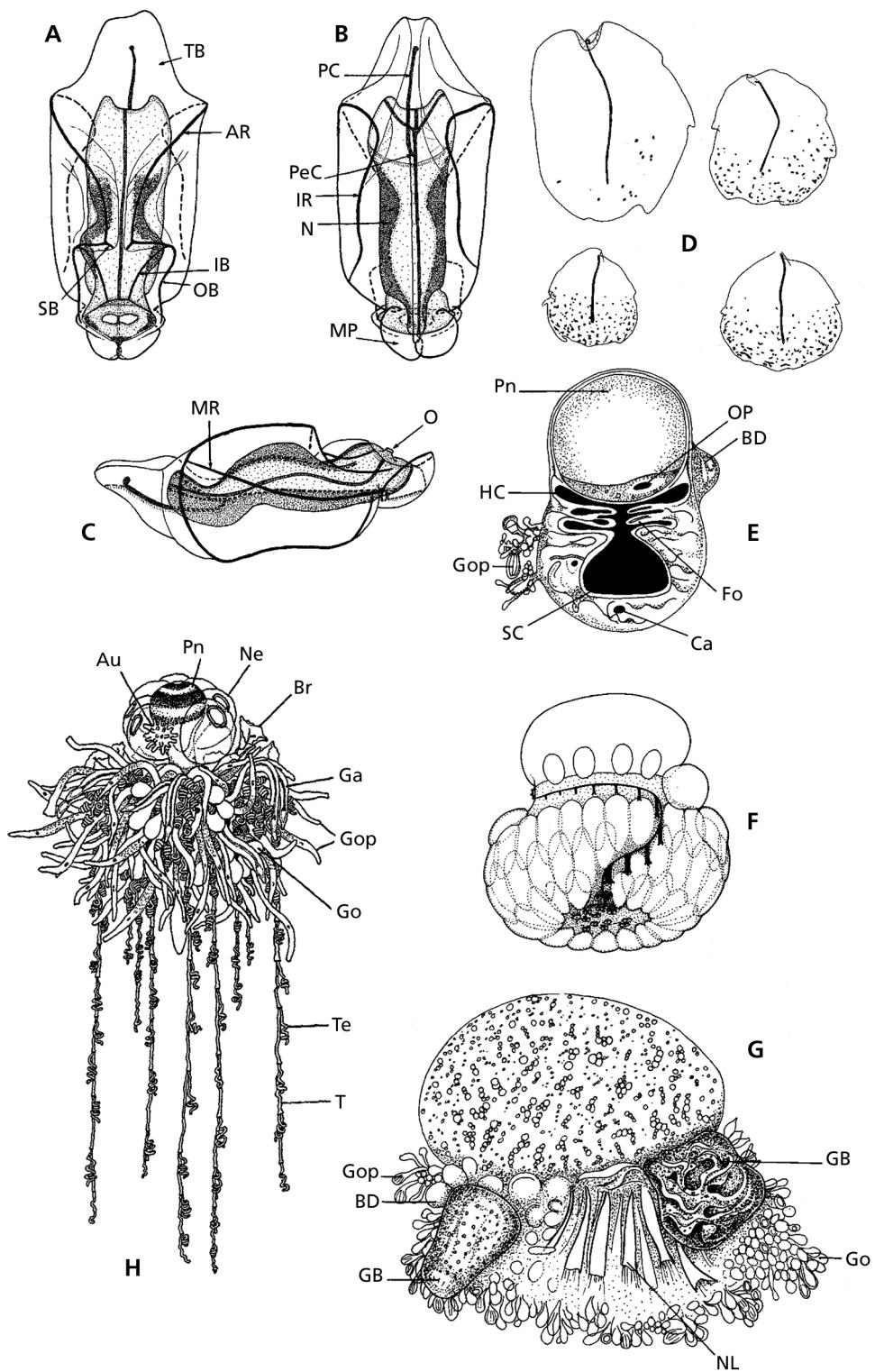
Genus **BARGMANNIA** Totton, 1954

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, Rhodalidiidae, *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 nectophor 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 = gastrozoid; 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, Rhodalidiidae, *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 cormidielles le long du spécimen depuis leur origine dans la zone de prolifération jusqu'à ce qu'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 = gastrozooïde; GB = corps globulaire (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.



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 cha-

racteristic structure the europhore, 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 europhore 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

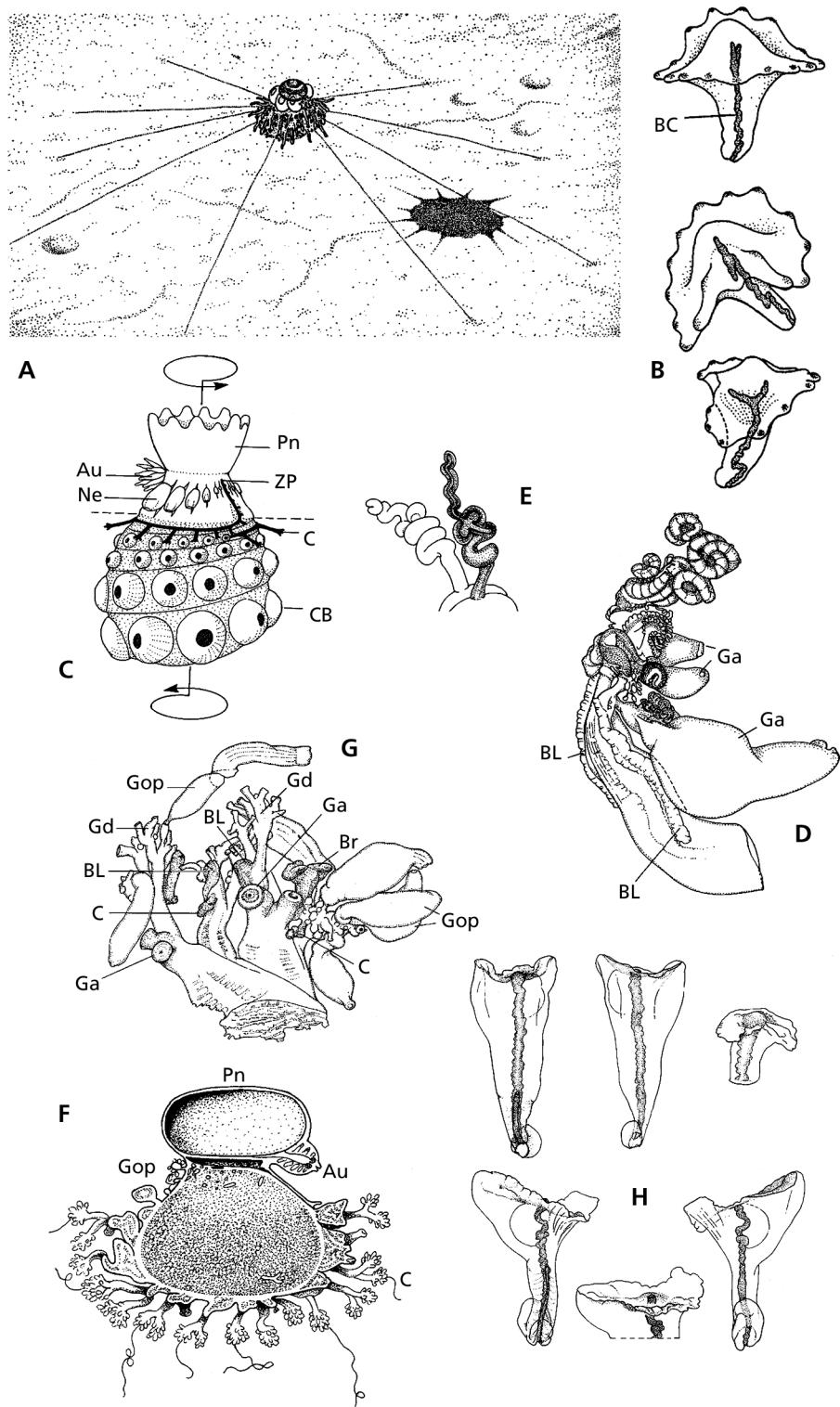
Genus **ARCHANGELOPSIS** Lens & van Riemsdijk, 1908

Figs 216H, 217A-B

Rhodaliids with smooth-walled pneumatophore. Europhore 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 through 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 = europhore; BC = bracteal canal; BL = bracteal lamella; Br = bract; C = cormidium; CB = cormidial 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 cormidiés, notez la série d'unités cormidielles en développement au niveau des anneaux apicaux siphosomaux. Leur présence indique la possibilité que les régions nectosomale et siphosomal 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 tricornu. F-H, *Rhodalia miranda* : F, section sagittale au travers d'une cormidie ; G, deux unités cormidielles en développement ; H, bractées (A-B d'après Hissmann et al., 1995 : p. 677, figs 7-6 ; C-H d'après Pugh, 1984). Au = europhore ; 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.



