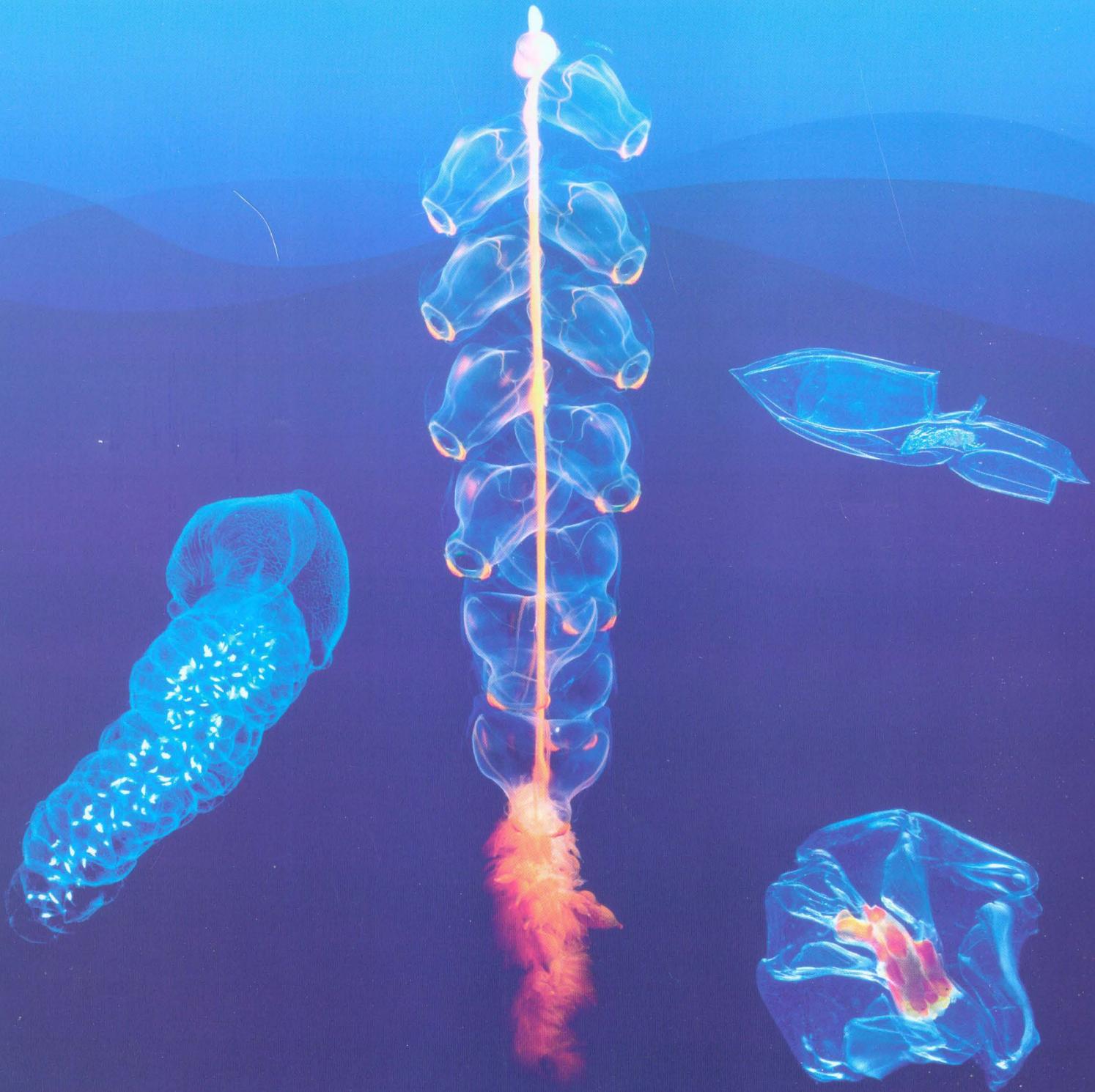
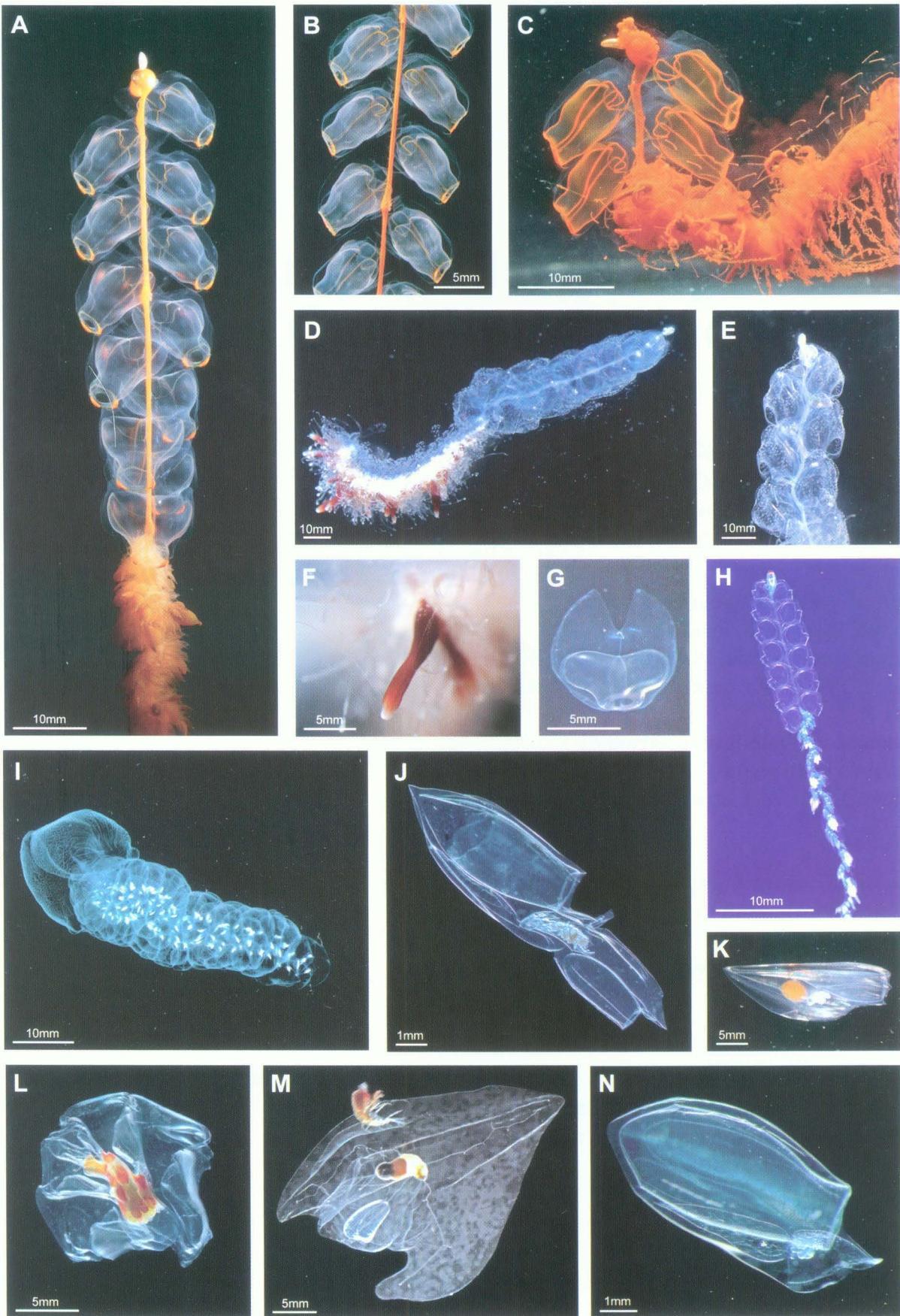


Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific Waters



Frontispiece: Selected images illustrating the variety and complexity of siphonophore morphology: **A:** physonect *Murru orthocanna*, colony with pneumatophore, twelve nectophores on (orange) nectosomal stem, part of (orange) contracted siphosome below, with gastrozooids; **B:** detail of part of nectosome in A; **C:** *M. orthocanna* young colony with four nectophores and part of relaxed siphosome, with expanded tentacles and gelatinous bracts; **D:** physonect *Apolemia* sp., colony with pneumatophore, nectophores and contracted siphosome bearing (red) gastrozooids, thin translucent palpons, bracts, thread-like tentacles (and palpacles), without tentilla; **E:** detail of *Apolemia* sp. nectosome showing six nectophores and some nectosomal polyps (pale pink); **F:** detail of *Apolemia* sp. gastrozooid; **G:** detached physonect nectophore, with axial wings and expanded nectosac with four radial canals; **H:** physonect *Nanomia bijuga*, colony with pneumatophore (red tip), nectophores, contracted siphosome with translucent gastrozooids and prominent tentilla (appear white here but red in life); **I:** prayomorph calycophoran colony swimming, with nectosome of two apposed nectophores and contracted siphosome with large bracts and gastrozooids with tentilla (white); **J:** diphymorph calycophoran *Chelophyses appendiculata*, colony of two linearly adjoined nectophores, anterior nectophore with translucent somatocyst, posterior nectophore, and siphosomal stem contracted within hydroecia of both nectophores; **K:** anterior nectophore only of diphymorph *Chuniphyes multidentata*, showing swollen (orange) somatocyst, and siphosome contracted within hydroecium (white); **L:** hippopodiid prayomorph colony of six nectophores with shallow nectosacs, enclosing central chamber containing contracted siphosome with (orange) gastrozooids; **M:** eudoxid of prayomorph *Nectadamas diomedae*, with gastrozooid and gonophore in hydroecium (and adherent crustacean on outer surface); **N:** anterior nectophore only of diphymorph *Dimophyes arctica*, with translucent carrot-shaped somatocyst, and siphosome contracted within hydroecium. Images kindly supplied, with permission, by: Kevin Raskoff, Monterey Peninsula College, CA (A and B); Casey Dunn, Brown University, RI (C and K); Dhugal Lindsay, JAMSTEC, Japan (D - G); Picture Library, Natural History Museum, London (H); Edie Widder, HBOI, FL (I); Russ Hopcroft, UAF/NOAA/ CoML, AK (J and L - N). Minor enhancements to some images using Adobe Photoshop CS (levels, contrast, shadow/highlight, crop) to better show the gelatinous morphology of siphonophores. Scale bars are approximate: 10 mm (A, C - E, H and I); 5 mm (B, F, G, K - M); 1 mm (J and N).



Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

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Abstract

Thirty-seven species of Siphonophora (Cnidaria: Hydrozoa) are described from Canadian Pacific waters off British Columbia and a key is provided. Twenty-five species are newly recorded from the area: *Apolemia contorta*, *Apolemia* sp., *Frillagalma vityazi*, *Bargmannia elongata*, *Marrus orthocanna*, *Amphicaryon acaule*, *Maresearsia praeclarula*, *Rosacea cymbiformis*, *R. plicata*, *Praya dubia*, *P. reticulata*, *Nectopyramis thetis*, *Nectadamas richardi*, *Vogtia pentacantha*, *V. serrata*, *V. spinosa*, *Sulculeolaria quadrivalvis*, *Lensia havock*, *L. hostile*, *L. multicristata*, *Gilia reticulata*, *Chuniphyes moserae*, *Kephyses ovata*, *Clausophyes moserae*, and *Heteropyramis crystallina*. Other species found include *Agalma elegans*, *Nanomia bijuga*, *Bargmannia lata*, *Nectadamas diomedae*, *Lensia achilles*, *L. conoidea*, *Dimophyes arctica*, *Muggiae atlantica*, *Chelophyes appendiculata*, and *Chuniphyes multidentata*. *Cordagalma ordinata* and *Sphaeronectes köllikeri* are also included because, though absent from the present collection, they were previously collected from Canadian Pacific waters. The recently proposed clade Codonophora is ranked here as an order, and the two traditional groups Physonectae and Calycophorae are retained for the present. Diagnoses are given for taxonomic rankings from suborder through to species, and species synonymies are included. *Tottonia contorta* is referred to the genus *Apolemia*, and *Lensia baryl* is shown to be conspecific with *L. achilles*, *L. multicristoides* conspecific with *L. multicristata*, and *Sphaeronectes gracilis* conspecific with *S. köllikeri*. Descriptions of nectophores, and bracts and gonophores when collected, are given for all species and are based on a recently published holistic terminology for the Siphonophora. Axes are introduced for zooids of amphicaryonine, nectopyramidine, hippopodiid, diphyid, and sphaeronectid calycophorans, and the revised terminology is applied to describe the course of the nectophore pedicular canal from stem to nectosac. The somatocyst, an important diverticulum from the pedicular canal in calycophorans, is restricted for the first time to canal(s) that penetrate the mesogloea. Surface diverticula from the pedicular canal, previously regarded as part of the somatocyst in prayid calycophorans, are here described separately and shown to be closely related to the muscular lamella(e) that connect(s) the nectophore to the stem, as in physonects. The application of the new axes and terminology to both physonects and calycophorans is summarized. Three extended general sections are included: life cycles, budding, and autotomy; the ecology of siphonophores of Canadian Pacific waters; and a summary of the worldwide distribution of siphonophores from Canadian Pacific waters. Notes on taxonomy, nomenclature, and biology are given for each species where appropriate, and data on winter–spring depth distribution and abundance are included for the most common species, *N. bijuga*, *L. conoidea*, and *C. multidentata*.

Résumé

L'ouvrage renferme une description de 37 espèces de siphonophores (cnidaires hydrozoaires) des eaux canadiennes du Pacifique (près de la Colombie-Britannique) et une clé d'identification. De ces 37 espèces, 25 y sont nouvellement répertoriées, soit *Apolemia contorta*, *Apolemia* sp., *Frillagalma vityazi*, *Bargmannia elongata*, *Marrus orthocanna*, *Amphicaryon acaule*, *Maresearsia praecleara*, *Rosacea cymbiformis*, *R. plicata*, *Praya dubia*, *P. reticulata*, *Nectopyramis thetis*, *Nectadamas richardi*, *Vogtia pentacantha*, *V. serrata*, *V. spinosa*, *Sulculeolaria quadrivalvis*, *Lensia havock*, *L. hostile*, *L. multicristata*, *Gilia reticulata*, *Chuniphyes moserae*, *Kephyses ovata*, *Clausophyes moserae* et *Heteropyramis crystallina*. Au nombre des autres espèces traitées figurent *Agalma elegans*, *Nanomia bijuga*, *Bargmannia lata*, *Nectadamas diomedae*, *Lensia achilles*, *L. conoidea*, *Dimophyes arctica*, *Muggiae atlantica*, *Chelophyes appendiculata* et *Chuniphyes multidentata*. De plus, même si exclues de la présente collection, les espèces *Cordagalma ordinata* et *Sphaeronectes köllikeri* y sont également abordées, car elles ont déjà été répertoriées dans les eaux canadiennes du Pacifique. Le clade Codonophora, récemment proposé, est placé au rang de l'ordre, et les deux groupes classiques Physonectae et Calycophorae sont maintenus. On y trouve également des diagnoses du sous-ordre jusqu'à l'espèce, ainsi que des synonymies de diverses espèces. Outre le classement de *Tottonia contorta* dans le genre *Apolemia*, on établit la conspécificité de *Lensia baryi* et de *L. achilles*, de *L. multicristoides* et de *L. multicristata*, et de *Sphaeronectes gracilis* et de *S. köllikeri*. On offre une description des ombrelles, ainsi que des aspidozoïdes et des gonophores (le cas échéant), pour toutes les espèces - description qui s'appuie sur une terminologie globale récemment publiée pour les siphonophores. On présente des axes pour les zoïdes des calycophores amphicaryonines, nectopyramidines, hippopodiides, diphyides et sphaeronectides, ainsi qu'une terminologie révisée pour décrire le trajet du canal pédiculaire du nectophore, à partir du pédoncule jusqu'au nectosac. Le somatocyste, diverticule important du canal pédiculaire des calycophores, est limité, pour la première fois, au canal ou aux canaux qui pénètrent dans la mésoglée. En plus de décrire séparément les diverticules à la surface du canal pédiculaire, considérés auparavant chez les calycophores prayides comme éléments du somatocyste, on montre qu'ils sont étroitement associés à lamelle musculaire ou aux lamelles musculaires reliant le nectophore au pédoncule, comme chez les physonectes. L'ouvrage comprend un résumé de l'application des nouveaux axes et de la terminologie chez les physonectes et les calycophores. On y trouve également trois sections élargies sur un certain nombre d'aspects généraux : cycles de vie, bourgeonnement et autotomie; écologie des siphonophores des eaux canadiennes du Pacifique; résumé de la répartition mondiale des siphonophores recensés dans les eaux canadiennes du Pacifique. Enfin, l'ouvrage renferme des notes sur la taxinomie, la nomenclature et la biologie de chaque espèce (le cas échéant) et des données hivernales et printanières sur l'abondance et la répartition verticale des espèces les plus communes, *N. bijuga*, *L. conoidea* et *C. multidentata*.

1. Introduction

Siphonophores are complex polymorphic marine Hydrozoa. Views vary concerning their relationship to the rest of the class and too few molecular data are available to decide which view is correct (Collins et al. 2006). The most recent review of phylogenetic patterns within the phylum Cnidaria ranks Siphonophora as an order within the subclass Hydroidolina, together with the two much larger orders Anthoathecata and Leptothecata (Daly et al. 2007). This classification does not fit well with the recent introduction of a new rank for two major groups of siphonophores, so for the purposes of the present work, the Anthoathecata, Leptothecata and Siphonophora are raised to the status of superorders.

The modern interpretation of siphonophore taxonomy has until recently been based on the comprehensive monograph of Totton (1965a), modified after several more recent authors. Additional work was reviewed by Mackie et al. (1987), and major contributions since 1987 include Margulis (1988), Pugh and Youngbluth (1988a and b), Pugh (1992a–c, 1995, 1999a and b, 2001, 2003, 2005, 2006a and b), Pugh and Pagès (1993, 1995), Carré and Carré (1995), Pagès and Pugh (2002), Hissmann (2005), Mapstone (2003, 2004, 2005), Dunn (2005), Dunn et al. (2005a and b), Haddock et al. (2005a and b), and Dunn and Wagner (2006). From this list, four recent papers, Haddock et al. (2005a), Dunn et al. (2005b), Dunn and Wagner (2006), and Pugh (2006b), provide the groundwork for a modern view of siphonophores. The first paper introduces a holistic terminology for siphonophore axes and surfaces (from colony to zooid), the second gives the first detailed molecular phylogeny of siphonophores based on an analysis of 43 species, and the third collates a new study on budding and cormidia in five long-stemmed siphonophore species with the above-mentioned molecular work to reconstruct some key transitions in early siphonophore phylogeny. The fourth paper, Pugh (2006b), extrapolates the findings of the second and third papers to give a new view of physonect phylogeny, although a few of the conclusions drawn by Pugh have since been reconsidered (P.R. Pugh, pers. comm., 2007).

Siphonophores have traditionally been divided into three lineages: Cystonectae, Physonectae, and Calycophorae (Totton 1965a). However, the work of Dunn et al. (2005b) and Dunn and Wagner (2006) indicates that cystonects are sister to all other siphonophores, and these authors group physonects and calycophorans together as the Codonophora, or “bell-bearers”. The results obtained by Dunn et al. (2005b) also suggest that physonects are paraphyletic and gave rise to the Calycophorae.

Previous records of siphonophores from Canadian Pacific waters are sparse, and include only 12 codonophoran species (Bigelow 1913; McMurrich 1916; Berkeley and Berkeley 1960; Totton 1965b; Mackie and Mills 1983; Mackie 1985; Mapstone and Arai 1992; Mapstone 1998). Although Agassiz (1865) recorded the cystonect *Physalia* sp. from the Strait of Georgia, there are no more recent records of this conspicuous organism so far north (Savilov 1961).

In the present work, 37 species of siphonophores are described from Canadian Pacific waters, including all siphonophores dependably recorded off British Columbia (B.C.). Species are listed in the Table of Contents. Thirty-five of these species come from collections of samples provided by Fisheries and Oceans Canada’s Pacific Biological Station (PBS), Nanaimo, B.C., and Fisheries and Oceans Canada’s Institute of Ocean Sciences (IOS), Sidney, B.C., taken between 1979 and 1990. Preliminary notification of 12 of these species is given in Arai et al. (1993) and Mapstone (1998). Two species known to occur in Canadian Pacific waters (Mackie 1985), but not present in the samples noted above, are described from Atlantic Ocean samples in the Discovery Collections held at the National Oceanography Centre (NOC), Southampton, United Kingdom (UK). The present collections include both physonects and calycophorans but no cystonects, although the latter have been collected to the south, off southern California (Mackie et al. 1987; Alvariño 1991; Cairns et al. 2002).

2. Systematics, Morphology, and Terminology

2.1. Systematics

The systematic framework introduced by Totton (1965a) and followed by Pugh (1999b) is updated here to include the new findings of Dunn et al. (2005b) and Dunn and Wagner (2006). Thus, the subclass Siphonophora is split into two orders, the Cystonecta and the Codonophora. The former order includes the Portuguese man-of-war, *Physalia physalis*, a species better known to nonspecialists than any other siphonophore, and the latter order includes all species so far collected from Canadian Pacific waters. The Codonophora is characterized by the presence of swimming bells, or nectophores, and by the formation of each cormidium from a probud (Dunn and Wagner 2006). In the present work the Codonophora is taken to comprise two suborders, the traditional Physonectae and Calycophorae.

Two families are currently recognized within the order Cystonecta (Pugh 1999b) and 14 families within the order Codonophora. The latter comprises eight families within the suborder Physonectae (see Section 10.1) and six families within the suborder Calycophorae (see Section 10.2).

2.2. Morphology

Siphonophores are polymorphic colonial animals, and schematic representations of the main asexual (or polygastric) colony types found in Canadian Pacific waters are given in Figures 1A, 2A and E, and 3A and G. Most physonects are long-stemmed and have many swimming bells and many cormidia, as shown in Figure 1A. In contrast, most calycophorans have only two bells, together with a long stem of many cormidia, with the bells arranged in one of two ways. In prayomorph calycophorans the bells are apposed (Fig. 2A) and in diphyomorph calycophorans one bell lies anterior (in front) of the other (Fig. 3A). Prayomorphs include the families Prayidae and Hippopodiidae (see Sections 10.2.1 and 10.2.2 and the definition in Section 9 (glossary)) and diphyomorphs include the families Diphyidae, Clausophyidae, Sphaeronectidae, and Abylidiae. All diphyomorphs except the family Abylidiae have been

positively recorded from Canadian Pacific waters (see Sections 7, 10.2.3, 10.2.4, and 10.2.5 and the definition in Section 9 (glossary)).

Members of a colony are termed zooids and are connected by a long contractile stem that may or may not have a pneumatophore or float at its apex. Individual zooids are derived from both polypoid and medusoid forms, and in the past there has been much confusion over the identity of various colony members. Codonophoran colonies are divisible into an anterior nectosome and a posterior siphosome, illustrated most clearly in physonects (Fig. 1A), whereas in calycophorans (Figs 2A and 3A) the nectosome partially overlaps the youngest part of the siphosomal stem when relaxed. The nectosome typically bears two or many asexual mature (definitive) medusoid nectophores for (propulsive) locomotion, and the siphosome bears zooids that are arranged in a regularly repeating pattern, a single iteration of which is called a cormidium. The cormidium varies in composition across species, but contains, at a minimum, a polypoid gastrozooid for feeding and sexual medusoid gonophores for reproduction. A cormidium is either retained throughout life or breaks off when mature to become a free-living sexual stage, termed a eudoxid. Bracts, additional polyps (such as palpons), and other zooids may also be present.

Nectophores have a muscular nectosac that contracts rhythmically during swimming and forces water out through a distal aperture termed the ostium (Figs 1G, 2A, 3D and E). Calycophoran nectophores also have a cavity known as the hydroecium, which houses the stem (Figs 2A, 3D and E), and typically contain a swollen somatocyst that varies in shape, is often filled with oil droplets, and may aid flotation (Totton 1954) (Fig. 3D).

Bracts are asexual and typically protect the other siphosomal cormidial zooids. They are either simple, as in physonects (Figs 1D and E), and probably polypoid in origin (Pugh 1974a; Dunn and Wagner 2006), or complex, as in calycophorans (Figs 2D, 3C), and probably medusoid in origin (Pugh 1974a). The latter type are often cloak-like and wrap around

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

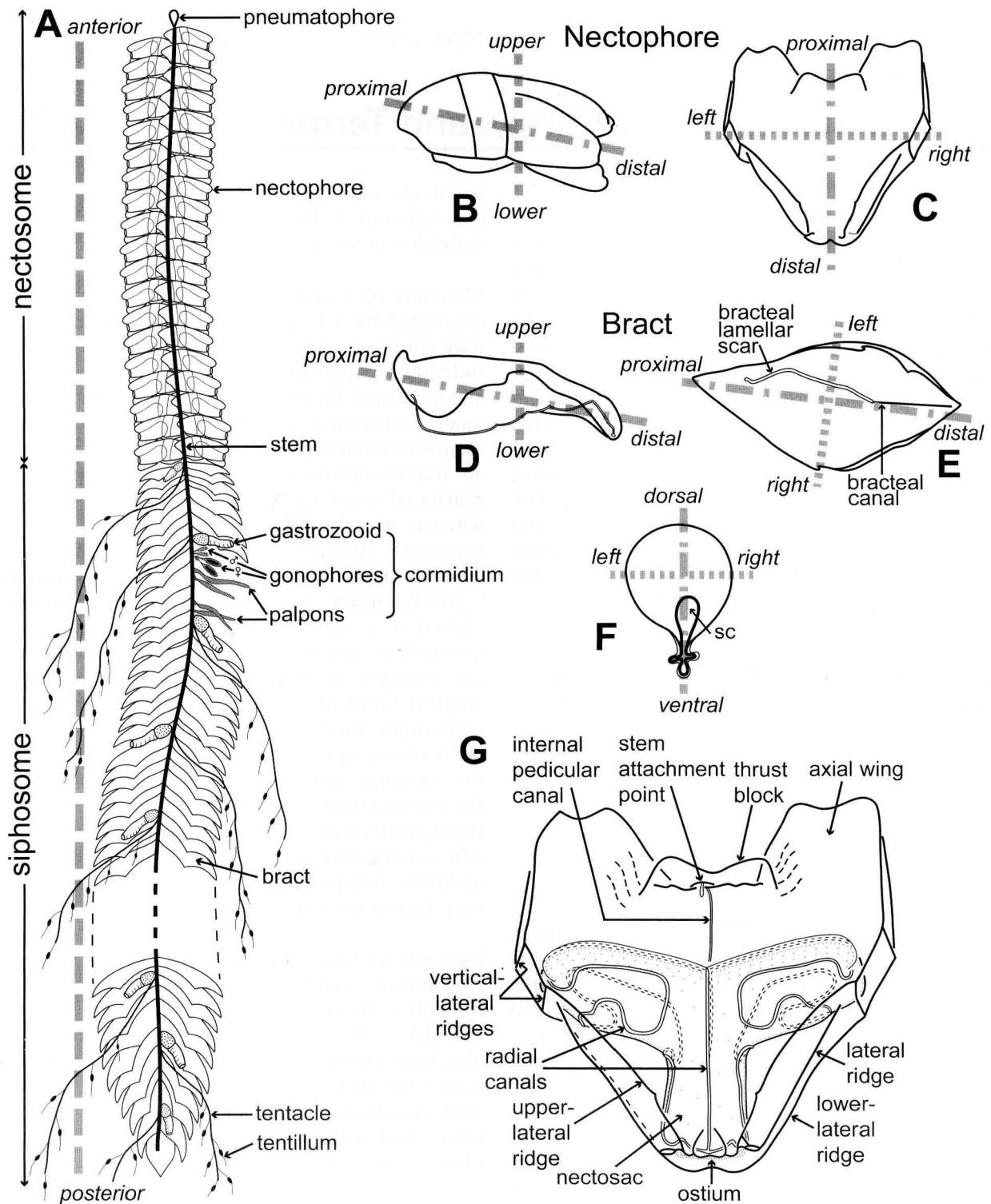


Fig. 1. General morphology and axes of a physonect siphonophore: **A**: schematic diagram of a colony, with exemplar cormidium (gastrozooid, male and female gonophores, palpons); **B**: nectophore, lateral view; **C**: nectophore, upper view; **D**: bract, lateral view; **E**: bract, lower view; **F**: transverse section through the siphosomal stem, showing stem canal (sc) and buds for bracts and gastrozooid; **G**: nectophore morphology, upper view. A–C, E, and G are derived from *Halistemma amphyridis* after Mapstone (2004) but are now referred by Pugh (2006b) to *H. foliacea* Quoy and Gaimard, 1833, except for the exemplar cormidium in A, which is derived from Bigelow (1911b, pl. 18 fig. 2); F is derived from an agalmatid stem illustrated by Garstang (1946, fig. 26). Not drawn to scale.

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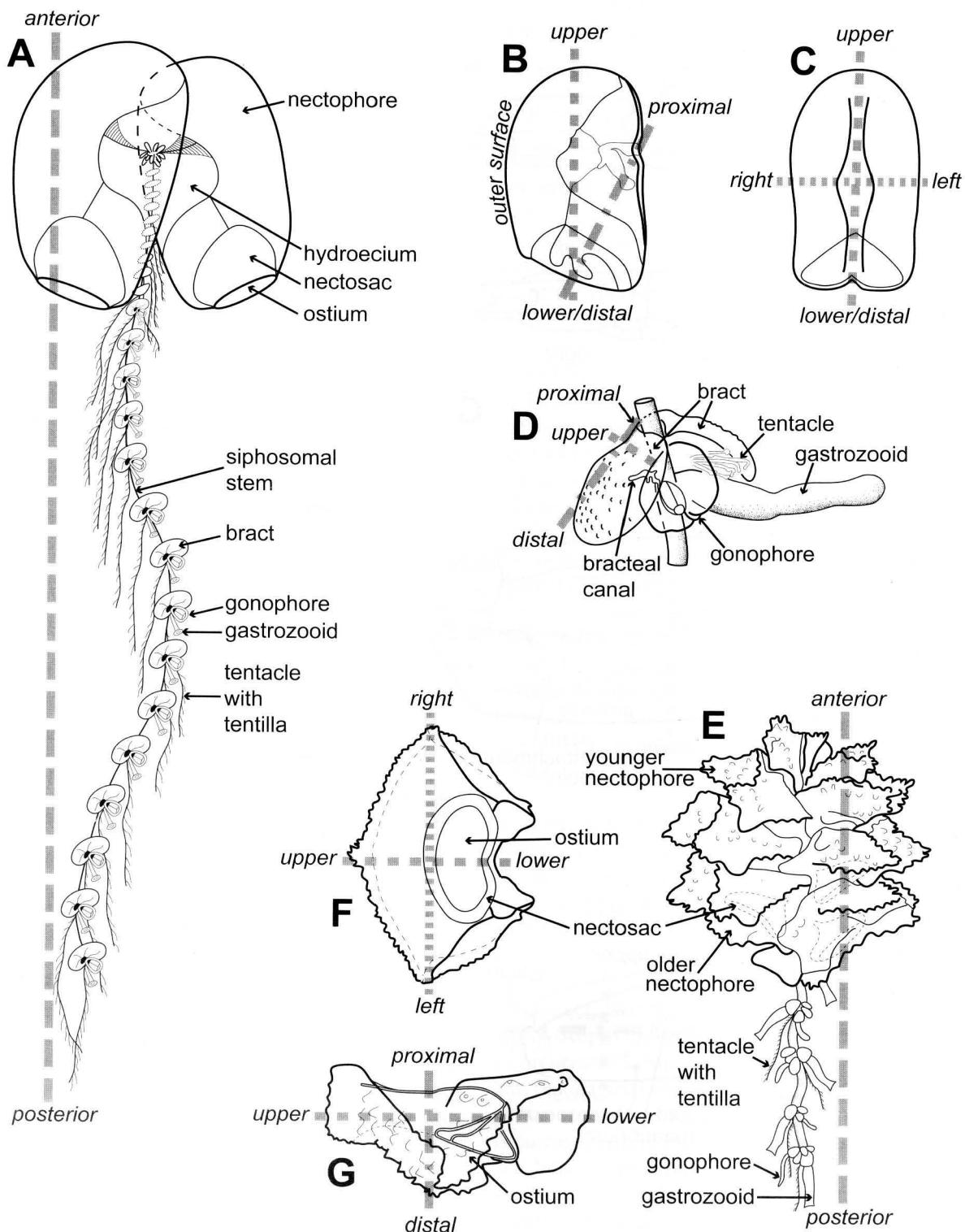


Fig. 2. General morphology and axes of two prayomorph calycophoran siphonophores based on the prayine genus *Rosacea* (A–D) and the hippopodiid genus *Vogtia* (E–G): **A:** schematic diagram of a prayine colony; **B:** prayine nectophore, right lateral view; **C:** prayine nectophore, proximal view; **D:** cormidium, lower view, illustrating the cloak-like protective bract; **E:** schematic diagram of a hippopodiid colony; **F:** hippopodiid nectophore, distal view; **G:** hippopodiid nectophore, right lateral view. A is based on Kawamura (1915b, pl. 7 fig. 4); D is derived from Mapstone (2005, fig. 4A); and E is compiled from Bigelow (1911b, pl. 15 fig. 5) and Haeckel (1888b, pl. 29 fig. 1). Not drawn to scale.

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

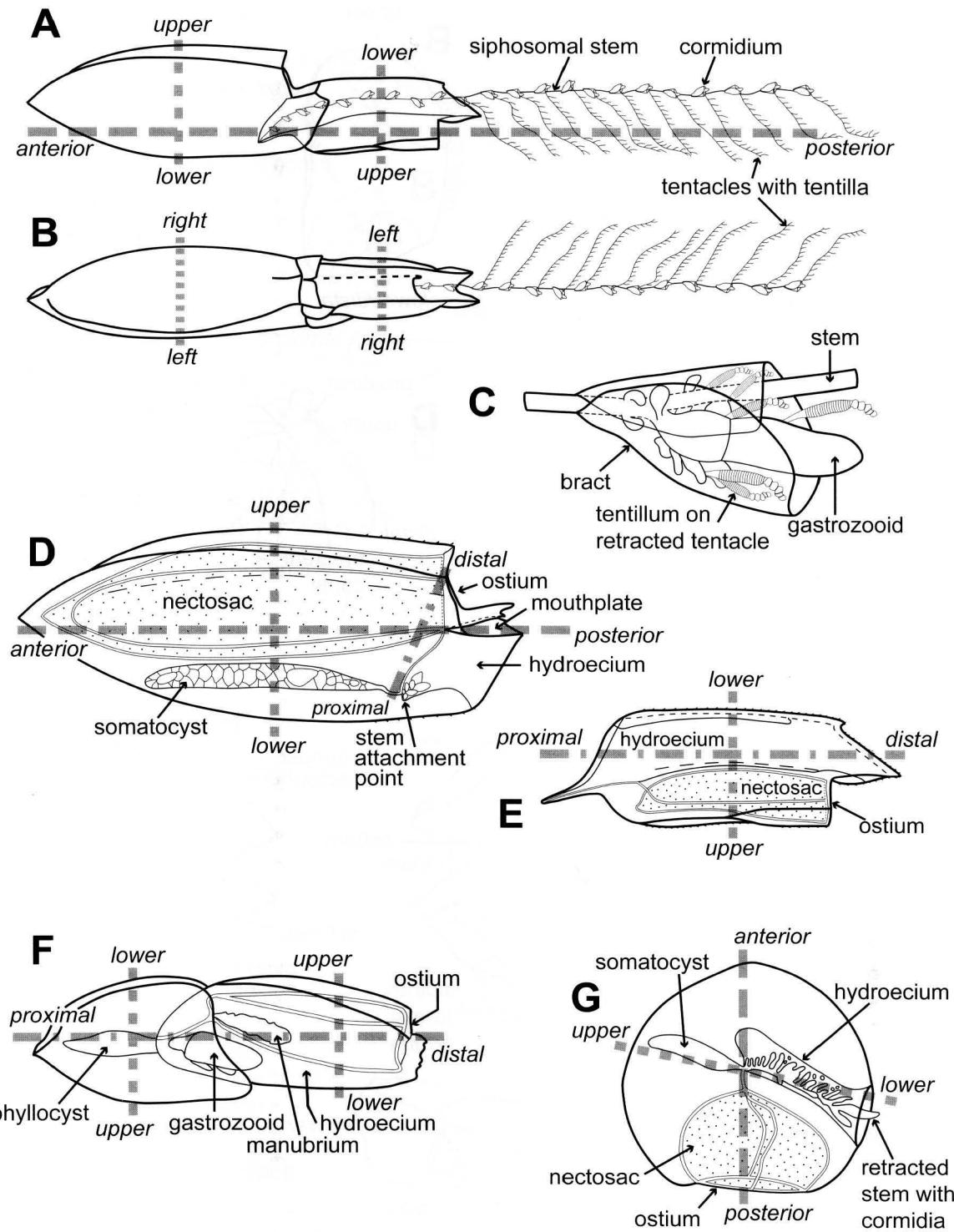


Fig. 3. General morphology and axes of two diphyomorph calycophoran siphonophores, *Chelophyses appendiculata* (A–F) and *Sphaeronectes köllikeri* (G): **A:** schematic diagram of a diphyid colony, lateral view; **B:** same, upper/lower view; **C:** cormidium, lateral view, illustrating the cloak-like protective bract; **D:** anterior nectophore, left lateral view; **E:** posterior nectophore, right lateral view; **F:** eudoxid, comprising a bract (right lateral view) and gonophore (left lateral view); **G:** *Sphaeronectes köllikeri* colony, lateral view. B is derived from Bigelow (1911b, pl. 8 fig. 8 and pl. 10 fig. 6); C is derived from Bigelow (1911b, pl. 11 fig. 1); and F is derived from Totton (1965a, fig. 124B). Not drawn to scale.

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the other zooids of the cormidium. Bracts differ from nectophores and most gonophores in having no nectosac.

In physonects the siphosomal cormidia also include modified gastrozooids called palpons, with associated simple tentacles termed palpacles. Palpons have a chemosensory or excretory function (Mackie and Boag 1963). Calycophorans do not bear palpons (with one exception; see Section 10.3).

A nectosome is absent in cystonects, and it has recently been suggested that in codonophorans this structure might have arisen by tandem duplication of the siphosome (Dunn and Wagner 2006). The nectosome remained elongate in long-stemmed physonects, but in other codonophorans it apparently shortened again during evolution, as, for example, in calycophorans.

Each gastrozooid has a tentacle for prey capture, and in codonophorans this tentacle typically includes a number of side branches that each bear a complex nematocyst stinging battery termed a tentillum (Figs 1A, 2A, retracted in 3C). In cystonects these batteries are absent, and nematocysts are instead arranged in simple aggregations, or pads, either on the tentacle itself, as in *Physalia* or on tentacular side branches, as in rhizophysids. All codonophoran siphonophores except the Apolemidae (Section 10.1.1) have tentilla. The palpacles of physonect palpons also typically bear nematocysts, and these are distributed in simple lines or aggregations, as in cystonects.

Each gonophore of a siphonophore is either male or female, as in other cnidarians, and releases gametes of one sex only. In cystonects and a minority of physonects the colony bears gonophores of only one sex, whereas in calycophorans and most physonects, gonophores of both sexes develop on the same individual colony (Fig. 1A), making these colonies hermaphrodite (see Dunn et al. 2005b, fig. 7). In physonects and cystonects, gonophores are usually borne on branching gonodendra. However, calycophoran gonophores probably arise directly from the pedicel of the gastrozooid.

2.3. Taxonomic terminology

Since the mid-19th century, most taxonomic descriptions of siphonophore colonies have been based on the position adopted at rest, with the

pneumatophore and (or) nectophores directed upwards and the stem with its bracts, gastrozooids, and gonophores hanging below. Mackie (1986), however, emphasized the anterior-posterior axis of the colony during swimming, when the single pneumatophore, or two or more nectophores, progress in an anterior direction and the stem trails behind. Haddock et al. (2005a) have now introduced a comprehensive terminology based on this anterior-posterior axis, giving new names for axes that they identify within the colony, including those of attached zooids. Anterior and posterior are restricted to the colony axis, dorsal and ventral to the orthogonal stem axis, and proximal and distal to the primary axis of any zooid (including nectophores and bracts). In large physonect colonies zooids are attached to the ventral surface of the siphosomal stem, although nectophores (when present) can attach to either the dorsal or the ventral surface of the nectosomal stem (Dunn et al. 2005b). In calycophorans, siphosomal zooids are likewise attached to the ventral surface of the siphosomal stem. Each zooid is attached to the stem at its proximal end and has a free distal end, an orthogonal upper-lower axis identifiable in lateral view, and an orthogonal right-left axis identifiable when the upper surface is viewed from outside the colony. A right-left axis can also be identified in the stem itself when viewed dorsally, so it is useful if this axis is preceded by “nectophore”, “bract”, or “stem”.

In their new terminology, Haddock et al. (2005a) adopt a holistic approach that allows siphonophores to be compared with other metazoans. These authors apply it in detail to two species of prayid calycophorans. In the present work their terminology is extended to all 37 species of codonophorans from Canadian Pacific waters. Axes for a typical physonect, two typical prayomorph calycophorans, and two diphyomorph calycophorans are summarized in Figures 1–3. Siphonophores are linear organisms, and the original mouth of the larva (protozooid) lies at the extreme posterior end of the adult colony; it is carried posteriorly as more mouths (gastrozooids) are budded in front during growth. However, in diphyomorph calycophorans this terminal mouth breaks off and becomes a free-living eudoxid, and this is followed by the production of many more similar eudoxids (see Section 10.3.3). The anterior end of the colony is marked either by the pneumatophore (in physonects; Fig. 1A) or by one or more definitive nectophores (in calycophorans; Figs 2A, 3A and B).

2.3.1. Zooid axes. Nectophore axes for a typical physonect are shown in Figures 1B and C, although in some physonects (*Apolemia* species, *Nanomia bijuga*, and *Cordagalma ordinata*) the upper-lower axis is relatively longer than that shown in Figure 1B (see Sections 10.1.1 and 10.1.3). The axes for a typical pair of apposed prayomorph calycophoran nectophores, as used in the descriptions given below, are shown in Figures 2B and C. The axes for the two dissimilar linearly adjoined (previously regarded as superimposed) nectophores typical of most diphyomorph calycophorans are shown in Figures 3A, B, D, and E.

In physonects, prayomorphs, and the posterior nectophore of diphyomorph calycophorans the primary nectophore axis is typically a proximal-distal axis (Figs 1B and C, 2B, 3E), as shown by Haddock et al. (2005a). However, in the more derived anterior nectophore of diphyomorphs the proximal-distal axis is short, and clearly not the primary axis of the zooid (Fig. 3D). Instead, it appears that during evolution, the nectosac of the anterior nectophore has become elongated into a point along an axis approximately orthogonal to the proximal-distal axis; this axis is here termed the anterior-posterior axis (Fig. 3D). Additionally, the likely evolution of the diphyomorph condition from the prayomorph condition is that one of the two originally apposed prayomorph nectophores (Fig. 2A) gradually moved posteriorly until its proximal hydrocial cavity came to occupy a position immediately posterior of the ostium of the anterior nectophore (Fig. 3A). A possible sequence for this nectophore migration is showed schematically in Figure 4. Thus, in diphyomorphs the upper surface of the anterior nectophore faces the same direction as the lower surface of the posterior nectophore and vice versa (Figs 3A, D, and E). The effect of this arrangement on the alignment of ridges between the two nectophores in a typical diphyomorph colony is explained in Section 10.2.3.

Other nectophores with unusual axes include those of hippopodiid calycophorans (Figs 2F and G), which are explained in Section 10.2.2, and those of sphaeronectid calycophorans (Fig. 3G), which are explained in Section 10.2.5. The axes of amphicaryonine and nectopyramidine prayine calycophoran nectophores are explained in Sections 10.2.1.1 and 10.2.1.3, respectively.

The axes of a typical physonect bract are shown in Figures 1D and E, and although a portion of this bract

extends beyond the proximal end of the bracteal canal, this pointed extension is still considered here to represent the proximal end of the bract. Physonect bracts connect to the stem via a bracteal muscular lamella, or pedicel, that attaches to the lower surface on each side of the bracteal canal, sometimes along a considerable part of its length (Fig. 1E; Dunn and Wagner 2006, p. 745). Calycophoran bracts vary in shape, and their axes are more difficult to determine. In some prayomorphs, bracts wrap around the stem like a cloak when young (Fig. 2D), attaching to the stem near the narrow proximal “neck” end of the cloak, where the bracteal canals connect to the stem canal. A proximal-distal axis extends outwards from the point of connection through the median point of the bract to the middle of the broad distal edge, or “hem”, of the cloak (Fig. 2D; see also Mapstone 2005, fig. 4). More mature bracts of this type flatten out, particularly when detached, with the proximal neck region forming a median indentation on one side (see *Praya reticulata* bract in Section 10.2.1.2). In other prayomorph bracts, such as those of *Lilyopsis fluoracantha*, attachment is along the length of the stem, as is well shown by Haddock et al. (2005a, figs 5B and C). Herein, bract axes in diphyomorph calycophorans are derived from the point where the bract was originally attached to the stem of the parent colony, as shown by Mackie et al. (1987, fig. 36). This end becomes the proximal end, and a proximal-distal axis extends through the bract, as shown in Figure 3F. A gonophore is always attached to the common pedicel of a eudoxid, and this attachment point marks the proximal end of the gonophore (Fig. 3F). Diphyomorph bract and gonophore axes are explained further in Section 10.2.3.

2.3.2. Gastrovascular canals. Siphonophores have a gastrovascular canal system that serves to circulate food from the feeding gastrozoooids to the nonfeeding nectophores, bracts, and gonophores, and also to distribute oxygen around the colony and remove wastes. An elongate canal within the stem forms the hub of the gastrovascular system and connects to each nectophore, bract, and gonophore via a pedicular canal. The pedicular canal typically passes through a muscular lamella to reach each individual zooid. In the nectophore the pedicular canal passes to the nectosac and divides into four radial canals that pass over the nectosac to a circular canal around the ostium. Diverticula, or blind-ending branches, arise from the pedicular canal, and in the nectophores of many diphyomorphs and some prayomorphs one branch swells to form a somatocyst. In physonect bracts the pedicular canal passes through a muscular

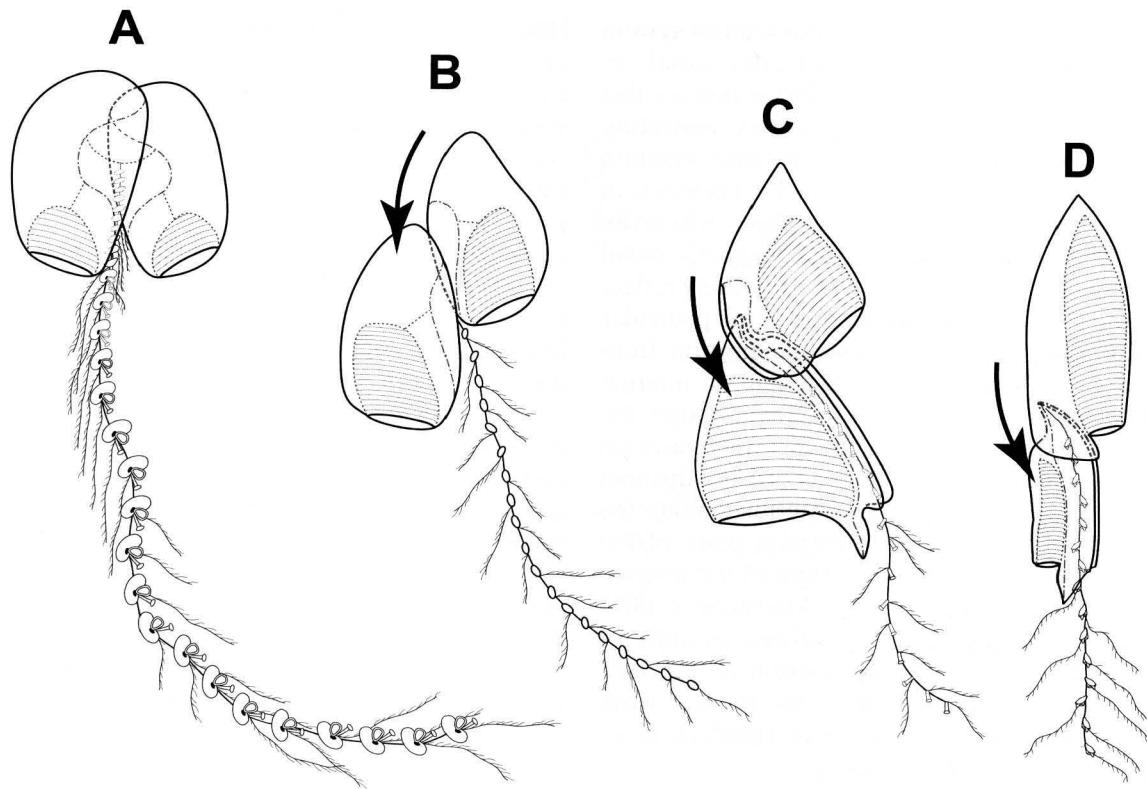


Fig. 4. Suggested nectophore migration in calycophorans from the apposed prayomorph condition (A) to the linearly adjoined (formerly “superimposed”) diphymorph condition (D): **A:** based on *Rosacea plicata*; **B:** interpretation of intermediate condition; **C:** based on *Clausophyes moserae*; **D:** based on *Chelophyses appendiculata*. Not drawn to scale.

lamella to give rise to one or more bracteal canals. In calycophoran bracts the pedicular canal from the stem passes into the bract via the pedicel of a gastrozooid (Pugh 1974a). Calycophoran bracts have one to six bracteal canals. The pedicular canal of gonophores typically divides into four radial canals that pass over the nectosac to a circular canal around the ostium, as in nectophores.

The arrangement of some gastrovascular canals is a diagnostic taxonomic character, and some long-standing canal names have changed because of the newly defined axes of Haddock et al. (2005a). In the nectosac of nectophores the dorsal radial canal has become the upper radial canal, and the ventral radial canal has become the lower radial canal (Haddock et al. 2005a, figs 2, 5A). In bracts that have more than one canal (those of prayomorph calycophorans, for example) the paired left and right hydroecial canals have become the anterior and posterior hydroecial canals, respectively, and where distinct left and right paired longitudinal canals are also present, these have become the anterior and posterior longitudinal canals. Also, the dorsal canal has become the upper

bracteal canal, and the ventral canal the lateral bracteal canal (Haddock et al. 2005a, figs 5B and C).

Haddock et al. (2005a) also divide the pedicular canal, from stem to nectophore, into discrete portions, and their names for these portions are *external pedicular canal*, *disjunct pedicular canal*, and *internal pedicular canal*. Diverticula also typically arise from the pedicular canal, as noted above, but one of the names applied to them by Haddock et al. (2005a), *somatocyst along the hydroecium*, refers only to calycophorans. This is because many calycophoran nectophores have a somatocyst, whereas physonect nectophores do not. Nevertheless, surface diverticula from the pedicular canal are also present in physonects, and the present author interprets these as being structurally homologous with the surface diverticula of calycophorans. As a result, it is necessary to change herein some of the names applied by Haddock et al. (2005a) to surface diverticula, and to introduce two new names, *ascending surface diverticulum* and *descending surface diverticulum*. Full justification for these names is given below.

Pedicular canal. The gastrovascular (canal) system of siphonophores includes a pedicular canal, as noted above, and A.K. Totton (1965a) defines this canal for nectophores and gonophores as connecting the nectophore to the stem. Totton's interpretation of the pedicular canal is followed by Haddock et al. (2005a), who rightly state on page 705, "Any nomenclature that implies that the pedicular canal is not a continuous entity does not accurately reflect its significance". These authors divide the pedicular canal into two sections, an external portion from the stem to the nectophore surface and an internal portion from the nectophore surface through the mesogloea to the nectosac. They also recognize an extra section in prayine calycophorans, the disjunct pedicular canal, which passes posteriorly along the nectophore surface from the insertion point of the external pedicular canal to the origin of the internal pedicular canal. Unfortunately, Mapstone (2005) used different names for the various sections of the pedicular canal in her description of *Rosacea cymbiformis* nectophores, but in the present work the pedicular canal terminology of Haddock et al. (2005a) is followed throughout.

Nectophore attachment and gastrovascular canals. The external portion of the pedicular canal passes through a structure known as the nectophoral muscular lamella, which in life attaches the nectophore to the stem. A lamella of this type is described by Totton (1954, 1965a), Pugh (1992c), and Mapstone (1998, 2003, 2004, 2005) for several codonophorans. Where the lamella attaches to the nectophore, a surface canal is typically present that is given the name *mantle* or *pallial* canal by Totton (1965a, p. 35). A mantle or pallial canal is also mentioned in numerous descriptions of siphonophores, by, for example, Totton (1954, 1965a), Mapstone (1998, 2003, 2004, 2005), Pugh (1998, 1999a, 2002, 2003, 2005, 2006b), Pugh and Harbison (1986), and Pugh and Youngbluth (1988a). The present author considers that this "pallial canal" canal may fulfill an important function in many species by facilitating the shedding of nectophores during autotomy. Autotomy is reviewed by Mackie et al. (1987) and discussed further in Section 3.4. However, Haddock et al. (2005b) do not use "pallial canal" because, as they note on page 705, "Historically the term pallial canal has been used to describe a variety of gastrovascular extensions in siphonophore nectophores". Instead, they term the various parts of the pallial canal in prayine calycophorans the *somatocyst along the hydroecium*, the *descending branch*, and the *disjunct pedicular canal* (Haddock et al. 2005b, table 3).

Haddock et al. (2005b, p.705) conclude, like the present author, that "It is probable that the pallial canals of physonects are homologous to the somatocyst and descending branch of the pedicular canal in calycophorans." Indeed, the definition given by Totton (1965a, p. 35) for the mantle or pallial canal as the "upper and lower diverticula of the pedicular canal at the point of entry into a nectophore or gonophore, eg. in *Rosacea* spp. The muscular pedicular lamella is attached to its proximal wall" lends further support to this interpretation. Totton does not restrict this definition to any one group of codonophorans. However, *somatocyst along the hydroecium*, the name used by Haddock et al. (2005a) for that diverticulum from the pedicular canal which extends anteriorly along the nectophore surface, can be applied only to calycophorans, since physonects have neither a somatocyst nor a hydroecium. Historically the somatocyst has been defined as "a caecal part of the common gastric cavity found in calycophoran nectophores" (Totton 1965a, p. 35), but it is clear that when Totton made this statement he was really referring to the somatocyst of a typical diphyomorph calycophoran, because he refers to figures of the larval nectophores of two diphyomorph species, *Muggiae atlantica* and *Sulculeolaria quadrivalvis* (Totton 1965a, text-figs 3, 4).

The relationship between the nectophoral muscular lamella and the median gastrovascular canal on the proximal surface of the nectophore is shown for selected codonophorans in Figure 5, with the lamella indicated as a shaded area. While the extent of this median canal varies among species, in all examples the external pedicular canal passes either through the lamella, or along one edge of it, from the stem (or stem mass where the stem is much contracted) to the nectophore. Here the external pedicular canal then either passes directly to the nectosac (Fig. 5A) or penetrates the mesogloea to reach the nectosac via an internal pedicular canal (Figs 5B and C); alternatively, it passes first posteriorly along the nectophore surface as a disjunct pedicular canal and then either penetrates the mesogloea and passes to the nectosac via an internal pedicular canal (Figs 5D–F and I) or connects directly to the nectosac without an intervening internal pedicular canal (Figs 5G and H).

In several species the lamella is attached along an ascending surface diverticulum and this diverticulum extends anteriorly from the pedicular canal, as shown in Figure 5 for three physonects (Figs 5A–C, *asd*) and two prayids (Figs 5D and E inset, *asd*). A similar diverticulum is present in hippopodiids

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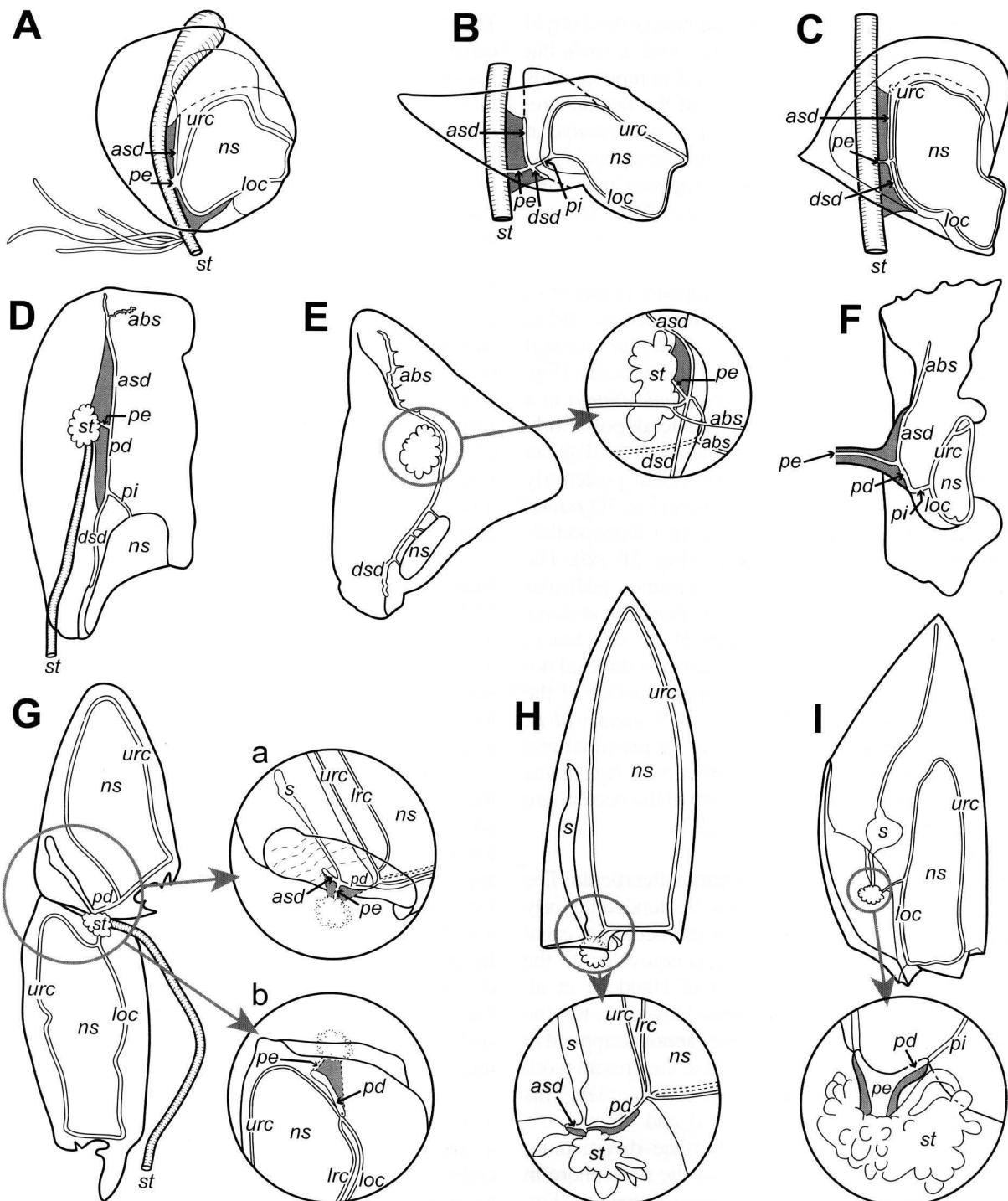


Fig. 5. Schematic diagram of muscular lamella attachment (shaded) and median gastrovascular canals in selected codonophorans from Canadian Pacific waters and elsewhere (lateral canals are shown in insets only): (A–C) Physonects: A: *Apolemia uvaria* (after Totton 1965a, fig. 15); B: *Agalma elegans* (after Fig. 19B, stn. LB13); C: *Nanomia bijuga* (derived from Totton 1965a, figs 12, 32, and Strait of Georgia sample); (D–I) Calycocephorans: D: *Praya reticulata* (after Bigelow 1911b, pl. 3 fig. 2, Fig. 30B, stns A4, LC10); E: *Nectopyramis thetis* (after Pugh 1992a, fig. 2c; Fig. 35C, stn. LC11); F: *Vogtia pentacantha* (after Fig. 40B, stn. B-7R); G: *Sulculeolaria quadrivalvis* (derived from C. Carré 1979, fig. 1, stn. A4); H: *Lensia conoidea* (after Fig. 47A, stns LB17, LC9); I: *Chuniphyes multidentata* (after Figs 57A, 58D, stn. LB14) (abs, ascending branch of somatocyst; asd and dsd, ascending and descending surface diverticula; ns, nectosac; pe, pd, and pi, external, disjunct, and internal branches of pedicular canal; s, somatocyst; st, stem, either extended or retracted; urc, lrc, and loc, upper, lateral, and lower radial canals of nectosac). Not drawn to scale.

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(Fig. 5F, *asd*) and in the anterior nectophore of the diphid *Sulculeolaria quadrivalvis* (Fig. 5G, inset a, *asd*), but here it is not directed anteriorly. Instead, in hippopodiids it passes towards the upper surface of the nectophore, while in the anterior nectophore of *S. quadrivalvis* it passes towards the lower surface of the nectophore. This is because, in these species, the nectophore axes were modified during evolution, as explained in Sections 2.3.2, 10.2.2, and 10.2.3.

The lamella also attaches to the nectophore posterior of the external pedicular canal in several species, and to different canals in other species. In *Apolemia uvaria* it attaches to the lower radial canal of the nectosac (Fig. 5A, *loc*), in *Agalma elegans* and *Nanomia bijuga* to a descending surface diverticulum that extends posteriorly (Figs 5B and C, *dsd*), in *Praya reticulata* to the disjunct pedicular canal and part of the equivalent posteriorly directed descending surface diverticulum (Fig. 5D, *pd* and *dsd*), and in *Vogtia pentacantha* and other hippopodiids to the disjunct pedicular canal only (Fig. 5F, *pd*). The lamella similarly attaches to the disjunct pedicular canal in *Sulculeolaria quadrivalvis*, *Lensia conoidea*, and *Chuniphyes multidentata* (Figs 5G–I, *pd*), but in these species the disjunct pedicular canal is directed not posteriorly but towards either the upper surface of the nectophore (in anterior nectophores of *S. quadrivalvis*, *L. conoidea*, and *C. multidentata*) or its proximal end (in posterior nectophores of *S. quadrivalvis*). Again, this occurs because of the modified nature of the nectophore axes in these species (see Section 2.3.2).

New names for some pedicular canal diverticula. The ascending surface diverticulum, which extends anteriorly along the nectophore surface from the pedicular canal in physonects and prayids (Fig. 5), is equivalent to the *somatocyst along the hydroecium* of Haddock et al. (2005a) in prayine calycophorans. However, for the reasons given above, the latter name cannot be applied to physonects and is therefore replaced in the present work by the new name *ascending surface diverticulum*. This name applies equally well to prayid and hippopodiid diverticula, since the ascending surface diverticulum is directed towards the upper end of the nectophore in both types (Figs 2B and F). In *Praya reticulata* (Fig. 5D) the muscular lamella is attached along the length of the ascending surface diverticulum, at least as far as the origin of the ascending branch of the somatocyst (see below), but in *Nectopyramis thetis* (Fig. 5E) it is attached only along the proximal portion of the ascending surface diverticulum, and the diverticulum extends anteriorly along the surface of the hydroecium beyond the end of the muscular lamella before penetrating the mesogloea as the ascending branch of the somatocyst (see below).

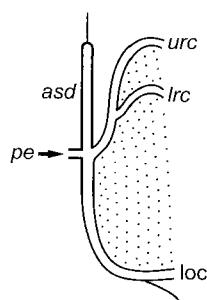
The descending surface diverticulum from the pedicular canal is directed towards the lower surface of the nectophore in the two agalmatid physonects shown in Figures 5B and C (*Agalma elegans* and *Nanomia bijuga*) and also in the two prayid calycophorans shown in Figures 5D and E (*Praya reticulata* and *Nectopyramis thetis*). However, the descending surface diverticulum is much longer in *P. reticulata* than in the two agalmatids, and in preserved specimens extends beyond the region of attachment of the muscular lamella, as shown in Figure 5D. In *N. thetis* the descending surface diverticulum is short (Fig. 5E, *dsd*), and the muscular lamella is not attached to any part of it. This is probably because, in nectopyramidines, only a single nectophore is developed (see Section 10.2.1.3). In prayine prayids this descending surface diverticulum is termed by Haddock et al. (2005a, table 3) the *descending branch*, but because it is regarded as the complement of the ascending surface diverticulum, in the present work its name is, regrettably, changed to descending surface diverticulum.

New definition of the somatocyst. Haddock et al. (2005a) include their *somatocyst along the hydroecium* as part of the somatocyst proper, while excluding the *descending branch*, but in the present work both these surface canals are excluded from the somatocyst, for the reasons given above. Thus, the somatocyst is here restricted to those diverticula from the pedicular canal or its ascending surface diverticulum that penetrate the mesogloea. The name *ascending branch* (of the somatocyst) is used by Haddock et al. (2005a, table 3) for this diverticulum in prayines, and the same name is applied here to any such penetrating diverticula from the pedicular canal, or from the ascending surface diverticulum, that develop in prayomorph calycophorans. In diphymorph calycophorans, only a single such diverticulum develops, typically from the point where the external pedicular canal inserts onto the nectophore surface, and the traditional name somatocyst is therefore used herein for this diverticulum, when present.

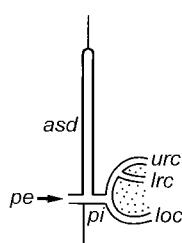
This new definition of the somatocyst necessitates a reevaluation of this structure in prayomorph codonophorans, and the types of somatocysts found in selected species from Canadian Pacific waters are shown in Figure 6, following the style of the schematic diagrams introduced for prayine siphonophores by Haddock et al. (2005a, table 3). It is evident from this figure that an ascending branch of the somatocyst is absent from nectophores of *Amphicaryon acaule* and *Rosacea plicata*, while it is present in nectophores of the five other prayomorph species shown. In hippopodiids, only a single ascending branch of the somatocyst is developed, but in *Praya*

Physonects:

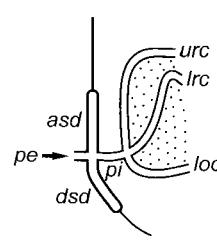
Apolemia contorta



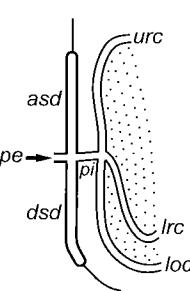
Bargmannia elongata



Agalma elegans

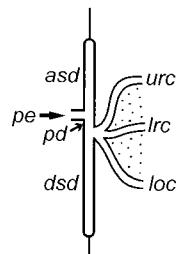


Nanomia bijuga

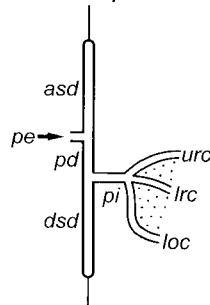


Calycophorans:

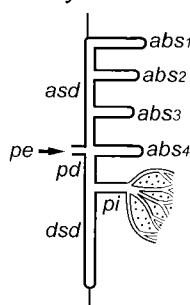
Amphicaryon acaule



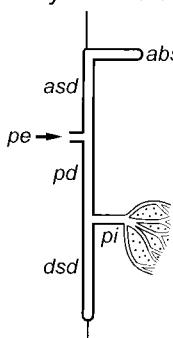
Rosacea plicata



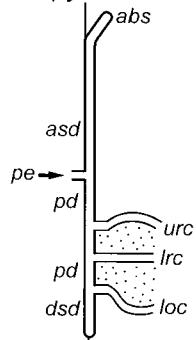
Praya dubia



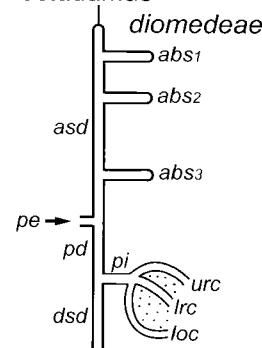
Praya reticulata



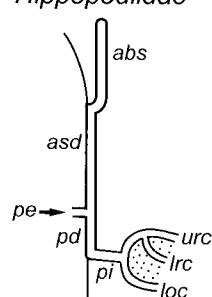
Nectopyramis thetis



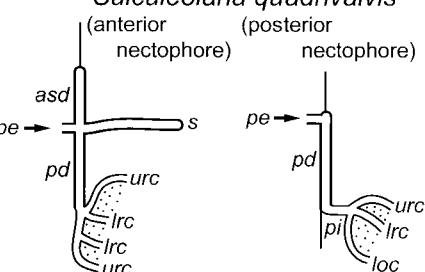
Nectadamas



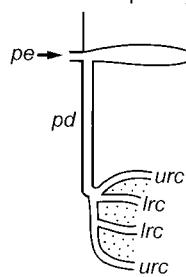
Hippopodiidae



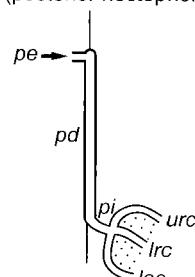
Sulculeolaria quadrivalvis



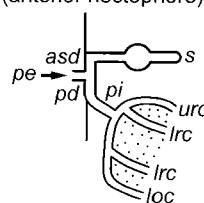
Chelophyses appendiculata
(anterior nectophore)



Chelophyses appendiculata
(posterior nectophore)



Chuniphyes multidentata
(anterior nectophore)



Chuniphyes multidentata
(posterior nectophore)

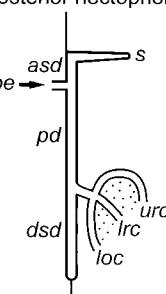


Fig. 6. Diagrammatic arrangement of the pedicular canal and diverticula arising from it (lateral view) in selected Canadian Pacific codonophoran siphonophores (*abs*, ascending branch of somatocyst; *asd* and *dsd*, ascending and descending surface diverticula; *pe*, *pd*, and *pi*, external, disjunct, and internal branches of pedicular canal; *s*, somatocyst; *urc*, *lrc*, and *loc*, upper, lateral, and lower radial canals of nectosac; the stippled area shows the nectosac). Not drawn to scale.

dubia and *Nectadamas diomedae* there are several such branches, most of which sub-branch, and these all arise from the ascending surface diverticulum (see Sections 10.2.1.2 and 10.2.1.3). In *P. reticulata* there is only a single ascending branch of the somatocyst, and this arises from near the anterior end of the ascending surface diverticulum; in mature nectophores it sub-branches numerous times, as described in Section 10.2.1.2. In *Nectopyramis thetis* there is a similar ascending branch of the somatocyst in the midline, but this species also uniquely develops two lateral ascending branches that arise from two lateral surface diverticula, close to their origin from the insertion point of the external pedicular canal, as shown in the inset in Figure 5E and described in detail in Section 10.2.1.3. Other prayine species not collected in Canadian Pacific waters also lack a somatocyst according to the present definition, including other species of the genera *Rosacea*, *Craseoa*, and *Prayola* (Haddock et al. 2005a, table 3), and these are discussed further in Section 10.2.1.2.

The disjunct pedicular canal in diphyomorphs. A disjunct pedicular canal can be identified in all the diphyomorph nectophores collected from Canadian Pacific waters that have retained some or all of the stem, and in others it is represented by a gutter-like scar on the nectophore surface previously considered by other authors to be part of the pallial canal (see above). A disjunct pedicular canal is found to pass along the hydroecium from the insertion point of the external pedicular canal towards the nectosac on the upper side of the nectophore in anterior nectophores of *Sulculeolaria quadrivalvis*, *Chelophyses appendiculata*, and *Chuniphyes multidentata*. The disjunct pedicular canal in the anterior nectophore is longer in the two diphyid species (Fig. 6; see Sections 10.2.3.1 and 10.2.3.2) than in the single clausophyid shown, where it is very short (Fig. 6; see Section 10.2.4.1). In the posterior nectophores of the two diphyid species there is no somatocyst and the disjunct pedicular canal extends distally from the insertion point of the external pedicular canal to the nectosac without continuing as a descending surface diverticulum (Fig. 6, *S. quadrivalvis*, *C. appendiculata*). In the posterior nectophore of the clausophyid *C. multidentata* (Fig. 6) a short ascending diverticulum passes proximally from the insertion point of the external pedicular canal to give rise to a somatocyst. Distally, a disjunct pedicular canal extends along the hydroecium to a short internal pedicular canal, which passes through the mesogloea to the nectosac, and the surface diverticulum continues farther distally as a descending surface diverticulum (Fig. 6).

2.4. Systematic descriptions and diagnoses

The layout of the systematic account (Section 10) follows current conventions. Diagnoses are based on features of the mature colony, including the nectophore, and of reproductive stages if appropriate. A full synonymy is also given prior to each species description. Where more than one view of a nectophore is illustrated, such views are of the same nectophore unless otherwise stated. Detached physonect nectophores in a dish orientate naturally with the upper surface uppermost (Fig. 1G); however, those of most calycophorans tend to lie with a lateral surface uppermost (Figs 3D and E). A typical view is illustrated for each species, with other views added where needed for a fuller interpretation of morphology. Physonect bracts are typically leaf-like with a pointed distal end, flattened in the upper-lower plane, and attached to the stem via a bracteal lamella from the proximal part of the lower surface, as noted above. They are illustrated in either upper or lower view (Fig. 1E), whichever best shows relevant morphological features. Calycophoran bracts vary in shape (Figs 2D, 3C) but are typically illustrated in lateral view (Fig. 3F). In bracts of the family Prayidae, the bracteal canals are typically not swollen, whereas those of bracts of the families Diphyidae and Clausophyidae typically contain the bracteal equivalent of the somatocyst, which is a discrete swollen structure termed the phyllocyst (Fig. 3F).

Taxonomic drawings are based on certain conventions. The profile or ridges are indicated by heavy lines, internal structures by thinner lines, and, in many, the swimming muscles of the nectosac by shading. Canals are shown as fine double lines. Furrows (see legends) or a continuation of structures behind other structures, and occasionally the stem or the presumed outline of damaged structures, are indicated by broken lines.

Gelatinous protuberances arising from nectophores and bracts may be rounded or pointed. In the literature quoted, rounded structures are typically referred to as protuberances and pointed protuberances are referred to as teeth. However, in a wider zoological sense the latter term is used to describe structures involved in feeding, and is arguably inappropriate in the present context. Thus, the term cusp is used herein to refer to such pointed protuberances.

3. Life Cycles, Budding, and Autotomy

The asexual siphonophore colony is the dominant stage in the life cycle. Siphonophores are holoplanktonic (except the Rhodaliidae) and lack a benthic stage, unlike most other pelagic cnidarians. This enables them to inhabit deeper offshore waters, where they are often the dominant gelatinous predators (see below). Most are hermaphrodite, or monoecious, although the sexes are separate in a few, i.e., they are dioecious. It seems likely that the first siphonophores were dioecious, and underwent a major transition to monoecy early in phylogeny, although further evidence is needed to verify this hypothesis (Dunn and Wagner 2006).

Siphonophores are difficult to breed in captivity. However, 11 species have been successfully reared to the young-colony stage in the laboratory by Claude and Danièle Carré (C. Carré 1967, 1968e; D. Carré 1967, 1969a and b, 1971, 1973; Carré and Carré 1969, 1991) from mature eudoxids or polygastric colonies collected in the Bay of Villefranche, Nice, Mediterranean Sea, although only one of these (*Muggiaeae kochi*) was cultured through its entire life cycle (Carré and Carré 1991). Another species, *Muggiaeae atlantica*, was reared by Russell (1938a) from eudoxids collected in the English Channel, and Freeman (1983) cultured the same species, together with *Nanomia bijuga*, from material obtained in Friday Harbor in the San Juan Islands, Washington State, USA, adjacent to Canadian Pacific waters. Most recently, Sherlock and Robison (2000) raised *N. bijuga* to the siphonula stage at two different temperatures using specimens from farther south, in Monterey Bay, California.

Some 19th-century workers, including Metschnikoff (1874) and Haeckel (1869b), also fertilized eggs of various physonect and calycophoran species and followed their early development. Metschnikoff (1874) reared *Agalma elegans* and *Sulculeolaria quadrivalvis*, which are both represented in Canadian Pacific waters, but none of the species raised by Haeckel are from this area.

Planktonic larval stages of *Agalma elegans* collected by Totton (1955) form a continuous series, with young colonies bearing identifiable definitive

nectophores. Larval nectophores of prayomorph calycophorans have also been obtained from the plankton and related to known species because they either contain an identifiable definitive nectophore in the hydroecium, or are attached to a larger and older such nectophore. They include *Praya dubia* and *P. reticulata* (Pugh 1992c), *Rosacea cymbiformis* (Moser 1924a), *R. plicata* and *Vogtia glabra* (Totton 1954), *Hippopodius hippopus* (D. Carré 1968), *Amphicaryon ernesti* (Totton 1954), and *Nectopyramis thetis*, *N. natans*, and *Nectadamas diomedaeae* (Pugh 1992a). All these species except *H. hippopus*, *V. glabra*, and *A. ernesti* are represented in Canadian Pacific waters.

The life cycles of a typical physonect and a typical calycophoran siphonophore are illustrated in Figure 7. Gametogenesis, fertilization, and larval development are summarized by Mackie et al. (1987) and Carré and Carré (1995). Eggs and sperm are shed directly into the sea, and fertilization is external (Fig. 7). Sperm are attracted to the egg by a unique species-specific chemical; the egg extrudes an extracellular cupule at the animal pole, over the polar bodies, and this gradually dissolves, releasing a high molecular weight chemo-attractant (Carré and Sardet 1981; Cosson et al. 1986); sperm then concentrate around the cupule until one penetrates and fertilizes the egg. Seven siphonophore species have so far been shown to produce such an attractant (Carré and Carré 1986), including four that occur in Canadian Pacific waters (*Muggiaeae atlantica*, *Lensia conoidea*, *Chelophyses appendiculata*, and *Nanomia bijuga*).

3.1. Early development

Gonophores are always of one sex, as mentioned in Section 2.2, and may or may not shed their gametes close to the asexual parent colony; the relevant observations have not been made for most species. In diphyomorph calycophorans, cormidia break off from the end of the stem and become free-swimming eudoxids, as mentioned in Section 2.3. At this time the gonophores may or may not be mature, but gonophore/gamete release from the eudoxid has

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

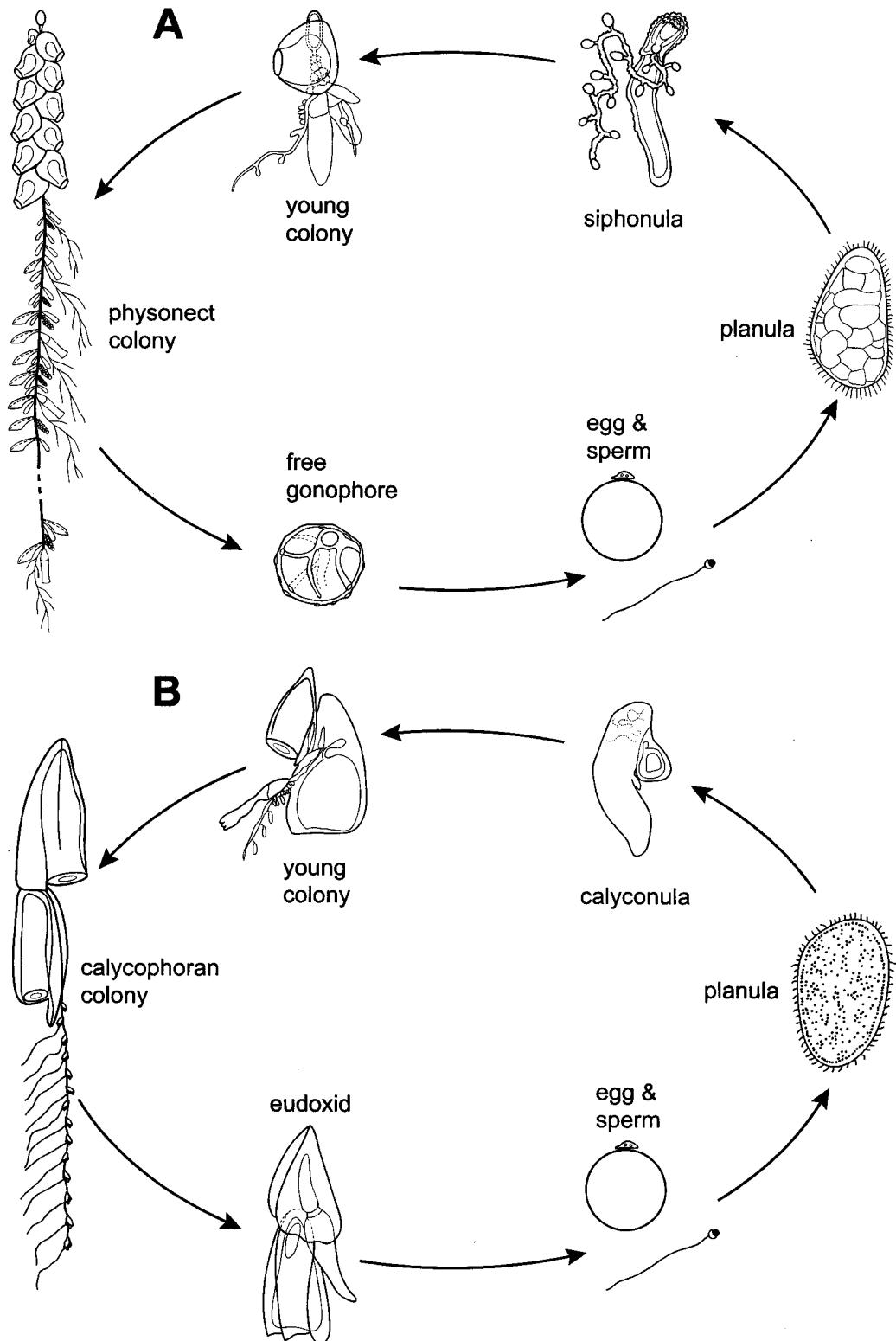


Fig. 7. Diagrammatic life cycles of two siphonophore species: **A:** typical physonect (*Nanomia bijuga*); **B:** typical calycophoran (*Lensia conoidea*). Parts of A are derived from D. Carré (1969b, pl. 2 fig. 6), Mackie et al. (1987, fig. 38B), and Metschnikoff (1874, pl. 12); parts of B are derived from D. Carré (1967, pl. 1). Not drawn to scale.