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 dextrotropic 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

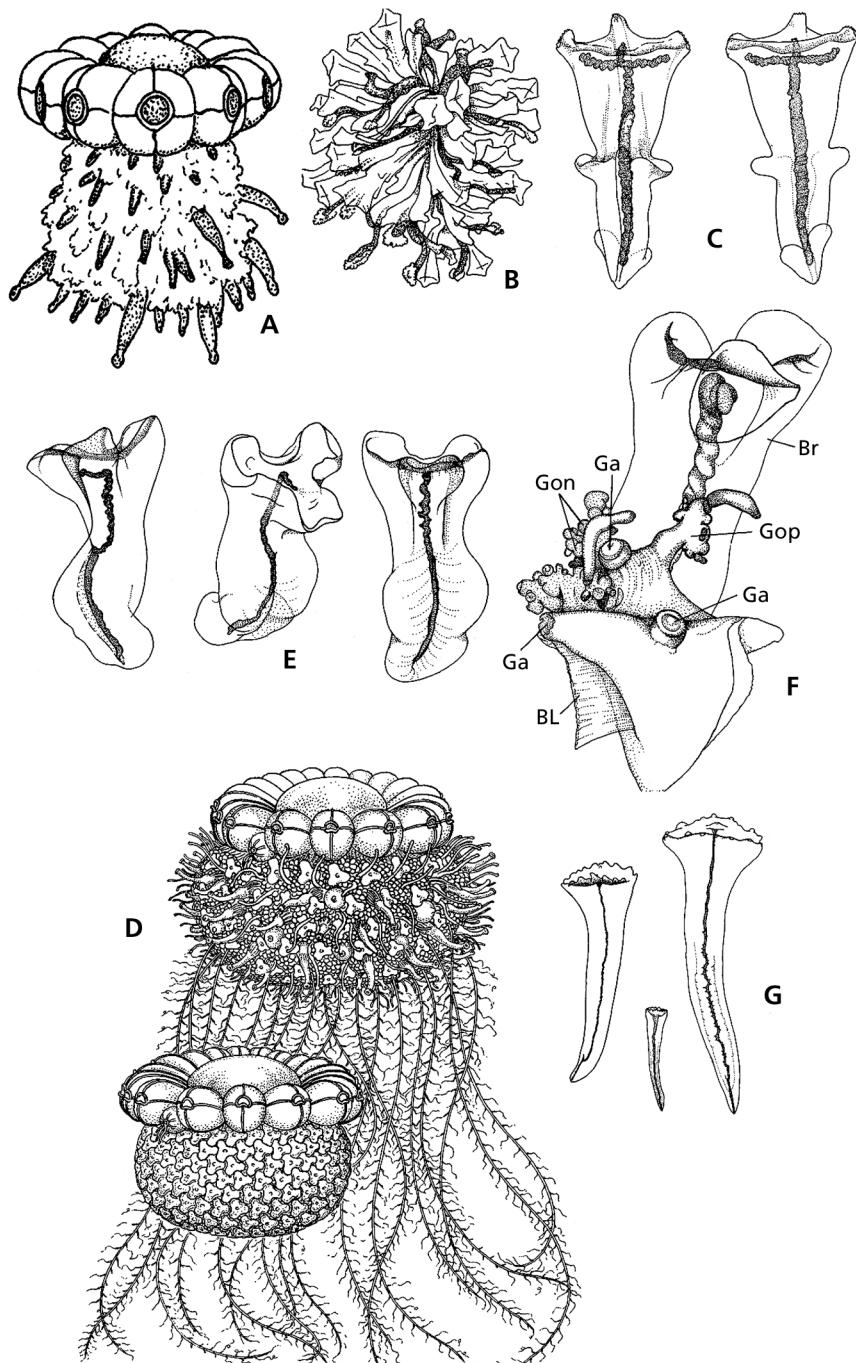


FIG. 218. Siphonophorae, Physonectae. A-C, Rhodaliidae, *Sagamalia hinomaru*: A, croquis d'animaux complets, avant fixation ; B, vue aborale du siphosome ; C, bractées ; D-F, *Stephalia corona* : D, reconstruction d'un animal complet, au-dessus en extension, en-dessous contracté ; E, différents aspects 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.

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 flattened 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 obsolescent. 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. | |
| – 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 | |
| Abylidiae | |

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 ante-

rior 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 phyllocysts, 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 haackeli Lens & Van Riemsdijk, 1908

Abyla ingeborgae Lens & Van Riemsdijk, 1908 [perhaps a syn. of *A. haackeli*]