3. Life Cycles, Budding, and Autotomy

so far been studied in only one species, *Muggiae kochi*, which liberates a succession of gonophores, as shown by Carré and Carré (1991).

Siphonophore eggs are yolk, and this food store is utilized during the early development of the larva and its metamorphosis into a young colony. Segmentation (cleavage) and gastrulation are described by Carré and Carré (1995, pp. 551–553). The fertilized egg undergoes total and equal cleavage up to the 32-blastomere stage, producing a solid ball of cells known as a stereoblastula. Each blastomere consists of an outer cortex comprising the nucleus and cellular organelles and an inner vitelline mass of yolk granules (see D. Carré 1969b, fig. 2). Cleavage then becomes partial and superficial and a periblastula is formed, comprising an outer layer of small flat cells and an inner mass of larger yolk cells (Mackie et al. 1987, fig. 1). Gastrulation follows, by delamination, as the outer layer of small cells divides by tangential cleavage to form an outer ectoderm and an inner endoderm. In the ventral region only, further division of the endodermal cells occurs, and some of these cells migrate into the yolk. At the same time, the ectodermal cells become ciliated and an ovoid or elongate planula larva is formed (Fig. 7). Buds soon appear on various zooids in the ventral “plaque”, and within 24 h the planula has transformed into a siphonula in physonects and a calyconula in calycophorans (Fig. 7).

In the physonect siphonula, either a pneumatophore or a larval bract typically appears early in development to give initial buoyancy to the larva. For example, the first structures to appear in *Nanomia bijuga* are the pneumatophore and the tentacle of the first gastrozooid (protozooid), followed later by a larval bract and later still by the first nectophore (D. Carré 1969b). The pneumatophore starts to function just 6–7 days after fertilization (D. Carré 1969b; Freeman 1983; Sherlock and Robison 2000), and around the same time the posterior end of the larva transforms into the first gastrozooid as the yolk supply starts to dwindle. By 20 days the larval bract has appeared (D. Carré 1969b, pl. 2 fig. 5). Later this bract is lost and replaced by the first nectophore, the stem starts to lengthen, more nectophore buds form, and a second gastrozooid starts to function (Fig. 7A). In *N. bijuga*, development from planula to siphonula larva is faster at 12 °C than at 8 °C (Sherlock and Robison 2000).

During the early development of two other physonects, *Agalma elegans* and *Cordagalma*

ordinata, the first structure to appear is a larval bract (Carré and Carré 1995). Such a bract is illustrated for *A. elegans* by Metschnikoff (1874, pl. 8 figs 6, 7) and for *C. ordinata* by D. Carré (1973, pl. 1 fig. 7, as *C. cordiforme*). In the latter species the larval bract is particularly large. Totton (1955) tried unsuccessfully to rear *A. elegans* larvae at the Carré's lab in Villefranche, but was able to collect a number of larvae at different developmental stages and these were illustrated in a series of clear and detailed figures (Totton 1955, figs 2–9). In *A. elegans* several larval bracts are produced and can be distinguished from the many hundreds of definitive bracts formed later by a characteristic pit of nematocysts at their distal tips (Totton 1955, fig. 2). Larval bracts surround the first and second gastrozooids and are carried posteriorly at the end of the stem as it lengthens and produces more cormidia. Totton showed this unique terminal structure in a figure of a young colony with five cormidia (frontispiece from Totton 1954, reproduced in Totton 1965a, fig. 7). In contrast, *C. ordinata* produces only a single larval bract, which is rounded and lacks a distal pit of nematocysts; the definitive bracts produced subsequently are prismatic and quite different in shape (see Section 10.1.3).

A small colony comprising a single nectophore (2 mm in length) and stem was collected by Margulies (1982) from Antarctic waters and introduced as *Mica micula*. Further specimens from a similar area were described and figured by Pagès and Gili (1989, fig. 2). They note that the pneumatophore of this colony seems immature, and small relative to the nectophore. Thus, they suggest that it might be the siphonula of a physonect, but not from a species that first develops a larval bract (see above), because no bract was found in any specimen. Also, although *M. micula* first develops a larval nectophore, like *Halistemma rubrum* (D. Carré 1971), the proportions of this nectophore are different, as also is the arrangement of the radial canals on its nectosac. In *Mica micula*, this arrangement resembles that displayed by the definitive nectophore of *Bargmannia elongata* (see Section 10.1.2), which led Pugh (1999b) to tentatively refer *M. micula* to *B. elongata*, and the present author concurs (see Section 10.1.2).

In the calycophoran calyconula the first structure to appear is the bud for a larval nectophore (Fig. 7B). At the same time another bud forms below it, which is destined to become the tentacle of the first gastrozooid (Carré and Carré 1995, figs 180A–C). The life cycle shown in Figure 7B is

based on the diphyomorph *Lensia conoidea*; the larval nectophore grows rapidly and by the time the calyconula is 3–4 days old, the ostium has opened and the nectosac has begun to pulsate. A few days later, as the yolk is used up, the posterior end of the planula starts to develop into the first gastrozooid, or protozooid. A mouth soon opens at its posterior end and nematocysts appear in a thickening in the midregion; these start to migrate into the developing tentacle to form the tentilla. By this stage, at about 10 days of age, the portion of the larva between the larval nectophore and the gastrozooid has thinned to form a stem, and on this stem, or possibly on the pedicel of the larval nectophore, a small bud develops (see D. Carré 1967, p. 242 and pl. 1 figs 5, 6) that is destined to become the anterior nectophore of the adult colony. Anterior of the nectosac the larval nectophore consists of a conical thickening of mesogloea, which is hollowed out on the lower side where the stem is developing. This hollow represents the hydroecium of the larval nectophore. Over the next week the anterior nectophore appears and the two-bell stage, or young colony, is formed (Fig. 7B). By 3 weeks the gastrozooid tentacle has also started to capture prey. After this, the anterior nectophore grows larger than the larval nectophore, and in *L. conoidea* the latter is shed and replaced by a definitive posterior nectophore (D. Carré 1967).

The course of development of other diphyomorph calycophorans from Canadian Pacific waters, including *Muggiae atlantica* (Russell 1938a; Freeman 1983), *Chelophyses appendiculata* (Carré and Carré 1995), *Sulculeolaria quadrivalvis* (Metschnikoff 1874; C. Carré 1979), and *Sphaeronectes köllikeri* (D. Carré 1969a, as *S. gracilis*), is similar to that shown in Figure 7B. These species differ from *Lensia conoidea* only in the following: in *M. atlantica*, after the larval nectophore is shed following the two-bell stage, no posterior nectophore forms, and the colony consists of an anterior nectophore only (Russell 1938a); in *S. köllikeri* the bud for a larval nectophore appears at the anterior end of the planula instead of on the lateral surface (D. Carré 1969a), and once this larval nectophore has formed it is retained throughout life, without a definitive nectophore ever being developed (see Section 10.2.5).

Only two prayomorph calycophorans, *Lilyopsis rosea* (Carré and Carré 1969) and *Hippopodius hippopus* (Metschnikoff 1874, as *H. gleba*), have so far been reared from fertilized eggs; adults of both were collected in the Mediterranean. During

the development of *L. rosea* the first bud to arise develops into a large larval tentacle that dwarfs the other siphosomal portion of the calyconula. Later this tentacle (*filament larvaire* of Carré and Carré 1969, p. 360) is resorbed and the primary gastrozooid maintains its position. In *L. rosea* the yolk and primary endoderm together form the somatocyst of the larval nectophore (Carré and Carré 1969), and the ascending surface diverticulum of *H. hippopus* larvae shown by Chun (1888b, p. 13, as *H. luteus*, pl. 2 fig. 3, as *saftebehälter*) may form in the same way, although larvae reared by Metschnikoff (1874) did not survive to this stage. While neither of these two species has been recorded from Canadian Pacific waters, the early development of those prayomorphs that are present is likely to follow a similar course.

Larvae of the prayomorph genus *Amphicaryon* were identified in the plankton by Totton (1954, fig. 45) and found to display characters of one of the two nectophores of mature *A. ernesti* colonies. Totton therefore concluded that in these prayomorphs the larval nectophore is retained into the adult stage (see Section 10.2.1.1). However, no prayomorphs of this type have been reared in the laboratory, so other stages in the life cycle are at present unknown.

3.2. Budding

Budding is a fundamental mechanism of colony growth in siphonophores that begins in the larva, as described above, and continues throughout life. In codonophorans, two budding sites, or growth zones, are typically identifiable, with the buds of one zone developing into nectophores and those of the other into siphosomal cormidia. By the time the colony matures, these zones will either have become separated through growth of the nectosomal stem, as in long-stemmed physonects, or not, as in calycophorans.

The siphosomal growth zone has recently been studied in detail in mature colonies of three long-stemmed physonects, *Bargmannia elongata* (Dunn 2005) and *Nanomia bijuga* and *Agalma elegans* (Dunn and Wagner 2006). All three species occur in Canadian Pacific waters (see Sections 10.1.2 and 10.1.3). Although there are no recent studies on growth in any calycophoran, budding has been described and figured for *Sphaeronectes köllikeri* by Chun (1885, as *Monophyses gracilis*); this species is also present in Canadian Pacific waters (see Section 10.2.5).

3. Life Cycles, Budding, and Autotomy

In physonects, siphosomal buds form on a small protrusion from the stem that Dunn (2005) and Dunn and Wagner (2006) term a *horn*. This structure is particularly well developed in young larvae of *Agalma elegans*, where it initially projects anteriorly, alongside the developing pneumatophore (well shown by Totton 1955, figs 2–9, as *nectostyle*). As the colony matures, the horn shrinks until it becomes quite small and insignificant (Dunn and Wagner 2006, figs 4d–j, labelled “T”). The horn is slightly larger in *Nanomia bijuga* than in *A. elegans* (Dunn and Wagner 2006, fig. 5d), while in *Bargmannia elongata* it is larger still and forms a distinctive sinistral coil (Dunn 2005, figs 5a, b). No horn is identifiable in Chun’s figure of the siphosomal budding zone of a mature colony of *Sphaeronectes köllikeri* (1885, pl. 2 fig. 2, as *Monophyes gracilis*).

Dunn (2005) and Dunn and Wagner (2006) have shown that each cormidium of the above-mentioned species arises from a probud, as already noted (Section 2.1), and the shape of the youngest probuds varies. In *Bargmannia elongata*, probuds can appear as transverse ridges across the ventral surface of the stem (Dunn 2005, fig. 5c), whereas in *Nanomia bijuga* they are rounded and more discrete (Dunn and Wagner 2006, fig. 5d). In *Agalma elegans* the youngest probud found by Dunn and Wagner (2006, figs 4d–j) had already split into six sub-buds, all arising from a common pedicel or stalk. Most zooids arise from the probud in a species-specific pattern, and in two of the species studied by Dunn (2005) and Dunn and Wagner (2006) the posteriormost zooid of each cormidium is a gastrozooid. However, in *A. elegans* the posteriormost zooid is a precociously developed B-palpon (Dunn and Wagner 2006, fig. 4a), which may be unusual; more growth zones must be investigated before any firm conclusions are drawn. Zooids of the three species studied recently also display some directional asymmetry within each cormidium. Zooids may arise on one side of the midventral line only, or alternately on the right and left sides of the midventral line. This asymmetry is most marked in *B. elongata* (see Dunn 2005, fig. 4), is displayed by the sexual gonodendra in *N. bijuga*, and is limited to a single gastrozooid-associated bract in each cormidium of *A. elegans* (Dunn and Wagner 2006).

Nectophores of physonect codonophorans form from simple buds that arise in a nectosomal growth zone immediately posterior of the pneumatophore, as shown for *Bargmannia elongata* by Dunn (2005, fig. 6). This zone is always simpler than the

siphosomal growth zone because fewer zooids are produced. Surprisingly, a second, much smaller bud was found immediately posterior of the bud for each definitive nectophore in specimens of *B. elongata* (see Dunn 2005, fig. 6), *Agalma elegans*, and another physonect species, *Forskalia formosa* (Dunn and Wagner 2006). In apolemiids, definitive nectophores alternate with elongate structures previously known as nectosomal tentacles (see Mapstone 2003, figs 2, 3, 9, 15), which are herein termed *nectosomal polyps*. They may actually be modified tentacle-less polyps (C.W. Dunn, pers. comm., 2007). Thus, the presence of these small extra buds in a pyrostepheid, an agalmatid, and a forskaliid suggests that the nectosome of physonects might have been more complex when it first evolved, with iterative polypoid as well as medusoid zooids, and that the ability to form polypoid zooids was subsequently lost in most physonects, as postulated by Dunn and Wagner (2006).

In calycophorans the siphosomal cormidia lack palpons, and this has led Dunn and Wagner (2006) to suggest that cormidial paedomorphy has occurred in this group. Calycophorans also have a much reduced nectosomal growth zone, and as Totton (1954, 1965a) points out, in those species where this has been studied, only one nectophore is budded from the stem, with each subsequent nectophore arising from the pedicel (or foot-stalk) of its predecessor. However, evidence for this is scant because this region is always much contracted in preserved material. Mapstone (2005) was unable to identify even a short nectosomal stem in one prayomorph calycophoran she studied, and she was similarly unable to confirm the origin of one elongate nectosomal lamella (or pedicel) from the other, even though these structures were quite large (Mapstone 2005, figs 3C and D). In contrast, the muscular lamella, or pedicel, of each nectophore of hippopodiid prayomorphs does arise from that of its predecessor, as is shown by Chun (1897b, fig. 11). In these species the pedicels form a “false” nectosome that hangs down around the central siphosome and carries a number of nectophores (Fig. 2E). Nectophores bud from an anterior growth zone and become progressively older towards the posterior end (also see Section 10.2.2). Similarly, the growth zone of a diphyomorph calycophoran, *Sulculeolaria quadrivalvis*, is clearly shown in two figures by Bigelow (1931, figs 198, 201, as *Galettea quadrivalvis* or *G. quadridentata*). In Bigelow’s figure 198 a reserve bud has clearly arisen from the pedicel of another nectophore, while in his figure 201 both the posterior nectophore and

at least one of the two reserve buds appear to have arisen from what is concluded to be the pedicel of the anterior nectophore (on the right, the nectophore itself having detached).

3.3. Nectophore replacement

Mackie et al. (1987, pp. 191 and 192) note that in long-stemmed physonects, while new nectophores are budded serially at the anterior end of the nectosome, they are also “shed spontaneously” at the posterior end, where there is “a zone of stem resorption”. These authors make the additional comment (p. 107) “It is thought that the nectophores of prayids and hippopodiids are produced continually throughout life”. Thus, it seems likely that in physonects and prayomorph calycophorans, nectophores are constantly being replaced, though no one has yet succeeded in rearing any beyond the young-colony stage to test this hypothesis.

Supporting evidence for nectophore replacement in long-stemmed physonects comes from Mapstone (2003). In her figure 1A this author shows an accumulation of scars of nectophoral muscular lamellae at the posterior end of the siphosome of *Apolemia uvaria*, which suggests that nectophores are indeed shed from this region. However, a similar accumulation could not be identified in *A. contorta* (as *Tottonia contorta*). Similarly, Chun (1885) comments that in the prayine prayid *Rosacea cymbiformis* both nectophores are replaced within a week. Mapstone (2005) studied 29 specimens of *R. cymbiformis* from the collections in the Natural History Museum (NHM), London, UK, and suggests that nectophores are continually regenerated. A larval nectophore is produced, as described above, shed after a N_1 nectophore grows inside its hydroecium, and the latter then matures. Subsequently, a definitive N_2 nectophore develops inside the N_1 hydroecium, and after it matures, the latter is shed. The hydroecium of the N_2 then broadens to clasp a new “ N_2' ”, which developed inside its hydroecium, and so replacement continues. Prior to nectophore loss, the lower part of each nectophoral muscular lamella is apparently resorbed, since this portion is only present in the N_2 of intact colonies of *R. cymbiformis*, not the N_1 (see

Mapstone 2005, fig. 1A). Thus, in the generalized prayine colony shown in Figure 2A, this lamella portion is omitted.

Mackie et al. (1987) comment that in some colonies of another prayomorph calycophoran genus, *Hippopodius*, the oldest nectophores at the posterior end of the “nectosome” are smaller than younger, more anterior nectophores; they deduce that these old nectophores were formed at an earlier growth stage, when the colony was smaller, and eventually replaced by larger nectophores. This replacement has already occurred in the generalized hippopodiid colony shown in Figure 2E, and the largest nectophores are at the posterior end. *Vogtia serrata*, together with two other *Vogtia* species, are represented in Canadian Pacific waters and are described below (Section 10.2.2)

The most detailed study of nectophore replacement so far undertaken is C. Carré’s (1979) on three species of the diphyomorph genus *Sulculeolaria*. This author, who collected his specimens from the Mediterranean, reared three species in the laboratory and showed that both nectophores can be replaced up to 3 times. Replacement nectophores of *S. quadrivalvis* have shorter upper and lateral cusps than the initial pair produced (given as NA_1 and NP_1 by C. Carré 1979), until in the second nectophore pair (NA_2 and NP_2 of C. Carré 1979) the upper cusps (as *dorsal teeth*) are reduced and the lateral cusps (as *lateral teeth*) have typically disappeared. The mouthplate also becomes reduced in regenerated nectophores, with shorter lappets (as *plates*) and loss of an upper (as *dorsal*) protuberance (pad) on each lappet (C. Carré 1979). Prior to C. Carré’s work, replacement nectophores were identified as separate species, thus complicating the nomenclature of *Sulculeolaria* (well illustrated here by the long synonymy for *S. quadrivalvis* in Section 10.2.3.1).

In other diphyomorph calycophorans, nectophore replacement is known only for the posterior nectophore of abyliids and both nectophores of certain diphyids (C. Carré, pers. comm., quoted in Mackie et al. 1987). As nectophores became progressively more complex in this group, it seems that the ability of most species to regenerate nectophores was lost.

3.4. Autotomy

Autotomy is defined by Lincoln et al. (1998, p. 32) as “the self-amputation of an appendage or other part of the body”, and may be a relatively common occurrence in the Siphonophora. Mackie et al. (1987) recognize three types of autotomy, serving three functions: discarding of worn-out parts, defence, and dispersal of sexual products. The first type includes the loss of larval nectophores and bracts as they are replaced by definitive nectophores during early development (Section 3.2) and the probable loss of worn-out definitive nectophores in physonects and prayomorph calycophorans as new nectophores are produced in the nectosomal growth zone (Section 3.3).

Defensive autotomy involves the spontaneous detachment of a nectophore or bract along a special *autotomy joint* after strong and persistent mechanical stimulation, such as pinching with a pair of forceps (Mackie et al. 1987, p. 190). This joint lies along the line of attachment of the nectophore or bract to its muscular lamella, or pedicel. Extensions of longitudinal muscles from the stem insert onto this line (Mackie et al. 1987) after they have fanned out from a narrower region where the lamella arises from the stem, and muscle contraction brings about autotomy. Close observation of the detachment line in large nectophores and bracts reveals a canal (as a gutter, or scar) in the centre flanked on each side by a line where the muscle fibres were inserted, as described in Section 2.3.2. In nectophores this canal is either an ascending or a descending surface diverticulum from the pedicular canal, or a disjunct section of the latter, as defined above (Figs 5, 6; see Section 2.3.2). In bracts the canal forms the

proximal portion of the bracteal canal, and when the lamella is torn away, the canal leaves a gutter-shaped scar similar to that found in nectophores (Fig. 1E; Mapstone 2003, figs 8d, 13b; 2004, figs 3c, d, g, and h, as *bracteal canal scar*).

Autotomy for dispersal of sexual products can involve fragmentation of whole portions of siphosomal stem (with all attached zooids), detachment of free-living eudoxids from the end of the siphosome as in diphyomorph calycophorans, or shedding of gonophores. All increase the opportunities for gamete dispersal. Autotomy of lengths of siphosome is a particular character of apolemiid physonects (Totton 1965a), which, as Mackie et al. (1987, p. 190) point out, occurs “as a normal part of development or growth” in some siphonophores. Fragments of *Apolemia uvaria* have been observed to be more common in Messina Harbour (in the Mediterranean) than whole colonies (Schaeppi 1906), and many apolemiid stem fragments were photographed by Båmstedt et al. (1998) off the Norwegian coast in the North and Norwegian seas. Another fragment was photographed by Wrobel and Mills (1998) off the Pacific coast of the USA and Canada. The authors of the latter paper did not record or photograph any nectophores, which suggests that they found only siphosomal fragments in these localities. Short lengths of stem of another physonect, *Cordagalma ordinata*, have also been observed floating freely in the water column by Mackie (1985) from a submersible in the Strait of Georgia, B.C. Free-floating stem fragments of the prayomorph calycophoran *Praya dubia* have also been recorded from submersibles (Mackie et al. 1987).

4. Ecology

The geographical and vertical distribution of each siphonophore species in Canadian Pacific waters is given in detail in Section 8 after the species description. Though little other work has been done on the ecology of siphonophores in these waters, it is included in this account where relevant. Much more can be predicted from their ecology elsewhere in the northeast Pacific and farther afield. The most abundant, and presumably ecologically significant, species in shallow water inshore is the diphyid calycophoran *Muggiae atlantica*. In other locations in the region, common species are the diphyids *Dimophyes arctica* and *Lensia conoidea* as well as the agalmatid physonect *Nanomia bijuga*. These four species are common in temperate latitudes worldwide. The ecology of these species, among others, was reviewed 20 years ago in an excellent paper by Mackie et al. (1987). The present discussion will draw on that paper and more recent literature to describe the ecology of Canadian Pacific species.

4.1. Physical ecology and distribution

Muggiae species are the best documented neritic (confined almost exclusively to nearshore waters) codonophoran siphonophores worldwide (Mackie et al. 1987). *Muggiae atlantica* is often the dominant siphonophore in the upper 100 m of temperate and subtropical coastal waters (Gili et al. 1987a and b, 1988; Toyokawa and Terazaki 1994; Palma and Rosales 1995). In the northeast Pacific it was the dominant siphonophore in Friday Harbor during the period 1976–1980 (Mills 1981; Purcell 1982) and in Saanich Inlet, B.C., during 1980–1981 (Mackie and Mills 1983; Larson 1986; Fig. 8A).

In the Strait of Georgia and various deep fjords the most abundant siphonophores are *Dimophyes arctica* and *Nanomia bijuga* (Mackie 1985; Mapstone and Arai 1992). *Dimophyes arctica* was the dominant siphonophore in the central Strait of Georgia in samples taken in the spring and summer of 1979, with a maximum density of 4.8 anterior nectophores·m⁻³ (Mapstone and Arai 1992; Fig. 8B). *Nanomia bijuga* was the second most abundant siphonophore (Fig.

8C). Off the west coast of Vancouver Island the present study showed that the most abundant species above 700 m depth in winter and spring are *N. bijuga* and *Lensia conoidea* (Sections 10.1.3 and 10.2.3.2). Farther north, in 2000–2001, investigations of Haida eddies that originate off the southern tip of the Queen Charlotte Islands and propagate westwards into the Alaska Gyre showed that *D. arctica* was the most abundant species (Mackas et al. 2005). In deeper water a greater number of species are present but less is known about their abundance.

The biology of siphonophores is affected by various physical factors, including temperature, salinity, oxygen concentration, levels of various pollutants, pressure, and light intensity. For example, in the laboratory a higher temperature increases the rate of various processes such as respiration and excretion (Biggs 1977a). The development rate may also increase at a higher temperature. For example, development of planulae of *Nanomia bijuga* is faster at 12 °C than at 8 °C (Sherlock and Robison 2000).

Mackie et al. (1987) reviewed the pitfalls of relating this laboratory research on the effects of physical factors to the actual geographical and vertical distribution of siphonophores in the field. Problems with field research include inadequate sampling programs and difficulty in differentiating between direct responses to physical factors and changes in currents or other hydrographic conditions. An example of the latter problem was the 1989 bloom of *Muggiae atlantica* in the German Bight. *Muggiae atlantica* was usually rare in the North Sea, being carried into it by variable-strength currents, primarily around the north of Scotland (Fraser 1967). In the summer of 1989 the population increased dramatically in the German Bight, up to 500·m⁻³, and decreased again the following year (Greve 1994). This bloom was coincident with the widespread temperature-regime shift of 1988–1989. It was considered that the increase in temperature in the German Bight might have been the primary cause of the bloom (Greve et al. 1996; Niermann et al. 1998). On the other hand, an exceptional influx of other southern oceanic species coincided with current changes in the North Atlantic and

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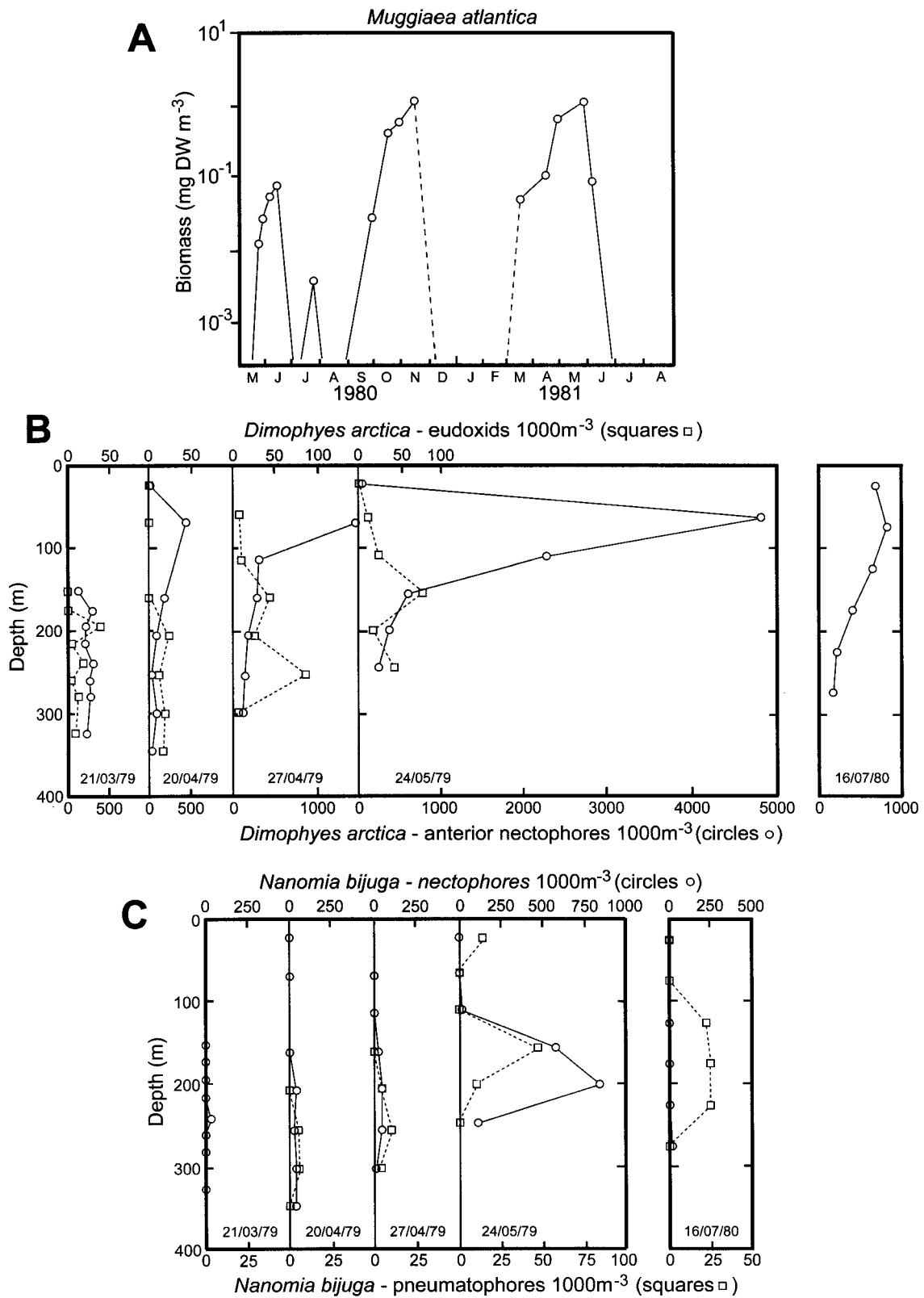


Fig. 8. Seasonal biomass and inshore depth profiles. A: *Muggiae atlantica*, B: *Dimophyes arctica* anterior nectophores (\circ) and eudoxids (\square). C: *Nanomia bijuga* nectophores (\circ) and pneumatophores (\square). A represents Saanich Inlet (modified from Larson (1986, fig. 1)); B and C represent the central Strait of Georgia (modified from Mapstone and Arai (1992, Figs 5a, 5b, 7)).

increased inflow from the Atlantic to the northern North Sea (Båmstedt et al. 1998; Edwards et al. 1999; Reid et al. 2001). Similarly, *M. atlantica* was first recorded from the southern Adriatic Sea in 1995, and strong northerly currents brought it to the northern Adriatic Sea by 1996. In 1997, it attained maximum densities of $450 \text{ nectophores} \cdot \text{m}^{-3}$ and $630 \text{ eudoxids} \cdot \text{m}^{-3}$ in the northern Adriatic Sea (Kršinic and Njire 2001). This was coincident with another widespread temperature-regime shift and an influx of oceanic species into the North Sea (Edwards et al. 1999). In neither of these locations is it possible to distinguish between the direct effects of temperature on *M. atlantica* populations and the indirect effects of changes in currents.

In spite of the difficulty of distinguishing the manner in which temperature is limiting the distribution of siphonophores, each species can be generally characterized by its latitudinal distribution (Mackie et al. 1987). The four common species in Canadian Pacific waters are also common in the temperate areas of the North Atlantic and the Southern Hemisphere.

The abundance of temperate-zone siphonophores is usually seasonal. This may be a direct reflection of temperature, but may also reflect seasonal changes in currents or supply of prey. In surface waters near Friday Harbor, *Muggiae atlantica* nectophores were abundant in May–June and also in September–November (Mills 1981; Mills and Strathmann 1987). Similar spring and fall peaks have been observed in Saanich Inlet (Fig. 8A). Seasonal peaks have also been documented for this species in the western Mediterranean (Razouls and Thiriot 1968; Gili et al. 1987b), Tokyo Bay (Toyokawa and Terazaki 1994), Valparaiso Bay (Palma and Rosales 1995), and the Humboldt Current (Palma and Apablaza 2004), but similar spring and fall peaks have not been described elsewhere.

On the continental shelf and slope off Vancouver Island the complex currents vary (and, at the shelf break, even reverse) with season (Thomson 1981). There are also El Niño – Southern Oscillation events, which increase the temperature and introduce southern taxa at approximately 7-year intervals, as well as longer term (decadal) regime shifts. Zooplankton in the upper 250 m has been sampled off Vancouver Island seasonally since 1979 (Mackas 1992; Mackas et al. 2001; Mackas and Galbraith 2002), but siphonophores have not usually been analyzed separately. A summary graph in Mackas (1992, fig. 12) shows a seasonal peak of

all siphonophore populations in the shelf break and slope region in May–June. Farther south, Keister and Peterson (2003) found that the normally neritic *Muggiae spp.* were present in the shelf water off Oregon only during an El Niño event. Still farther south, seasonal peak abundance of *Nanomia bijuga* in Monterey Bay, California, occurs during October intrusions of oceanic water (Robison et al. 1998). Small calycophorans such as *Lensia conoidea* and *Chuniphyes multidentata* peak about 48 days earlier and primary production peaks earlier still (Silguero and Robison 2000).

Peak populations of calycophoran eudoxids may precede those of the polygastric colonies. This was shown for *Dimophyses arctica* in the central Strait of Georgia by Mapstone and Arai (1992) (Fig. 8B) but had earlier been described from Saanich Inlet by Mills (1982, cited in Mackie et al. 1987).

In addition to temperature, salinity may also affect the horizontal and vertical distribution of siphonophores. Here again, in field observations it is difficult to separate responses to salinity from those to temperature and from the effects of currents. No siphonophores have been reported to enter fresh water. Siphonophores have, however, been reported from areas of low salinity, such as those species that repopulate the estuaries leading into the Bay of Bengal following the monsoon season (Daniel 1985; Sai Sastry and Chandramohan 1989).

Both the temperature and salinity of the near-surface water in coastal areas of the northeast Pacific vary widely with location and season. Details of currents, tides, input of fresh water, and local physiography of the B.C. coast are presented by Thomson (1981). Temperature decreases and salinity increases with depth, often with a gradual temperature gradient (thermocline) and a steeper salinity gradient (halocline) beneath the level of wind-induced mixing and convective overturning. Beneath 200–300 m in the open ocean there is little seasonal change in temperature or salinity.

The thermocline and halocline, and the associated changes in water density (pycnocline), may act as barriers to vertical movement of phytoplankton and zooplankton. For example, Pugh and Boxshall (1984) examined the physical, chemical, and biological structure of a 60 m water column at a shelf station off the coast of northwest Africa. The phytoplankton peak, indicated by the chlorophyll concentration, was close to the base of the pycnocline. Copepods

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were distributed throughout the water column, with a peak in the main phytoplankton layer, and eudoxids of *Muggiae atlantica* showed a very similar distribution. The distribution of the less abundant polygastric stage of *M. atlantica* was also similar, except that it did not extend above the thermocline. The distribution of this siphonophore probably reflects the distribution of prey rather than direct effects of physical gradients, except for a possible physical barrier to upward movement of the polygastric stage above the thermocline.

Water density, governed by temperature and salinity and to a lesser extent by hydrostatic pressure, increases with depth. To minimize the swimming effort needed to remain at a certain depth, a siphonophore colony must adjust its density, i.e., it must become as close to neutrally buoyant as possible. Protein-based tissues are denser than seawater, and too little low-density oil is present in somatocysts or elsewhere to be significant. This is counteracted for physonects by gas-filled floats and for both physonects and calycophorans by isosmotic replacement of sulphate ions with lighter chloride ions in the gelatinous nectophores and bracts (Mackie et al. 1987). Siphonophores have been found to replace 41%–75% of their sulphate content relative to seawater (Bidigare and Biggs 1980).

For physonect siphonophores such as *Nanomia bijuga*, gas glands secrete carbon monoxide into the float (Pickwell et al. 1964). Gases are highly compressible under the very high hydrostatic pressure at depth. As *N. bijuga* rises in the water column it releases bubbles of the expanding gas from an apical (terminal) pore surrounded by a sphincter muscle (Mackie et al. 1987; Pickwell 1970). The importance of the float for flotation varies with species. For example, Mackie (1985) states that *Cordagalma ordinata* (as *C. cordiformis*) is neutrally buoyant in spite of having a minute float, owing to its abundant gelatinous structures.

Dissolved oxygen is usually abundant in the near-surface layer but may be depleted at depth. Often, high productivity at the surface results in elevated amounts of organic carbon falling to intermediate depths, and microbial respiration decreases the oxygen concentration, forming an oxygen-minimum layer. Oxygen may also be depleted by eutrophication or industrial pollution. In upwelling areas, such as the eastern Pacific from Vancouver Island south, northwesterly winds in summer push surface water offshore and deeper water with less oxygen rises to

replace it. Since 2000 this phenomenon has greatly increased and has depleted the fish and benthic fauna in the northern California Current (Chan et al. 2008).

Although oxygen is necessary for aerobic respiration, some siphonophore species are known to be resistant to at least mild hypoxia in the field. Palma and his co-workers investigated the physical factors correlated with the distribution and abundance of siphonophores in various waters off Chile (Palma and Rosales 1997; Palma et al. 1999). Abundance of *Lensia conoidea* was found to be correlated with lower levels of dissolved oxygen. The same species was abundant in Bunnefjord, a eutrophic basin near the Norwegian city of Oslo (Tveite 1969). *Muggiae atlantica* is seasonally common in the polluted inner portion of Tokyo Bay (Toyokawa and Terazaki 1994). Off California, apolemiid siphonophores appear primarily in hypoxic waters from 450 to 800 m depth (Båmstedt et al. 1998). In contrast, the depth range of *Nanomia bijuga* in Monterey Bay during upwelling is truncated below 400 m by the oxygen-minimum layer (Robison et al. 1998).

Light intensity is another factor that varies with depth. The euphotic zone in which light is sufficient to support phytoplankton growth and reproduction is shallow, extending to a maximum depth of about 150 m in clear tropical oceanic water but to only a few metres in turbid inshore regions of the temperate zone. The zone in which fish and some invertebrates can see extends some distance further, but in much of the deeper oceanic water column light comes only from bioluminescence. No ocelli have been identified in siphonophores, but extraocular photosensitivity in many Hydrozoa has been indicated by their activities (Martin 2002). Mackie and Boag (1963) elicited swimming of *Nanomia bijuga* (as *N. cara*) when they were suddenly illuminated by a bright light. Mackie (1985) described diel vertical migration of this species in Jervis Inlet, B.C. Similarly, Mackie et al. (1987) reviewed the diel vertical migration of siphonophores such as *Chelophys appendiculata* and *Lensia conoidea* in the Atlantic.

4.2. Locomotion

Locomotion of a siphonophore colony requires the coordinated contraction of the nectophores to provide jet propulsion. It also requires streamlining of the colony from the feeding configuration to one with a minimum of drag. It has been analyzed

primarily in a few small species that can be maintained in the laboratory, such as *Nanomia* spp. among the Physonectae and *Chelophyses appendiculata* in the Calycophorae. The unusual properties of muscle and nerve, especially epithelial conduction, have attracted the attention of physiologists (Spencer and Schwab 1982; Bone 1985, 2005; Mackie et al. 1987).

In individual nectophores the thrust produced varies with the size and shape of the nectophore, the extent of the muscle relative to that of the mesogloea, and the frequency and strength of contraction and refilling. In the colony the swimming pattern also depends on the number and orientation of the nectophores and the configuration of the colony. The small diphyid siphonophore *Chelophyses appendiculata* has two streamlined nectophores. It swims slowly if only the smaller posterior nectophore is active, but much faster if both are utilized (Bone and Trueman 1982). A physonect colony such as those of *Nanomia* spp. has a number of nectophores arranged in a nectosome. It can swim in three principal ways. A rapid-escape response in *Nanomia* spp. involves simultaneous contraction of all nectophores and results in forward swimming at $20\text{--}30 \text{ cm}\cdot\text{s}^{-1}$ (Mackie 1964; Biggs 1977b). Asynchronous nectophore contraction in spontaneous bursts results in forward swimming at lower speeds ($8\text{--}10 \text{ cm}\cdot\text{s}^{-1}$; see Mackie 1964). Backward swimming, also considered an escape response, is brought about by contraction of radial velar muscles in such a way that the water jet from each nectophore is reversed (Mackie 1964).

Epithelial conduction across nerve-free but electrically conducting epithelia is widespread in members of the Hydrozoa (Spencer and Schwab 1982). The myoepithelium of the siphonophore nectophore is a unitary muscle without any intrinsic nerve plexus. In the nectophores of *Chelophyses appendiculata*, cross-striated muscle fibres, which are simple, with invaginated tubules but lacking a sarcoplasmic reticulum, are coupled by numerous gap junctions into a single subumbrellar myoepithelium (Bone et al. 1999). In the early portion of the burst of action potentials that controls a bout of active swimming, the action potentials increase in amplitude and duration and so does the force of each contraction and of the jet triggered by each action potential (Inoue et al. 2005). It is believed that this delay in attaining maximum contractions allows the siphosome to become streamlined before being subjected to maximum stress. There are also radial muscles in the velum that in *C. appendiculata* are symmetrically arranged and reduce the jet

aperture during expulsion but relax and enlarge it during inhalation (Bone and Trueman 1982). They correspond to those muscles that redirect the jet in the backward swimming of *Nanomia* spp.

The impulses for swimming presumably arise in the marginal nerve rings of the nectophore and are transmitted to the myoepithelium (Mackie et al. 1987). Coordination between the individual nectophores and with the siphosome is carried out by nerves and conducting epithelia in the stems of calycophoran and physonect colonies (Grimmelikhuijen et al. 1986; Mackie et al. 1987). Specialized sense organs such as ocelli or statocysts have not been identified, but touch-sensitivity is widespread. Such information is brought from the exumbrella of nectophores and bracts by means of non-myoid epithelial conduction.

4.3. Feeding

Most siphonophores capture their prey by trapping it with special side branches on the tentacle of each gastrozooid (Fig. 9A). These branches are termed tentilla, and each comprises a pedicel, a thickened cnidosac of cnidae and associated structures, and usually an elongate retractile terminal filament (Fig. 9B). Cnidae are manufactured in a cuff at the base of the gastrozooid, the cnidogenic band or basigaster, whence they migrate into the tentillum, where they are incorporated in a particular species-specific pattern into the cnidosac (especially in a concentrated outer battery, the cnidoband) and usually into the terminal filament (Skaer 1988; Kass-Simon and Scappaticci 2002). The cnidosac also contains a long-looped elastic filament of modified mesogloea attached to the cnidoband and to the axial mesogloea, together with muscles, nerves, and a gastrovascular canal (Mackie and Marx 1988). In some physonects the elastic filament contains phosphatic spicules.

Siphonophores are ambush predators. During feeding, the tentilla (if present) and the tentacles are extended into the water to form a largely transparent net. The prey is usually first ensnared by the terminal filament and its entangling cnidae. The terminal filament contracts, bringing the prey into contact with the cnidoband. The structures in the cnidosac erupt in a rapid and violent event involving stretching of the elastic ligament, eversion of the cnidoband, and discharge of many more cnidae. The forces involved in this complex event are not yet understood (Mackie and Marx 1988; Mackie 1999).

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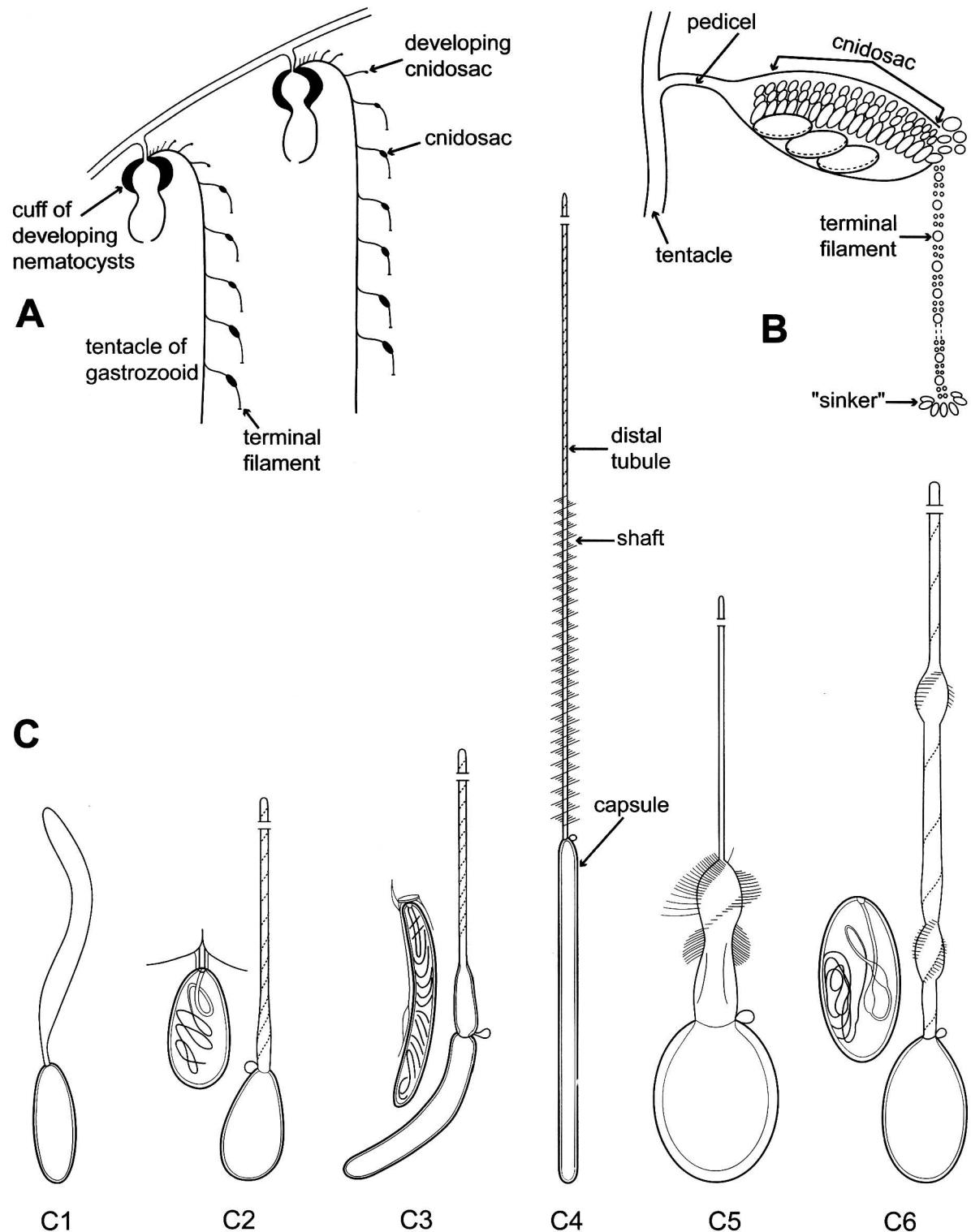


Fig. 9. Schematic diagrams of siphonophoran tentilla and nematocysts: **A:** portion of a tentacle with two tentilla (modified from Skaer 1988, fig. 1a); **B:** calycocephoran tentillum (modified from Skaer 1988, fig. 1b); **C:** discharged and some undischarged nematocysts (derived from Iwanzoff 1896, pl. 5); **C1:** rhopaloneme anacrophore of *Rosacea cymbiformis*; **C2:** holotrichous isorhiza of *Agalma elegans*; **C3:** homotrichous anisorhiza of *Agalma elegans*; **C4:** microbasic mastigophore of *Rosacea cymbiformis*; **C5:** rhopaloid stenotele of *Apolemia uvaria*; **C6:** rhopaloid birhopaloid of *Apolemia uvaria*. Not drawn to scale.

The complex tentillum is considered a cnidarian organ (Mackie 1999). It is found in all codonophoran siphonophores except the family Apolemiidae. Variations in the structure are of diagnostic importance in the suborder Physonectae and are discussed further in Section 10.1. Tentacles of the Apolemiidae lack side branches, and instead bear cnidae in one or more rows aligned along the tentacle (Carré and Carré 1973; Mapstone 2003). In cystonects, sister to codonophorans (see Section 1), cnidae are grouped into simple pads, and these occur either on discs on the tentacles (Physaliidae) or on short side branches arising from them (Rhizophysidae). Some workers have described the latter as tentilla (Totton 1965a; Pagès and Gili 1992b; Pugh 1999b), but in the present work this term is restricted to side branches that bear cnidosacs with cnidobands and terminal filaments.

The several varieties of cnidae that have been observed in siphonophores are all nematocysts. Each consists of a thick-walled capsule containing a highly folded tubule that everts on discharge. They develop within cells (cnidocytes), with the tubule forming attached to the apex of the capsule and then inverting into it. This process has been observed in several codonophorans, including *Rosacea cymbiformis* (Skaer 1973, 1991) and *Apolemia uvaria* (Carré and Carré 1973; D. Carré 1974a). It is still in progress as the cnidocytes migrate into the tentilla or tentacle.

The presently accepted classification of nematocysts was first devised by Weill (1934) and has since been modified by several workers, including Mariscal (1974) and Östman (2000). Bouillon et al. (2004) also summarize the types of nematocysts and their occurrence within many of the families of Hydrozoa, including most of the families of Siphonophora. Astomocnidae are closed at the tip of the tubule and generally entangle the prey, whereas in stomocnidae, most tubules are open at the tip and may penetrate or entangle the prey. Astomocnidae found in codonophorans include rhopalonemes with club-shaped tubules and spironemes in which the undischarged tubule is coiled. Rhopalonemes may have a short apical projection on the discharged tubule (acrophore) or lack this structure (anacrophore); an example of the latter is the rhopaloneme anacrophore of *Rosacea cymbiformis* (Fig. 9C, C1). In desmoneme spironemes the undischarged tubule forms a corkscrew-like coil (not illustrated).

Stomocnidae are classified according to the absence (haplonemes) (Figs 9C, C2 and C3) or presence

(heteronemes) (Figs 9C, C4–C6) of a rod-shaped basal shaft of the tubule, which can be visible even inside the undischarged capsule and is then usually attached to a thinner distal portion of the tubule. Haplonemes may be isorhizas, in which the tubule is nearly isodiametric proximal to the midpoint (Fig. 9C, C2), or anisorhizas, in which the tubule is dilated towards the base (Fig. 9C, C3). The nematocysts in either of these categories may be atrichous (without spines on the tubule), holotrichous (armed with tiny spines throughout), or basitrichous (armed with spines at the base of the tubule), and if armed may also be homotrichous (with spines all of the same kind) or heterotrichous (with two or more kinds of spines). In heteronemes the prominent shaft may be approximately isodiametric (rhabdoid) or of variable diameter (rhopaloid). All rhabdoid heteronemes described from codonophorans are microbasic (the shaft is less than 1½ times the capsule length) and mastigophores (the tubule continues beyond the shaft) (Fig. 9C, C4). Rhopaloids may be euryteles, with the discharged shaft dilated distally (not illustrated), stenoteles, with the discharged shaft dilated at the base (Fig. 9C, C5), or birhopaloids, with a distal and a proximal dilation of the shaft (Fig. 9C, C6). Birhopaloids with the swellings widely separated along the shaft are unique to apolemiid siphonophores, although birhopaloids with the swellings close together are present in some scyphozoans (Östman 2000).

The terminal filaments of the tentilla in most codonophorans contain rhopaloneme and desmoneme astomocnidae that entangle the prey, and the terminal sinker contains desmonemes (Purcell 1984; Skaer 1988). The straight or curved cnidobands of Calycophorae such as *Sphaeronectes köllikeri*, *Rosacea cymbiformis*, *Muggiae atlantica*, *Chelophyses appendiculata*, and *Sulculeolaria quadrivalvis* contain 50–2000 small homotrichous anisorhiza haplonemes packed in rows (Purcell 1984; Mackie et al. 1987). In addition, the cnidosac contains 4–30 larger microbasic mastigophore heteronemes as well as several isorhiza haplonemes or desmonemes (Purcell 1984; Skaer 1988). In agalmatid Physonectae such as *Agalma elegans*, *Cordagalma ordinata*, *Frillagalma vityazi*, and *Nanomia bijuga*, cnidobands vary from short banks to coiled structures and contain between 30 and 20 500 small homotrichous anisorhiza haplonemes (Purcell 1984; Pugh 1998). The associated heteronemes include 3–120 stenoteles or microbasic mastigophores. The scanning electron microscopic (SEM)

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pictures in Purcell (1984) show that the very numerous small haplonemes of the cnidoband also primarily entangle the prey. They do not clearly demonstrate the functions of the remaining nematocysts, although in Purcell and Mills (1988) a few stenoteles are seen penetrating prey. The feeding functions of the birhaploids described in the tentacles and palpacles of apolemiids such as *Apolemia uvaria* and *A. contorta* (as *Tottonia contorta*) have not yet been analyzed (Mapstone 2003).

Siphonophores alternate a motionless fishing phase, during which the tentacles (and, if contractile, the stem) relax, with a streamlined swimming phase, during which the stem and tentacles contract while the colony moves to a new position. A small active diphyid calycophoran such as *Chelophys appendiculata* may repeat this cycle about 100 times per hour, whereas larger physonect and prayid colonies change position less often (Biggs 1977b). Colonies may employ various mechanisms to deploy the tentacles and tentilla and take up different fishing configurations (Biggs 1977b; Mackie et al. 1987). In the 1970s, colonies were examined *in situ* by scuba divers. More recently, manned submarines and remotely operated vehicles have allowed direct observation of deeper colonies. Nectophores of the diphids *C. appendiculata*, *Muggiae atlantica*, and *Sulculeolaria quadrivalvis* swim in a spiral and come to rest above the stem and tentacles (Mackie and Boag 1963; Biggs 1977b; Purcell 1984). Mackie and Boag (1963) termed this the veronica movement after the bullfighter's pass. A nectophore may contract gently to drive the fishing colony slowly upwards. The prayid *Rosacea cymbiformis* and some physonects adopt a "longline" posture when fishing (Biggs 1977b, fig. 5). This involves partially relaxing the more or less horizontal stem, aided by contractions of the gonophores and spreading of the transparent tentacles to hang vertically beneath the stem in a single plane to form a fishing net (Totton 1965a; Purcell 1981a). A similar colony of *Praya dubia* may extend its fishing net for up to 40 m in Monterey Bay (Robison and Connor 1999). The stem of *Agalma elegans* lies in arcs and the tentacles hang ventrally in more than one plane (Biggs 1977b). *Nanomia bijuga* sits in a "J" shape with the tentacles splayed out until a prey is contacted, when it begins to swim actively to streamline the colony and reel in the prey (Robison and Connor 1999).

The type of prey caught is affected by the number, type, and size of the nematocysts and by the size

of the gastrozoids and of the colony, as well as by feeding behaviour and, of course, availability of prey (Purcell 1980, 1984; Mackie et al. 1987; Purcell and Mills 1988). Opaque cnidosacs and terminal filaments may mimic small animals and hence attract larger prey (Purcell 1980).

The diet of small active diphyid calycophorans such as *Muggiae atlantica*, *Chelophys appendiculata*, and *Sulculeolaria quadrivalvis* consists almost entirely of small arthropods, largely copepods (Purcell 1981b, 1982). *Lensia conoidea* eudoxids in a Norwegian fjord fed primarily on copepods but also on cladocerans (Pagès et al. 1996a). Off Catalina Island, California, the diet of *Sphaeronectes köllikeri* in the spring consisted entirely of copepods (Purcell 1981b; Purcell and Kremer 1983). Purcell (1981b) showed that *Hippopodius hippopus* feeds selectively and possibly exclusively on ostracods. Although the diets of the hippopodiid *Vogtia* species are not known, the correlation of their abundance with that of ostracods indicates that they may also prey on ostracods (Pugh 1991). The larger colonies of prayid calycophorans such as *Rosacea cymbiformis* capture prey of a wide variety of sizes and types, including arthropods, molluscs, chaetognaths, and fish larvae (Purcell 1980, 1981b). Similarly, the diet of agalmatid physonects such as *Agalma elegans* and *Nanomia bijuga* includes not only large copepods but also larger arthropods such as hyperiid amphipods, shrimp, and euphausiids, as well as chaetognaths and fish larvae (Purcell 1980, 1981a and b; Purcell and Mills 1988; Robison and Connor 1999). The apolemiid *Apolemia uvaria* also utilizes arthropods and chaetognaths but may include in its diet a large proportion of gelatinous zooplankton such as salps, ctenophores, and hydromedusae (Purcell 1981b; Båmstedt et al. 1998).

Once a prey is captured by the tentillum of *Nanomia* spp. the gastrozoid begins to elongate and writhe. Ingestion is conducted not just by the gastrozoid to which the tentillum is attached but often also by neighbouring ones (Mackie et al. 1987). The reaction can be induced either by tactile stimuli or by chemicals such as prey fluids or reduced glutathione in the water (Mackie and Boag 1963). Ingestion by the gastrozoids is presumably aided by the nematocysts surrounding the mouth (Mackie and Boag 1963). For example, the buccal area of gastrozoids of *Apolemia uvaria* contains microbasic mastigophores and stenoteles (Carré and Carré 1973).

Digestion occurs first extracellularly within the gastrozooid and then intracellularly within the endoderm of the walls of the gastrozooid (Mackie and Boag 1963). The epithelio-musculo-glandular cells of the gastrozooid of *Chelophyses appendiculata* are illustrated by Carré and Carré (1995). In the physonects, such as the genera *Nanomia* and *Apolemia*, particulate matter is also transmitted through the stem canal to the palpons and digested intracellularly there (Mackie et al. 1987). Large objects that resist extracellular digestion are egested through the gastrozooid mouth. In physonects such as *Nanomia* spp., smaller particles accumulate in the terminal bulb of the palpon and are discharged through its terminal orifice (Mackie and Boag 1963).

To date, no complete energy budget for a siphonophore has been calculated. A complete budget includes all intake, including animal prey and possibly symbionts, microorganisms, or dissolved organic material. This is balanced by output of food wastes, excretion (ammonia and other nitrogenous products), respiration (maintenance and active), anaerobic metabolism, somatic growth, and other production, such as mucus, cnidae, and reproductive products (Arai 1997). For siphonophores the intake consists primarily of animal prey. Statements in the early literature that symbionts may be present usually refer to the chondrophore *Velella* sp., then classed with the siphonophores. To determine uptake of dissolved organic material, amino acids labelled with ^{14}C are taken up and incorporated into tissue and mesogloea (Ferguson 1988), but no quantitative studies have been done.

Rates of ingestion of prey have been obtained either directly by measuring clearance in laboratory containers or by calculation, i.e., gut contents divided by the time required for egestion of the prey (for tabulated data see Mackie et al. 1987). In the laboratory, the feeding rate of *Muggiae atlantica* increased linearly with prey density until prey density exceeded that in the field (Purcell 1982). Feeding rates are also affected by the type and size of prey and by laboratory conditions (Purcell 1982; Purcell and Kremer 1983). Feeding rates of pelagic cnidarians estimated from gut contents in the field have always been higher than laboratory-determined rates (Purcell 1997). In October 1980, daily prey consumption by *M. atlantica* in the surface waters of Friday Harbor was estimated to be $5.5\text{--}10.5 \text{ prey}\cdot\text{colony}^{-1}\cdot\text{day}^{-1}$ (Purcell 1982). Digestion rates in siphonophores vary with type and size of prey as well as with temperature (Purcell 1981a, 1983).

Measurements of food waste have been confined to the coherent pellets, each containing the remains of a single copepod or fish larva, egested by siphonophore gastrozooids after the colony has been feeding (Mackie et al. 1987). Comparison of the carbon and nitrogen contents of the copepod exoskeleton in the pellet with those in the intact prey yielded assimilation efficiencies circa 90% or greater for siphonophores such as *Rosacea cymbiformis* (Purcell 1983). However, as noted above, it is known that smaller particles may also be egested, so actual assimilation efficiency may be somewhat lower.

Data obtained from measurements of excretion and respiration are summarized by Mackie et al. (1987). Measurements of excretion of nitrogenous compounds have concentrated on ammonia. On the other hand, preliminary measurements on *Sphaeronectes köllikeri* showed that ammonia constituted only about half of the total nitrogen released by these siphonophores, so amino acids or urea may also be released (Purcell and Kremer 1983).

Respiration as a measure of aerobic metabolism has been investigated in a number of species of both Physonectae and Calycocephorae (Mackie et al. 1987). Smaller siphonophores generally have higher mass-specific metabolic rates than larger ones. Slow-swimming, inactive species such as *Rosacea cymbiformis* generally have lower metabolic rates than fast-swimming, active species such as *Sulculeolaria quadrivalvis*, *Agalma elegans*, and *Nanomia bijuga*. Rough comparisons of the quantity of assimilated prey with the respiration rate show that when prey levels in the environment are high, there may be much excess energy production, but that at lower prey densities, intake may approximately balance metabolism (Mackie et al. 1987).

It has usually been assumed that anaerobic metabolism is unimportant to pelagic cnidarians, although some can survive in oxygen-depleted water (Arai 1997; Rutherford and Thuesen 2005). *Muggiae atlantica* is an oxyconformer (oxygen consumption decreases with oxygen concentration) down to approximately 10% oxygen saturation, where there is a marked increase in oxygen usage and then a rapidly declining consumption rate and high mortality as anoxia is approached (Rutherford and Thuesen 2005). Anaerobic metabolism has not been investigated in this species.

Direct measurements of production (somatic growth, reproductive products, mucus, and cnidae)

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by siphonophores are rare, in part because of the complexity of their life cycles. Purcell (1982) found that the production of eudoxids by *Muggiae atlantica* in laboratory containers increased with greater prey availability.

4.4. Biological interactions

In recent years it has been recognized that gelatinous coelenterates are an important source of food in the sea (Arai 2005). Water and salt contents are high relative to organic content, but the organic contents of these prey are digested (and presumably assimilated) very rapidly by predators and hence cnidarians may be sources of energy comparable to better recognized prey such as arthropods (Arai et al. 2003). In studies of predation based on predators' stomach contents the measured masses of different prey organisms are rarely scaled by their digestion rates. Nevertheless it is already becoming well documented that cnidarians and fish utilize gelatinous organisms such as siphonophores as prey, and data are accumulating, though more slowly, on predation by a number of other predators such as arthropods and reptiles (Arai 2005).

Among the vertebrates, marine birds, reptiles, and fish are known to eat gelatinous food. Birds, however, eat only near-surface prey such as Scyphomedusae, Hydromedusae, and Chondrophora (Mackas and Galbraith 1992). No siphonophore prey has so far been recorded. Reptiles, on the other hand, dive to greater depths. Leatherback sea turtles *Dermochelys coriacea* (Vandelli, 1761) are present off the Pacific coast of Canada (Benson et al. 2007) and in smaller numbers off B.C. and Alaska (L. Spaven and J. Ford, pers. comm., 2004). These turtles not only migrate long distances to areas where there are high surface concentrations of cnidarians, they can also dive to at least 500 m depth, and spend much of their time submerged (Hays et al. 2004). No study has been made of their prey in Canadian Pacific waters. The gut contents of leatherback sea turtles caught off southwest England and in the Mediterranean may include birhopaloid nematocysts (Hartog 1980; Hartog and van Neirop 1984). As noted above, to date, birhopaloid nematocysts with the swellings well separated along the shaft have only been described from apolemiid siphonophores, indicating that apolemiids form part of the turtles' diet.

Predation on gelatinous material by fish is of more ecological importance. Commercial species that include significant amounts of coelenterates (cnidarians and ctenophores) in their diet include the spiny dogfish, *Squalus acanthias* Linnaeus, chum salmon, *Oncorhynchus keta* (Walbaum in Artedi), sablefish, *Anoplopoma fimbria* (Pallas), and various gadoids, scorpaenids, and scombrids (Arai 1988, 2005; Purcell and Arai 2001). In midwater of the subarctic North Pacific, pelagic coelenterates are eaten by lanternfishes (family Myctophidae), grenadiers (family Macrouridae), and deep-sea smelts (family Bathylagidae) (Beamish et al. 1999).

Unfortunately, in studies of coelenterate prey in the gut contents of fish, siphonophores are often not distinguished from other cnidarians and ctenophores, and are seldom identified even to genus. One notable exception is the work of Hobson and his co-workers (Hobson and Chess 1988; Hobson et al. 1996), who found that the blue rockfish, *Sebastodes mystinus* (Jordan and Gilbert), was eating *Nanomia bijuga*, *Muggiae atlantica*, and other siphonophores in onshore currents during a relaxation of upwelling off northern California. Similarly, siphonophores have been observed in the guts of other scorpaenids, including the Puget Sound rockfish, *Sebastodes emphaeus* (Starks), widow rockfish, *Sebastodes entomelas* (Jordan and Gilbert), and black rockfish, *Sebastodes melanops* Girard, from the Gulf of Alaska (Rosenthal et al. 1988), as well as *S. melanops* and the squalid *Squalus acanthias* off Oregon (Brodeur et al. 1987).

Among invertebrates, other cnidarians are the best documented predators of siphonophores. In the Strait of Georgia the hydromedusa *Aequorea victoria* (Murbach and Shearer) has been observed eating *Muggiae atlantica*, *Dimophyes arctica*, and *Nanomia bijuga* (as *Nanomia cara*) (Mackie et al. 1987). In Kuleet Bay, Purcell (1991) found that *M. atlantica* was the most abundant coelenterate in the gut of *A. victoria*. She examined the possibility that this was a case of intraguild predation (where the predator is consuming species that potentially compete with it for food). This was not the case at this time, since *M. atlantica* was consuming copepods and *A. victoria* was largely consuming larvaceans. Off the Queen Charlotte Islands the scyphomedusan *Phacellophora camtschatica* Brandt also preys on *M. atlantica* (Mackie et al. 1987). In other parts of the world some siphonophores, such as *Rosacea*

cymbiformis, have been observed eating other siphonophores (Mackie et al. 1987).

The best documented predators of pelagic cnidarians from the phylum Mollusca are the neustonic nudibranchs and snails of the class Gastropoda (Lalli and Gilmer 1989). These predators utilize chondrophores such as *Velella* and the tropical siphonophore *Physalia*, though the latter does not extend into Canadian Pacific waters. In the water column the pelagic nudibranch *Cephalopyge trematoides* (Chun, 1889) has been reported feeding on *Nanomia bijuga* in the Mediterranean and the Gulf of California (Senz-Braconnot and Carré 1966; Mackie et al. 1987). The heteropod *Carinaria cristata* (Linnaeus) is widely distributed off the Pacific coast of North America. In the southern portion of its range, off southern California, it has been reported preying on the siphonophores *N. bijuga* and *Muggiae atlantica* (Seapy 1980). It is probably active in Canadian Pacific waters also.

Arthropods that prey on pelagic coelenterates include hyperiid amphipods, gammaridean amphipods, decapods such as crabs and shrimp, mysids, euphausiids, and copepods, but there are as yet few data relating to predation on siphonophores *per se* other than hyperiid amphipods (Arai 2005). In the eastern Gulf of Mexico siphonophores have been reported in the diet of penaeid shrimp (Heffernan and Hopkins 1981). Abundant unidentified coelenterate material was reported from the foreguts of similar mesopelagic shrimp off Oregon (Nishida et al. 1988).

Many hyperiid amphipods are associated with siphonophores, particularly large physonect and prayid colonies (Laval 1980; Mackie et al. 1987). The associations vary greatly in timing, degree of dependence of the hyperiids on their hosts for shelter or food, and extent of maternal care. This dependence may vary with stage of the hyperiid life cycle. Often, post-embryonic development is completed in the host, and the juveniles are obligate parasites, dependent for food on their cnidarian hosts. The adults vary from free-swimming with a wide-ranging diet to facultative parasites.

Trematode, cestode, and nematode larvae are also widely distributed parasites of pelagic coelenterates (Lauchner 1980). Predation by fish on these coelenterates allows transmission of helminth (metazoan worm) parasites to the fish (Arai 1988; Marcogliese 1995; Purcell and Arai 2001). Larval

stages of digenetic trematodes such as *Opechona* spp. include cercariae, which develop into rediae in gastropods, followed by metacercariae, which develop in coelenterates or other intermediate hosts. The definitive hosts, in which the trematode becomes sexually mature, are fish. Adult *Opechona bacillaris* (Molin, 1859) have been reported from a number of fish known to eat coelenterates in the Atlantic, Pacific, and Mediterranean (Bray and Gibson 1990). Metacercariae have been reported from cnidarian, ctenophore, and chaetognath hosts, including the siphonophore *Dimophyes arctica* in the North Sea (Reimer et al. 1971). It is probable that they would also be found in siphonophores of Canadian Pacific waters.

As noted by Mackie (1995), the protective responses of siphonophores must provide defence not only against predation but also against damage from simple contact with other organisms. The fragile colonies are easily damaged by interaction with arthropods or fish. Sometimes problems are simply avoided. For example, Purcell (1981a) found that in the laboratory, *Rosacea cymbiformis* extends its tentacles to feed primarily during light periods and she speculated that in the field this would allow the siphonophore to avoid damage from large vertically migrating fish and crustaceans. More specifically, protective responses may include transparency, blanching, bioluminescence, nematocyst discharge, escape locomotion, and autotomy (see Section 3.4).

Physonect siphonophores such as *Agalma okeni* have nectophores that are highly transparent but the siphosome may have pigmented regions (Johnsen and Widder 1998). Transparency reduces the distance at which prey can be recognized by a sighted predator. Pigment spots may disrupt the outline seen by a predator and also may lure prey (Mackie et al. 1987; Mackie 1995). *Nanomia bijuga* has chromatophores on the nectophores and gonophores that expand in light and contract at night (Mackie 1962; Mackie et al. 1987). Blanching, the formation of light-scattering granules in the mesogloea, has been described in *Hippopodius hippopus* but not in the closely related *Vogtia* spp. (Mackie and Mackie 1967).

Bioluminescence has been observed in a number of siphonophores, including physonects such as *Apolemia* spp., *Frillagalma vityazi*, and *Nanomia bijuga*, prayids such as *Maresearsia praecleara*, *Praya dubia*, *Rosacea plicata*, and *Nectadamas diomedaeae*, hippopodiids such as *Vogtia spinosa* and *V. serrata*, and clausophyids such as *Chuniphyes multidentata*.

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(Widder et al. 1983; Haddock and Case 1999). The wavelengths of the emissions vary from 442 to 500 nm, i.e., blue or green light. Some of these displays are spectacular. In *Vogtia* spp. the light is produced in waves that spread over the surface of the nectophores. In *N. bijuga* (as *N. cara*), patches of luminescent cells present on the nectophores and bracts produce a disruptive pattern (Freeman 1987; Mackie et al. 1987). In *P. dubia* the light originates from the bracts (Widder et al. 1989). These displays may deter sighted fish or arthropod predators or prevent destructive contact, although there is very little proof. It has been suggested that the light may actually attract deep-diving leatherback sea turtles (Davenport 1988).

Nematocysts on the tentilla, gastrozooids, and palpons are important in feeding by siphonophores as described in Section 4.3. It has been assumed that nematocysts present on other structures such as the pneumatophores, nectophores, and bracts are defensive in nature. These nematocysts are independent receptor-effectors, whereas the nematocysts involved in feeding by physonects, such as those in the cnidosac of *Cordagalma ordinata*, are directly or indirectly modulated by the nervous system (Carré and Carré 1980). It is not clear how much of a deterrent the nematocysts are. Some fish will eat cnidarians, as described above. On the other hand, Bullard and Hay (2002) demonstrated that nematocysts prevented predation by fish on the cystonect siphonophore *Physalia physalis*, whereas predation took place if the nematocysts were discharged.

Locomotion of colonies of most larger siphonophore species is too slow to deter predators. However, when *Chelophyses appendiculata* is disturbed, the stem is retracted and both nectophores contract at instantaneous velocities that can reach $30 \text{ cm} \cdot \text{s}^{-1}$ (Bone and Truman 1982). *Nanomia bijuga* can attain similar speeds during synchronous forward

swimming and can also swim in reverse, as described in Section 4.2. Fast transmission along the stem, which triggers these “escape” responses, is associated with giant fibres (Mackie 1984).

If a predatory attack is successful the damage may be minimized by autotomizing the attacked portion of the colony. Defensive autotomy in physonect siphonophores such as *Nanomia* spp. involves the detachment of a bract or nectophore at the pedicel attachment, and occurs if it is strongly and persistently stimulated (Mackie et al. 1987). The pedicel contains muscle that inserts on the attachment zone as described in Section 3.4. Contraction of the muscle is mediated by rapid flurries of impulses in the ectodermal epithelium. Detached nectophores swim vigorously for a short time and may distract a visual predator, allowing the main colony to escape. *Nanomia* colonies can tolerate the loss of several nectophores, the gaps being closed by contraction and torsion of the stem, followed by replacement budding (Mackie 1995).

The data on feeding and predation that were discussed in Sections 4.3 and 4.4 show that little is known concerning the trophic importance of siphonophores in Canadian Pacific waters. Even the place of the four most common species in the food webs is not well understood. In a neighbouring region, Friday Harbor, Washington, Purcell (1982) found that in the fall of 1980, *Muggiaeae atlantica* was the most abundant non-crustacean predator in surface waters. She calculated prey consumption *in situ* but had insufficient data to calculate the impact of predation on populations of the copepod prey. Elsewhere it is now recognized that at high densities gelatinous predators can seriously deplete populations of zooplankton and ichthyoplankton and can compete for food with fishes (Purcell 1997; Purcell and Arai 2001). Studies of this type are needed to further investigate the importance of siphonophores and other gelatinous predators in Canadian waters.

5. Worldwide Distribution

5.1. Oceanographic biomes and provinces

Siphonophores live primarily offshore, away from the coast, and are rarely encountered in shallow water. A few are limited to neritic regions above the continental shelf, but most inhabit both the neritic and the oceanic provinces of the world's oceans (see Lincoln et al. 1998, appendix 9). Their population nuclei are typically located in the epipelagic layer (upper 200 m of the water column), but some species have long distributional tails because their overall ranges extend downwards into the deeper meso- and bathypelagic layers (Mackie et al. 1987), at approximately 200–1000 m and below 1000 m, respectively (see Herring 2002, fig. 1.1). Other species have their population nuclei in these deeper layers (see below). One form, the well-known Portuguese man-of-war, *Physalia*, is pleustonic (floats at the surface). The worldwide distribution of siphonophores is influenced by a mix of factors including prey availability, geographical location, temperature, depth, and preferred water mass. These factors are well summarized by Mackie et al. (1987). Sampling with nets was the method used to capture most of the material upon which the species records given below are based; however, the particular destructive risks of net-sampling for fragile siphonophores are emphasized by Pugh (1989). Published data on siphonophore distributions vary worldwide, with many more records from the neritic zone than from the oceanic zone. Indeed, many parts of the three great oceans have yet to be sampled for siphonophores.

Ten years ago a scheme was introduced by Longhurst (1998) for dividing the world's oceans into four major "vegetation" types, or biomes, following from earlier schemes based mainly on the recognition that the chlorophyll concentration in phytoplankton in surface waters determines large-scale partitions of the pelagic realm. The defined extents of the four biomes (here termed Polar, Westerlies, Trades, and Coastal) take account of a multitude of currently available physical oceanographic and biogeographic data that characterize these oceanic water masses (on ecosystem diversity, especially zooplankton

and phytoplankton composition, wind and sun effects that control turbulent diffusion and thermal stratification, seasonal solar irradiance at the sea surface, depth layering and mixing, latitudinal zonation, circulation and stratification of surface water masses close to continental topographic areas, coastal wind patterns, and other factors). As a specific example, the polar fronts of each hemisphere are defined where the mixed-layer depth is constrained by a surface brackish layer in spring. Also, the physical forcing of water motion and stratification over continental shelves is a special case in that all continental-shelf regions, with the exception of those within the Polar biome, constitute a single Coastal biome. Longhurst's (1998) scheme has since become generally accepted by oceanographers, and was recently updated (Longhurst 2007). A simplified version of Longhurst's world ocean biomes is presented in Figure 10, and as their definition takes account of oceanographic and biogeographic parameters affecting ocean water masses (noted above), such biomes offer an improved water-mass reference base compared with the standard geographic reference (Lincoln et al. 1998, appendix 6). The four biomes are therefore adopted here in the summary, given below, of the worldwide distribution of 37 siphonophore species currently recorded from Canadian Pacific waters.

Longhurst (1998, 2007) subdivides each major biome into many regional provinces, but only the Coastal biome provinces covering the northeast Pacific continental shelf are specifically addressed in the present work.

Northeast Pacific coastal provinces. The principal oceanic water movement in the northeast Pacific is the eastward flow of the North Pacific Current across the Pacific Westerlies biome (Longhurst 1998, 2007; Fig. 10). It approaches the North American continent near Vancouver Island at about 47°–48°N, where it bifurcates into a northward stream along the B.C. to Alaska coastline as far as the Aleutian archipelago, and a southward stream down the western coastline of the USA. The exact position of this bifurcation varies with season and El Niño – Southern Oscillation events. These coastal zones

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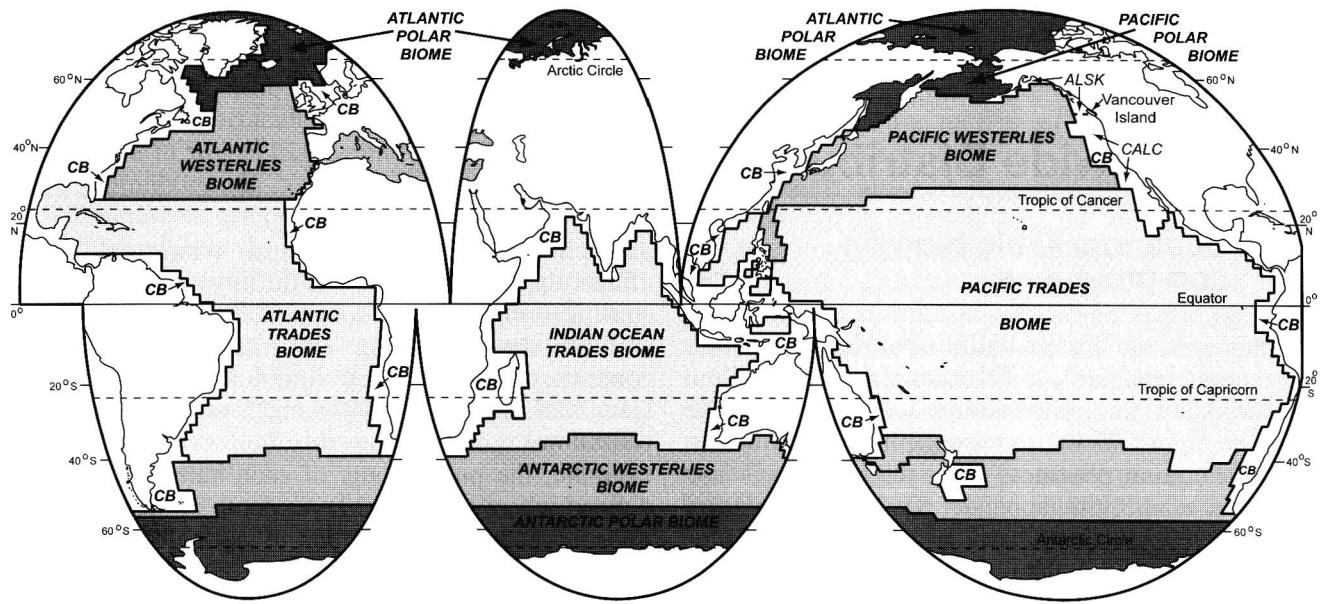


Fig. 10. Worldwide distribution of primary oceanographic biomes of the upper oceans (Polar, Westerlies, and Trades) and Coastal biome (CB), based mainly on the recognition that the phytoplankton chlorophyll concentration determines the large-scale partitions of the pelagic realm (derived primarily from Longhurst 1998). The Atlantic Polar biome includes the Arctic Ocean. The Alaska Coastal Downwelling Province (ALSK) and the California Current Province (CALC) are also identified within the Coastal biome in the northeast Pacific Ocean, extending northwards and southwards from Vancouver Island, respectively.

are referred to by Longhurst (1998, 2007) as the Alaska Coastal Downwelling (ALSK) province to the northwest and the California Current (CALC) province to the south. Longhurst (2007, pp. 389–404) gives an extended description of northeast Pacific continental-shelf topography, oceanography, and biogeography, and this is summarized below.

The present sampling stations off Vancouver Island are located near this major North Pacific Current bifurcation, and extend published siphonophore records from California, Oregon, and Washington northwards into Canadian Pacific waters. The boundary between Longhurst's ALSK and CALC provinces is imprecise; he defines the southern limit of the ALSK province (somewhat arbitrarily) as passing through Queen Charlotte Sound at 53°N (north of Vancouver Island), yet his CALC province extends southwards from the North Pacific Current bifurcation, some 5° farther south. The present sampling stations are here regarded as the northernmost part of the CALC province, near the North Pacific Current bifurcation, while the ALSK province includes the more usual inside waters of Queen Charlotte Strait.

With the exception of areas east of the Queen Charlotte Islands, the continental shelf along the

fjord coastline north of Vancouver Island is either narrow or absent, with high seasonal (glacial) freshwater discharge into the ocean from high coastal mountain ranges. The seaward edge of the continental shelf is also very steep and extends down to abyssal depths. The counterclockwise Alaska Current circulates around the shelf on the periphery of the subarctic gyre. Rapid tidal streams associated with river mouths and bays dominate the inner shelf. Cyclonic (counterclockwise) winds impose downwelling towards the coastline, with the main Alaska Current forced through the coastal passages. Thus, the dominant current maintains a course close to land.

The southward part of the current bifurcation provides cool subarctic water to the southwest tip of Baja California (22°–23°N). While the continental shelf is again narrow along the Washington, Oregon, and northern California coast, a wider continental borderland south of Point Conception (34°N) consists of many basins, shallow banks, and islands. Here, in contrast to the ALSK province, tidal streams do not dominate the alongshore flow of the coastal current. Current flows are complicated along this coastline, and the CALC province can experience contradictory conditions, with equatorward upwelling winds in summer and poleward downwelling winds in

winter. A further complicating narrow poleward undercurrent underlies the generally equatorward California Current at the continental slope from Baja California to Vancouver Island throughout the year.