Abyla peruana Sears, 1953

Abyla schmidti Sears, 1953

Abyla tottoni Sears, 1953

Abyla trigona Quoy & Gaimard, 1827

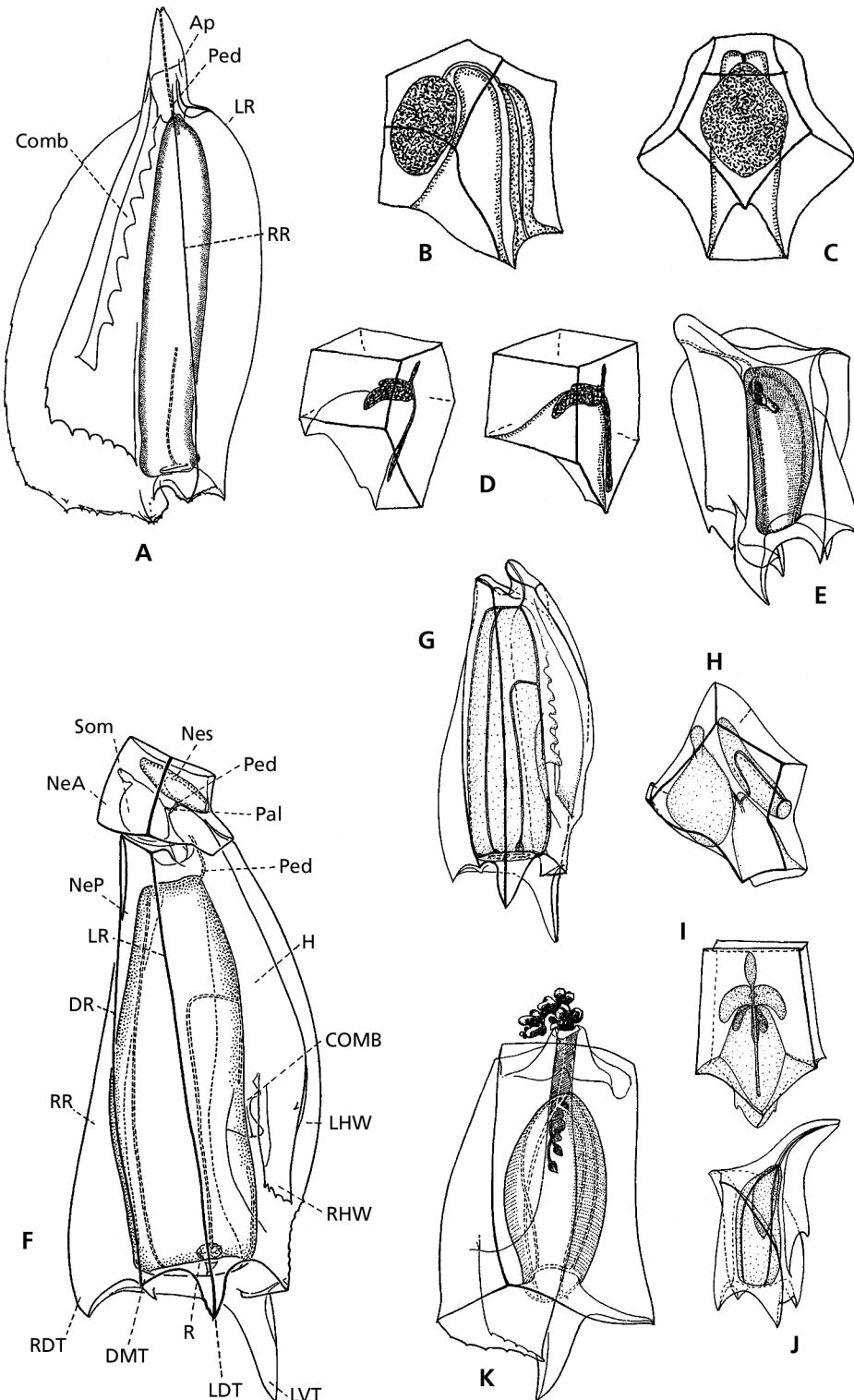


FIG. 219. Siphonophorae, Calycocephorae, Abyliidae. A-E, *Abyla*: A, *Abyla trigona*, polygastric stage; B-C, anterior nectophore of *Abyla haekeli*; B, ventral view; C, lateral view; D, bract of *Abyla eschschotzi* (left), bract of *Abyla tetragona* (right); E, eudoxid of *Abyla haekeli*. F-J, *Abylopsis teragona*: F, polygastric stage; G, posterior nectophore; H, anterior nectophore; I, eudoxid bract; J, gonophore. K, *Bassia bassensis*, polygastric 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 = dorsal 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 = somato-cyst.

FIG. 219. Siphonophorae, Calycocephorae, Abyliidae. A-E, *Abyla*: A, *Abyla trigona*, stade polygastrique; B-C, nectophore antérieur d'*Abyla haekeli*: B, vue ventrale; C, vue latérale; D, bractée d'*Abyla eschschotzi* (à gauche), bractée d'*Abyla tetragona* (à droite); E, eudoxie d'*Abyla haekeli*. F-J, *Abylopsis teragona*: F, stade polygastrique; G, nectophore postérieur; 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 = cormidié; COMB = peigne; DMT = dent dorsomédiane; DR = crête dorsale; H = hydroécie; Nes = nectosac; LDT = dent dorsale gauche; LHW = aile hydroéciale gauche; LR = crête gauche; LVT = dent ventrale gauche; NeA = nectophore antérieur; NeP = nectophore postérieur; Pa = canal pallial; Ped = canal pédi culaire; R = rete; RDT = dent dorsale droite; RHW = aile hydroéciale droite wing; RR = crête droite; Som = somato-cyste.

Genus CERATOCYMBIA 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

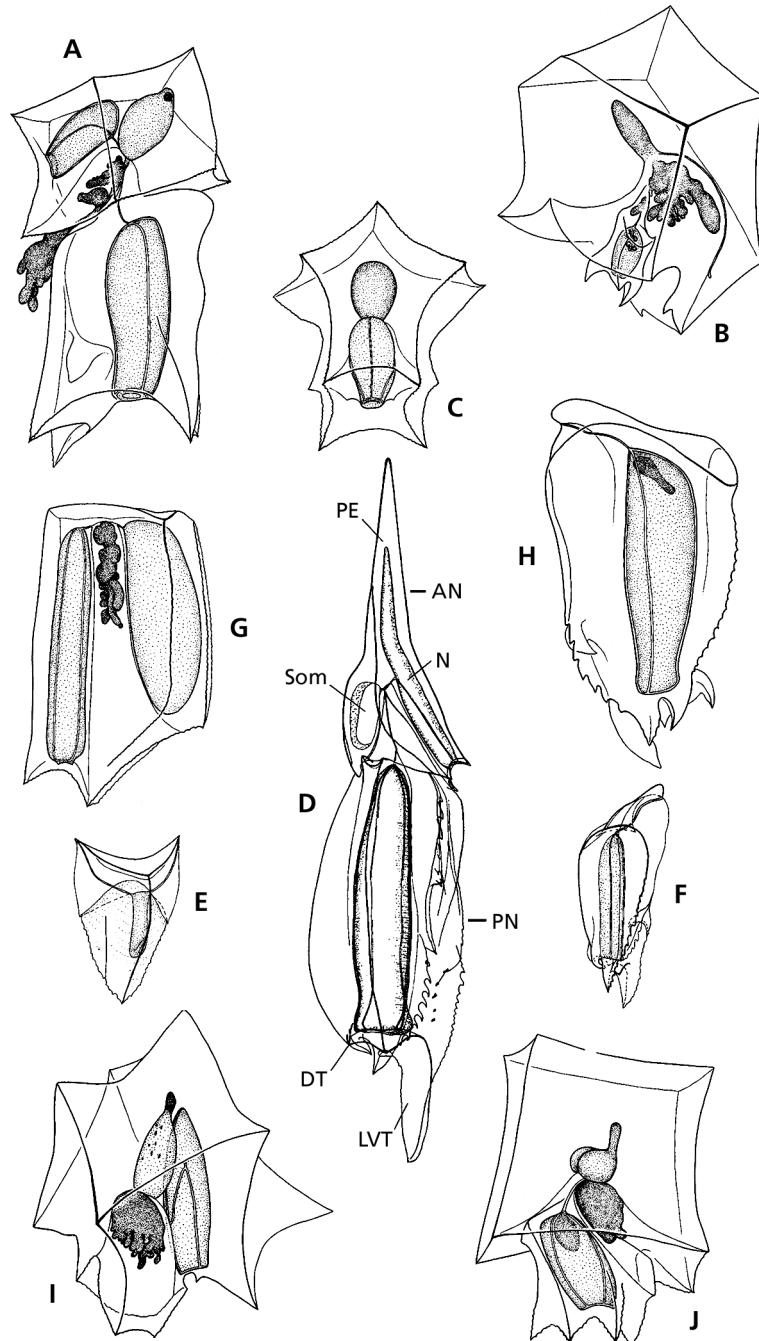


FIG. 220. Siphonophorae, Calycophorae, Abyliidae. A-C, *Bassia bassensis*: A, polygastric stage (lateral view); B, eudoxid (latero-ventral view); C, anterior nectophore (dorsal view). D-H, *Ceratocymbia*: D-F, *Ceratocymbia sagittata*: D, polygastric stage; E, eudoxid bract; F, gonophore; G, *Ceratocymbia leuckarti*, anterior nectophore; H, *Ceratocymbia 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 = pyramidal 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, *Ceratocymbia sagittata*: D, stade polygastrique; E, bractée de l'eudoxie; F, gonophore; G, *Ceratocymbia leuckarti*, nectophore antérieur; H, *Ceratocymbia 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 & Pages (1993); Pugh (1995).

Clausophyes galeata Lens & Van Riemsdijk, 1908

Clausophyes laetmata Pugh & Pages, 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); Pages & Pugh (2002).