In summary, therefore, the major currents in the northeast Pacific are strongly influenced by coastal and shelf topography, with the major bifurcation of the North Pacific Current close to the sampling locations in the present study. Thus, one might expect species identified in the present study from the western Vancouver Island shelf (48° – 49° N) to occur both northwards in the ALSK province and southwards in the CALC province. However, sampling in the ALSK province is scant, and almost all records so far published are from the CALC province.

Detailed distribution records covering the northeast Pacific for all fully named siphonophore species currently recorded from Canadian Pacific waters are also given in the Distribution section included after each species description in the systematic account (Section 10).

5.2. Data coverage and reliability

The misidentification of siphonophores in the literature is considerable and some records are known to be synonyms of other species. Only records considered valid after evaluation of high-quality figures and review of related published literature are included in the present work. The worldwide distribution section (Section 5.3) and systematic account (Section 10) discuss at length where records are questionable, decipher synonyms, and present an identification and distribution list for each of the 37 siphonophore species covered in the present work that is as reliable and up to date as possible.

Most Pacific siphonophore records come from a general review by Alvariño (1971) and an Antarctic review by Alvariño et al. (1990), with additional records from off California by the same authors. While these records are all depth-related, some of the species identifications are questionable. Only after review of figures in Alvariño (1981) and Alvariño et al. (1990), and review of related literature, are some records included in the present work. The California records by the same author (Alvariño 1967b, 1991; Alvariño and Kimbrell 1987) are treated similarly. Other records from this area and elsewhere in the Pacific are quoted where relevant (for example,

Gasca and Suárez 1992a; Lin 1993; Margulis and Vereshchaka 1994; Kitamura et al. 2003; Lindsay and Hunt 2005; Zhang et al. 2005). Similarly, records from the southeast Pacific off the coast of Chile are included (for example, Pagès et al. 2001; Palma and Aravena 2001; Palma and Silva 2006).

In the Atlantic, most records come from the northeast sector, where long-term studies have been ongoing for over a century (reviewed in Mackie et al. 1987), with recent surveys from the northwest Atlantic by Hosia et al. (2008) and Pagès et al. (2006). The Atlantic was also studied by Margulis (1974, 1976, 1978), whose records are quoted where appropriate, together with (validated) records from the South Atlantic by Alvariño (1981) and Alvariño et al. (1990). Reliable latitudinal information from the Atlantic as a whole is presented by Pugh (1999b, table 1). Arctic records are given by Fraser (1967) and Kramp (1963). Mediterranean records come from a number of sources, including Gamulin and Kršinic (2000), Gili et al. (1991), and Mills et al. (1996), and Caribbean records from Gasca (1999b) and Suárez et al. (2002). Records from the southeast Atlantic off the coast of Namibia and South Africa are included (for example, Pagès and Gili 1992a and b; Gibbons and Thibault-Botha 2002). A number of studies are also quoted from the Antarctic sector of the Atlantic, including the Southern Ocean (Antarctic Ocean) and Weddell Sea, which cover extensive depth ranges (Pagès and Gili 1989; Pagès and Kurbjewitz 1994; Pagès and Schnack-Schiell 1996; Pagès et al. 1994, 1996b; Pugh et al. 1997). For the Indian Ocean most records come from Daniel (1985), who compiled earlier data in addition to her own records, and there are also records from Musaeva (1976) and Totton (1954, 1965a). Siphonophores from the Antarctic sector of the Indian Ocean are recorded by Margulis (1992) and Moser (1925).

In the northeast Atlantic, latitudinal variation in both species diversity and number of siphonophore specimens has been observed. There are many epipelagic species in the warm tropical waters at low latitudes, whereas in cooler temperate waters at higher latitudes the number of species is reduced (see Mackie et al. 1987, p. 147). In the northeast Atlantic, two peaks of numerical abundance are identified, one between 11° and 18° N and the second between 40° and 53° N (Mackie et al. 1987). Also, at higher latitudes biomass is greater and species diversity less. No similar information is available for the Pacific as yet, but such a study might show similar trends.

5.3. Worldwide distribution of species recorded from Canadian Pacific waters

5.3.1. Physonects. Physonects are harder to quantify than calyphorans because each colony comprises a number of nectophores. Nectophore number is species-specific and also can increase with age (Pugh 1984, p. 487). However, numbers of nectophores present can give an indication of relative abundance; an example is *Nanomia bijuga* in the present work (see Section 10.1.3). The presence or absence of physonect nectophores also gives an indication of the distribution of different physonect species worldwide, both horizontally and vertically, although sampling effort must also be taken into account. Of the eight formally named physonect species found in Canadian Pacific waters, only two are common worldwide: *Agalma elegans* and *N. bijuga*. Published records for the remaining six species represent only a few captures worldwide.

Family Apolemidae. *Apolemia contorta* has so far been recorded from four localities worldwide, all under the earlier name *Tottonia contorta* (see Section 10.1.1). It was originally described from the area of the Indian Ocean Trades biome (Margulis 1976), and subsequently from the Pacific Trades biome, near the equator (Margulis 1980b). More recently it has been recorded from the Pacific Westerlies biome in Sagami Bay, Japan (Lindsay and Hunt 2005; Lindsay 2006), and from the CALC province, off Point Conception, California (Mapstone 2003). The present work extends its distribution to the northern limit of the CALC province, off Vancouver Island (see Section 10.1.1). Unpublished records from the Atlantic Trades biome are also known (pers. obs.).

Family Pyrostephidae. Two *Bargmannia* species occur in Canadian Pacific waters: *B. lata*, introduced by Mapstone (1998), and *B. elongata*. The genus was revised by Pugh (1999a), who introduced two further species and showed that previous records for *B. elongata* had sometimes included nectophores of a new species, *B. amoena*. Thus, many *B. elongata* records are unreliable, although the nectophores listed in Section 10.1.3 are all identified as *B. elongata*. This species is typically mesopelagic, preferring depths of 200–600 m in the northeast Atlantic (Pugh 1999a), and has been found at similar depths off Vancouver Island. In the Pacific the only reliable records for *B. elongata* are from the California Current coastal province (first quoted in Arai et al. 1993; Pugh 1999a; Dunn 2005; Dunn et al. 2005b;

present work). This species almost certainly occurs in other regions of the Pacific, where it was recorded prior to 1999 (for example, Stepanjants 1967, 1977b; Alvariño 1971), but so far these specimens have not been rechecked. In the Atlantic, *B. elongata* has been collected from both the Westerlies and Trades biomes (Pugh 1984, 1999a; Hosia et al. 2008), and also in the Atlantic sector of the Antarctic Westerlies biome (Pugh 1999a). It is widely distributed in the northeast Atlantic, where it extends from the equator to 60°N, and may be more common than *B. amoena* at lower latitudes (Pugh 1999a). However, as yet there are no reliable records for *B. elongata* from the Indian Ocean, where one might expect to find this species, or from lower latitudes in the Pacific.

Bargmannia lata was first described from Canadian Pacific waters (Mapstone 1998) and has subsequently been reported farther south in the CALC province, off San Diego, by Pugh (1999a). There are no other Pacific records, but this species has been collected a number of times in the Atlantic, from both the Westerlies and Trades biomes, although more frequently from greater mesopelagic depths at lower latitudes (Pugh 1999a). Possibly, *B. lata* prefers warmer water than *B. elongata*. *Bargmannia lata* has so far been recorded only once from the Indian Ocean, from the coastal province incorporating the Gulf of Aden, on the John Murray Expedition (Pugh 1999a).

Family Agalmatidae. *Agalma elegans* and *Nanomia bijuga* are both widely distributed in the Trades, Westerlies, and Coastal biomes of the three oceans referred to above, although the number of records is not great for either species. *Agalma elegans* is epipelagic (Margulis 1984), with records scattered throughout warmer waters of the Pacific and Atlantic and, perhaps more abundantly, from the Indian Ocean (Musaeva 1976; Daniel 1985; Thibault-Botha and Gibbons 2005). In the Pacific this species inhabits both the Westerlies biome (Kawamura 1954; Berkeley and Berkeley 1960; Honma and Kitami 1978; Lindsay and Hunt 2005) and the Trades biome (Bigelow 1911b; Stepanjants 1977b; Gasca and Suárez 1992a). There are more records for *A. elegans* from the coastal provinces adjacent to these oceanic biomes than from the biomes themselves, with most records coming from the CALC province (Alvariño 1991; Gasca and Suárez 1992b; Dunn et al. 2005b; present records), several from the associated coastal province of the southeast Pacific (Palma 1986; Palma and Rosales 1995; Pagès et al. 2001; Palma and Silva 2006), and several more

from the associated western coastal provinces of the Pacific (Totton 1932; Gao 1982; Pagès et al. 1990; He et al. 1992; Zuo et al. 2005; Yin et al. 2006). In the Atlantic, *A. elegans* inhabits both the Westerlies biome (Totton 1936; Fraser 1961; Dunn et al. 2005b; Pagès et al. 2006) and the Trades biome (Alvariño 1981; Purcell 1981b; Gasca and Suárez 1991b; Suárez et al. 2002), with sparse records from the associated coastal provinces (Sars 1846; Abreu and Noguiera 1989; Pagès and Gili 1992b; Hosia and Bämstedt 2007). There are no records from either the Pacific or the Atlantic Polar biomes, and the few given by Alvariño et al. (1990) from the Antarctic Westerlies and Polar biomes are questionable, since *A. elegans* has not yet been reported from the latter region by any other workers.

Nanomia bijuga has often been recorded under the name *Stephanomia bijuga* (see synonymy in Section 10.1.3), and has also been muddled with its congener *Nanomia cara*. However, the latter species is restricted to the North Atlantic, where it may be allopatric with *N. bijuga* (Mackie et al. 1987). It has been suggested that *N. bijuga* is a neritic species (Pugh 1974b), and certainly there are frequent reports in the literature of its collection from the epipelagic and upper mesopelagic zones (Margulis 1980b; Alvariño et al. 1990; Pugh 1999b), although not exclusively from the Coastal biome. There are many more records for *N. bijuga* from the Pacific than from the Atlantic, with most coming from the CALC province (Berkeley and Berkeley 1960; Mackie 1964 (as *N. cara*); Alvariño 1967b, 1980c, 1991; Pearcy 1972; Mackie 1985 (as *N. cara*); Alvariño and Kimbrell 1987; Widder et al. 1989; Gasca and Suárez 1992b; Haddock and Case 1999; Silguero and Robison 2000; present records). Alvariño's records for this species are recognized herein because the nectophore figures seem to be correct for *N. bijuga*, even though the bract figures are suspect (Alvariño 1981, figs 4A and B; Alvariño et al. 1990, figs 8A and B; see Section 10.1.3). There are very few records for *N. bijuga* from the Pacific Westerlies biome (Alvariño 1971; Lindsay and Hunt 2005; Lindsay 2006), and similarly few from the Pacific Trades biome (Bigelow 1911b; Stepanjants 1977b; Zhang and Xu 1980; Gasca and Suárez 1992a; Margulis and Vereshchaka 1994). More records, however, exist for *N. bijuga* from the associated western coastal provinces of the Pacific, where it may be a common species (Totton 1932; Dawyoff 1937; Gao 1990; Pagès et al. 1990; He et al. 1992; Zhang et al. 2005; Zuo et al. 2005).

Records for *Nanomia bijuga* from the Atlantic are infrequent, for the reasons noted above, with very few from the Westerlies biome (Pugh 1974b, 1975; Casanova 1980; Bouillon et al. 2004; Dunn et al. 2005b) and also few from the Trades biome (Margulis 1969; Alvariño 1981; Alvariño et al. 1990; Gasca and Suárez 1991b; Gasca 1993, 1999b). The majority of *N. bijuga* records from these two Atlantic biomes come from the somewhat enclosed regions of the Mediterranean and the Gulf of Mexico. Additional records for *N. bijuga* come from the coastal provinces of these biomes (Abreu and Noguiera 1989), including those in the southeast Atlantic, where there has been much sampling effort (Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002). Farther north, on the eastern side of the Atlantic, the range of *N. bijuga* is thought to overlap that of *N. cara*, depending on water movements. Thus, during years with incursions of warmer water into the English Channel (part of the coastal province around the UK), *N. bijuga* might be present, while during other years it might be replaced by *N. cara* (Mackie et al. 1987). However, it seems unlikely that *N. bijuga* extends into the Atlantic Polar biome, and the record of Margulis (1978) from southwest of Iceland might represent *N. cara*, since the latter species is typical of this region (Kramp 1939, 1942; Hosia et al. 2008). In contrast, a few nectophores of *N. bijuga* have been recorded from the Antarctic Westerlies and Polar biomes (Pagès and Gili 1989; Alvariño et al. 1990). As might be expected, there are scattered records for *N. bijuga* from the Indian Ocean Trades biome, and more from the associated coastal provinces of this ocean (Totton 1954; Musaeva 1976; Daniel 1985; Thibault-Botha et al. 2004).

Cordagalma. *Cordagalma ordinata* is an epipelagic species that can extend into the mesopelagic zone (Pagès and Gili 1992b; Bouillon et al. 2004), and has most often been recorded under the name *Cordagalma cordiformis(e)*. It is rare worldwide, and has not been recorded from the Polar biomes. *Cordagalma ordinata* may be more common than records suggest because the nectophores are small and not always captured by nets (see Section 10.1.3). In the Pacific there are single records from the Westerlies biome (Kitamura et al. 2003) and Trades biome (Stepanjants 1977b), but most come from the CALC province, where *C. ordinata* has been observed from a submersible at several locations around Vancouver Island (Mackie 1985; see Section 10.1.3). There are also scattered records from other

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Pacific coastal provinces, including off Chile (Palma 1994; Pagès et al. 2001) and on the Great Barrier Reef (Totton 1932). In the Atlantic, *C. ordinata* has been recorded from the Westerlies biome (C. Carré 1968a; D. Carré 1973; Biggs 1977a and b; Casanova 1980; Purcell 1980; Gili et al. 1987b; Mills et al. 1996; Bouillon et al. 2004; Dunn et al. 2005b; Pagès et al. 2006) and, less frequently, from the Trades biome (Totton 1932; Gasca 1993). In this ocean, as in the Pacific, there are more records from various coastal provinces than from the oceanic biomes, including northeastern Norwegian fjords (Pagès et al. 1996a; Hosia and Båmstedt 2007) and the southeastern coastal province off Africa (Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002). The very few records for *C. ordinata* from the Indian Ocean come from both the Trades biome and the associated coastal provinces (Totton 1954; Daniel 1985); there are also a couple of records from the Pacific sector of the Antarctic Westerlies biome (Margulis 1987).

Frillagalma. *Frillagalma vityazi* is a rare species worldwide. It is typically collected from mesopelagic depths, where most of the present specimens from Canadian Pacific waters were taken (see Section 10.1.3). *Frillagalma vityazi* records also include some from the North Atlantic (Pugh 1974b, as physonect "C"), although in this ocean *F. vityazi* has been recorded at all depths from the surface to 2000 m (Pugh 1998). The present recorded samples are the first from the Pacific Westerlies biome (previously reported in Arai et al. 1993). Almost all other records worldwide are from the Trades biomes in both the Atlantic (Stepanjants 1975; Gasca 1997a and b; Pugh 1998) and the Indian Ocean (Totton 1954; Daniel 1966, 1974, 1985; Rengarajan 1975). There are also a few records from the Atlantic Westerlies biome (Pugh 1974b, 1975), but none from high latitudes in either hemisphere, which suggests that *F. vityazi* is a warmer water species (Mackie et al. 1987) and cannot survive in cold polar waters.

Marrus. In the present work the physonect *Marrus antarcticus* is considered conspecific with *M. orthocanna* (see Section 10.1.3), and is therefore classified here as a rare cold-water species that mainly inhabits the two Polar biomes. In the Antarctic Polar biome it was collected at all depths from the surface to 2600 m (Alvariño et al. 1990; Pagès et al. 1994; Pugh et al. 1997). In the Northern Hemisphere it has been recorded from both the Atlantic Polar biome (Kramp 1942; Zelickman 1972; Margulis 1978; Andersen 1981; Stepanjants 1989) and the Pacific Polar biome (Stepanjants 1967).

Marrus orthocanna has also been recorded from the Pacific Westerlies biome (Stepanjants 1967; Arai et al. 1993; Lindsay and Hunt 2005; Lindsay 2006) but not from the Pacific Trades biome. Similarly, in the Atlantic there are records from the Westerlies biome (Fraser 1967; Pugh 1974b; Kirkpatrick and Pugh 1984; Bouillon et al. 2004) but many fewer from the Trades biome (Pugh 1974b; Alvariño 1981). In the Indian Ocean there is only a single published record, as *M. orthocanna*, from the Trades biome (Daniel et al. 1969). Alvariño et al. (1990, maps A11–15) show a number of records from both the Pacific and West Atlantic sectors of the Antarctic Westerlies biome, mainly as *M. antarcticus*, and there is also a single record from the Coastal biome east of New Zealand (Totton 1954).

5.3.2. Calycophorans

Most calycophorans are epipelagic, including most members of the family Diphyidae (except some species of the genus *Lensia*) and prayids of the genus *Amphicaryon* (Mackie et al. 1987). Other epipelagic calycophorans, such as species of the family Abylidae and the genus *Hippopodius* of the family Hippopodiidae, are not represented in the present Canadian Pacific collection and are typical of warmer tropical waters (see Section 2.3.2). In contrast, meso- and bathypelagic siphonophore assemblages are dominated by calycophorans of the family Clausophyidae, together with some species of the family Prayidae, species of the hippopodiid genus *Vogtia*, and species of the diphyid genus *Lensia* (Mackie et al. 1987). The present Canadian Pacific collection contains five clausophyid species, nine prayids, three *Vogtia* species, and five *Lensia* species. The worldwide distributions of these 22 species, together with those of the 6 other calycophorans found in the area, are discussed below.

Family Prayidae: Subfamily Amphicaryoninae. The two amphicaryonine species recorded here from Canadian Pacific waters are both typical of warmer water masses (Kirkpatrick and Pugh 1984).

Amphicaryon. *Amphicaryon acaule* is sometimes confused with a similar species, *A. ernesti*, introduced by Totton in 1954, but in *A. acaule* the nectosac of the smaller definitive nectophore is functional, whereas in *A. ernesti* it is vestigial and nonfunctional; there are also some minor differences in the larger larval nectophore (see Section 10.2.1.1). Most modern authors have collected, and often illustrated, both species, and thus their records for *A. acaule* are reliable. In the Pacific there are very

few records from the Westerlies biome (Stepanjants 1967; Alvariño 1971), and only a few more from the Trades biome (Bigelow 1911b, 1931 (station 51 only); Alvariño 1971; Stepanjants 1977b; Zhang and Xu 1980; Zhang 1984; Lin 1993; Palma and Silva 2006); most records are from the associated coastal provinces of this ocean. In particular, *A. acaule* has been collected in the CALC province in the northeast Pacific (Alvariño 1967b, 1971, 1980c, 1991; present records) and the associated coastal provinces in the southeast Pacific (Palma 1973, 1994; Palma and Rosales 1995; Pagès et al. 2001; Palma and Apablaza 2004), northwest Pacific (Gao 1982; He et al. 1992; Gao et al. 2002), and southwest Pacific (Totton 1932; Pagès et al. 1990).

In the Atlantic, Pugh (1999b) gives a latitudinal range of 60°N–37°S for *Amphicaryon acaule*, and this conforms with published records for this species from the Westerlies biome (Margulis 1974; Pugh 1974b, 1975, 1984; Casanova 1980; Kirkpatrick and Pugh 1984; Bouillon et al. 2004; Pagès et al. 2006) and the Trades biome (Margulis 1974; Stepanjants 1975; Alvariño 1981; Gasca 1999a). In addition, the species has been recorded from the Coastal biome of South Africa in the Atlantic (Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002), with one possible record also from the South American Coastal biome (Alvariño et al. 1990). Records from the Indian Ocean are scattered, being distributed fairly equally between the Trades biome and the associated coastal provinces (Totton 1954; Patriti 1970a; Margulis 1979; Daniel 1985; Thibault-Botha et al. 2004). There are no records for *A. acaule* from the Indian sector of the Antarctic Westerlies and Polar biomes, but the species has been recorded from the Pacific and western Atlantic sectors of these biomes (Alvariño et al. 1990), though such records are not recognized by Pugh (1999b). *Amphicaryon acaule* has not been found in other studies of these biomes. It is an epipelagic species that is also found in the mesopelagic zone (Bouillon et al. 2004).

Maresearsia. *Maresearsia praeclara* is a rare species worldwide (Alvariño 1981), and so far has only been collected from the mesopelagic zone in the Atlantic (Pugh 1999b). The present Canadian Pacific *M. praeclara* eudoxids probably come from the same zone (see Section 10.2.1.1), as do other *M. praeclara* specimens from somewhat farther south (Widder et al. 1983; Haddock and Case 1999). Previous records for *M. praeclara* in the Pacific come from the border of the Pacific Westerlies biome with the CALC province (Haddock and Case 1999)

and also from the Borderlands region of southern California (Widder et al. 1983). Additionally, there is one record for *M. praeclara*, as *M. sphaera*, from the Pacific Polar biome (Stepanjants 1967; see Section 10.2.1.1) and a second from the Pacific Trades biome off Chile, close to the border with the associated southeastern coastal province (Pagès et al. 2001). Records for the Indian Ocean are given by Daniel (1985) and include both *M. praeclara* and another synonym, *M. intermedia* (see Section 10.2.1.1). In the Atlantic, *M. praeclara* has been recorded from both the Westerlies biome (Pugh 1974b, 1975; Kirkpatrick and Pugh 1984) and the Trades biome (Totton 1954; Margulis 1974; Alvariño 1981), and is said to be widespread in warmer waters of the North Atlantic, to latitude 53°N (Kirkpatrick and Pugh 1984). It has not been collected from the Atlantic Polar biome, the Antarctic Westerlies biome, or the Antarctic Polar biome.

Subfamily Prayinae. Distributions of the four species of prayine prayids collected from Canadian Pacific waters vary worldwide, with only *Rosacea plicata* considered common (Kirkpatrick and Pugh 1984; Bouillon et al. 2004). Published records for the remaining three species are far fewer, with *R. cymbiformis* noted as being “more abundant in the Atlantic” than in the Mediterranean (Bouillon et al. 2004, p. 229) and *Praya dubia* being described as “widespread” (Kirkpatrick and Pugh 1984, p. 58) and *P. reticulata* as “not uncommon in the Atlantic” (Pugh 1974b, p. 38). The two *Rosacea* species are “generally more abundant at, or restricted to, higher latitudes” (Mackie et al. 1987, p. 151), with *R. plicata* typically inhabiting deeper layers than *R. cymbiformis* (Bouillon et al. 2004). The definitive nectophores of *R. cymbiformis* are difficult to distinguish from those of *R. plicata*, as noted by Mapstone (2005) and discussed in Section 10.2.1.2, and the bracts can also be difficult to distinguish when poorly preserved. This may well explain the paucity of records for *Rosacea* species, particularly *R. cymbiformis*, in the literature.

Praya. There are more records for *Praya dubia* worldwide than for *P. reticulata*, with some *P. dubia* records given under the synonym *Nectocarmen antonioi* Alvariño, 1983 (see Section 10.2.1.2). Other records for *P. dubia* may be unreliable because the bracts have been incorrectly assigned. These mistakes, including many records published by Alvariño for this species as *Nectodroma dubia* (Alvariño 1967b, 1980c, 1983, 1991; Alvariño and Kimbrell 1987), have mostly been pointed out by

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Pugh (1992c). Alvariño's figures of a *P. dubia* bract (Alvariño 1981, figs 174–19B; Alvariño et al. 1990, fig. 19B) show an elongate recurved upper bracteal canal more typical of *P. reticulata* bracts, as discussed in Section 10.2.1.2. Records for *P. dubia* by some other authors may also be questionable, particularly if only bracts were collected. Good bract figures are essential, since distinguishing the bracts of *P. dubia* from those of *P. reticulata* remained difficult before the full redescription by Pugh (1992c). Therefore, of records published before 1992, only those based on definitive nectophores of *P. dubia* are deemed valid in the present work.

Praya dubia has therefore been recorded relatively infrequently worldwide. In the Pacific there are only two reliable records from the Westerlies biome (Haddock and Case 1999; Lindsay 2006) and a few from the Trades biome (Bigelow 1911b; Palma and Silva 2006), but most come from the CALC province (Totton 1965a; Stepanjants 1967; Pearcy 1972; Hobson and Chess 1988; Widder et al. 1989; Dunn et al. 2005b; present work). One additional valid record from the latter province is from the San Pedro Channel in southern California, as *Nectocarmen antonioi* (Alvariño 1983), and 85 nectophores are also recorded from this province by Alvariño (1980c, as *Nectodroma dubia*). *Praya dubia* has also been recorded from the Coastal biome in the southeast Pacific (Moser 1925; Palma 1973; Palma and Apablaza 2004). In the Atlantic, most records for *P. dubia* come from the Westerlies biome (Pugh 1974b, 1975, 1984, 1990; Kirkpatrick and Pugh 1984; Larson et al. 1988; Hosia et al. 2008), with fewer from the Trades biome (Totton 1965a; Pugh 1992c) and two from the northeast coastal province of the Atlantic, around the UK (Kirkpatrick and Pugh 1984). Pugh (1999b) gives a latitudinal range of 60°N–44°S for *P. dubia* in the Atlantic. There are several records from the Indian Ocean Westerlies biome for this species (Daniel 1974, 1985) and a few from the associated coastal provinces (Quoy and Gaimard 1833; Daniel 1985; Gibbons and Thibault-Botha 2002). Additionally, there are scattered records for *P. dubia* from the Antarctic Westerlies and Polar biomes by both Totton (1965a) and Alvariño et al. (1990, map A55, as *N. antonioi* only).

Praya reticulata has been recorded most often from the Pacific, where there are more records from the Trades biome (Bigelow 1911b, 1931; Alvariño 1971) than from the Westerlies biome (Stepanjants 1967). Most records for *P. reticulata* from this ocean,

however, come from the CALC province (Bigelow and Leslie 1930; Bigelow 1931; Alvariño 1967b, 1971, 1980c, 1991; Stepanjants 1967; Pearcy 1972; Mills 1981; Arai et al. 1993; present records), where this species seems to be more common than *P. dubia*. There is also one record of “an unusually fine colony” from the associated coastal province off the Pacific coast of Panama (Boone 1933, p. 35). *Praya reticulata* records from the Atlantic are restricted to very few from both the Westerlies biome (Pugh 1974b, 1984; Pagès et al. 2006) and the Trades biome (Totton 1965a; Pugh 1992c), and one from the associated eastern coastal province off South Africa (Pagès and Gili 1992b). In the Indian Ocean *P. reticulata* has been found only once in the Trades biome, from the Arabian Sea (Daniel 1985), and also from the associated coastal provinces in both the east (Margulis 1979) and the west (Gibbons and Thibault-Botha 2002). There are also two records from the Antarctic Westerlies biome, both in the Pacific sector (Totton 1965a).

Rosacea. Bracts of the two *Rosacea* species collected from Canadian Pacific waters are difficult to distinguish, as noted above, while the nectophores of *R. cymbiformis* also have limited characters for species identification (Mapstone 2005). However, both Bigelow (1911b) and Totton (1965a) give good figures of typical definitive nectophores for both *R. cymbiformis* and *R. plicata*, and it is likely that these figures have been used by most authors to distinguish their *Rosacea* material. Bracts are more problematic, but it is also concluded herein that most authors' records are based on nectophore material when the life stage collected is not mentioned. *Rosacea plicata* is a common species worldwide, and this is supported by Totton's (1954, pp. 88–89) comment “In the course of many years during which I have been searching plankton samples for Siphonophora, I have found outside the Mediterranean ... many Rosacean nectophores all of which, except a few of *Rosacea cymbiformis*, appear to belong to one species, *R. plicata*”.

Rosacea plicata is a cosmopolitan species and, as noted above, has been recorded from all biomes worldwide except the Atlantic Polar biome. In the Pacific, records come from the Westerlies biome (Bigelow 1913; Stepanjants 1967; Alvariño 1971; Kubota 1998; Haddock and Case 1999), the Trades biome (Bigelow 1911b; Stepanjants 1967; Margulis 1987), and the associated coastal provinces in both the east (Alvariño 1967b, 1980c, 1991; Palma 1973, 1994; Palma and Rosales 1995; Palma and

Silva 2006; present records) and the west (Bigelow 1913; Gao 1982; Zhang et al. 2005). There are more records for *R. plicata* from the Atlantic than from the Pacific, and these come from both the Westerlies biome (Bigelow 1911a; Bigelow and Sears 1937; Grice and Hart 1962; van Soest 1973; Margulis 1974; Pugh 1975, 1984, 1990; Casanova 1980; Pugh and Harbison 1987; Bouillon et al. 2004; Pagès et al. 2006; Hosia et al. 2008) and the Trades biome (Leloup and Hentschel 1935; Margulis 1974; Alvariño 1981; Haddock and Case 1999). Similarly, there are records of *R. plicata* from the associated coastal provinces of these two biomes in the northeast Atlantic (Patriti 1965b; Fraser 1967; Radziejewska et al. 1973; Kirkpatrick and Pugh 1984; Pagès et al. 1996a), and southeast Atlantic (Totton 1954; Stepanjants 1975; Pagès and Gili 1991b, 1992b; Gibbons and Thibault-Botha 2002). There are also a number of records for *R. plicata* from the Indian Ocean Trades biome (Totton 1954; Daniel 1973, 1974, 1985; Musaeva 1976) and the associated coastal provinces (Totton 1954; Daniel 1985; Gibbons and Thibault-Botha 2002). In the Southern Hemisphere, published records exist for *R. plicata* from the Antarctic Westerlies biome (Totton 1954; Alvariño et al. 1990) and Antarctic Polar biome (Totton 1954; Alvariño et al. 1990; Margulis 1992; Pagès et al. 1994; Pugh et al. 1997).

Rosacea cymbiformis has yet to be recorded from any Polar biome, and indeed there is only one reasonably reliable record for this species from the Antarctic Westerlies biome (Margulis 1987). Records from the Pacific are also sparse, and come from both the Westerlies biome (Kawamura 1954; Kubota 1998) and the Trades biome (Bigelow 1911b; Alvariño and Ambros 1986; Gasca and Suárez 1992a; Margulis and Vereshchaka 1994). There are a few more records from the CALC province in this ocean (Bigelow 1911b; Alvariño 1980c, 1991; Alvariño and Kimbrell 1987; present record), but only scattered records from the associated coastal provinces in the southeast Pacific (Palma 1973; Purcell 1980; Gasca and Suárez 1991a; Palma and Rosales 1995) and southwest Pacific (Huxley 1859; Bigelow 1919). More records for this species come from the Atlantic, particularly the Westerlies biome (delle Chiaje 1822–1829; Leloup 1933, 1934, 1936, 1955; Bigelow and Sears 1937; Totton 1965a; van Soest 1973; Pugh 1974b; Bidigaire and Biggs 1980; Casanova 1980; Purcell 1981a; Gamulin and Kršinic 2000; Bouillon et al. 2004; Mapstone 2005) and the associated eastern coastal provinces (Fraser 1955, 1967; Kirkpatrick and Pugh 1984). Farther south

in the Atlantic, there are fewer records from the Trades biome (Leloup and Hentschel 1935; Biggs 1977a) and the associated southeastern coastal province (Pagès and Gili 1991b, 1992b; Gibbons and Thibault-Botha 2002). In the Indian Ocean there are a few records for *R. cymbiformis* from the Trades biome (Rengarajan 1975; Musaeva 1976; Daniel 1985) and the associated coastal provinces (Daniel 1985; Thibault-Botha et al. 2004).

Subfamily Nectopyramidinae. Worldwide, published records for the three ectopyramidine prayid species recorded from Canadian Pacific waters are fewer than those for the prayine prayid *Rosacea plicata*, though similar in number to the records published so far for the other three prayine species (see above), at least for *Nectopyramis thetis* and *Nectadamas diomedae*. Records for *Nectadamas richardi* are very few. To the records for *N. thetis* must be added a number previously given as *Nectopyramis spinosa* (see Section 10.2.1.3), although only for larval nectophores that possess a small and nonfunctional nectosac (Pugh 1992a). Other *N. spinosa* nectophores (with a functional nectosac) represent records of larval nectophores of *Nectopyramis natans* (Pugh 1992a), a species not so far encountered in Canadian Pacific waters. Additionally, records for eudoxids of *N. spinosa* actually represent eudoxids of *N. richardi* (Pugh 1992a) and are included in the distribution summary for the latter species below.

Nectopyramidines typically inhabit the mesopelagic zone, although at higher latitudes more specimens have been collected at shallower depths (Kirkpatrick and Pugh 1984; Pugh 1992a). There is also evidence that the definitive nectophores of *Nectopyramis thetis* occupy a slightly deeper depth range than eudoxids in the North Atlantic, since Pugh (1992a) found the former to be most abundant at 400–600 m depth and the latter at 300–400 m. There is insufficient evidence for *Nectadamas diomedae*, but for *N. richardi*, Pugh (1992a) also found that in the North Atlantic, eudoxids are distributed at slightly greater depths than definitive nectophores.

Nectopyramis. *Nectopyramis thetis* is described by Pugh (1992a, p. 292) as “the best known ectopyramidine species” and indeed, Pugh examined over 3000 specimens from the North Atlantic. In the Atlantic there are a number of records from the Westerlies biome (Bigelow 1911a; Leloup 1933, 1936; Patriti 1965b; Fraser 1967; van Soest 1973; Pugh 1974b, 1975, 1984, 1990; Casanova 1980; Kirkpatrick and Pugh 1984), some from the Trades

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biome (Totton 1954; Alvariño 1981), and a few from the associated eastern coastal provinces (Fraser 1961; Kinzer 1977). Pugh (1999b) gives a latitudinal range of 63°N–34°S for *N. thetis* in the Atlantic, which includes one record by Fraser (1961) from the Atlantic Polar biome south of Iceland. In the Pacific there are fewer records from either the Westerlies biome (Stepanjants 1967; Alvariño 1971) or the Trades biome (Bigelow 1911b; Alvariño 1971), including one from the Banda Sea (Sears 1952). There are also some records from the CALC province in the eastern Pacific (Alvariño 1967b, 1971, 1980c, 1991; present work). However, there are no published records for *N. thetis* from the Pacific Polar biome. Records from the Indian Ocean Trades biome are few (Sears 1952; Totton 1954; Alvariño 1964; Daniel 1974), with none from the Antarctic sector of the Indian Ocean. In the Antarctic Westerlies and Polar biomes a number of records are given by Alvariño et al. (1990) for “*Nectopyramis spinosa*” from both the Pacific and Atlantic sectors, but these are questionable because although some might represent larval nectophores of *N. thetis*, this life stage of *N. thetis* has not yet been recorded by any other authors this far south.

***Nectadamas*.** Published records for *Nectadamas diomedaeae* are far fewer than those for *Nectopyramis thetis* by a factor of at least 7 (for nectophores) for the North Atlantic region (Pugh 1992a). Pugh also comments that although *N. diomedaeae* is poorly known, it has a “widespread distribution in the Atlantic, Pacific, and Indian oceans as well as occurring in the Antarctic and Arctic oceans” (Pugh 1992a, p. 320). In the North Atlantic *N. diomedaeae* is most abundant between 15° and 21°N (Pugh 1992a, table 8) in the northern sector of the Atlantic Trades biome, although there is only one other published record, by Stepanjants (1975), for this species from this sector of the Trades biome, and more records by other authors from farther south (Margulis 1974; Alvariño 1981; Alvariño et al. 1990). Records for *N. diomedaeae* by authors other than Pugh come mainly from the Atlantic Westerlies biome (Totton 1954, 1965a; Fraser 1961; van Soest 1973; Margulis 1974; Casanova 1980; Haddock and Case 1999). There are also very occasional records for *N. diomedaeae* from the coastal province to the east of the Atlantic Westerlies biome (Fraser 1961, 1967), and a few from the Atlantic Polar biome (Fraser 1961; Stepanjants 1963, 1989; Pugh 1992a). In the Pacific there are similar numbers of records for this species from the Westerlies biome (Bigelow 1913; Stepanjants 1970; Pugh 1992a; Haddock and Case

1999) and the Trades biome (Bigelow 1911b, 1931; Stepanjants 1977b; Pugh 1992a), with a few also from the Pacific Polar biome (Stepanjants 1963; Pugh 1992a). Pacific records for *N. diomedaeae* also come from the CALC province (Alvariño 1967b, 1991; Dunn et al. 2005b; present records). In the Indian Ocean this species has been recorded from both the Trades biome (Totton 1954; Pugh 1992a) and the associated western coastal province (Totton 1954). In the Southern Ocean there are scattered records for *N. diomedaeae* from the Antarctic Westerlies biome (Alvariño 1971; Alvariño et al. 1990; Pagès et al. 1996b) and the Antarctic Polar biome (Totton 1954; Alvariño 1971; Alvariño et al. 1990; Pugh et al. 1997).

Nectadamas richardi is a rare species, although it is said to be more common in the Atlantic than published records suggest, with a latitudinal distribution from the equator to 60°N (Pugh 1992a). Records by the latter author also suggest that *N. richardi* is most abundant between 45° and 50°N, and indeed, most published records for this species come from the Westerlies biome in the Atlantic (Pugh 1974b and Casanova 1980, both as eudoxids of *N. spinosa*; Pugh 1990 as *Nectopyramis* sp. nov., Pugh 1992a). In the Pacific there is only one published record so far for *N. richardi*, from the CALC province off the Mexican coast at latitude circa 32°N (Totton 1954), as a eudoxid of the now invalid species *N. spinosa* (see above), and the present records extend the range of this species northwards in the Pacific to 48°N.

Family Hippopodiidae. Records for the three hippopodiid species currently found in Canadian Pacific waters are somewhat similar for the other oceans worldwide, although in general, *Vogtia serrata* and *V. spinosa* are more frequently collected than *V. pentacantha*. Some of the early records for the latter two species are unreliable, owing to identification problems (see Section 10.2.2). For example, when considering the distribution of *V. serrata*, it is important to include published records for the synonym *V. kuruae* (Alvariño 1967a). *Vogtia serrata* is the deepest living of all hippopodiids (Pugh 1991), and is generally regarded as epi- and meso-pelagic by Pagès et al. (1994); it is a dominant species between 30° and 40°N in the northeast Atlantic at depths below 700 m (Mackie et al. 1987), although it is occasionally collected from shallower depths, and sometimes even from the surface (Stepanjants 1970).

Vogtia. *Vogtia pentacantha* is an infrequently collected species, although it has a widespread distribution worldwide (Kirkpatrick and Pugh 1984). It is rare in the Pacific, with only a few records from the Westerlies biome (Alvariño 1971) and Trades biome (Alvariño 1971; Gasca and Suárez 1992a; Lin 1993). This species has also, though only occasionally, been collected from the CALC province in the northeast Pacific (Bigelow and Leslie 1930; Alvariño 1991; Dunn et al. 2005b; present work), and less often from the coastal province in the southeast Pacific (Palma and Rosales 1997; Palma and Apablaza 2004). *Vogtia pentacantha* has been more frequently reported from the Atlantic, with some records from the Westerlies biome (Fraser 1967; van Soest 1973; Pugh 1974b, 1975, 1984, 1990, 1991; Casanova 1980; Kirkpatrick and Pugh 1984; Bouillon et al. 2004) and a few from the Atlantic Trades biome (Pugh 1991; Gasca 1997a). However, there is only one published record so far from the Atlantic Polar biome (Fraser 1967). More *V. pentacantha* records have been published for the Indian Ocean than elsewhere in the world's oceans, with several from the Indian Ocean Trades biome (Musaeva 1976; Daniel 1985) and others from the associated coastal provinces of this ocean (Rengarajan 1973; Daniel 1985; Thibault-Botha et al. 2004). The only records for *V. pentacantha* from the Antarctic Westerlies and Polar biomes all come from Alvariño et al. (1990).

Vogtia serrata is possibly a cold-water species (Daniel 1985), although it has been collected from all biomes of the world's oceans. There are more published records worldwide for this species than for either *V. pentacantha* or *V. spinosa*, including the synonym *V. kuruae* mentioned above, as well as records by Bigelow (1913) under the synonym *V. pentacantha* (see Section 10.2.2). Records for *V. serrata* from the Pacific come from the Polar biome (Bigelow 1913; Stepanjants 1967; Motoda and Minoda 1974; Cooney 1981), the Westerlies biome (Bigelow 1913; Stepanjants 1967, 1970; Alvariño 1971; Margulis and Vereshchaka 1994; Haddock and Case 1999; Lindsay and Hunt 2005; Lindsay 2006), and the Trades biome (Bigelow 1911b; Alvariño 1967a; Alvariño and Ambros 1986; Margulis 1987). There are further records in the northeast Pacific from the CALC province (Bigelow and Leslie 1930; Alvariño 1967b, 1980c, 1991; Arai et al. 1993; Haddock and Case 1999; Burd and Thompson 2000; present records), the associated coastal provinces in the southeast Pacific (Alvariño 1967a; Palma and Rosales 1997), and the associated coastal provinces

in the western Pacific (Bigelow 1911b; Alvariño 1967a; Alvariño and Ambros 1986; Margulis 1987). In the Atlantic there are more published records for *V. serrata* from the Westerlies biome (for example, Bigelow 1931; Bigelow and Sears 1937; Grice and Hart 1962; Fraser 1967; van Soest 1973; Margulis 1974, 1978; Pugh 1974b, 1975, 1984, 1990, 1991; Casanova 1980; Kirkpatrick and Pugh 1984; Mackie et al. 1987; Hosia et al. 2008) than from the Trades biome (Alvariño 1967a, 1981; Margulis 1974; Stepanjants 1975; Pugh 1991), with no records from any associated coastal provinces. *Vogtia serrata* has been less frequently recorded from the Indian Ocean, with few records from the Trades biome (Musaeva 1976; Margulis 1992) and the associated western coastal provinces (Totton 1954; Margulis 1992). *Vogtia serrata* also penetrates Antarctic waters, with sparse records from the Antarctic Westerlies biome (Alvariño et al. 1990; Pagès et al. 1996) but more from the Antarctic Polar biome (Moser 1925; Margulis 1992; Pagès and Kurbjewitz 1994; Pagès et al. 1994; Pugh et al. 1997). Overall, these records show that *V. serrata* is a cosmopolitan oceanic species.

Vogtia spinosa is a widely distributed species, primarily in the tropical and subtropical regions of the three great oceans, although it has only been collected infrequently (Bouillon et al. 2004). There are scattered records from the Pacific, with a few from the Westerlies biome (Alvariño 1971), more from the Trades biome (Bigelow 1911b, 1931; Alvariño 1971, 1976; Hong and Zhang 1981; Alvariño and Ambros 1986; Lin 1993), and some from the CALC province (Stepanjants 1967; Alvariño 1971, 1980c, 1991; Pearcy 1972; present records) and an associated eastern coastal province in the Southern Hemisphere (Palma 1994; Palma and Rosales 1995). More records come from the Atlantic, including a number from the Westerlies biome (van Soest 1973; Pugh 1974b, 1975, 1984, 1990, 1991; Kirkpatrick and Pugh 1984; Bouillon et al. 2004; Pagès et al. 2006; Hosia et al. 2008), some from the Trades biome (Margulis 1974; Alvariño 1981; Alvariño et al. 1990; Pugh 1991) and the associated eastern coastal province (Pagès and Gili 1991b, 1992b), and three from the Atlantic Polar biome (Fraser 1967; Margulis 1974; Pugh 1991). There are fewer records for *V. spinosa* from the Indian Ocean, from the Trades biome (Musaeva 1976; Daniel 1985) and the associated coastal provinces (Rengarajan 1975; Margulis 1979; Daniel 1985; Gibbons and Thibault-Botha 2002). This species is apparently more common in the Indian Ocean than *V. serrata*, but less

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common than *V. pentacantha*. *Vogtia spinosa* has also been occasionally recorded from the Antarctic Westerlies and Polar biomes (Alvariño et al. 1990; Pagès et al. 1994).

Family Diphyidae. The widely distributed and successful calycophoran family Diphyidae is represented by 10 species from the current Canadian Pacific collection, including 5 commonly recorded species (*Sulculeolaria quadrivalvis*, *Lensia conoidea*, *Dimophyes arctica*, *Muggiae atlantica*, and *Chelophyses appendiculata*) and 5 less frequently or rarely recorded species (*L. achilles*, *L. havock*, *L. hostile*, *L. multicristata*, and *Gilia reticulata*).

Subfamily Sulculeolariinae. *Sulculeolaria quadrivalvis* has been described as “a common species in [the] warmer waters of the world’s oceans” (Kirkpatrick and Pugh 1984, p. 80), and also as an “epiplanktonic species, dwelling mainly in the surface layers” (Pagès and Gili 1992b, p. 83). It is widely distributed in the Trades and Westerlies biomes and the associated coastal provinces of the Pacific, Atlantic, and Indian oceans. However, as it is a warm-water species, there are no records from either the Antarctic Westerlies biome or the two Polar biomes. In the Pacific, *S. quadrivalvis* has been recorded only occasionally from the Westerlies biome (Moser 1913a; Stepanjants 1967; Alvariño 1971; Margulis 1989), and more often from the Trades biome (Lens and van Riemsdijk 1908; Bigelow 1911b, 1919, 1931; Moser 1925; Dawydyoff 1937; Alvariño 1963, 1971, 1976; Stepanjants 1977b; Xu and Zhang 1978; Hong and Zhang 1981; Zhang 1984; Gasca and Suárez 1992a; Lin 1993; Palma and Silva 2006). There are also many records for this species from the CALC province (Alvariño 1971, 1980c, 1991; Pearcy 1972; Purcell 1980, 1981b; Suárez and Gasca 1991; Margulis and Vereshchaka 1994; Dunn et al. 2005b), although it is likely to be at the extreme northern limit of its range in Canadian Pacific waters (present record). It has also been recorded from the southeastern coastal provinces in the Pacific (Palma 1973, 1994; Gasca and Suárez 1991a) and the associated coastal provinces in the northwest (Hong 1964; Zhang and Xu 1980; Gao 1982, 1990; Zuo et al. 2005) and west (Bigelow 1919; Totton 1932).

In the Atlantic there are more published records for *Sulculeolaria quadrivalvis* from the Westerlies biome (Bigelow and Sears 1937; Alvariño 1971; Pugh 1974b, 1975; Casanova 1980; Purcell 1981b; Kirkpatrick and Pugh 1984; Dunn et al. 2005b; Pagès et al. 2006) than from the Trades biome

(Alvariño 1969, 1981; Margulis 1972b; Stepanjants 1975; Gasca 1998), although this may reflect sampling effort. However, there is only one record from the northeastern associated coastal province, which includes British waters (Totton 1954), but many more from the warmer southeastern coastal province off southern Africa (Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002). *Sulculeolaria quadrivalvis* has been collected numerous times in the Mediterranean sector of the Atlantic Westerlies biome, where it is found year-round in both the eastern and western regions (Bouillon et al. 2004). There are also a number of records for *S. quadrivalvis* from the Indian Ocean, from both the Trades biome (Musaeva 1976; Daniel 1985) and the associated coastal provinces (Daniel 1985; Gibbons and Thibault-Botha 2002), including the Red Sea and Gulf of Aden (Totton 1954).

Subfamily Diphyinae. Five species of the diphyine diphyid genus *Lensia* are found in the present collection from Canadian Pacific waters, and of these only two, *L. conoidea* and *L. multicristata*, are considered common worldwide. The remaining three, *L. achilles*, *L. havock*, and *L. hostile*, are mostly deep-living and rare, although records for *L. achilles* also include those under the synonyms *L. baryi* and *L. eltanin* (see Section 10.2.3.2). *Lensia achilles* and *L. havock* both have widespread latitudinal distributions, penetrating the Arctic and Antarctic Polar biomes.

Lensia. *Lensia conoidea* is a typically mesopelagic species (Kirkpatrick and Pugh 1984), and has been defined by Margulis (1972a) as a broadly tropical species inhabiting deeper layers in the tropics and shallower layers at temperate latitudes. This distribution is supported, in general, by published records, which are mostly from the northern Westerlies biomes of the world’s oceans and their associated coastal provinces. There are fewer records from the Trades biomes, where very deep water is rarely sampled. In the Pacific there are some records from the Westerlies biome (Yashnov 1952; Stepanjants 1967; Alvariño 1971; Kitamura 1998) and more from the CALC province in the east, where *L. conoidea* has frequently been encountered (Alvariño 1967b, 1980c, 1985; Pearcy 1972; Mills 1981; Alvariño and Kimbrell 1987; Gasca and Suárez 1992b; Arai et al. 1993; Silguero and Robison 2000; Dunn et al. 2005b). Several records also exist from the associated western coastal provinces of the Pacific (Chiu 1954; Zhang and Xu 1980; Gao 1982). Records from the Pacific Trades biome are fewer

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(Alvariño 1971; Zhang 1984; Gasca and Suárez 1992a; Lin 1993; Zhang and Lin 1997; Palma 1999), with some also from the associated eastern coastal provinces (Palma and Rosales 1997; Palma et al. 1999; Palma and Aravena 2001).

Lensia conoidea is largely confined to northern latitudes in the North Atlantic, where it makes an important contribution to several siphonophore assemblages, in both shallow and deep water masses (Mackie et al. 1987). In the Atlantic in general, it extends into the Polar biome (Kramp 1963; Margulis 1978; Hosia et al. 2008), and has been recorded many times from the Westerlies biome (Grice and Hart 1962; Pugh 1975, 1977, 1984, 1990; Casanova 1980; Kirkpatrick and Pugh 1984; Larson et al. 1988; Mills et al. 1996; Andersen et al. 2001a; Bouillon et al. 2004; Pagès et al. 2006; Hosia et al. 2008), with a number of records also from the associated eastern coastal provinces (Stuwitz 1836; Sars 1846; Totton and Fraser 1955b; Fraser 1967; Kirkpatrick and Pugh 1984; Pagès et al. 1996a; Hosia and Båmstedt 2007). In the Atlantic Trades biome there are fewer records (Leloup and Hentschel 1935; Alvariño 1981; Alvariño et al. 1990), with more from the associated eastern coastal provinces (Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002). There are also fewer records for *L. conoidea* from the Indian Ocean, with some from both the Trades biome (Musaeva 1976; Daniel 1985) and the associated coastal provinces (Patriti 1970a; Daniel 1985; Gibbons and Thibault-Botha 2002). Scattered records exist for *L. conoidea* from the Antarctic Westerlies and Polar biomes (Alvariño 1981; Margulis 1987; Alvariño et al. 1990), and Pugh (1999b) reports 59°S as the southern limit for this species in the South Atlantic.

Lensia multicristata is typically a mesopelagic species (Pugh 1984), although it may also occur in the epipelagic zone and occasionally has an extensive distributional tail into the bathypelagic zone (Angel et al. 1982; Pugh 1990). At some locations it can be more common than *L. conoidea* (Pugh 1974b; Stepanjants 1975). Worldwide records come from all biomes except the Pacific Polar biome, with perhaps more from the Trades biome than from the Westerlies biome. In the Pacific there are a few records from the Westerlies biome (Stepanjants 1967; Alvariño 1971), with many more from the associated CALC province (Alvariño 1967a, 1980c, 1985; Stepanjants 1967; Suárez and Gasca 1991; Gasca and Suárez 1992b; Arai et al. 1993; Margulis and Vereshchaka 1994), a number also from the Trades biome (Bigelow 1911b; Alvariño 1976;

Zhang 1984; Margulis 1987; Gasca and Suárez 1992a; Lin 1993; Margulis and Vereshchaka 1994; Zhang and Lin 1997; Palma 1999), and one from an associated southeastern coastal province (Palma and Silva 2006). In the Atlantic there are records for *L. multicristata* from the Polar biome (van Soest 1973; Hosia et al. 2008), the Westerlies biome (Bigelow and Sears 1937; Margulis 1971; van Soest 1973; Pugh 1974b, 1975, 1984, 1990; Kirkpatrick and Pugh 1984; Bouillon et al. 2004; Pagès et al. 2006), and the Trades biome (Totton 1954; Margulis 1971; Stepanjants 1975; Alvariño 1981; Alvariño et al. 1990). There are also several records from the associated southeastern coastal provinces of the Atlantic (Totton 1954; Pagès and Gili 1992b). Records from the Indian Ocean cover both the Trades biome (Totton 1954; Musaeva 1976; Daniel 1985) and the associated coastal provinces (Totton 1954; Margulis 1979; Daniel 1985; Thibault-Botha et al. 2004), and *L. multicristata* has also been recorded from the Antarctic Westerlies and Polar biomes (Totton 1954; Alvariño et al. 1990).

Lensia achilles has a worldwide distribution, with more published records from high than from low latitudes. In the Pacific it has been recorded from the Polar biome (Stepanjants 1967; Motoda and Minoda 1974), the Westerlies biome (Stepanjants 1967), and once from the Trades biome (Margulis and Vereshchaka 1994), with more records from the CALC province (Totton 1965b; Alvariño 1967b, 1985; Mackie 1985; Mapstone and Arai 1992; Margulis and Vereshchaka 1994; present work) and a few also from coastal provinces in the southeast Pacific (Alvariño et al. 1990 as *L. eltanin*). Atlantic records for *L. achilles* include a few from the Polar biome (Margulis 1978; Hosia et al. 2008) and the Trades biome (Totton 1941; Margulis 1971; Alvariño 1981; Alvariño et al. 1990), and more from the Westerlies biome (Fraser 1961; Margulis 1971; Pugh 1974b, 1975, 1984, 1990; Casanova 1980; Hosia et al. 2008). *Lensia achilles* has also been found in some eastern associated coastal provinces (Totton 1941; Fraser 1961; Kinzer 1977) and western associated provinces (Alvariño et al. 1990). More records for *L. achilles* come from the Antarctic Westerlies and Polar biomes, including several by Alvariño under the synonyms *L. baryi* and *L. eltanin* (Alvariño et al. 1990; Margulis 1992; Pagès et al. 1994; Pagès and Schnack-Shiel 1996; Pugh et al. 1997).

Lensia havock is another rare diphyne with few records from any ocean. Records by Margulis are given under the synonym *Muggiaeae havock*. In the

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Pacific there is one record from the Polar biome (Stepanjants 1967), one from the Trades biome (in the South China Sea; Zhang and Lin 1997), and a few from the Westerlies biome (Stepanjants 1970; Margulis and Vereshchaka 1994). There are also records from the CALC province (Alvariño 1967a, 1985; Margulis and Vereshchaka 1994; present record). Mackie et al. (1987) report that in deeper waters of the North Atlantic at 53° and 60°N, *L. havock* occurs in relatively large numbers, but published records from the Atlantic are few. They include a single record from the Polar biome (Margulis 1978) and a few records from both the Atlantic Westerlies biome (Totton 1941; Margulis 1972b; Kirkpatrick and Pugh 1984; Pugh 1990; Hosia et al. 2008) and the Trades biome (Totton 1941; Stepanjants 1975; Alvariño 1981). Very few records exist for the Indian Ocean Trades biome and the associated coastal provinces (Totton 1941; Daniel 1985). Most published records for *L. havock* come from the Antarctic Westerlies and Polar biomes (Totton 1941; Alvariño 1981; Alvariño et al. 1990; Margulis 1992; Pagès et al. 1994; Pagès and Schnack-Schiel 1996; Pugh et al. 1997).

Lensia hostile has only infrequently been collected worldwide, with very few records from most regions. Records from the Pacific come from the southeastern sector of the Trades biome (Alvariño et al. 1990) and the CALC province (Alvariño 1967b, 1971, 1985; Margulis and Vereshchaka 1994; present work), whereas records from the Atlantic, including a few as the synonym *L. zenkevitchi* Margulis, 1970 (see Section 10.2.3.2), come from the Trades biome (Margulis 1970, 1971; Stepanjants 1975; Alvariño 1981) and the Westerlies biome (Pugh 1974b, 1975, 1984, 1990; Casanova 1980; Kirkpatrick and Pugh 1984). There is also a single record from an associated coastal province in the southeast Atlantic (Totton 1941). *Lensia hostile* has so far only been recorded 5 times from the Indian Ocean, all in the Trades biome or the associated coastal provinces (Totton 1941; Daniel 1985), whereas there are more published records for this species from the Antarctic than from any other region of the world's oceans. These come from both the Antarctic Westerlies and Polar biomes (Alvariño et al. 1990; Pagès et al. 1994; Pugh et al. 1997).

Dimophyes. *Dimophyes arctica*, the most cosmopolitan of all siphonophores, is collected mainly from the top 500 m of the water column at higher latitudes (Pugh 1990) and below 200 m at lower latitudes (Daniel 1985). It can extend deep into

the mesopelagic zone, down to 1000 m (Bouillon et al. 2004) and in the northeast Atlantic south of 50°N the population is found at greater depths as the isotherms deepen (Pugh 1990). This may also be true for the Pacific, since Alvariño (1971, fig. 4) shows a few deeper records at lower latitudes, but more data are needed. *Dimophyes arctica* has been recorded from the Polar, Westerlies, and Trades biomes in all oceans. In the Pacific, records come from the Polar biome (Stepanjants 1967; Motoda and Minoda 1974; Cooney 1981; Coyle and Hunt 2000), the Westerlies biome (Bigelow 1913; Kawamura 1954; Berkeley and Berkeley 1960; Stepanjants 1970; Alvariño 1971; Liu et al. 1990; Margulis and Vereshchaka 1994), and the Trades biome (Alvariño 1971; Zhang and Xu 1980; Zhang 1984; Lin 1993; Margulis and Vereshchaka 1994; Palma and Silva 2006). *Dimophyes arctica* has also been collected from most coastal provinces in the Pacific, including the CALC province (Alvariño 1967b, 1971, 1980c, 1991; Mills 1981, 1982; Mackie and Mills 1983; Mackie 1985; Purcell 1989, 1991; Mapstone and Arai 1992; Arai et al. 1993; Margulis and Vereshchaka 1994; present records), southeastern provinces (Palma and Rosales 1997; Pagès and Orejas 1999; Palma et al. 1999; Palma and Aravena 2001), northwestern provinces (Gao 1990), and southwestern provinces (Totton 1932; Alvariño et al. 1990).

There are more records from the Atlantic Polar biome for *Dimophyes arctica* than for any other siphonophore (Bernstein 1932, 1934; Kramp 1942; Stepanjants 1963, 1967, 1989; Zelickman 1972; Mohammed and Grainger 1974; Grainger and Grohe 1975; Margulis 1978; Huntley et al. 1983; Sameoto 1984; Raskoff et al. 2005; Hosia et al. 2008), with many records also from the Atlantic Westerlies biome (van Soest 1973; Pugh 1974b, 1975, 1977, 1984, 1990; Margulis 1978; Casanova 1980; Kirkpatrick and Pugh 1984; Bouillon et al. 2004; Pagès et al. 2006; Hosia et al. 2008) and the associated coastal provinces to the east (Totton and Fraser 1955a; Fraser 1967; Hosia and Båmstedt 2007) and west (Bigelow 1926). *Dimophyes arctica* is also found in the Atlantic Trades biome (Leloup 1934; Leloup and Hentschel 1935; Alvariño 1972, 1981; Stepanjants 1975; Gasca 1998, 1999b) and the associated coastal provinces (Alvariño 1968a; Pagès and Gili 1991b, 1992b), and in the Indian Ocean Trades biome (Totton 1954; Musaeva 1976; Daniel 1985) and the associated coastal provinces (Totton 1954; Daniel 1985; Thibault-Botha et al. 2004). Since *D. arctica* is a truly cosmopolitan species, it is not surprising that there are also many records from

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the Antarctic Westerlies and Polar biomes (Alvariño 1981; Hopkins 1985; Zhang and Liu 1989; Alvariño et al. 1990; Margulis 1992; Pakhomov 1993; Pagès and Kurbjewit 1994; Pagès et al. 1994; Pagès and Schnack-Schiell 1996; Pugh et al. 1997).

Muggiaeae. *Muggiaeae atlantica* is a neritic species that is “rarely found in deep water” (Kirkpatrick and Pugh 1984, p. 104) and inhabits “warm and temperate regions over the continental shelf in the three great oceans and the Mediterranean” (Pagès and Gili 1992b, p. 95). Thus, there are no records from the Atlantic and Pacific Polar biomes, and only a few from the Antarctic Polar biome (Alvariño et al. 1990). It has been suggested (M. Sears, cited in Alvariño 1971) that in the Pacific, *M. atlantica* has its habitat base in Japanese waters and travels eastwards in the North Pacific Current across to the CALC province, where there are many records. This is perhaps borne out by the distribution of *M. atlantica* in the North Pacific, where there are relatively few records from mid-ocean in the Westerlies biome, and more from close to land masses. The latter include records from the East China Sea (Stepanjants 1967; Alvariño 1971; Arai 2001; Kitamura et al. 2003) and the CALC province (Alvariño 1967b, 1971, 1980c; Pearcy 1972; Mills 1981, 1982; Freeman 1983; Mackie and Mills 1983; Alvariño and Kimbrell 1987; Hobson and Chess 1988; Purcell 1990; Gasca and Suárez 1992b; Margulis and Vereshchaka 1994; Dunn et al. 2005b; present records). In the Pacific Trades biome there are also very few records from mid-ocean (Bigelow 1911b; Alvariño 1971), with more from “shelf” waters of the South China Sea and East China Sea in the west (Zhang 1977; Hong and Zhang 1981a; Gao 1982, 1990; Lin and Zhang 1990; Liu et al. 1990; Lin 1993; Zuo et al. 2005) and the associated coastal provinces in the east (Alvariño 1972; Gasca and Suárez 1991a, 1992a; Palma 1994; Palma and Rosales 1995, 1997; Palma et al. 1999; Pagès et al. 2001; Palma and Aravena 2001; Palma and Apablaza 2004; Palma and Silva 2006).

The distribution of *Muggiaeae atlantica* in the Atlantic is similar, with very few records from mid-ocean; in the Westerlies biome most records come from the land-locked Mediterranean (Bigelow and Sears 1937; Carré and Carré 1991; Bouillon et al. 2004) and from associated eastern coastal provinces (Totton and Fraser 1955a; Beaudouin 1971; Pugh 1974b; Southward and Barrett 1983; Greve 1994; Båmstedt et al. 1998; Fosså et al. 2003). However, only one record is so far published for *M. atlantica* from a western coastal province in the North

Atlantic (Bigelow and Sears 1939). In the Atlantic Trades biome there are, again, very few records from mid-ocean (Alvariño 1981) and many from adjacent eastern coastal provinces (Cervigon 1961; Pugh and Boxshall 1984; Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002), and two also from western coastal provinces (Moncaleano and Niño 1979; Girola 1991). Similarly, in the Indian Ocean, records for *M. atlantica* are mainly from water over continental shelves. Thus, there are very few records from mid-Indian Ocean (Daniel 1985) and more from the associated coastal provinces (Totton 1954; Daniel 1985; Pagès and Gili 1992a; Gibbons and Thibault-Botha 2002). As noted above, records from colder water are very few, with only scattered records from the Antarctic Westerlies and Polar biomes (Alvariño et al. 1990).

Chelophyes. *Chelophyes appendiculata* is probably the most common species of siphonophore worldwide, and is abundant in the warmer waters of the world’s oceans (Kirkpatrick and Pugh 1984). It is an epipelagic species that also inhabits the mesopelagic zone (Bouillon et al. 2004). The present specimens collected off Vancouver Island are at the northern limit of their range. In warmer water *C. appendiculata* may be allopatric with its congener *C. contorta* (Alvariño 1971). It has been suggested that *C. appendiculata* prefers more oceanic offshore water, while *C. contorta* is more abundant closer to land masses (Daniel 1985) and in less saline equatorial water (Stepanjants 1977a), but the two species can coexist in tropical waters (Rengarajan 1975; Alvariño and Ambros 1986; Lin 1993). In the Pacific there are records for *C. appendiculata* from both the Pacific Westerlies biome (Kawamura 1954; Stepanjants 1967; Alvariño 1971; Honma and Kitami 1978) and the Trades biome (Agassiz and Mayer 1902; Rees and White 1966; Alvariño 1971, 1976; Stepanjants 1977a and b; Hong and Zhang 1981a; Chen 1983; Zhang 1984; Alvariño and Ambros 1986; Margulis 1987; Alvariño et al. 1990; Gasca and Suárez 1992a; Lin 1993; Margulis and Vereshchaka 1994; Palma 1999; Palma and Silva 2006), and even more from the southern sector of the CALC province (Alvariño 1967b, 1971, 1980c, 1991; Alvariño and Kimbrell 1987). There are also isolated records from farther north in this province, including around Vancouver Island as noted above, and these occurrences are noted also in Section 10.2.3.2. *Chelophyes appendiculata* is also found in most other Pacific coastal provinces, including the northwest (Bigelow 1913; Hong 1964; Zhang 1977; Gao 1982, 1990; Zuo et al. 2005; Zuo et al. 2005),

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southwest (Bigelow 1919; Totton 1932; Margulis 1987), and southeast (Alvariño 1972; Palma 1973; Palma et al. 1999; Pagès et al. 2001).

In the Atlantic, *Chelophyses appendiculata* has been frequently recorded from the Westerlies biome, including the Mediterranean (Bigelow 1911a, 1918, 1931; Leloup 1933, 1956; Totton 1936; Grice and Hart 1962; van Soest 1973; Pugh 1974b, 1977, 1990; Casanova 1980; Purcell 1981b; Lo and Biggs 1996; Gamulin and Kršinic 2000; Andersen et al. 2001a and b; Bouillon et al. 2004; Dunn et al. 2005b; Pagès et al. 2006; Hosia et al. 2008) and the Trades biome (Leloup and Hentschel 1935; Leloup 1955; Moore and Corwin 1956; Alvariño 1972, 1981; Stepanjants 1975; Michel and Foyo 1976; Gasca and Suárez 1989a and b, 1991b; Alvariño et al. 1990; Suárez et al. 2002). It has occasionally been recorded from Atlantic coastal provinces in the northeast (Totton and Fraser 1955a; Furnestin 1964; Kirkpatrick and Pugh 1984) and northwest (Bigelow 1914; Bigelow and Sears 1939), but has only very occasionally penetrated the Atlantic Polar biome (Kramp 1939). In warmer Atlantic coastal provinces there are more records, including from the southeast (Cervigon 1961; Kinzer 1977; Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002) and southwest (Alvariño 1968a, 1981; Moncaleano and Niño 1979; Abreu and Nogueira 1989; Alvariño et al. 1990).

Chelophyses appendiculata occurs all over the Indian Ocean, particularly in the Southern Hemisphere (Daniel 1985). There are many published records from both the Trades biome (Totton 1954; Daniel 1974, 1985; Musaeva 1976; Margulis 1979; Rengarajan 1983) and the associated coastal provinces (Totton 1954; Patriti 1970a; Rengarajan 1975; Daniel 1985; Gibbons and Thibault-Botha 2002). *Chelophyses appendiculata* also extends into the Antarctic Westerlies biome (Totton 1954; Margulis 1987; Alvariño et al. 1990) and occasionally into the Antarctic Polar biome (Alvariño et al. 1990), but is unlikely to be breeding this far south, although a few eudoxids were identified in these biomes by Alvariño et al. (1990). Possibly these authors mistook the eudoxids of another diphyid for those of *C. appendiculata*, since their figure of a *C. appendiculata* eudoxid (Alvariño et al. 1990, fig. 34D) is taken from Totton (1965a, fig. 124B), though not acknowledged, rather than from an original specimen. Such records can only be verified by reexamining the original material, which is a task beyond the scope of the present work.

Subfamily Giliinae. The small diphyid species *Gilia reticulata* is rare worldwide, and most published records are given under the earlier synonym *Lensia reticulata* (see Section 10.2.3.3). It is largely confined to higher latitudes in both hemispheres (Pugh and Pagès 1995) and thus most records come from the Westerlies and Polar biomes. It may have been missed in some hauls because of its small size (length 4 mm; see Pugh 1999b), and is typically collected between 500 and 2000 m depth (Pugh and Pagès 1995) in the mesopelagic and upper bathypelagic zones (Alvariño et al. 1990). Although the nectophores and bracts have a reticulate surface, the gonophore is not reticulate (Pugh and Pagès 1995), and gonophores described by Alvariño and Wojtan (1984) and Alvariño et al. (1990) are not referable to *G. reticulata*. Thus, records for eudoxids by these authors (as *L. reticulata*) are unreliable and are not included in the distribution summaries given here. In the Pacific, *G. reticulata* has been recorded from the Polar biome (Stepanjants 1967; Motoda and Minoda 1974; Margulis and Vereshchaka 1994) and the Westerlies biome (Stepanjants 1970; Margulis 1992; Margulis and Vereshchaka 1994). There are also several records from the CALC province (Alvariño 1967b, 1985; Gasca and Suárez 1992b; Margulis and Vereshchaka 1994).

In the Atlantic, *Gilia reticulata* has been recorded from the Polar biome (Margulis 1978; Pugh and Pagès 1995), several times from the Westerlies biome (Pugh 1990; Pugh and Pagès 1995; Pagès et al. 2006; Hosia et al. 2008), but only rarely from the Trades biome (Alvariño 1972) and the associated western coastal province (Alvariño et al. 1990). There are very few records for *G. reticulata* from the Indian Ocean Trades biome (Totton 1954) and the associated coastal provinces (Alvariño et al. 1990), and few also from the Antarctic Westerlies biome (Alvariño et al. 1990; Pugh and Pagès 1995; Pugh et al. 1997). More records exist for this species from the Antarctic Polar biome (Daniel 1985; Alvariño et al. 1990; Pagès and Kurbjewitz 1994; Pagès et al. 1994; Pugh and Pagès 1995; Pagès and Schnack-Siel 1996).

Family Clausophyidae. Species of the calyphoran family Clausophyidae are typically meso- and bathypelagic in distribution, and in siphonophore assemblages in the northeast Atlantic are co-dominant with species of the families Prayidae and Hippopodiidae (Mackie et al. 1987). The family is represented in the current Canadian Pacific collection by five species, *Chuniphyes multidentata*,

C. moserae, *Kephyses ovata*, *Clausophyes moserae*, and *Heteropyramis crystallina*, with eudoxid gonophores of *C. multidentata* being one of the most common siphonophore life stages encountered in the region (see Section 10.2.4.1). This fits with the general findings of Mackie et al. (1987) that at higher latitudes, larger, less active, deeper living clausophyids, hippopodiids, and prayids tend to predominate in deeper horizons, together with the large diphyid *Lensia conoidea*, whereas at lower latitudes, smaller and more active diphyid and abylid siphonophores predominate in shallower epipelagic horizons.

Subfamily Chuniphyinae. The two species of *Chuniphyes* have large definitive anterior and posterior nectophores and a much smaller gonophore. In life the latter exists as a free-living eudoxid, although when it is preserved, the delicate scale-like bract is typically lost (see Section 10.2.4.1). Such gonophores are numerous in the present Canadian Pacific collection, and were also abundant in deeper samples from latitude 44°N in the northeast Atlantic (Pugh 1984). Although gonophores of the two *Chuniphyes* species are at present indistinguishable (Pugh 1999b), it is almost certain that most of the gonophores collected off Vancouver Island are referable to *C. multidentata*, since this species is common and breeding throughout the region, whereas *C. moserae* has been collected only once from above the hydrothermal vent some distance from the main current sampling stations (Fig. 11; see Section 10.2.4.1). Indeed, Mackie et al. (1987) suggest that in the northeast Atlantic the two *Chuniphyes* species have an allopatric distribution, with *C. multidentata* preferring higher latitudes and *C. moserae* latitudes south of 40°N, and surmise that where their ranges overlap, these two species probably occupy different depth horizons. The two *Chuniphyes* species are also likely to be more common than records suggest, because they primarily inhabit meso- and bathypelagic zones (Alvariño et al. 1990; Pugh 1990; Margulis and Vereshchaka 1994; Pugh et al. 1997), where worldwide sampling effort has been scant (Pagès et al. 1994).

Chuniphyes multidentata is a well-known species in the Atlantic (Kirkpatrick and Pugh 1984), but has less frequently been collected from the Pacific and Indian oceans. In the Pacific there are scattered records from the Westerlies biome (Bigelow 1913; Stepanjants 1967; Alvariño 1971; Haddock and Case 1999; Gao et al. 2002; Lindsay 2006), with more from the CALC province (Alvariño 1967b,

1971, 1980c, 1991; Pearcy 1972; Arai et al. 1993; Margulis and Vereshchaka 1994; Silguero and Robison 2000; Dunn et al. 2005b; present records) and also several from the associated western coastal provinces (Bigelow 1913; Zhang and Xu 1980; Zhang and Zhang 1980). *Chuniphyes multidentata* has also been recorded from the Pacific Trades biome (Bigelow 1911b, 1919; Alvariño 1971; Zhang and Xu 1980; Chen 1983) and occasionally from the associated western coastal provinces (Lens and van Riemsdijk 1908; Alvariño et al. 1990) but not from any associated eastern coastal provinces, nor from the Pacific Polar biome. In the Atlantic there are a few published records from the Polar biome (Kramp 1942; Fraser 1967; Hosia et al. 2008), with many more from the Westerlies biome (Bigelow 1918, 1931; Leloup 1955; Patriti 1965a and b; van Soest 1973; Pugh 1974b, 1975, 1984, 1990; Margulis 1978; Casanova 1980; Angel et al. 1982; Pagès et al. 2006; Hosia et al. 2008) but fewer from the Trades biome (Alvariño 1971, 1981; Stepanjants 1975; Alvariño et al. 1990) and the associated western coastal provinces (Alvariño 1981). Records for *C. multidentata* from the Indian Ocean Trades biome are few (Totton 1954; Musaeva 1976; Daniel 1985), with only occasional records also from the associated coastal provinces (Totton 1954). Farther south, in the Antarctic Westerlies biome, there are more records (Totton 1954; Margulis 1987; Alvariño et al. 1990; Pagès et al. 1996), plus a few from the Antarctic Polar biome (Totton 1954; Alvariño et al. 1990; Pagès et al. 1994).

Chuniphyes moserae is a little-known species most often collected from bathypelagic depths (Totton 1954; Alvariño 1971; Stepanjants 1975; Daniel 1985; Pagès et al. 1994). In the Pacific there are records from the Polar biome (Stepanjants 1967; Motoda and Minoda 1974; Margulis 1988), the Westerlies biome (Stepanjants 1967, 1970; Alvariño 1971), the Trades biome (Alvariño 1971; Zhang and Xu 1980; Alvariño et al. 1990), and the CALC province (Alvariño 1967b; Margulis and Vereshchaka 1994; present work). In the Atlantic, *C. moserae* has been recorded from the Westerlies biome (Totton 1954; Margulis 1972b; Larson et al. 1988; Pugh 1990; Pagès et al. 2006) and the Trades biome (Alvariño 1971, 1981; Margulis 1972b; Stepanjants 1975; Alvariño et al. 1990) but not from the Polar biome. There are very few records from the Indian Ocean Trades biome and the associated coastal provinces (Totton 1954; Daniel 1985). In the Antarctic region there are more records, mostly from the Polar biome (Totton 1954; Alvariño et al. 1990; Pagès et al. 1994;

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Pugh et al. 1997), with some also from the Westerlies biome and the associated coastal provinces (Alvariño et al. 1990; Pagès et al. 1996b).

Subfamily Kephyinae. *Kephyes ovata* has frequently been confused with *Clausophyes moserae* in the past, and was originally introduced under the name *Diphyes ovata* by Keferstein and Ehlers (1860) from a specimen collected in the Mediterranean. Later, Moser (1925), who thought she had found more specimens of this species, moved it into the genus *Clausophyes*. However, unbeknown to Moser, her specimens were a new species and not the same as that of Keferstein and Ehlers (1860). This error was not brought to light until 1988, when Margulis revised the clausophyids and changed the name of Moser's specimens from *C. ovata* to *C. moserae*. Unfortunately, Margulis (1988) also relegated Moser's species to a subspecies of another clausophyid, *Clausophyes galeata*. This was later rectified by Pugh and Pagès (1993), who gave full species status to *C. moserae*. In addition to describing the anterior and posterior nectophores of her species “*C. ovata*”, Moser (1925) also linked some new bracts that she found to her species, but Pugh (2006a) has since shown that bracts are not developed in the genus *Clausophyes*. They are, however, characteristic of the species originally described by Keferstein and Ehlers (1860), and Pugh (2006a) has now transferred this species to a new genus, *Kephyes*. The bracts of *K. ovata* are therefore identical with those described by Moser (1925), and it is concluded here that all records for bracts under the name *C. ovata* in the literature represent records for *K. ovata*.

Another twist to this tale is that in 1969, the species described by Keferstein and Ehlers (1860) was reintroduced as a new species, *Clausophyes massiliiana*, by Patriti. Thus, some records for *K. ovata* appear in the literature under the name *C. massiliiana*, and others, as mentioned above, for the eudoxid stage of *K. ovata* appear under the name *Clausophyes ovata*. These synonyms are therefore included, where relevant, in the distribution summary for *K. ovata* given below.

Kephyes ovata is a rare species worldwide, and typically lives at mesopelagic depths (Casanova 1980; Kirkpatrick and Pugh 1984; Mills et al. 1996; Pagès et al. 2006). It has only very infrequently been recorded in the Pacific, with a single record from the Westerlies biome (Stepanjants 1970) and two records from the CALC province (Dunn et

al. 2005b; present work). There are also scattered records for eudoxids from the associated eastern and western coastal provinces of the Pacific Trades biome (Alvariño et al. 1990 as *Clausophyes ovata*). In the Atlantic, in contrast, *K. ovata* is said to be widely distributed (Pugh 2006a), and it has a range in the North Atlantic that extends from the equator to latitude 60°N (Kirkpatrick and Pugh 1984 as *C. massiliiana*). Other Atlantic records for *K. ovata* all come from the Westerlies biome (Pugh 1974b, 1975, 1984, 1990, 2006a; Casanova 1980; Bouillon et al. 2004; Pagès et al. 2006) including a number of records from the Mediterranean sector (Keferstein and Ehlers 1861; Patriti 1969; Mills et al. 1996; Gamulin and Kršinic 2000), but there are no specific records as yet from either the Trades biome or the Polar biome of the Atlantic. *Kephyes ovata* has only been recorded once so far from the Indian Ocean, and this record comes from a western associated coastal province (Totton 1954). Most published records for *K. ovata* come from the Southern Ocean, from the Antarctic Westerlies and Polar biomes, as eudoxids of “*C. ovata*” (Alvariño et al. 1990, maps A202–A208 and A210–A213).

Subfamily Clausophyinae. *Clausophyes moserae* is the only species of this subfamily so far found in Canadian Pacific waters, with 147 anterior nectophores collected during the present study (see Section 10.2.4.3). It has frequently been recorded under the name *Clausophyes ovata*, but such records are only valid when applied to the nectophores, since records for bracts are now referable to *K. ovata* (see above and Section 10.2.4.3).

Clausophyes moserae is a meso- to bathypelagic species (Mackie et al. 1987, fig. 18; Pagès et al. 1994), which is said to have a “widespread distribution” in the North Atlantic (Mackie et al. 1987, p. 151, as *C. ovata*), although it has only been occasionally recorded from the Pacific, between the equator and latitude 40°N (Margulis 1988). There are very few individual published records from the Pacific, with one from the Westerlies biome (Lindsay 2006), two from the Trades biome (Margulis and Vereshchaka 1994), and a few more from the CALC province (Alvariño 1967b, 1991; Margulis and Vereshchaka 1994; present records). There is also a single record for *C. moserae* from the Gulf of California (Margulis and Vereshchaka 1994). Records from the Atlantic include one from the Polar biome (Mackie et al. 1987) and a number from the Westerlies biome (Leloup 1933, 1934; Pugh 1974b, 1975, 1984, 1990; Casanova 1980; Angel et al. 1982; Mackie et

al. 1987; Pugh and Pagès 1993; Hosia et al. 2008), as well as one from an associated eastern coastal province (Patriti 1965b). No reliable records exist for the Mediterranean, where *C. moserae* has often been confused with *K. ovata* (see above). There are also several records for *C. moserae* from the Atlantic Trades biome (Moser 1925; Leloup 1934; Totton 1954; Phillips 1972; Alvariño 1981; Alvariño et al. 1990; Pugh and Pagès 1993) and two from the associated eastern coastal province (Totton 1954). In contrast, there are few records for *C. moserae* from the Indian Ocean Trades biome and the associated coastal provinces (Totton 1954; Daniel 1985), and few also from the Antarctic Westerlies biome (Totton 1954; Pugh and Pagès 1993) with more records from the Antarctic Polar biome (Totton 1954; Alvariño et al. 1990; Pugh and Pagès 1993; Pagès et al. 1994; Pugh et al. 1997).

Subfamily Heteropyramidinae. *Heteropyramis crystallina* is a small rare species that inhabits meso- and bathypelagic layers (Kirkpatrick and Pugh 1984), though most records come from the mesopelagic zone (Pagès and Kurbjewit 1994; Pagès et al. 1994; Pugh 1999b). Many early records are given under the synonym *Thalassophyes crystallina*, but this species was then reduced to a junior synonym of *H. maculata* by Margulis (1988). Thus, her records are unreliable. All subsequent records list *H. crystallina* as a separate species, albeit under the name *T. crystallina*, until Pugh (1999b) finally reduced *Thalassophyes* to a junior synonym of *Heteropyramis* (see Section 10.2.4.4). Since Totton (1954, fig. 71A) illustrated a eudoxid of *H. crystallina* under the name *H. maculata*, eudoxid records for the latter species may also include eudoxids of *H. crystallina*.