Crystallophyes amygdalina Moser, 1925

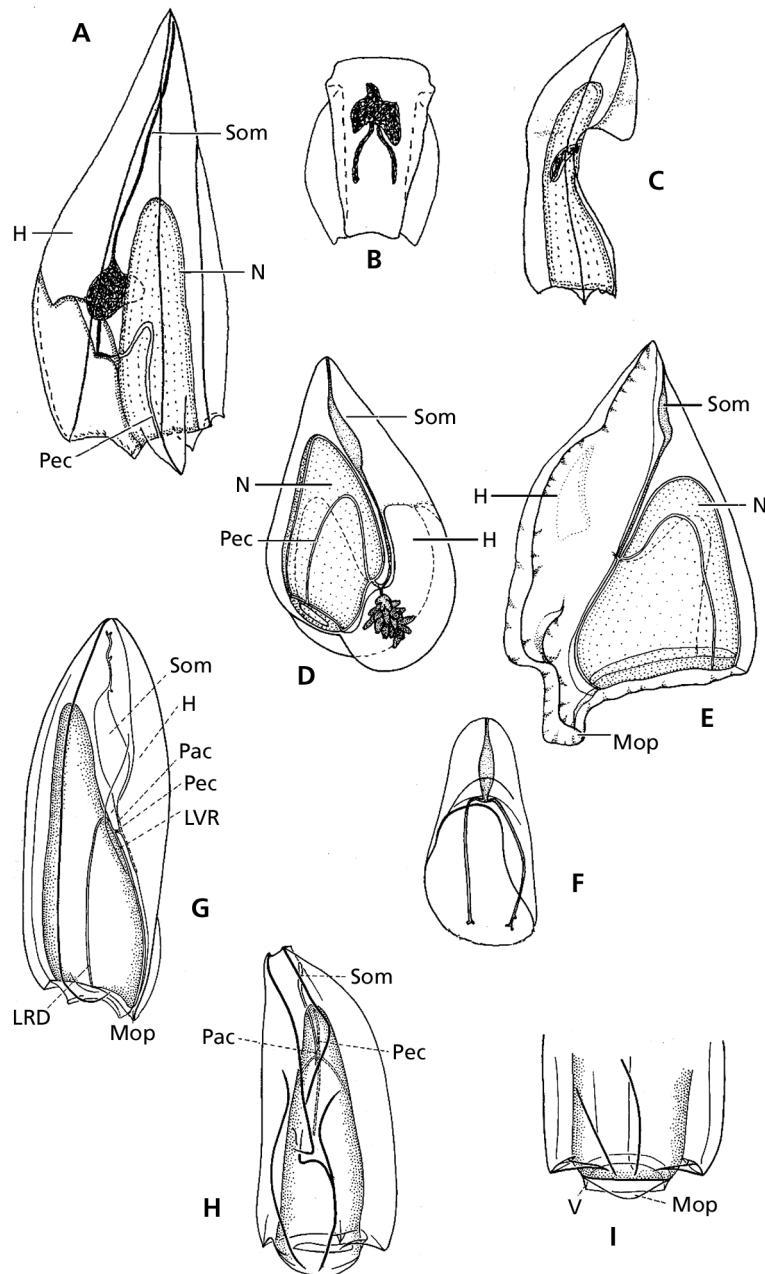


FIG. 221. Siphonophorae, Calycothorae, Clausophyidae. A-C, *Chuniphyes multidentata*: A, lateral view of the anterior nectophore; B, bract; C, gonophore. D-F, *Clausophyes ovata*: D, anterior nectophore (lateral view); E, posterior nectophore (lateral view); F, eudoxid bract (ventral view). G-I, *Crystallophyes 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, Calycothorae, 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 péiculaire ; 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 *CHELOPHYYES* 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)

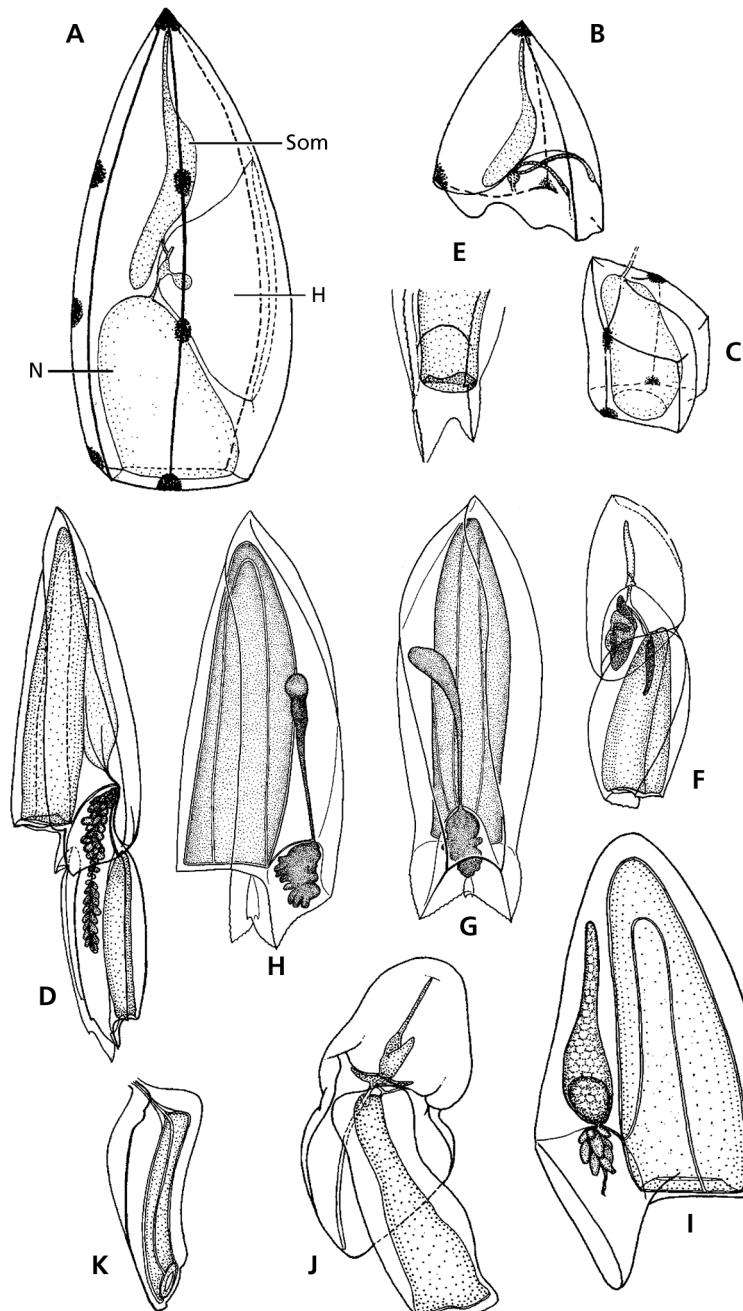


FIG. 222. Siphonophorae, Calycophorae, Clausophyidae. A-C, *Heteropyramis maculata*: A, anterior nectophore (lateral view); B, eudoxid bract; C, gonophore. Diphididae. D-H, *Chelophyses*. D-F, *Chelophyses appendiculata*: D, polygastric stage; E, detail of mouth-plate of posterior nectophore; F, eudoxid stage; G-H, *Chelophyses 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. Diphididae. D-H, *Chelophyses*. D-F, *Chelophyses appendiculata*: D, stade polygastrique; E, détail de la plaque buccale du nectophore postérieur; F, stade eudoxie; G-H, *Chelophyses 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 eudoxoids 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 challengerii 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 gnamuthui Daniel & Daniel, 1964 [doubtful status]

Lensia grimaldi Leloup, 1933

Lensia hardyi Totton, 1941

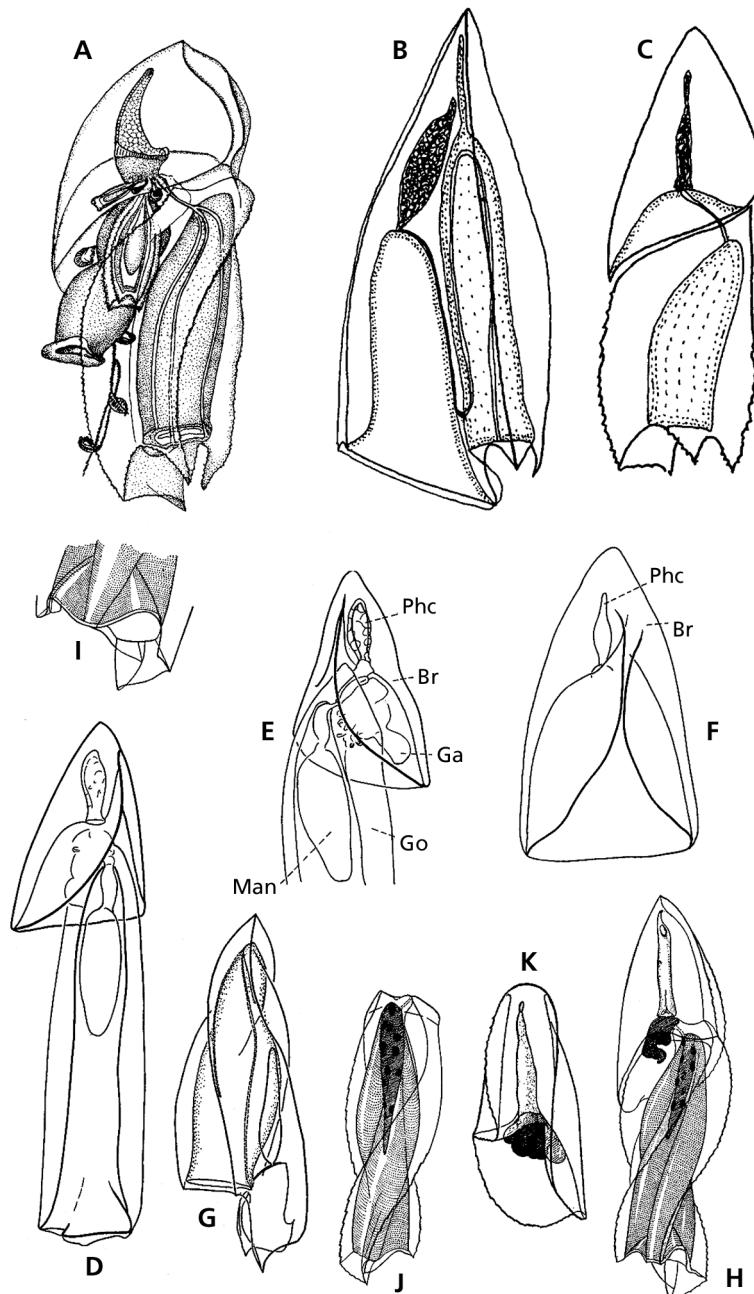


FIG. 223. Siphonophorae, Calycothorae, Diphyidae. A-C, *Diphyes dispar*: A, polygastric phase; B, anterior nectophore (lateral view); C, bract and gonophore. D-F, *Eudoxia macra*: D, whole eudoxid stage; E, detail of the eudoxial bract and of the apical part of the gonophore; F, eudoxid bract. G-K, *Eudoxoides 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 female gonophore; K, ventral view of the bract (A after Trégoüeff, 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, Calycothorae, 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 Trégoüeff, 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.

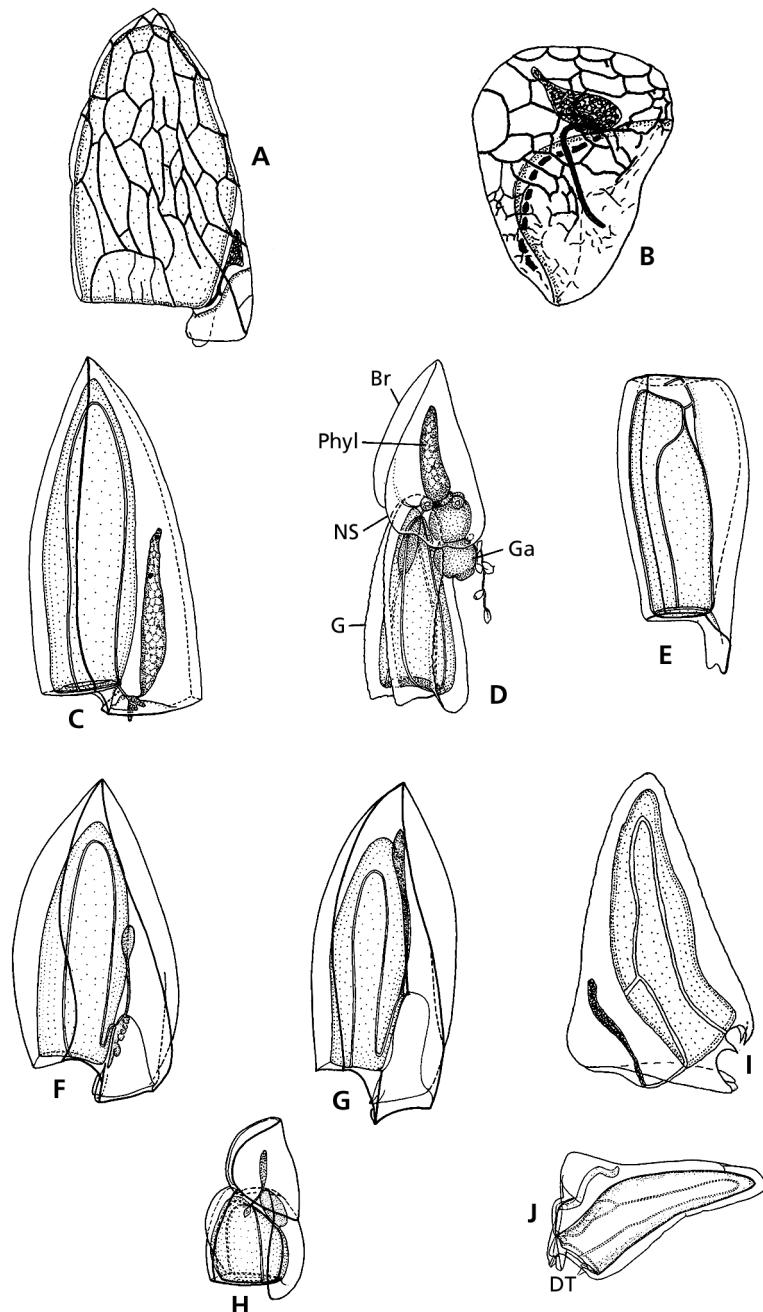


FIG. 224. Siphonophorae, Calycophorae, Diphyidae. A-B, *Gilia reticulata*: A, lateral view of an anterior nectophore; B, bract with gonophore. C-E, *Lensia conoidea*: C, anterior nectophore; D, eudoxid stage; E, posterior nectophore. F-H, *Muggiaeae*: F, *Muggiaeae kochi*, anterior nectophore (lateral view); G, *Muggiaeae atlantica*, anterior nectophore (lateral view); H, *Muggiaeae 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, *Muggiaeae*: F, *Muggiaeae kochi*, nectophore antérieur (vue latérale) ; G, *Muggiaeae atlantica*, nectophore antérieur (vue latérale) ; H, *Muggiaeae 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 lelopi 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 nagabushanami 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).

Muggiae atlantica Cunningham, 1892
Muggiae bargmannae Totton, 1954

Muggiae delsmani Totton, 1954
Muggiae 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 hippocampus (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 Alvarino, 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 defini-

tive 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.