The present record for *Heteropyramis crystallina* from the northern limit of the CALC province is the first from the northern Pacific. The only other records from this ocean come from the Trades biome in the southern Pacific and the associated coastal provinces of Australia (Alvariño et al. 1990). In the Atlantic, *H. crystallina* has a latitudinal range of 60°N–67°S (Pugh 1999b), with some records in the northeast Atlantic from the equator to 11°N and more from 40° to 60°N (Kirkpatrick and Pugh 1984). *Heteropyramis crystallina* has not been recorded from the Atlantic Polar biome, but there are several published records from the Westerlies biome (Totton 1954; Fraser 1961; van Soest 1973; Pugh 1975, 1990; Kirkpatrick and Pugh 1984; Hosia et al. 2008), and a few also from the Trades biome (Leloup and

Hentschel 1935; Totton 1954; Alvariño 1981), with two records from the associated western coastal provinces (Totton 1954; Alvariño 1981). Records from the Indian Ocean are infrequent, with one from the Trades biome (Daniel 1985) and three from the associated western coastal provinces (Totton 1954). All remaining records for *H. crystallina* come from the Southern Ocean, with several from the Antarctic Westerlies biome (Totton 1954; Alvariño 1981; Daniel 1985) and more from the Antarctic Polar biome (Moser 1925; Hardy and Günther 1935; Totton 1954; Alvariño 1981; Pagès and Gili 1989; Alvariño et al. 1990; Pagès and Kurbjewit 1994; Pagès et al. 1994; Pagès and Schnack-Shiel 1996; Pugh et al. 1997).

Family Sphaeronectidae. The only species of this calycophoran family so far recorded from Canadian Pacific waters is *Sphaeronectes köllikeri* from Jervis Inlet by Mackie (1985, as *S. gracilis*). The name *S. gracilis* has been used for most records worldwide, although some are given under the older name *S. köllikeri* used in this work (see Section 10.2.5). *Sphaeronectes köllikeri* is a small species measuring only 5–6 mm long when mature, and is thus unlikely to have been retained in the nets used in the present study. It may also have escaped the nets used in other studies, and if so it may be more common than records suggest. It is a typically epipelagic species, and inhabits warmer water close to the surface (Kirkpatrick and Pugh 1984), where it frequently forms large aggregations (Pagès and Gili 1991a and b, 1992b). *Sphaeronectes köllikeri* has not been recorded from the Polar biomes, and typically exhibits a neritic distribution (Mackie et al. 1987), preferring waters from an oceanic source, at least along the Chilean coast (Palma et al. 1999; Palma and Aravena 2001).

Sphaeronectes köllikeri is a rare species worldwide, and most records come from the associated coastal provinces of the Westerlies and Trades biomes in all three oceans. In the Pacific there are only two records from the Pacific Westerlies biome (Kitamura et al. 2003, off Japan), with slightly more from the Pacific Trades biome (Bigelow 1911b; Alvariño 1971; Xu and Zhang 1978; Lin 1993; Margulis and Vereshchaka 1994; Palma and Silva 2006), while all others are from the associated coastal provinces. A few of these records come from the CALC province (Bigelow and Leslie 1930; Purcell and Kremer 1983; Mackie 1985; Alvariño and Kimbrell 1987; Alvariño 1991), with more from the associated coastal provinces in the southeast (Palma 1985, 1986, 1994; Palma and

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Rosales 1997; Palma et al. 1999; Pagès et al. 2001; Palma and Aravena 2001), and also from the coastal provinces in the northwest (Zhang and Xu 1980; Gao 1982; Zhang et al. 2005; Zuo et al. 2005) and southwest (Huxley 1859; Pages et al. 1990).

Sphaeronectes köllikeri has also been found from the Atlantic Westerlies biome (Fraser 1961, 1967; Totton 1965a; Lakkis and Zeidane 1997; Gamulin and Kršinic 2000; Pagès et al. 2006) and the associated eastern coastal provinces (Fraser 1961, 1967; Moreno and Fdez-Alcazar 1984; Gili et al. 1991) and western coastal provinces (Fewkes 1881; Dunn et al. 2005b). There are also a few records from

the Atlantic Trades biome, including the specimen described in this work (see Section 10.2.5), in the Gulf of Mexico and Caribbean Sea (Mayer 1904; Sears 1950), many more from the associated eastern coastal provinces (Seguin 1966a and b; Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002), and one record also from a western coastal province (Seguin 1965). In the Indian Ocean there is only a single record for *S. köllikeri* from the Trades biome (Daniel 1985) and several more from the associated coastal provinces (Patriti 1970a; Daniel 1974, 1985; Gibbons and Thibault-Botha 2002). Only one author has recorded *S. köllikeri* from the Antarctic Westerlies biome (Margulis 1987).

6. Material Examined

6.1. Localities

Samples were collected from Canadian Pacific coastal waters at latitudes between approximately 48° and 52°N. The main stations where samples from PBS were obtained were aligned along three parallel tracks extending southwest from Pachena Point and Barkley Sound (Fig. 11, Table 1) from inshore to beyond 1500 m water depth. Samples from IOS were obtained in the vicinity of a deep thermal vent at 47°57'N, 129°06'W (Fig. 11, inset), and further samples from PBS came from a larger area of coastal waters between 48°5'N, 126°9'W and 52°00'N, 128°56'W. The depth range of samples extended from the surface to below 2200 m. Other samples include *Nanomia bijuga*, *Lensia achilles*, and *Dimophyes arctica* taken from the Strait of Georgia in 1979; locality details are given in Mapstone and Arai (1992).

Distributional records by other authors are given in full for Canadian Pacific and other northeast Pacific waters, followed by a comment on distribution in the remainder of the Pacific and other oceans. Records from Canadian Pacific waters include those taken between latitudes 30° and 60°N and from the North American west coast to longitude 160°W.

Cordagalma ordinata and *Sphaeronectes köllikeri* are included in the present work because they were previously found in Canadian Pacific waters (Mackie 1985), although none were identified in the present samples. Consequently, the species descriptions are drawn from material collected from the North Atlantic (6°20'N, 31°46'W), the Sargasso Sea (circa 38°N, 67°W), and the Mediterranean (36°03'N, 2°48'E).

6.2. Collection and sorting methods

The majority of field samples studied were supplied by the Groundfish Section of PBS and taken during an investigation into the recruitment of larval sablefish, which is a food fish of commercial importance in western Canada. These samples

come from four cruises conducted between 22 January and 25 April 1987 and were taken at the stations shown in Figure 11 using a 1 m² Tucker sampler with 335 µm mesh nets, which retained all except the smallest siphonophoran nectophores and bracts. Nets were opened and closed at specified depths (McFarlane and Beamish 1992). Typically, horizontal tows were taken at depths near 300, 500, and 700 m, and also from the surface to 300, 500, and 700 m depth and in the reverse direction. Each trawl unit comprised three nets. When the gear was deployed, the bottom net was open and the middle and top nets were closed. At the desired depth the middle net was opened and the top and bottom nets were closed. Tow duration was approximately 15 min. During retrieval the top net was open. Mean depth was calculated on the basis of the length and angle of the cable. Volume fished was recorded by flowmeters and data were corrected to 1000 m³. Specimens were fixed in 4% formaldehyde in seawater buffered with sodium borate. Cnidarians and ctenophores were sorted from the field samples and transported to the University of Calgary.

Additional samples taken in 1988 at the same stations and depths as those shown in Figure 11 were scanned for undescribed species or species rare in the area.

Samples from IOS were collected between 19 and 21 June 1990 over the central hydrothermal-vent field on the Endeavour segment of the Juan de Fuca Ridge and were also examined and counted. They come from three sets of Tucker trawls using 1 mm mesh nets (Fig. 11 inset, Table 1) and the specimens were preserved in isopropyl alcohol.

Further samples taken in 1980, 1982, and 1986 were also scanned as above. Oblique Bongo-tows were made at precise depths using 351 µm mesh nets during 1980 (44 samples from 95–640 m depth) and 1982 (22 samples from 600–1650 m depth). Paired Bongo-tows were made using 230 and 350 mm mesh nets during 1986 (46 samples from 0–200 to 0–800 m depth). No new species were found during sample scanning, indicating that the species list in the Table of Contents (based on the 1987 samples)

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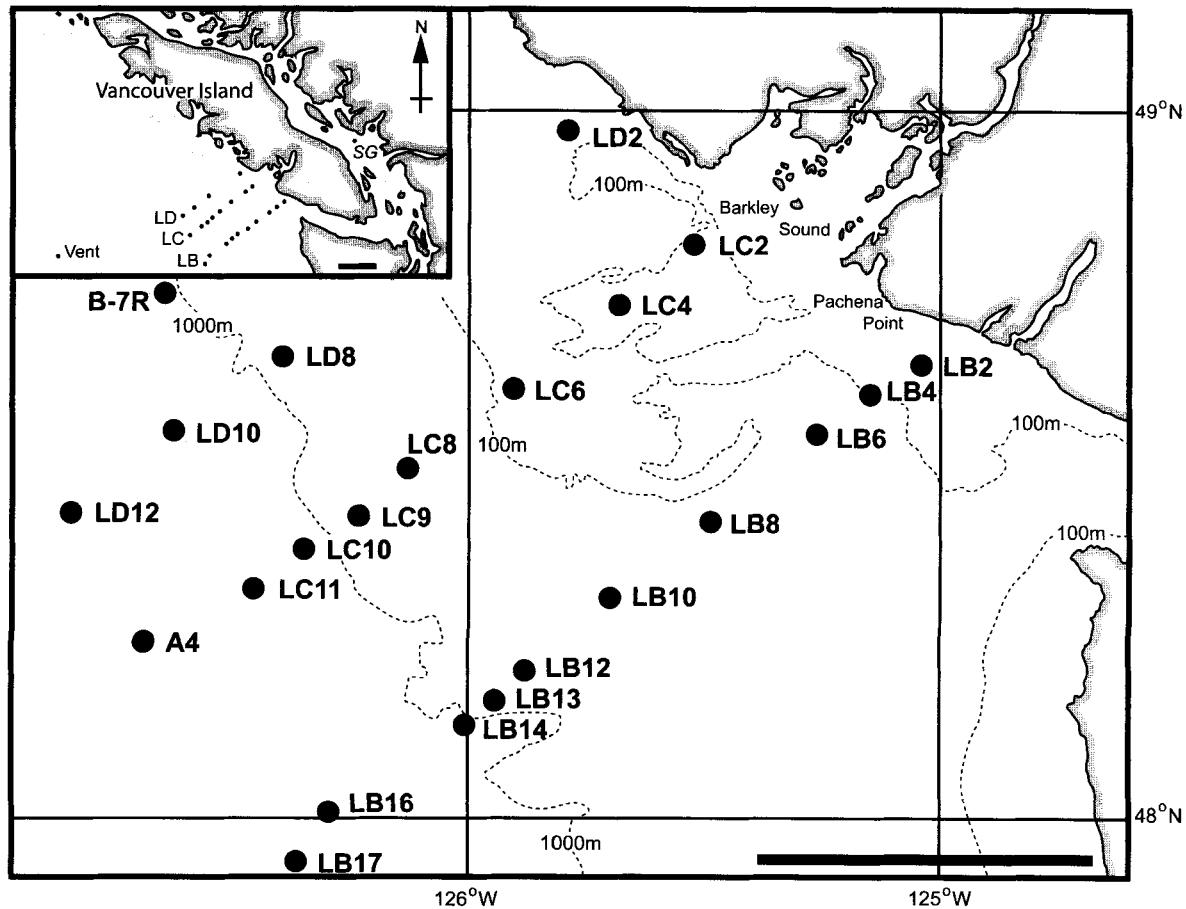


Fig. 11. Locations of sampling stations off the west coast of Vancouver Island, B.C., the offshore hydrothermal-vent sampling station, and one station in the Strait of Georgia (SG) (see Table 1). Scale bars = 50 km.

is a true representation of the siphonophore fauna of Canadian Pacific waters between 1979 and 1990.

Nectophores of specimens in which the ridges and other structures could not easily be discerned were stained with Steedman's Triple Stain (Kirkpatrick and Pugh 1984). It is normal convention that the lengths of the various structures are expressed as a fraction of the length of the nectophore, and in the present work the latter is measured from the base

of the ostium, excluding the mouthplate and ostial cusps. Well-preserved nectophores were used for all measurements.

Specimens are deposited in the Royal British Columbia Museum (as BCPM), Victoria, and the NHM. Other specimens from the NHM collection were examined to aid identification and clarify points of taxonomic detail; these are also listed below. Most were originally identified by A.K. Totton.

6. Material Examined

Table 1. Stations occupied off Vancouver Island.

Station Number	Latitude (N)	Longitude (W)	Bottom depth (m)
1987 and 1988			
LB2	48°39.0'	125°02.4'	55
LB4	48°35.7'	125°08.7'	105
LB6	48°32.2'	125°15.5'	110
LB8	48°25.3'	125°28.7'	145
LB10	48°18.6'	125°41.4'	150
LB12	48°12.9'	125°51.9'	510
LB13	48°10.6'	125°56.1'	810
LB14	48°08.5'	126°00.0'	1180
LB16	48°00.5'	126°17.0'	1530
LB17	47°56.5'	126°26.1'	>1200
LC2	48°48.7'	125°31.0'	105
LC4	48°43.4'	125°40.8'	162
LC6	48°36.5'	125°54.0'	95
LC8	48°29.5'	126°07.1'	197
LC9	48°25.9'	126°13.7'	660
LC10	48°22.4'	126°20.2'	1150
LC11	48°19.0'	126°26.7'	1470
A4	48°15.0'	126°40.0'	>1200
LD2	48°58.4'	125°47.1'	42
LD8	48°39.2'	126°23.4'	760
LD10	48°32.2'	126°36.6'	1475
LD12	48°25.4'	126°49.4'	Not known
1990			
Vent tow 1	47°57.30'N, 129°05.6'W to 47°56.32'N, 129°05.2'W		2200–2200
Vent tow 2	47°59.24'N, 129°05.6'W to 48°00.77'N, 129°04.1'W		2130–2200
Vent tow 3	47°57.17'N, 129°06.1'W to 47°56.30'N, 129°06.5'W		2150–2200
Other stations			
B-7R (1982)	48°43.28'	126°39.83'	1200
Strait of Georgia (1979–1982)	49°16'	123°40'	Not known

7. Key to Siphonophores from Canadian Pacific Waters

The compilation of a successful identification key for siphonophores is a complex task, and the key given below is relevant only to the area covered by Canadian Pacific waters. It is divided into three sections. The first section (7.1) addresses families and is based upon whole colonies, including the two suborders so far recorded from Canadian Pacific waters. It covers the three long-stemmed physonect families found in the present study, Apolemiidae, Pyrostephidae, and Agalmatidae, with the addition of the Forskaliidae because an immature colony of *Forskalia* sp. was recorded just north of the study area, west of Graham Island, B.C. (Berkeley and Berkeley 1960). It also covers the short-stemmed families Physophoridae and Rhodaliidae because of an unconfirmed report of *Physophora hydrostatica* from off Tofino, Vancouver Island, and records of an unidentified benthic rhodaliid siphonophore from the

Juan de Fuca Ridge region (Pugh 1983). Five of the six known families of calycophorans are included in the key because all are represented in the present collection. The sixth, Abylidiae, is included because unidentified species, which may have been abyliids, were also reported from the Endeavour segment of the Juan de Fuca Ridge (Burd and Thompson 2000).

The second section of the key (7.2), to genera and species, is entered from the first section (7.1, the key to siphonophore families). It is based on nectophore characters only, and restricted to species recorded from Canadian Pacific waters.

The third section (7.3) is a separate key to calycophoran bracts identified so far from Canadian Pacific waters.

7.1. Key to siphonophore families (based on the whole mature colony)

1	Pneumatophore present (Order Physonectae)	2
-	Pneumatophore absent (Order Calycophorae)	7
2	Colony with linear stem (long-stemmed families)	4
-	Colony with linear stem absent, siphosomal elements borne on a bulbous structure (short-stemmed families)	3
3	Pneumatophore enlarged; aurophore present; nectosome and siphosome short, forming large distinctive swollen corm. Pneumatophore not enlarged; Family Rhodaliidae	
-	Aurophore absent; nectosome long, siphosome short and forming laterally expanded sac Family Physophoridae	
4	Nectosome conical, with many nectophores in whorls; bracts on both siphosome and elongate pedicels of gastrozooids Family Forskaliidae	
-	Nectosome not conical, with fewer nectophores, not in whorls; bracts on siphosome only Family Apolemiidae	5
5	Elongate nectosomal polyps present between nectophores (Family Apolemiidae)	15
-	No elongate nectosomal polyps between nectophores	6
6	Nectophore with axial wings developed; nectosac muscular throughout (except in <i>Marrus</i> spp.) (Family Agalmatidae)	16
-	Nectophore with lower-lateral wings developed; nectosac with muscle-free proximal face (Family Pyrostephidae)	20
7	Nectophore(s) approximately spherical or angular but not streamlined; nectosac small relative to nectophore (prayomorph families)	8
-	Nectophore(s) conical, typically streamlined with nectosac large relative to nectophore (diphyomorph families)	10

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- 8 Mature colony comprising six or more definitive nectophores, angular or not, flattened proximodistally, and lacking bracts (Family Hippopodiidae) 21
- Colony comprising two to four rounded nectophores with bracts, or a single nectophore with or without bracts 9
- 9 Nectophore single and approximately spherical (Family Sphaeronectidae or larval nectophore of *Vogtia* spp.) 23
- Nectophores typically two to four and approximately spherical or cylindrical, atypically single and angular (Family Prayidae) 24
- 10 Anterior nectophore alone developed 11
- Anterior and posterior nectophores both developed, dissimilar 13
- 11 Nectophore pyramidal with rectangular facets; nectosac tubular with narrow ostium Family Abylidiae
- Nectophore conical with elongate triangular facets; nectosac with broad ostium 12
- 12 Anterior nectophore with hydroecium opening posteriorly; nectosac filling nectophore (Family Diphyidae) 33
- Anterior nectophore with hydroecium opening proximally; nectosac not filling nectophore (Family Clausophyidae) 42
- 13 Somatocyst in anterior nectophore only 14
- Somatocyst in both nectophores (Family Clausophyidae) 42
- 14 Anterior nectophore conical, with nectosac filling nectophore (Family Diphyidae) 33
- Anterior nectophore angular, with small tubular nectosac Family Abylidiae

7.2. Key to nectophores of siphonophore species recorded from Canadian Pacific waters (based on morphology of definitive nectophores only, unless otherwise indicated)

- 15 Nectophores with undulating upper and lateral radial canals, long ascending surface diverticulum, and small ostial process *Apolemia contorta*
- Nectophores with straight radial canals, short ascending surface diverticulum, and large ostial process *Apolemia* sp.
- 16 Lateral radial canals of nectosac following sinuous, looped course 17
- Lateral radial canals of nectosac not following looped course 18
- 17 Nectophore longest along proximal-distal axis; nectosac small, not filling nectophore *Agalma elegans*
- Nectophore longest along upper-lower axis; nectosac large, filling nectophore *Nanomia bijuga*
- 18 Nectophore heart-shaped in distal view, with lower process developed below ostium *Cordagalma ordinata*
- Nectophore not heart-shaped in distal view, lacking lower process 19
- 19 Axial wings extending beyond thrust block, nectosac with muscular proximal face *Frillagalma vityazi*
- Axial wings not extending beyond thrust block, nectosac with broad muscle-free proximal face *Marrus orthocanna*
- 20 Upper-lateral ridges each with short inner ridge at 4/5 nectophore length and nectosac undulating in lateral view *Bargmannia elongata*
- Upper-lateral ridges without short inner ridge at 4/5 nectophore length and nectosac straight in lateral view *Bargmannia lata*

7. Key to Siphonophores from Canadian Pacific Waters

- 21 Nectophore without deep furrow and flap between lower and ostial facets 22
 - Nectophore with deep furrow and flap between lower and ostial facets *Vogtia serrata*
- 22 Upper and proximolateral facets with a few or no large cusps *Vogtia pentacantha*
 - Upper and proximolateral facets with many small cusps *Vogtia spinosa*
- 23 Hydroecium tubular, opening small, circular *Sphaeronectes köllikeri*
 - Hydroecium spherical, opening elongate, slit-like; typically containing developing angular definitive nectophore Larval nectophore of *Vogtia serrata*
- 24 Colony comprising single nectophore only, larval or definitive 25
 - Colony comprising two nectophores, one or both definitive 28
- 25 Nectophore ridges prominent, cusped Larval nectophore of *Nectopyramis thetis*
 - Nectophore ridges smooth 26
- 26 Nectophore definitive, pyramidal *Nectopyramis thetis*
 - Nectophore definitive, laterally flattened 27
- 27 Nectophore rhomboidal; somatocyst complexly branched *Nectadamas diomedae*
 - Nectophore ovate with truncate distal surface; somatocyst with few branches *Nectadamas richardi*
- 28 Colony with two nectophores of dissimilar sizes, one representing retained larval nectophore, together forming an approximate sphere 29
 - Colony with typically two elongate, approximately uniformly sized definitive nectophores 30
- 29 Smaller definitive nectophore of pair shield-shaped, nectosac nonfunctional
 - Smaller definitive nectophore of pair subspherical, nectosac functional
 *Amphicaryon acaule*
 *Maresearsia praecleara*
- 30 Nectophores with ascending and descending surface diverticula and complexly divided somatocyst, and nectosac with ramified radial canals 31
 - Nectophores with ascending and descending surface diverticula, without somatocyst, nectosac with four radial canals, including laterals following W-shaped courses 32
- 31 Somatocyst of up to six median and two lateral ascending branches (from median branch), latter subdividing extensively *Praya dubia*
 - Somatocyst of single median ascending branch subdividing extensively *Praya reticulata*
- 32 Lower end of hydroecium not marked by lower sill *Rosacea cymbiformis*
 - Lower end of hydroecium marked by lower sill *Rosacea plicata*
- 33 Nectophore(s) not ridged 34
 - Nectophore(s) ridged 35
- 34 Nectophores with mouthplate of anterior nectophore divided *Sulculeolaria quadrivalvis*
 - Nectophores with mouthplate of anterior nectophore undivided *Dimophyes arctica*
- 35 Ridges parallel with long axis of nectophore 36
 - Ridges parallel with and orthogonal to long axis of nectophore, anastomosing
 *Gilia reticulata*
- 36 All ridges on anterior nectophore complete 37
 - Some ridges on anterior nectophore incomplete 40
- 37 Five ridges on anterior nectophore 38
 - Seven ridges on anterior nectophore *Lensia havock*
- 38 Hydroecium of anterior nectophore less than 2/5 of nectophore length 39
 - Hydroecium of anterior nectophore reaching 1/3 nectophore length *Muggiaeaa atlantica*

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- 39 Lateral ridges of anterior nectophore bending towards upper surface near ostium *Lensia achilles*
- Lateral ridges of anterior nectophore not bending towards upper surface near ostium *Lensia conoidea*
- 40 Anterior nectophore with five or seven ridges 41
- Anterior nectophore with more than seven ridges *Lensia hostile*
- 41 Mesogloea soft, upper ridge complete; hydroecium a shallow channel lying posterior of ostium *Lensia multicristata*
- Mesogloea turgid, upper ridge incomplete; hydroecium claw-like and deeper, ending anterior of ostium *Chelophyses appendiculata*
- 42 Anterior nectophore ridged 43
- Anterior nectophore smooth 45
- 43 Anterior nectophore with six ridges at posterior end 44
- Anterior nectophore with five ridges at posterior end *Heteropyramis crystallina*
- 44 Lateral ridges of anterior nectophore uniting close to anterior end of nectophore; somatocyst without lateral expansions or distinctly demarcated anterior branch *Chuniphyes moserae*
- Lateral ridges of anterior nectophore uniting some distance beyond anterior end of nectophore; somatocyst with lateral expansions and distinctly demarcated thin anterior branch *Chuniphyes multidentata*
- 45 Ostium at oblique angle to long axis of anterior nectophore; nectosac up to 3/4 nectophore length *Clausophyes moserae*
- Ostium orthogonal to long axis of anterior nectophore; nectosac at least 8/10 nectophore length *Kephyses ovata*

7.3. Key to bracts of calycophoran species recorded from Canadian Pacific waters

- 1 Bract without distinctive neck-shield 2
- Bract with distinctive neck-shield 11
- 2 Bract with system of branched canals 3
- Bract subspherical, with simple (unbranched) phyllocyst *Sphaeronectes köllikeri*
- 3 Bracteal canals comprising a pair of hydroecial canals only 4
- Bracteal canals comprising a pair of hydroecial canals and up to four additional canals 5
- 4 Bract helmet-shaped; hydroecial canals straight *Amphicaryon acaule*
- Bract round in lateral view; hydroecial canals recurved *Maresearsia praecleara*
- 5 Bract either globular or hemispherical with smoothly curved contours 6
- Bract typically angular, either pyramidal or triangular 9
- 6 Bract hemispherical, flattened; two distinct lobes comprising lateral lobe and hydroecial lobe (of two fused lobes); inner surface of hydroecial lobe without flap; gonophore symmetric 7
- Bract globular; three distinct lobes comprising lateral lobe and two separate hydroecial lobes; small flap on inner surface of posterior hydroecial lobe; gonophore asymmetric 8
- 7 Lateral and hydroecial lobes same size; posterior hydroecial canal almost as long as hydroecium; upper canal long and recurved *Praya reticulata*
- Lateral lobe larger than hydroecial lobe; posterior hydroecial canal less than 1/2 length of hydroecium; upper bracteal canal not recurved *Praya dubia*
- 8 Mesogloea turgid, giving bract a compact shape; upper canal originating from posterior hydroecial canal *Rosacea plicata*
- Mesogloea flaccid, giving bract an imprecise shape; upper canal originating from posterior longitudinal (spur) canal *Rosacea cymbiformis*

7. Key to Siphonophores from Canadian Pacific Waters

- 9 Bract pyramidal, not flattened laterally; cormidial bell and also sometimes smaller gonophores, typically present in hydroecium *Nectopyramis thetis*
- Bract laterally flattened; large gonophore typically present in hydroecium, but cormidial bell absent 10
- 10 Bract over 7 mm long; apex pointed; hydroecial opening flanked by two lobes
..... *Nectadamas diomedae*
- Bract 6 mm or shorter; apex not pointed; hydroecial opening without flanking lobes
..... *Nectadamas richardi*
- 11 Bract conical; phyllocyst typically prominent, with or without single thin elongate distal branch 13
- Bract leaf-like; phyllocyst with two thin elongate distal bracteal canals 12
- 12 Phyllocyst triangular with broad distal end, proximal end not reaching proximal end of bract *Chuniphyes multidentata*
- Phyllocyst narrow, reaching proximal end of bract, with or without swelling in midregion ..
..... *Kephyses ovata*
- 13 Phyllocyst with thin proximal branch reaching proximal end of bract and thin distal branch extending to distal end of elongate neck-shield *Dimophyes arctica*
- Phyllocyst without thin proximal and distal branches 14
- 14 Bract with deep notch or right angle on right side of lower border 15
- Bract without notch in lower border 16
- 15 Bract with shallow notch on left side of lower border; phyllocyst up to 4/5 length of head-piece of bract *Lensia conoidea*
- Bract without notch on left side of lower border; phyllocyst typically 1/2 length of head-piece of bract *Lensia achilles*
- 16 Gonophore with flat proximal end and without spur from either lower ridge
..... *Muggiaeaa atlantica*
- Gonophore with proximal end consisting of bluntly pointed apophysis and with spur projecting from either right or left lower ridge *Chelophyes appendiculata*

8. Abbreviations Used in Figures

The following abbreviations are used in Figures 12–65.

<i>abs</i>	Ascending branch of somatocyst	<i>ipe</i>	Insertion point of external pedicular canal
<i>abs₁₋₄</i>	Ascending median somatocyst branches	<i>kn</i>	Knob
<i>abs_{l-r}</i>	Ascending left and right lateral somatocyst branches	<i>la</i>	Lateral angle
<i>ahc</i>	Anterior hydroecial canal (bract)	<i>laf</i>	Lateral furrow
<i>ahl</i>	Anterior hydroecial lobe (bract)	<i>lal</i>	Lateral lobe (bract)
<i>ala</i>	Anterior lateral angle	<i>lbc</i>	Lateral bracteal canal
<i>alc</i>	Anterior longitudinal canal (bract)	<i>lc</i>	Lateral cusp
<i>an</i>	Anterior nectophore	<i>lcu</i>	Lower cusp
<i>anc</i>	Annular constriction	<i>ldr</i>	Laterodistal ridge
<i>ap</i>	Apophysis	<i>lf</i>	Lateral facet
<i>asd</i>	Ascending surface diverticulum (nectophore)	<i>lfl</i>	Lower flap
<i>aw</i>	Axial wing	<i>lfu</i>	Lower furrow
<i>bc</i>	Bracteal canal	<i>lgr</i>	Longitudinal ridge
<i>blc</i>	Branch of lower radial canal	<i>lhw</i>	Left hydroecial wing
<i>br</i>	Bracteal ridge	<i>lipf</i>	Limit of proximolateral facet
<i>ca</i>	Commissure	<i>lla</i>	Left lateral angle
<i>cb</i>	Cormidial bell	<i>llar</i>	Lower lateral ridge
<i>cfr</i>	Circumferential ridge	<i>llc</i>	Lower lateral cusp
<i>co</i>	Central organ	<i>llf</i>	Left lateral facet
<i>cp</i>	Small cross-process	<i>lllr</i>	Left lower lateral ridge
<i>cr</i>	Cusped ridge	<i>llof</i>	Left lower facet
<i>cu</i>	Cusp	<i>llor</i>	Left lower ridge
<i>da</i>	Distal angle	<i>l-lr</i>	Lower lateral ridge
<i>dbp</i>	Distal branch of phyllocyst	<i>lmh</i>	Limit of hydroecium
<i>de</i>	Distal edge	<i>ln</i>	Larval nectophore
<i>df</i>	Definitive nectophore	<i>loa</i>	Lower angle
<i>df</i>	Distal facet	<i>loc</i>	Lower radial canal (nectophore)
<i>dl(l)</i>	Distal lamella (lappets)	<i>lof</i>	Lower facet
<i>dn</i>	Developing definitive nectophore	<i>lofu</i>	Longitudinal furrow
<i>dsd</i>	Descending surface diverticulum (nectophore)	<i>lor</i>	Lower ridge
<i>dv</i>	Diverticulum	<i>lp</i>	Lower process
<i>fl</i>	Flap	<i>lpa</i>	Lower proximal angle
<i>fl</i>	Left flap	<i>lr</i>	Lateral ridge
<i>fr</i>	Right flap	<i>lrc</i>	Lateral radial canal (nectophore)
<i>fu</i>	Furrow	<i>ls</i>	Longitudinal septum
<i>g</i>	Gastrozooid(s)	<i>lsd</i>	Lateral surface diverticulum
<i>gb</i>	Gas bubble	<i>lsd_{l-r}</i>	Lateral surface diverticulum, left and right
<i>go</i>	Gonophore	<i>lulr</i>	Left upper lateral ridge
<i>h</i>	Hydroecium	<i>luf</i>	Left upper facet
<i>hcb</i>	Hydroecium of cormidial bell	<i>lur</i>	Left upper ridge
<i>hg</i>	Hydroecium of gonophore	<i>lw</i>	Left wing
<i>hl</i>	Hydroecial lobe (bract)	<i>lwr</i>	Lower lateral ridge
<i>ho</i>	Hydroecial opening	<i>mep</i>	Mesogloea plug
<i>hp</i>	Head-piece	<i>mfz</i>	Muscle-free zone of nectosac
<i>hr</i>	Hydroecial ridge	<i>mi</i>	Median indentation
<i>hw</i>	Hydroecial wing	<i>ml</i>	Muscular lamella
<i>ib</i>	Immature bract		

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

<i>mmp</i>	Median mesogloal protuberance	<i>rlof</i>	Right lower facet
<i>mn</i>	Manubrium (gonophore)	<i>rlor</i>	Right lower ridge
<i>mp</i>	Mouthplate	<i>rlr</i>	Right lateral ridge
<i>mr</i>	Marginal ridge	<i>rpf</i>	Right proximolateral facet
<i>mup</i>	Median upper protuberance	<i>rr</i>	Reticulum of ridges
<i>n</i>	Notch	<i>ruf</i>	Right upper facet
<i>nes</i>	Neck-shield	<i>rulr</i>	Right upper lateral ridge
<i>ns</i>	Nectosac	<i>rur</i>	Right upper ridge
<i>o</i>	Ostium	<i>rw</i>	Right wing
<i>oc</i>	Ostial chromatophore	<i>s</i>	Somatocyst
<i>of</i>	Ostial facet	<i>scr</i>	Semicircular ridge
<i>op</i>	Ostial process	<i>si</i>	Sill
<i>or</i>	Ostial ridge	<i>smr</i>	Smooth ridge
<i>orc</i>	Ostial ring canal	<i>sr</i>	Short ridge
<i>os</i>	Outer surface	<i>st</i>	Stem
<i>p</i>	Phyllocyst	<i>stp</i>	Stem-attachment point
<i>pa</i>	Proximal angle	<i>tb</i>	Thrust block (physonects)
<i>pbp</i>	Proximal branch of phyllocyst	<i>te</i>	Tentacle
<i>pd</i>	Disjunct pedicular canal	<i>tfu</i>	Transverse furrow
<i>pe</i>	External pedicular canal	<i>tp</i>	Terminal pore
<i>pf</i>	Proximal facet	<i>tu</i>	Tubercle
<i>phc</i>	Posterior hydroecial canal (bract)	<i>ua</i>	Upper angle
<i>phl</i>	Posterior hydroecial lobe (bract)	<i>ubc</i>	Upper bracteal canal
<i>phr</i>	Perihydroecial ridge	<i>uc</i>	Upper cusp
<i>pi</i>	Internal pedicular canal	<i>udr</i>	Upper distal ridge
<i>pla</i>	Posterior lateral angle	<i>uf</i>	Upper facet
<i>plc</i>	Posterior longitudinal canal (bract)	<i>ufu</i>	Upper furrow
<i>plf</i>	Proximolateral facet	<i>ulc</i>	Upper lateral cusp
<i>pn</i>	Posterior nectophore	<i>ul-r</i>	Upper-lateral ridge (physonect)
<i>pnd</i>	Pneumadenia (gas gland)	<i>ulr</i>	Upper lateral ridge (calycophoran)
<i>po</i>	Pocket	<i>u-lri</i>	Inner upper-lateral ridge
<i>pom</i>	Posterior margin of lower facet	<i>u-lro</i>	Outer upper-lateral ridge
<i>por</i>	Proximal ridge	<i>up</i>	Upper pad
<i>pr</i>	Protuberance	<i>upa</i>	Upper proximal angle
<i>ppr</i>	Proximal protuberance	<i>upr</i>	Upper proximal ridge
<i>ps</i>	Proximal surface	<i>ur</i>	Upper ridge
<i>r</i>	Rim, on larval nectophore	<i>urc</i>	Upper radial canal (nectophore)
<i>rb</i>	Reserve bell	<i>us</i>	Upper surface
<i>rc</i>	Radial canal (gonophore)	<i>v</i>	Velum
<i>re</i>	Rete mirabile	<i>ver</i>	Velar ridge
<i>rla</i>	Right lateral angle	<i>vf</i>	Vertical furrow
<i>rlf</i>	Right lateral facet	<i>v-lr</i>	Vertical-lateral ridge
<i>rllr</i>	Right lower lateral ridge		

9. Glossary of Siphonophore Terminology

Ampulla	Swollen vesicle(s) in tentillum of some physonects
Anterior hydroecial canal	One of a pair of bracteal canals in a prayomorph bract (previously “left hydroecial canal”). See also “posterior hydroecial canal”
Anterior hydroecial lobe	One of two lobes in a prayomorph bract (previously “left hydroecial lobe”)
Anterior longitudinal canal	One of a pair of bracteal canals in a prayomorph bract (previously “left longitudinal canal”). See also “posterior longitudinal canal”
Anterior nectophore	Leading heteromorphic nectophore in a diphyomorph calycophoran colony with two nectophores. Typically streamlined. See also “posterior nectophore”
Anterior–posterior axis	Main axis of siphonophore colony (previously “aboral–oral axis”). Most obvious during swimming, when nectophores propel colony forwards in anterior direction and elongate siphosomal stem trails behind
Apophysis	Prolongation of proximal end of posterior nectophore in some diphyomorph calycophorans. Fits tightly into hydroecium of anterior nectophore
Ascending branch of somatocyst	Penetrating branch(es) of gastrovascular system from pedicular canal in many calycophoran nectophores. Arise(s) either directly from pedicular canal or from ascending (or lateral) surface diverticulum of that canal. Branched or unbranched. Typically thin in prayomorphs, unbranched and swollen in many diphyomorphs, when it is termed a somatocyst
Ascending surface diverticulum	Blind-ending surface canal of gastrovascular system in many codonophoran nectophores. Arises from pedicular canal and typically extends anteriorly in proximal midline. Muscular lamella attached along part or all of its length. See also “descending surface diverticulum”
Auropore	Gas gland of pneumatophore in rhodaliid physonect. Projects from dorsal side of colony where pneumatophore joins nectosome. Surface smooth or papillate. Secretes gas into pneumatophore for buoyancy. In other physonects gas gland integral to pneumatophore and does not protrude
Autotomy	Self-amputation of a zooid, such as a larval nectophore, bract, or definitive nectophore. For defence, release of sexual products, or discarding of old nectophore prior to replacement. Applied also to fragmentation of siphosomal stem in apolemiid and some other physonects
Axial wing	One of two gelatinous extensions from each side of proximal midline in many physonect nectophores. Wings “clasp” stem and interdigitate with wings of nectophores on opposite side of stem
Basigaster	Thickened cuff of cnidocytes (nematoblasts) at base of a gastrozooid, where nematocysts are produced. See also “cnidogenic band”

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Bract	Asexual zooid in cormidium of most codonophorans. Leaf-like and simple in most physonects, more complex in most calycophorans, being rounded in most prayids. Conical or faceted in most diphyomorph calycophorans, with thin distal neck-shield. See also “larval bract”
Bracteal canal	Gastrovascular canal of bract. Typically one in physonect bracts, up to six in prayomorph calycophoran bracts, two in clausophyid bracts, and one (or possibly three) in most abylid diphyomorph calycophoran bracts. Modified into a phyllocyst in most diphyid diphyomorphs (see below)
Bracteal lamellar scar	Gutter-like scar on lower surface of detached physonect bract left by bracteal muscular lamella. Part of bracteal canal
Calyconula	Later larval stage of a calycophoran siphonophore
Central organ	Globular or ovoid structure associated with stem-attachment point in bracts, larval and definitive nectophores of some prayid calycophorans, and larval nectophores of some hippopodiid calycophorans
Chromatophore	Pigment spot on each side of ostium (or elsewhere) in some physonect nectophores
Cnida	Stinging or adhesive capsule with eversible tubule (thread) formed by a cnidocyte and diagnostic of phylum Cnidaria. Includes nematocysts, spirocysts, and ptychocysts, though only nematocysts present in siphonophores
Cnidoband	Ribbon-like band of many haploneme nematocysts in cnidosac of tentillum of most codonophorans. Flanked by two rows of larger nematocysts (mastigophores or stenoteles) and associated with a muscle, nerve, and looped elastic filament. Coiled in most physonects, straight or C-shaped in most calycophorans
Cnidocil	Bristle-like sensory process projecting from surface of a cnidocyte (nematoblast) that triggers discharge of a nematocyst when stimulated
Cnidocyte	Cell that secretes a cnida; also termed cnidoblast or, if a nematocyst is secreted, nematoblast
Cnidogenic band	See “basigaster”
Cnidome	Inventory of cnidae for a particular cnidarian species or taxon
Cnidosac	Swollen sac of a tentillum containing nematocysts. Typically includes a cnidoband, two lateral rows of large nematocysts, and an elastic ligament. Attached to stem of tentacle by a pedicel and typically bearing one or more distal terminal contractile filaments
Codonophoran	Siphonophore with nectophores (swimming bells). Includes physonects and calycophorans
Colony	Dominant asexual stage in life cycle of a siphonophore; see also “polygastric stage”
Commissural canal	Extra canal between upper and lateral radial canals in anterior nectophores of some species of <i>Sulculeolaria</i>
Cormidial bell	Special nectophore in cormidia of cystonects and cormidia and eudoxids of some calycophoran species (<i>Lilyopsis</i> , <i>Stephanophyes</i> , <i>Nectopyramis</i> , some species of <i>Diphyes</i>)