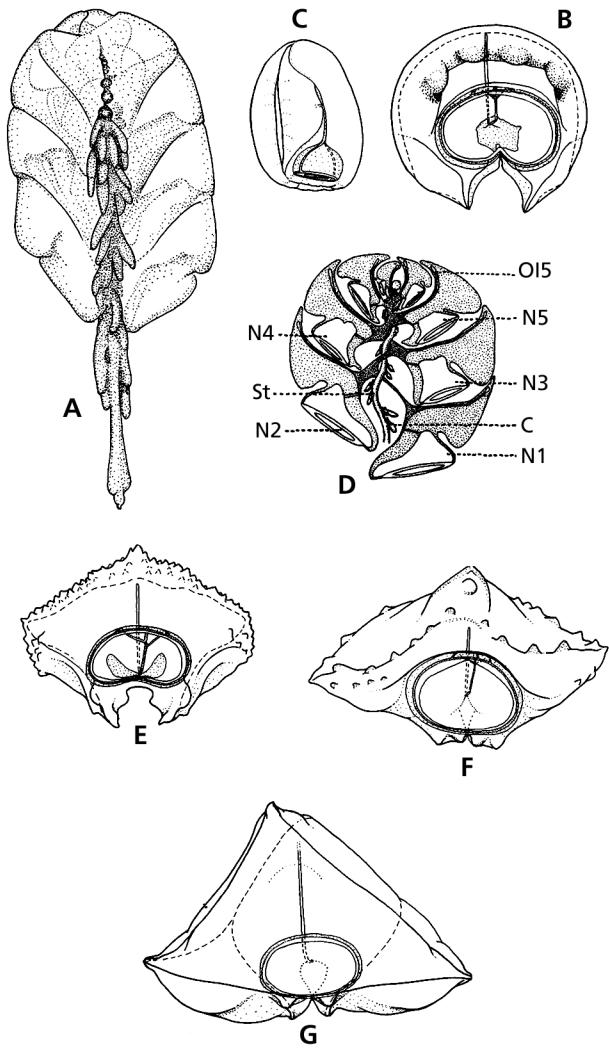


FIG. 225. Siphonophorae, Calyphorae, Hippopodiidae. A-D, *Hippopodius hippopus*: A, stade polygastrique; B, nectophore définitif; C, nectophore larvaire; D, schéma de la disposition des nectophores dans une colonie. E-G, *Vogtia*, nectophores définitifs (vue dorsale): E, *Vogtia spinosa*; F, *Vogtia 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; O15 = oleocyte du nectophore n° 5; St = stolon.

FIG. 225. Siphonophorae, Calyphorae, 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; O15 = 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)

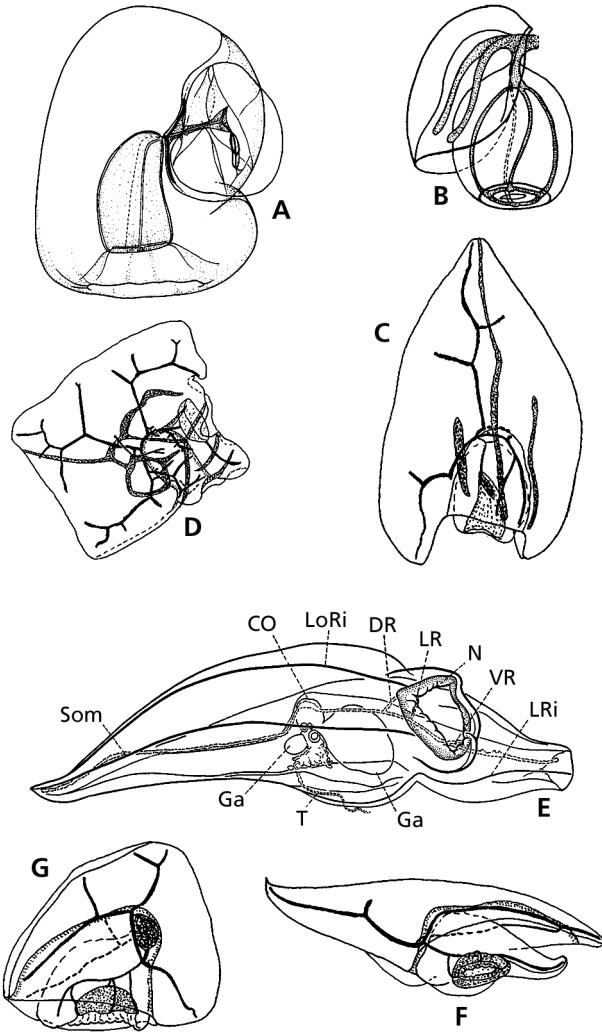


FIG. 226. Siphonophorae, Calycophorae. A-B, Prayidae, Amphicaryoninae, *Amphicaryon acaule*: A, nectophore of polygastric stage; B, eudoxid stage. C-D, Prayidae, Nectopyramidae, *Nectadamus diomedae*: C, eudoxid stage; D, definitive nectophore (lateral view). E-G, *Nectopyramis*: E-F, *Nectopyramis natans*: 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, Nectopyramidae, *Nectadamus diomedae*: 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 = gastéozoïde ; 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 diomedae (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

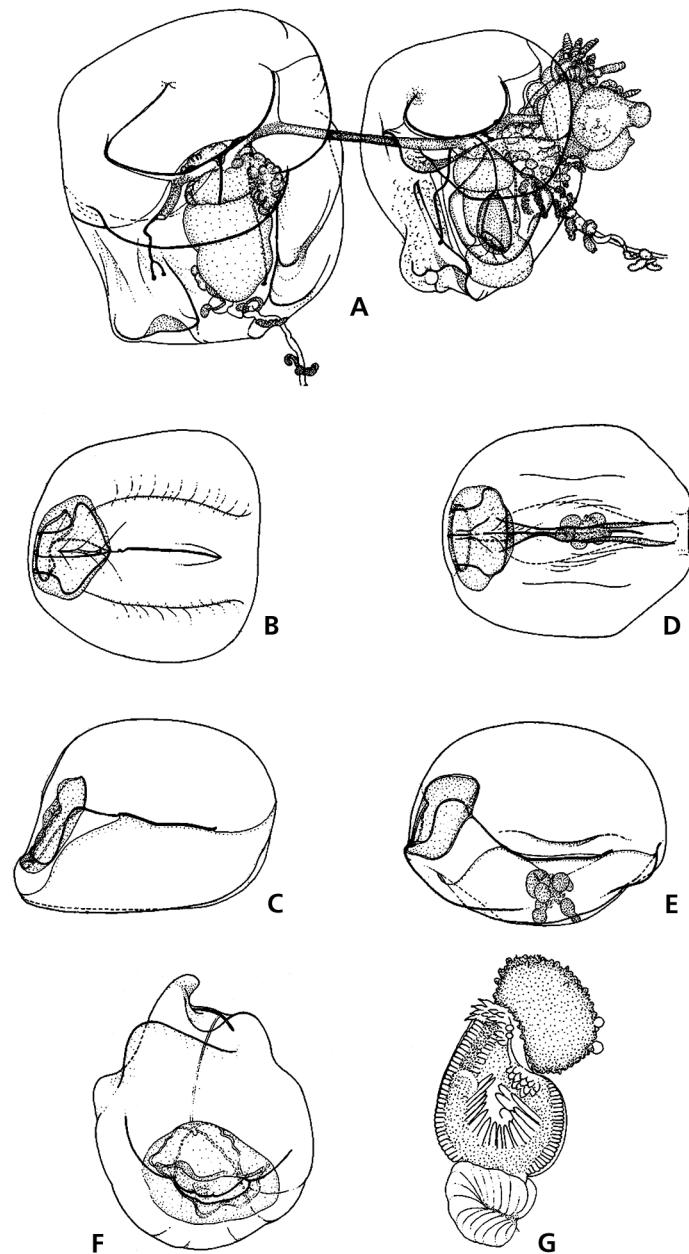


FIG. 227. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G, *Craseoa lathetica*: A, two attached stem groups viewed ventrally; B-C, nectophores n° 1: B, ventral view; C, lateral view; D-E, nectophore n° 2: D, ventral view; E, lateral view; F, gonophore; G, tentillum (all after Pugh & Harbison, 1987).

FIG. 227. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G, *Craseoa lathetica*: A, deux groupes cornidiaux 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 *DESMOPHYYES* 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 praecincta 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

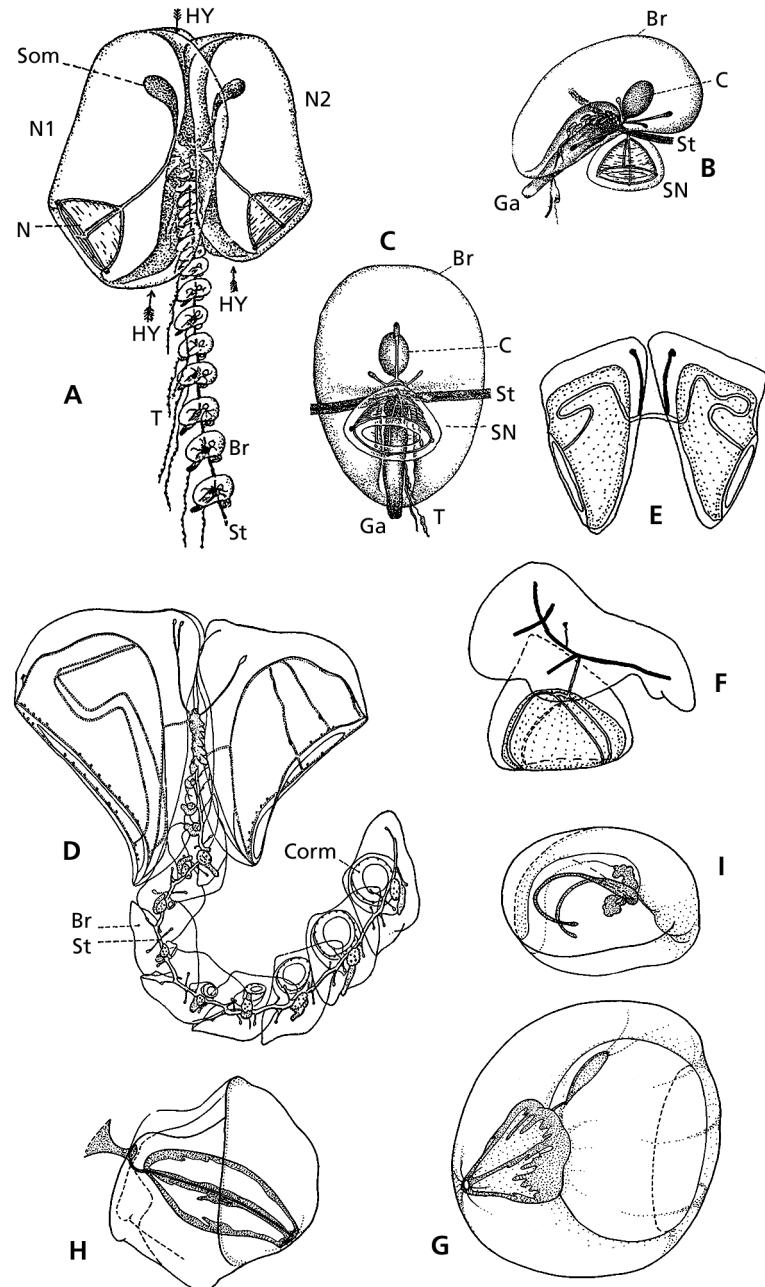


FIG. 228. Siphonophorae, Calyptophorae, Prayidae. A-C, *Desmophyes annectens*: A, polygastric stage; B, eudoxid phase (lateral view); C, eudoxid phase (dorsal view). D-F, *Lilyopsis rosea*: D, polygastric stage; E, nectophore (lateral view); F, bract. G-I, *Maresearia praecleara*: G, larger nectophore; 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 = gastozooid; HY = hydroecium; N = nectosac; N1, N2 = nectophore 1, nectophore 2; Som = somatocyst; SN = special nectophore; St = stolon; T = tentacle.

FIG. 228. Siphonophorae, Calyptophorae, Prayidae. 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, *Maresearia praecleara* : 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.

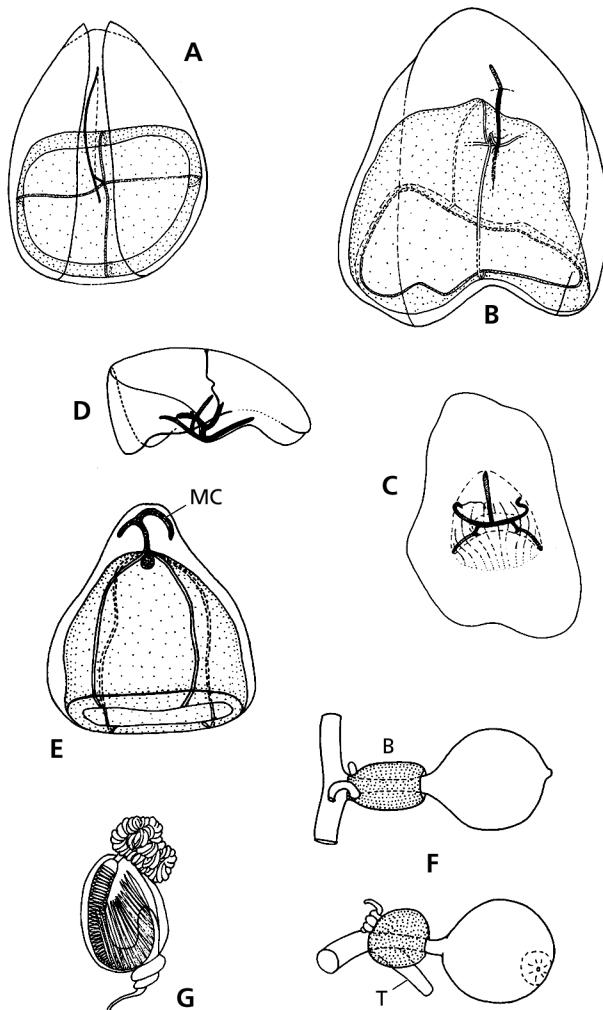


FIG. 229. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G, *Mistopraina fragosa*: A, nectophore n° 1; B, ventro-lateral view of nectophore n° 2; C, ventral view of a large bract; D, lateral view of a large bract; E, gonophore; F, gastrozooids with basigasters; G, tentillum (all after Pugh & Harbison, 1987). B = basigaster; MC = mantle canal; T = tentacle.

FIG. 229. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-G, *Mistopraina fragosa*: A, nectophore n° 1; B, vue ventro-latérale du nectophore n° 2; C, vue ventrale d'une grande bractée; D, vue latérale d'une grande bractée; E, gonophore; F, gastéozoïdes 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)

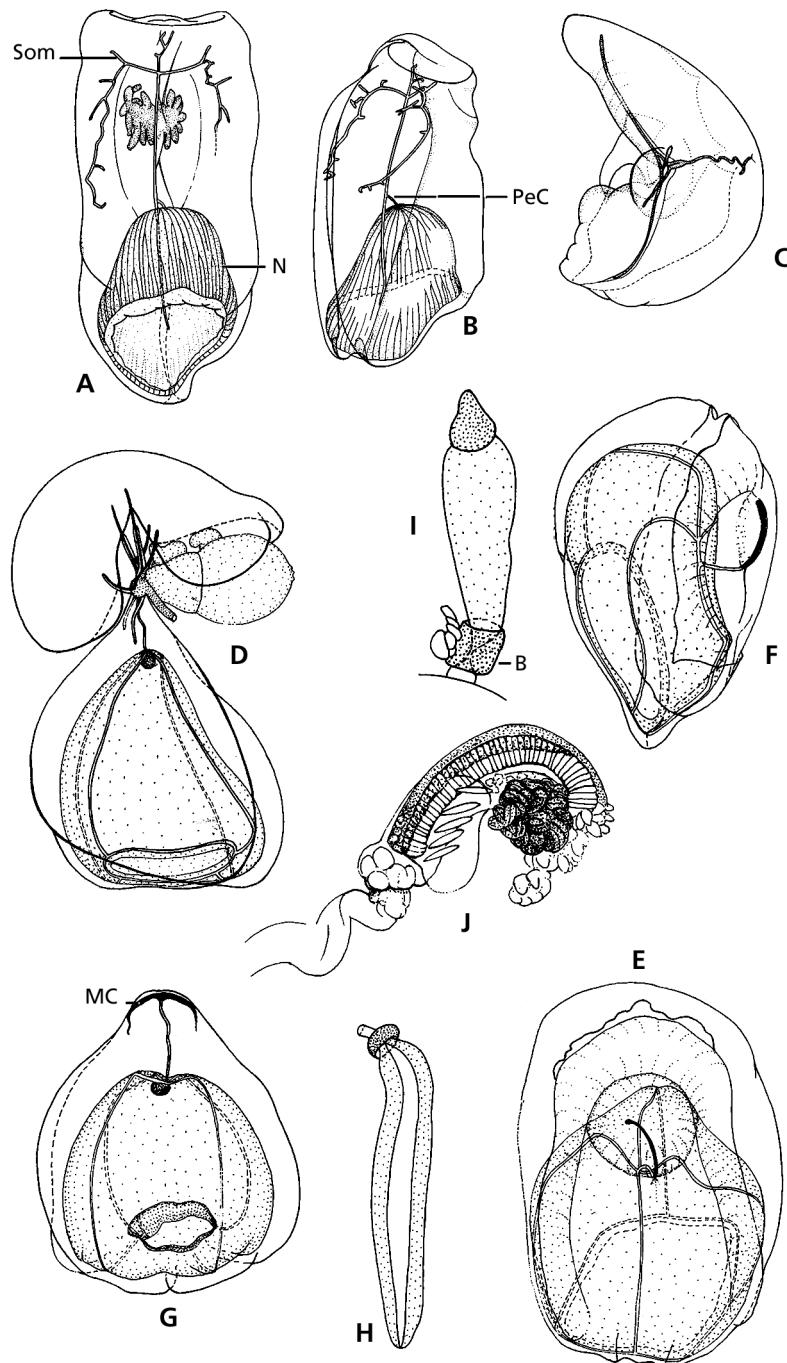


FIG. 230. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-C, *Praya dubia*: A, dorsal view of a definitive nectophore; B, lateral view of a definitive nectophore; C, eudoxid bract. D-J, *Prayola urinatrix*: D, polygastric stage; E, nectophore n° 1 (ventral view); F, nectophore n° 2 (ventro-lateral 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 limbata Pugh & Youngbluth, 1988

Rosacea cymbiformis (Delle Chiaje, 1822)

Rosacea plicata (Quoy & Gaimard, 1833)

Rosacea flaccida Biggs, Pugh & Carré, 1978

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 calyphorans, 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

Calyphora 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).

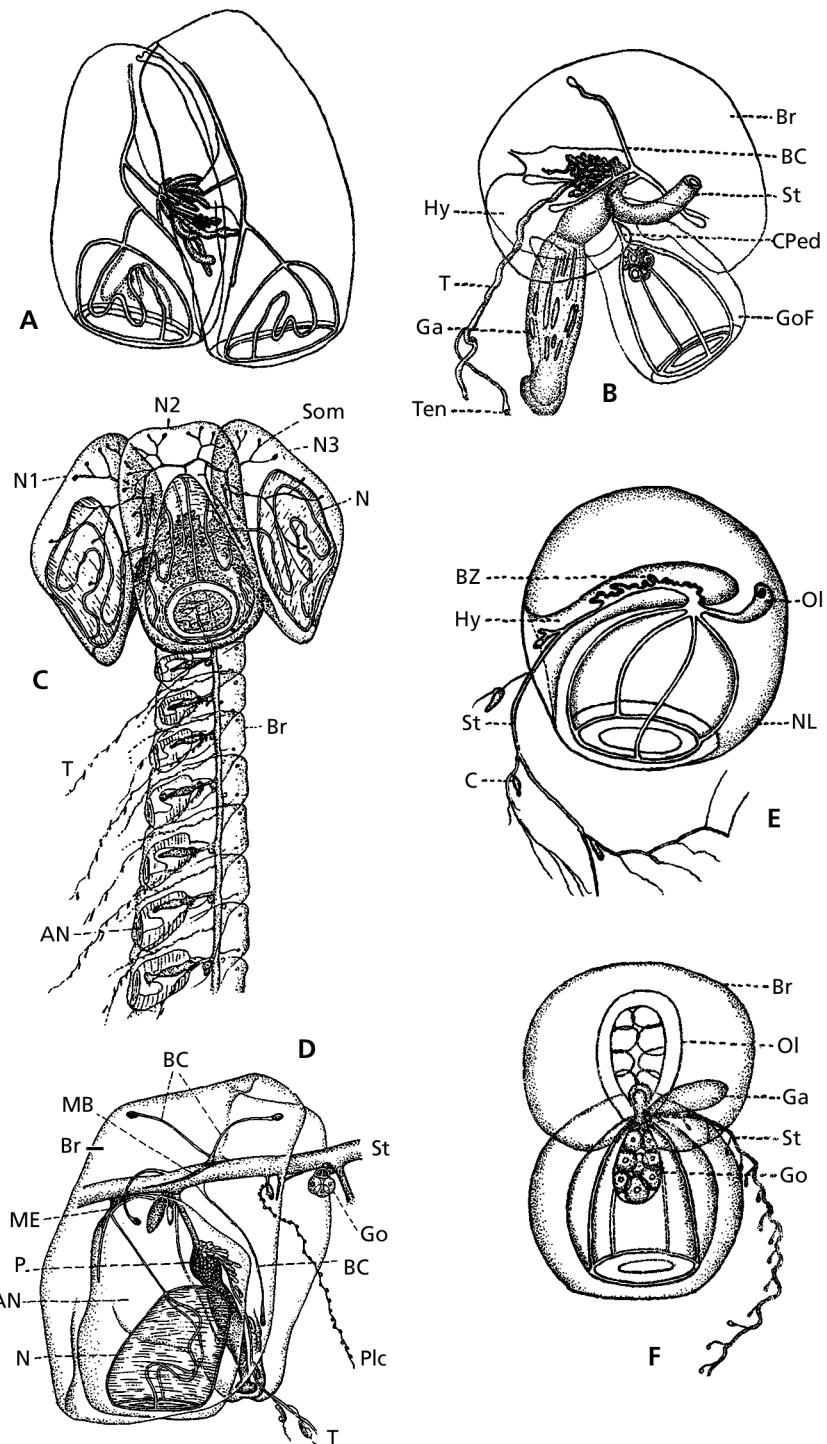


FIG. 231. Siphonophorae, Calycophorae, Prayidae, Prayinae. A-B, *Rosacea cymbiformis*: A, two definitive nectophores; B, adult cormidia. C-D, *Stephanophyes superba*: C, polygastric phase; D, single stem group. E-F, Sphaeronectidae, *Sphaeronectes gracilis*: E, polygastric stage; F, eudoxid stage (A-B, E-F after Trégueroff, 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 cormidal. E-F, Sphaeronectidae, *Sphaeronectes gracilis* : E, stade polygastrique ; F, stade eudoxie (A-B, E-F d'après Trégueroff, 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 péducale ; 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 = tentacle ; Ten = tentille.

Sphaeronectes bougisi Carré, 1968c
Sphaeronectes fragilis Carré, 1968c
Sphaeronectes gamulinini 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 previtellogenetic 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 *Polyodium hydriforme* Ussov, 1885, which was until recently the only known metazoan adapted to an intracellular parasitic life.

The taxonomic status of *Polyodium* 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.

Polyodium hydriforme Ussov, 1885