9. Glossary of Siphonophore Terminology

Cormidium	Serially repeated (iterative) group of zooids on siphosome. Includes gastrozooid(s) and one or more gonophores, and typically one or more bracts. Physonect cormidia also include palpons. Cormidia are typically discrete in calycophorans and rhodaliid and apolemiid physonects and diffuse in other physonects. In some prayomorph and most diphyomorph calycophorans, cormidia break off from end of siphosome to become free-living eudoxids
Cusp	Small gelatinous protuberance (previously “tooth”) from surface or edge of nectophore, gonophore, or bract. Typically arising from around the ostium in diphyomorph nectophores, when present
Dactylozooid	Modified swollen palpon in some physonects without palpacle (<i>Cordagalma</i> , <i>Frillagalma</i>). Filled with oil droplets and termed an oleocyst in <i>Pyrostephos</i> (see below)
Descending surface diverticulum	Blind-ending surface canal of gastrovascular system in some codonophoran nectophores. Arises from pedicular canal and extends posteriorly in proximal midline. Muscular lamella often attached along part or all of its length. See also “ascending surface diverticulum”
Dioecious	Sexes separate (i.e., male and female gonophores on different colonies)
Diphyomorph	Calycophoran with typically two dissimilar linearly adjoined nectophores and cormidia typically detaching from posterior end of siphosome to become free-swimming eudoxids
Disjunct pedicular canal	Subsection of pedicular canal (see below) in some prayomorph and many diphyomorph nectophores. Extends along nectophore surface from insertion point of external pedicular canal to origin of internal pedicular canal
Distal lamella	Thin extension from ostial region of anterior and posterior nectophores in many diphyomorph calycophorans (previously “basal lamella”). Aligned along right–left nectophore axis. Entire, notched (emarginate), or, in anterior nectophores, completely divided into two lappets. See “mouthplate”
Diverticulum	Blind-ending branch of a gastrovascular canal
Dorsal–ventral axis	Stem axis orthogonal to anterior–posterior axis of siphonophore colony. Nectophores arise from either ventral or dorsal surface of nectosomal stem, and siphosomal zooids arise mainly from ventral surface of siphosomal stem
External pedicular canal	Subsection of pedicular canal (see below) in codonophoran nectophores, extending between colony stem and nectophore surface
Eudoxid	Free-living sexual stage in life cycle of most diphyomorph and some prayomorph calycophorans; derived from cormidium detached from posterior end of siphosome. Can live independently in plankton for several weeks. Comprises bract, gastrozooid, and gonophore, with more gonophores budded later
Facet	Flat surface of ridged nectophore or bract. Delimited by certain ridges and also often with free edge; this edge straight, notched, or merging imperceptibly into anterior wall of hydroecium in lower facet of some diphyomorphs. Surfaces between some longitudinal ridges in diphyomorph anterior nectophores folding inwards along longitudinal furrow during swimming and not typically termed facets

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Furrow	Alternating with longitudinal ridges in diphyomorph calycophoran nectophore and present in ridged and ridgeless codonophorans
Fuseudoxid	Unique eudoxid comprising fused bract and gonophore. Present only in clausophyid diphyomorph genus <i>Crystallophyes</i>
Gas gland	See "pneumadenia"
Gastrovascular system	Circulatory system representing body cavity or enteron of a cnidarian. Comprises stem canal and branches to all zooids in a siphonophore. Distributes digested food from gastrozooids to rest of colony, circulates oxygen, removes wastes, and may also transport cnidae
Gastrozooid	Asexual feeding polyp in cormidium of colony or in eudoxid. Typically one per cormidium. Comprises proximal pedicel, basigaster (cnidogenic band), stomach, and distal proboscis with mouth. Pedicel typically short and atypically elongate (<i>Forskalia</i> , <i>Lychnagalma</i> , and <i>Sphaeronectes köllikeri</i>), with bracts and (or) palpons attached in some codonophorans
Gonodendron	Branched complex on siphosome of physonects and cystonects. Bears either male or female gonophores (and typically other zooids)
Gonophore	Sexual medusoid zooid arising from either a gonodendron (see above) or pedicel of a gastrozooid. Comprises manubrium (spadix) with one or more sex cells, enclosed (eumedusoid) or not (styloid) by a medusoid bell with radial canals. Each gonophore releases gametes of one sex only
Gonozooid	Specialized polypoid zooid that bears gonophores. See "gonodendron"
Growth zone	Zone on stem where zooids develop. Two growth or budding zones present in codonophorans, and buds develop into either nectophores or cormidia. Budding continues throughout life and growth zones may remain close together at maturity or become separated by a length of stem
Head-piece	Proximal portion of a diphyomorph eudoxid bract, containing phyllocyst. Typically ridged, with or without prominent facets, or smooth
Hydroecium	Hollowed out external cavity on proximal or lower surface of a calycophoran nectophore. Houses stem. Also present in many calycophoran bracts and gonophores
Internal pedicular canal	Subsection of pedicular canal (see below) in codonophoran nectophores, extending from external pedicular (or disjunct pedicular) canal through mesogloea to radial canals of nectosac
Involucrum	Fold (hood) from pedicel of tentillum in some physonects. Partially or completely encloses cnidosac and terminal filament(s)
Lappet	One of two subdivisions of a distal lamella (mouthplate) in anterior nectophores of diphyomorph calycophorans
Larval bract	First bract(s) to develop in many larval physonects and in abyiid calycophorans, for buoyancy. Typically shed (caducous) once definitive bracts and (or) nectophores start to function, but retained in terminal cormidium (protozooid) of some physonects
Larval nectophore	First nectophore to develop in many codonophorans. Typically caducous (shed) and replaced by one, two, or many definitive nectophores. Retained throughout life in some species

9. Glossary of Siphonophore Terminology

Lateral ascending branch of somatocyst	Diverticulum from a lateral surface diverticulum of pedicular canal. Penetrates mesogloea and develops only in prayid calycophoran <i>Nectopyramis thetis</i>
Lateral bracteal canal	Unpaired canal of prayomorph bract (previously “ventral canal”)
Lateral radial canal	One of a pair of canals passing over lateral surfaces of nectosac. Straight or sinuous, atypically with short diverticula or much branched. See “upper and lower radial canals”
Lateral ridge	One of a pair of ridges on lateral surfaces of some physonect nectophores, complete or incomplete and typically terminating at ostium. See “ridges” for lateral ridges of calycophorans
Lateral surface diverticulum	One of a pair of blind-ending surface canals of gastrovascular system in nectophore of <i>Nectopyramis thetis</i> . Arises from pedicular canal and extends outwards, first laterally and then posteriorly
Lower-lateral ridge	One of a pair of ridges delimiting lateral surface from lower lateral surface in many physonect nectophores. See “ridges” for lower lateral ridges of calycophorans
Lower-lateral wing	One of two gelatinous extensions from each side of proximal midline in some physonect nectophores that do not “clasp” stem and interdigitate with nectophores on opposite side (pyrostephids)
Lower radial canal	Paired with upper radial canal and passes over lower surface of nectosac (previously “ventral radial canal”). Typically asymmetric and straight, atypically sinuous or branched. Absent from anterior nectophores of many diphyine diphyid calycophorans. See “upper and lateral radial canals”
Manubrium	Tube in centre of gonophore (previously “spadix”) on which sex cells, either male or female, develop. Mouth absent. See “gonophore”
Median mesogloal protuberance	Swelling protruding from hydroecial wall of some diphyomorph anterior nectophores (<i>Sulculeolaria</i> , <i>Chuniphyes</i>)
Mesogloea	“Jelly” layer between ectoderm and endoderm in body wall. Typically noncellular. Thick in some siphonophore nectophores and bracts. Turgid or flaccid; flaccidity often increased after storage in preservative
Mesogloal plug	Enlarged block of mesogloea in nectophore of some physonects. Incorporated into thrust block of pyrostephids, orthogonal to thrust block in <i>Marrus</i> spp.
Monoecious	Hermaphrodite (male and female gonophores on same colony)
Mouthplate	Thin distal extension of nectophore beyond ostium in some physonects. Also used for distal lamella of diphyomorph calycophorans (see above)
Muscle-free zone	Region of proximal wall of nectosac lacking musculature. Present in nectophores of many dioecious physonects
Muscular lamella	Tissue sheet connecting nectophores, gonophores, and bracts to nectosomal or siphosomal stem in siphonophores. Pedicular canal from stem passing either through sheet or along one edge
Neck-shield	Distal portion of diphyomorph eudoxid bract

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Nectophore	Asexual medusoid swimming bell of codonophoran siphonophores, with muscular nectosac for propulsion. Many and similar (homomorphic) in physonects, few and similar in prayomorph calycophorans, few and dissimilar (heteromorphic) in diphyomorph calycophorans. Two types formed in most codonophorans, larval and definitive (mature). Third type found in cormidia of cystonects and some calycophorans. See "cormidial bell"
Nectophore replacement	Larval nectophore replaced by definitive nectophores in many codonophorans, and old definitive nectophores probably replaced throughout life by new ones in physonects, possibly replaced several times in prayomorph calycophorans, and up to 4 times in some diphyomorph calycophorans (<i>Sulculeolaria</i>). Buds for new nectophores form in growth zone, while old nectophores are discarded from either posterior end of nectosome (physonects) or from distalmost muscular lamella of a "false nectosome" in calycophorans
Nectosac	Internal (subumbrellar) cavity of nectophore or gonophore opening via an ostium and with muscular walls. Contracts rhythmically to pump out water for colony propulsion. Muscles thick or thin and shape variable
Nectosomal polyp	Polypoid zooid on nectosome of apolemiid physonects
Nectosome	Anterior portion of stem, bearing nectophores in codonophoran siphonophores (absent in cystonects). Reduced to swollen bulb in rhodaliid physonects and absent from agalmatid genus <i>Athorybia</i>
Nematoblast	See "cnidocyte"
Nematocyst	Type of cnida found in siphonophores, comprising capsule consisting of two or more layers. Secreted by a nematoblast
Oleocyst	Enlarged palpon unique to physonect genus <i>Pyrostephos</i> . Lacks a palpacle and contains oil for flotation of large, heavy stem
Ostium	Distal aperture of nectosac (of nectophore or gonophore)
Ostial ring canal	Circular gastrovascular canal around ostium of nectophore or gonophore
Palpon	Modified gastrozooid found in cystonects and many physonects (and calycophoran <i>Stephanophyes</i>). Each typically bearing a simple tentacle termed a palpacle. Chemosensory or excretory function. Termed a gonopalpon when in a gonodendron. Absent from <i>Bargmannia</i> and two species of <i>Marrus</i>
Pedicel	Stalk of a zooid
Pedicular canal	Gastrovascular canal connecting stem canal to zooid canal, specifically to radial canals of nectosac in nectophore
Pericystic cavity	See "pneumatophore"
Phyllocyst	Swollen branch (diverticulum) of gastrovascular system in a diphyomorph eudoxid bract; typically contains oil droplets
Planula	Ciliated larva formed from fertilized egg

9. Glossary of Siphonophore Terminology

Pneumadenia	Gas gland of pneumatophore (see above)
Pneumatophore	Anterior gas-filled float in physonect and cystonect siphonophores. Comprises gas gland (pneumadenia), central gas cavity (pneumatosaccus), and surrounding pericystic cavity (typically with septa) that connects to gastrovascular cavity of stem. Much enlarged in rhodaliid physonects and agalmatid physonect genus <i>Athorybia</i> . See “aurophore”
Polygastric stage	See “colony”
Posterior hydroecial canal	One of a pair of bracteal canals in a prayomorph bract (previously “right hydroecial canal”); see “anterior hydroecial canal”
Posterior hydroecial lobe	Lobe of prayomorph bract (previously “right hydroecial lobe(s)”)
Posterior longitudinal canal	One of a pair of bracteal canals in a prayomorph bract (previously “right longitudinal canal”). See “anterior longitudinal canal”
Posterior nectophore	Following heteromorphic nectophore in a diphymorph calycophoran colony with two nectophores. See “anterior nectophore”
Prayomorph	Calycophoran with typically two apposed nectophores, and cormidia typically retained on siphosome throughout life
Probud	Bud from which siphosomal cormidium develops in codonophorans
Protozooid	Original mouth of larval colony, at posterior end of siphosome in mature physonect and some prayomorph colonies
Proximal-distal axis	Primary axis of any zooid. Each zooid attaches to stem at proximal end and has a free distal end
Radial canals	Gastrovascular canals in nectosac of nectophore or gonophore. Typically four and bilaterally symmetric, atypically many and branched (<i>Praya</i>). Arise together from internal pedicular canal in most species, passing over nectosac to ostial ring canal
Reserve bell	Small extra nectophore in hydroecium of some calycophorans. Replaces a definitive nectophore
Rete mirabile	Network of fine canals from a gastrovascular canal of a nectophore
Ridges	Present on nectophores, bracts, and gonophores of many codonophorans. Often of diagnostic importance in nectophores. Ridges of diphymorph nectophores typically aligned along long axis (longitudinal ridges), typically seven (upper, two upper lateral, two lower lateral, and two lower) or fewer and complete, atypically incomplete, and with orthogonal velar ridge
Right-left axis	Axis of stem or zooid; orthogonal to dorsal-ventral axis of stem or to upper-lower axis of zooid (when viewed from outside the colony)
Siphonula	Later larval stage of a physonect siphonophore
Siphosome	Posterior portion of stem, bearing cormidia in all siphonophores
Somatocyst	Swollen diverticulum of gastrovascular system that penetrates mesogloea in some calycophoran nectophores. Shape of diagnostic importance in some diphymorphs
Stem	Comprising anterior nectosome and posterior siphosome. Elongate in most siphonophores, with nectosomal portion either elongate or short; no stem develops in <i>Physalia</i>
Stem-attachment point	Region on proximal surface of (preserved) nectophore or bract where stem is attached in life

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Tentacle	Arising from basigaster region of gastrozoid, only one per gastrozoid, typically bearing several side branches, or tentilla, for prey capture
Tentaculozoid	Siphosomal tentacle unique to physonect genus <i>Bargmannia</i> . Probably representing an atrophied polyp with a single hypertrophied tentacle
Tentillum	Specialized side branch of a siphonophore tentacle bearing complex nematocyst battery. Present in all codonophorans except <i>Apolemia</i> . Variable in physonects and of taxonomic importance. Similar in calycophorans. Typically comprising pedicel, cnidosac with cnidoband, one or more terminal filaments, and involucrum
Terminal filament	Thin filament(s) at distal end of cnidosac in most tentilla, with desmoneme and rhopaloneme nematocysts and with or without terminal thickening (sinker). Typically only one, atypically two or more, with or without ampulla(e) (see above)
Thrust block	Thickening (often a flap in preserved material) on proximal surface of physonect nectophore, between axial wings, that abuts stem. Size and shape can be diagnostic. Typically with ascending surface diverticulum on proximal surface and internal pedicular canal passing through mesogloea
Upper bracteal canal	Unpaired canal of prayomorph bract (previously “dorsal bracteal canal”)
Upper radial canal	Paired with lower radial canal and passing over upper surface of nectosac (previously “dorsal radial canal”). Typically asymmetric and straight, atypically sinuous or branched. Only median radial canal present in many diphyine anterior nectophores, looping over nectosac from disjunct pedicular canal on lower surface to ostial ring canal on upper surface. See “lateral and lower radial canals”
Upper-lateral ridge	One of a pair of ridges delimiting upper surface from lateral surface in many physonect nectophores. May subdivide distally into inner and outer branches
Upper-lower axis	Zooid axis orthogonal to proximal-distal axis; upper surface of zooid is directed anteriorly and lower surface is directed posteriorly
Velar ridge	Single ridge in some diphyomorph anterior nectophores lying near and orthogonal to ostium. Complete or incomplete
Velum	Thin ring of tissue projecting inwards around ostium of nectophore and gonophore. Typically damaged during preservation
Vertical-lateral ridge	One or more pairs of ridges connecting upper-lateral ridge with lower-lateral ridge in some physonect nectophores

10. Systematic Account

Phylum CNIDARIA Verrill, 1865

Class HYDROZOA Owen, 1843

Subclass HYDROIDOLINA Collins, 2000

**Superorder SIPHONOPHORA
Eschscholtz, 1829**

**Order CODONOPHORA Dunn, Pugh,
and Haddock, 2005b**

**10.1. Suborder PHYSONECTAE
Haeckel, 1888a**

Diagnosis

Codonophora with pneumatophore present; nectophores within colony similar and typically many (except *Athorybia* and *Melophysa*), attaching to either extended or reduced nectosome; siphosome with diffuse cormidia (except Apolemiidae and Rhodaliidae); each cormidium comprising gastrozooid with tentacle bearing complex nematocyst batteries on side branches (tentilla) (except Apolemiidae) of taxonomic importance, palpons, bracts, and gonophores on gonodendra (dioecious or monoecious).

Notes

Dunn and Wagner (2006) suggest that the Codonophora first evolved after the development of an ancestral nectosome and the accompanying derivation of each siphosomal cormidium from a single probud (see Sections 2.2 and 3.2), and that this group gave rise to the great variety of Siphonophora found in today's seas. The hypothesized phylogeny given by these authors in their figure 7 shows that physonects include a diversity of clades, some of which are monophyletic, others paraphyletic. Within the former group, some species are nested within groups of species previously referred to different families. However, only certain of these nodes

are significant, and considerable caution must be exercised when interpreting this phylogeny. Prior to Dunn and Wagner's work, most authors, including Totton (1954, 1965a) and Mackie et al. (1987), were unsure whether physonects were primitive or derivative. However, Dunn et al. (2005b) and Dunn and Wagner (2006) show that the Cystonectae are sister to the Codonophora, and that within the latter the family Apolemiidae is monophyletic.

The remaining codonophorans include a reasonably well supported monophyletic clade for the Calycophorae, and two monophyletic clades for the Forskaliidae and Agalmatidae; these three clades are all monoecious. Dunn and Wagner (2006) postulate a transition from dioecy to monoecy early in the phylogeny, before the evolution of the Calycophorae, but this node is poorly supported (it has a Bayesian posterior probability of less than 90%) and monoecy amongst the Codonophora might have arisen more than once (Dunn et al. 2005b).

In the present work the suborder Physonectae is retained, despite its apparent paraphyletic condition, because these codonophorans share a number of characters that distinguish them from those in the suborder Calycophorae (Section 10.2), as discussed below.

Historical. The name Physonectae was first proposed by Haeckel (1888a) for species described from the *Challenger* expedition, but the family Physophoridae was excluded. The latter was added later by Bigelow (1911b), and a new family, Pyrostephidae, introduced by Moser (1925). Totton (1965a) referred seven families to the Physonectae, including Apolemiidae, Agalmatidae (as Agalmidae), Forskaliidae, Pyrostephidae, Physophoridae, Athorybiidae, and Rhodaliidae. Pugh (1999a, 2001, 2003, 2006b) subsequently revised two of these, Pyrostephidae and Forskaliidae, added two new families, Erennidae and Resomiidae, and removed one family, Athorybiidae.

Relationships. In the past, physonects were grouped by Haeckel (1888b), Stepanjants (1967), Mackie et al. (1987), and Carré and Carré (1995) into long-stemmed and short-stemmed forms, but the new

molecular analysis of Dunn et al. (2005b) shows that amongst the codonophorans a short stem evolved more than once. Thus, the short-stemmed species *Athorybia rosacea* is nested within a long-stemmed group comprising *Nanomia bijuga*, *Halistemma rubrum*, and three species of the genus *Agalma*. The latter species were previously referred to the catch-all family Agalmatidae and are now referred to a subgroup within this family named the Agalmatidae *sensu stricto* (Dunn et al. 2005b; Pugh 2006b). Another short-stemmed species, *Stephalia dilata*, is not closely related to any other physonect tested, and a third species, *Physophora hydrostatica* (with a short siphosome but elongate nectosome), shows possible affiliations with a clade of four *Forskalia* species, although in the consensus tree of Dunn et al. (2005b, fig. 6) this node is poorly supported.

New characters shown in the molecular analysis of Dunn et al. (2005b) to be of possible importance in the phylogeny of the Siphonophora are reviewed by Pugh (2006b) and arranged into a tentative phylogeny for the Physonectae in his figure 21. Pugh (2006b) suggests that the presence of nectosomal polyps in the Apolemiidae might be an ancestral character that has been secondarily lost in other physonects, and nectosomal polyps are discussed further in Section 10.1.1. The ancestral codonophoran is postulated to have had a ventral nectosome (Pugh 2006b); in other words, the nectophores were budded from the same side of the nectosomal stem as the siphosomal zooids were budded from the siphosomal stem (see Fig. 1F). A ventral nectosome is exhibited by all physonects so far examined except for species of the families Pyrostephidae and Agalmatidae *sensu stricto*, which have a dorsal nectosome (Pugh 2006b). Physonects can also be divided into groups based on their reproductive state, and are thought to be primitively dioecious, with a transition to monoecy occurring early in phylogeny (Dunn and Wagner 2006; see Section 3). Another change that may have taken place at about this time is the appearance of a descending surface diverticulum on the proximal surface of the nectophore in monoecious physonects (Pugh 2006b, as *descending pallial canal*). Pugh (2006b) also notes that the musculature of the nectosac may be linked to reproductive state, since all dioecious physonects except the Rhodaliidae have a muscle-free zone on the lower proximal surface of the nectosac (see Section 2.3.2), whereas in monoecious physonects the musculature is complete. In the Rhodaliidae the nectophores appear to have reverted to the ancestral type (Pugh 2006b).

Dioecious physonect families include Erennidae, Pyrostephidae, and Rhodaliidae, and monoecious families include Agalmatidae *sensu stricto*, Forskaliidae, and Physophoridae, and an additional family recently introduced by Pugh (2006b), Resomiidae. Within the former group, Pugh also includes two genera previously placed in the Agalmatidae (*Marrus* and *Stephanomia*), and within the latter group he further separates the Agalmatidae *sensu stricto* from the other monoecious families because all agalmatids have a dorsal nectosome (2006b, fig. 21). The nectosome is ventral in the remaining monoecious families (Forskaliidae, Physophoridae, and Resomiidae) and also in three monoecious genera previously referred to the family Agalmatidae (*Cordagalma*, *Frillagalma*, and *Lychnagalma*). Thus, although Pugh (2006b) excludes a total of five genera from the Agalmatidae *sensu stricto*, here they are retained as indeterminate genera of the family Agalmatidae (Section 10.1.3). Further molecular analyses are needed to better resolve the relationships of these five genera to other physonect families, but this task is outside the scope of the present work.

The only physonect families so far collected from Canadian Pacific waters (apart from unconfirmed records) are the Apolemiidae, Agalmatidae, and Pyrostephidae. Their diagnoses are given below (Sections 10.1.1, 10.1.2, and 10.1.3) and are derived from a character matrix based on the eight physonect families herein recognized: Apolemiidae, Erennidae, Pyrostephidae, Rhodaliidae, Forskaliidae, Physophoridae, Resomiidae, and Agalmatidae. The relationships among these families (excluding the new family, Resomiidae) suggested by Dunn et al. (2005b) and Dunn and Wagner (2006) are summarized as follows: the Apolemiidae (represented by four unnamed species; see Dunn et al. 2005b, fig. 6) is sister to all other codonophorans; the Pyrostephidae (represented by two species of *Bargmannia*) is sister to three other dioecious physonects, two of which are presently assigned to different families (see Dunn and Wagner 2006, fig. 7); the Agalmatidae (represented by five core agalmatid species and *Athorybia rosacea*, but excluding *Cordagalma ordinata*, as *C. cordiforme*) is sister to a clade comprising the Forskaliidae (represented by four species) and possibly the Physophoridae (represented by one species), although the latter node is poorly supported. The agalmatid clade is distinguished from the forskaiid/physophorid clade by the acquisition of a new character: reiteration of the anteriormost cormidial element in mature cormidia (Dunn and Wagner 2006, fig. 7).

Characters used to distinguish zooids of the suborder Physonectae from those of the suborder Calycophorae (see Section 10.2) are reviewed below, followed by analyses of the physonect families, genera, and species found in Canadian Pacific waters.

Pneumatophore. All physonects possess a pneumatophore, and this structure is considered to be a neoformation (Mackie 1999). Cystonects (comprising only five valid species) also have a pneumatophore, but it is either exceptionally large (as in the pleustonic cystonect *Physalia*) or contains unique hypocystic villi that arise from the gas gland (Rhizophysidae). The short-stemmed physonect family Rhodaliidae also has an enlarged pneumatophore, and this is used to maintain a position in the water a short distance above the substratum, since this family is benthic (Hissmann et al. 1995). In *Athorybia* species the pneumatophore is also enlarged, but this genus is pelagic.

Nectophores. Physonects typically bear a number of identical asexual nectophores (except for the agalmatid genus *Athorybia*), and in seven of the eight families these are distributed along an elongate nectosome (Fig. 1A). In the Rhodaliidae the nectosome is reduced to a swollen bulb, and in the genus *Athorybia sensu stricto* of the family Agalmatidae, it is effectively absent. Nectophores arise from either the ventral midline or the dorsal midline of the nectosomal stem (Dunn et al. 2005b; Pugh 2006b).

The axes of a typical physonect nectophore shown in Figures 1B and C are based on those defined by Haddock et al. (2005a) and explained in Section 2.3.1. In most species the proximal–distal axis is longer than the orthogonal upper–lower axis (Fig. 1B), but in some it is the upper–lower axis that is longer, as seen in the apolemiids *Nanomia bijuga* and *Cordagalma ordinata*. Thus, the long axis of the latter nectophores is aligned approximately parallel to the anterior–posterior axis of the colony.

The nectophores of most long-stemmed physonects develop an axial wing on each side of the stem-attachment point (Fig. 1G), except in the Pyrostephidae, where the wings are lateral or lower-lateral in position. Typical physonect axial wings extend outwards beyond the proximal midline, and in the nectophore descriptions given below, the wing tips are taken as representing the proximal end of the proximal–distal nectophore axis. Most nectophores bear ridges that are of diagnostic importance (see

below), but in some families the ridges are either weak (Physophoridae and Forskaliidae) or absent (Apolemiidae and Rhodaliidae). Several of the ridge names adopted by earlier authors (Pugh and Youngbluth 1988a; Pugh 1998, 1999b; Mapstone 2004; Dunn et al. 2005a) do not correlate well with the recently defined upper–lower axis of the nectophore, so Pugh (2006b) recently revised some of the ridge names. These names are followed in the present work (with one exception; see Section 10.1.2), but are hyphenated to distinguish them from similar names applied here to the ridges of calycophoran nectophores (Section 10.2). Thus, for physonect nectophores the name upper-lateral ridge replaces the name apicolateral ridge and lower-lateral ridge replaces the name infralateral ridge (Fig. 1F). These names are preferred because these two ridges delimit the lateral borders of the upper and lower surfaces of the nectophore; the name upper-lateral ridge also follows an earlier application by Totton (1954, p. 47) to *Agalma elegans*. No homology is implied between these names and similar names used for the ridges of calycophorans described later (Section 10.2), where nectophore axes are defined differently. Additionally, hyphenation of physonect ridge names is extended to the vertical-lateral ridge of physonects, used by earlier authors but without a hyphen. The name lateral ridge as used by earlier authors is herein retained.

In physonects, nectophores typically have a thickened region on the proximal surface known as the thrust block (Fig. 1G). This structure is flanked by the axial wings and is assumed to cushion the nectophore against damage during swimming as powerful contractions of the nectosac force the nectophore against the stem. The size and shape of the thrust block are also of taxonomic importance, and it is enlarged in nectophores with a muscle-free zone on the proximal surface of the nectosac, particularly in the family Pyrostephidae. In the latter family the enlarged thrust block lies along the proximal–distal nectophore axis and is termed the mesogloea plug by Totton (1965a). Such a plug is also identified here in the agalmatid genus *Marrus*, but it extends across the right–left nectophore axis, orthogonal to the proximal–distal axis, and forms part of the nectophore body, not the thrust block; in *Marrus* species the latter structure is represented by a tongue-like extension from the proximal surface of the plug (see Section 10.1.3).

A pedicular canal connects each physonect nectophore to the stem, as discussed in Section

2.3.2. In physonects this canal is always direct, and develops either one or two surface diverticula, as shown in Figures 5 and 6. No penetrating somatocyst is present, although a very short branch may penetrate inwards from the ascending surface diverticulum, as in *Halistemma foliacea* (Mapstone 2004, fig. 2e, as *H. amphytridis*).

Siphosomal cormidia. Physonect cormidia are herein considered to be either diffuse or discrete. They must all form from a probud (Dunn and Wagner 2006), and in the diffuse cormidia typical of most physonects the zooids then spread out along the length of the siphosomal stem, with further zooids sometimes budded later from the anteriormost cormidial element, as mentioned above. In discrete cormidia, zooids develop on branches from a single pedicel instead of spreading out along the siphosome. Only a few families display this type of cormidium, including the Apolemiidae (Gegenbaur 1853, pl. 18 fig. 1) and Rhodaliidae (Hissmann 2005, fig. 10). The remaining families have diffuse cormidia, with zooids either spreading out along an elongate linear cormidium, as in long-stemmed physonects, or remaining close together, as in short-stemmed forms such as *Athorybia* and *Physophora*.

Zooids composing a typical physonect cormidium include a gastrozooid, a number of bracts and palpons, and gonophores borne on gonodendra, as mentioned above. In linear cormidia, a gastrozooid was thought to mark the limit of each cormidium (Totton 1965a), but Dunn and Wagner (2006) recently showed that this is the case in only two of the three agalmatid physonects they studied (*Nanomia bijuga* and *Forskalia formosa*); in the third (*Agalma elegans*) a particularly enlarged palpon, known as the B-palpon, marks the limit of each cormidium. Gastrozooids arise on one or several branches in the discrete cormidia of short-stemmed rhodaliids (Hissmann 2005), but the early development of these cormidia is unknown. Similarly, in long-stemmed Apolemiidae there are likely to be one or several gastrozooids per cormidium (Mapstone 2003), with each cormidium arising from a probud, as Dunn and Wagner (2006) concluded for one species, but budding sequences in this family have not yet been investigated.

Physonect gastrozooids are typically attached to the siphosome by a short pedicel, as is shown by Dunn (2005, fig. 4) for *Bargmannia elongata* and Pugh (2005, fig. 7) for *Physophora gilmeri*, and is inferable from Dunn and Wagner (2006) for

Agalma elegans and *Nanomia bijuga*. However, in species of the family Forskaliidae and the agalmatid genus *Lychnagalma* the gastrozooids are borne on elongate pedicels. These pedicels are reported by Dunn and Wagner (2006) to bear a number of bracts in *Forskalia formosa* and a single palpon near the proximal end of the gastrozooid in *Lychnagalma utricularia*. It is also worth noting here that bracts also arise from the shorter pedicels of the gastrozooids of *P. gilmeri* (Pugh 2005) and one or more palpons on the short gastrozooid pedicels of *A. elegans* (Dunn and Wagner 2006).

The tentacle that arises from the base of each gastrozooid typically bears a number of complex nematocyst batteries on the tentilla, or side branches, and these are used to catch prey, as discussed in Section 4.3. In physonects, tentilla are of taxonomic importance and occur in all physonects except the Apolemiidae. The tentacles of pyrostephids and erennids bear unique, but different in each case, tentilla that contain only three types of nematocysts, whereas in agalmatids and resomiids four types are typically present (Pugh 2001, 2006b). The tentilla of pyrostephids have a straight or slightly coiled cnidoband, with large nematocysts at the proximal end only and two smaller types throughout the remainder, including in the terminal filament (Pugh 1999a); this tentillum type is discussed further in Section 10.1.2. In erennids the cnidoband is also straight and bears one large type of nematocyst and two smaller types, but the terminal filament is rigid and devoid of nematocysts (Pugh 2001). Resomiids develop a cnidoband that first coils up as it matures and then unwinds to become folded into three zigzag sections (Pugh 2006b). In the Forskaliidae and core Agalmatidae *sensu stricto* (as defined in Section 10.1.3) the cnidoband is coiled and bears either a single terminal filament (unicornuate) or two terminal filaments and an ampulla (tricornuate). Agalmatid and resomiid tentilla are also typically protected by an involucrum, which grows up from the base to enclose the cnidoband either partially or completely. Such a growth sequence is clearly shown in the tricornuate species *Agalma okeni* by Bigelow (1911b, pl. 17 figs 3–7), and a mature tricornuate tentillum is also shown for *A. elegans* by Bigelow (1911b, pl. 18 fig. 10). Bigelow's figures also illustrate the trifid nature of a tricornuate tentillum of a core agalmatid, with the ampulla forming a swollen vesicle (in this case terminal) flanked by two (coiled-up) terminal filaments. Agalmatid tentilla are discussed further in Section 10.1.3.

Palpons and gonophores are also present in all mature physonect cormidia, and recent studies by Dunn (2005) and Dunn and Wagner (2006) show that these zooids mostly arise from a probud, but that in two species (*Agalma elegans* and *Nanomia bijuga*) they may also arise later, directly from the stem, as noted above. Bracts also arise from the probud at the bases of gastrozooids and palpons, but can also appear somewhat later directly on the stem. In older cormidia some of the zooids may be lost, so to study the complete arrangement, researchers must examine mature cormidia that still lie relatively close to the growth or budding zone (Dunn and Wagner 2006). Physonect bracts are relatively simple and typically have only one bracteal canal (Figs 1D and E), at the distal tip of which there is often a patch of nematocysts. A bracteal lamella, or pedicel, connects the bract to the stem from the lower surface, typically along the proximal third of the bract, and, if stimulated, the bract can detach easily by autotomy (see Section 3.4).

10.1.1. Family APOLEMIIDAE Huxley, 1859

Diagnosis

Physonectae with colony linear and having ventral nectosome with many similar nectophores and nectosomal polyps; nectophores ridgeless, with thrust block not enlarged and nectosac muscular throughout; nectophores without descending surface diverticulum from pedicular canal on proximal surface; dioecious; gastrozooid tentacles simple and without tentilla.

Monotypic for *Apolemia* Eschscholtz, 1829

Notes

The family Apolemiidae was introduced by Huxley (1859) for the genus *Apolemia* erected 30 years earlier by Eschscholtz (1829) for a physonect with simple tentacles that lack tentilla. The genus was monotypic for *Apolemia uvaria* (Lesueur, 1815) until 1967, when a second genus and species were added by Stepanjants (1967) for *Ramosia vitiazi*. Nine years later a third genus and species were added by Margulis (1976) for *Tottonia contorta*. More recently *A. uvaria* and *T. contorta* were redescribed by Mapstone (2003), who also made a brief reassessment of *R. vitiazi*. She found that in *A. uvaria* there are 4–6 nectosomal polyps per nectophore, whereas in *R. vitiazi* and *T. contorta*

there are only 1 or 2. She also noted that the courses of the radial canals of the nectophore and the morphology of the bract varied slightly amongst the three species (Mapstone 2003). However, the nectophores and bracts were of the same basic form in all three species, and these differences seem to be of only specific importance, as Mapstone herself noted. In other families of long-stemmed physonects, genera are distinguished by more fundamental characters such as nectophore shape and ridge pattern and tentillum type. Since tentilla are absent from apolemiids, and nectophore morphology is similar, the genera *Ramosia* Stepanjants, 1967 and *Tottonia* Margulis, 1976 are herein referred to the genus *Apolemia* Eschscholtz, 1829.

In the molecular consensus tree of Dunn et al. (2005b), four as yet unnamed species of apolemiids form a monophyletic clade that is sister to all other Codonophora, as noted in Section 10.1. Characters that distinguish these species include those in the family diagnosis given above, particularly the presence of nectosomal polyps and the absence of tentilla on the gastrozooid tentacles. Totton (1965a, p. 47) includes these among three characteristics of *Apolemia (uvaria)* that he considers “striking”: the presence of “bunches of tentacles [polyps] at the bases of the nectophores”, “the comparatively slight difference between the gastrozooids and their [tentilla-less] tentacles and the palpons with their palpacles”, and “the production of free cormidal groups”. These characters, together with separate sexes, or dioecy (see Dunn et al. 2005b, fig. 7), indicate that the family is primitive, and for this reason is treated first in most taxonomic works on siphonophores (for example, Kirkpatrick and Pugh 1984; Pugh 1999b; Totton 1965a) and in the present systematic account (Section 10).

Apolemiid nectophores are compressed along the proximal-distal axis, which makes their upper-lower axis either longer than, or similar in length to, the proximal-distal axis. Thus, their axes differ from those of typical physonects, where the proximal-distal nectophore axis is longer than the upper-lower axis (see Section 2.3.1; Fig. 1B). The proximal-distal axis of apolemiids is best seen in lateral view, but unfortunately, the present apolemiid nectophores were either too fragile or too laterally distorted to draw in this view. However, the reader can superimpose this axis onto lateral views of nectophores of two other apolemiid species in

Mapstone (2003, figs 6b, 11b). In those figures the proximal-distal nectophore axis extends between the ascending surface diverticulum (as *pallial canal scar, pas*) and the ostium. The upper-lower axis lies orthogonal to this axis and can be superimposed by the reader onto the figures of apolemiid nectophores given below, where it will lie parallel to the upper and lower radial canals and extend between the thrust block and the base of the ostial process.

Nectophores of apolemiids have nectosacs that fill more of the nectophore than do the nectosacs of most agalmatids (see Section 10.1.3). They are also deeply hollowed out proximally, as already noted by Totton (1965a), Pugh (1999b), and Mapstone (2003), and all three authors describe this hollowing out as axial. However, in the present work this surface is regarded as proximal and it is flanked by two extensive axial wings, well shown in two schematic views of an apolemiid nectophore by Mapstone (2003, figs 1b and c). In mature nectophores the axial wings lie farthest apart at their tips and converge on the proximal side of the nectophore, typically at the level where the ascending surface diverticulum originates from the pedicular canal. Here the proximal wing bases are swollen and typically lie close together (Mapstone 2003, figs 6c, 11c; see proximal views of the two apolemiid figures given in this work). They flank the lower furrow, which begins just below the ascending surface diverticulum. This furrow passes downwards and then turns distally towards the ostium (see Mapstone 2003, figs 1c, 6c, 11c, as *ventral furrow*), but peters out before reaching the latter, on the proximal side of the ostial process (see Mapstone 2003, figs 6b, 11b). Apolemiid lateral radial canals are looped, and may or may not give rise to short diverticula (see Mapstone 2003, figs 4, 11, 15b and c). There is also an ascending surface diverticulum from the pedicular canal, as shown in Figures 4 and 5 (see also Mapstone 2003, figs 6b and c, 11b and c, 15c, as *pallial canal scar (pas)*), but no descending surface diverticulum. The absence of the latter, as the *descending pallial canal*, is shown by Dunn et al. (2005b, p. 931) to be linked to a dioecious state.

In apolemiids, nectophores alternate with nectosomal polyps on the nectosome, as noted by Dunn (2005) and mentioned above (Section 3.2), suggesting that the nectosome of long-stemmed

physonects is perhaps more complex than was previously appreciated (Dunn and Wagner 2006). Small buds at the base (on the posterior side) of each developing nectophore in some agalmatids and a pyrostepheid also hint at this (Dunn 2005; Dunn and Wagner 2006). These buds may well represent the vestige of a nectosomal polyp, and in the apolemiid species studied by Mapstone nectosomal polyps were also found to arise from the posterior end of each nectophoral muscular lamella (as *nectosomal tentacles* or *nectosomal tentacle bases*; see Mapstone 2003, figs 2c and d, 3a–c, 9c, 15a).

The siphosomal cormidia of apolemiids are poorly understood at present because even after initial relaxation in MgCl₂, specimens still undergo considerable contraction on preservation, making detailed studies of zooid arrangement difficult. Dunn and Wagner (2006) found that in apolemiids, cormidia arise from a probud, as in other physonects, but did not follow the budding sequence or determine the organization of mature cormidia. Totton (1965a) noted that apolemiid cormidia are discrete, and not spread out along the siphosomal stem as in other long-stemmed physonects (see Sections 3.2 and 10.1); this is well shown in a figure by Gegenbaur (1853, pl. 18 fig. 1) of a young colony of *Apolemia uvaria* from the Mediterranean. Totton (1965a) also estimated that each mature cormidium of *A. uvaria* comprised up to 50 or more palpons, in addition to bracts and one or more gastrozooids. Mapstone (2003) typically found two gastrozooids per cormidium in *A. uvaria* where an individual cormidium could be identified, and it seems likely that in this species all zooids in each cormidium arise from a single pedicel. Similarly, Stepanjants (1967, fig. 78) shows an apparently discrete cormidium (or part of one) in *Ramosia vitiasi*, comprising two gastrozooids, two bracts, and 11 palpons. This arrangement recalls that found in the short-stemmed physonect family Rhodaliidae, where cormidia can be either polygastric, with several gastrozooids per cormidium as in the genus *Tridensa* (Hissmann 2005), or monogastric, with only a single gastrozooid per cormidium as in the genera *Arancialia* (Hissmann 2005) and *Archangelopsis* (Hissmann et al. 1995). However, further study of relaxed apolemiid cormidia is needed to confirm these preliminary observations.

Genus *Apolemia* Eschscholtz, 1829

Diagnosis

With the characters of the family.

Type species: *Apolemia uvaria*.

Notes

The generic names *Ramosia* and *Tottonia* are herein relegated to junior synonyms of the genus *Apolemia*, for the reasons given below.

The type species was first figured by Lesueur as *Stephanomia uvaria* in an unnumbered plate published in 1815 (see the Discussion in Mapstone 2003). As Totton (1965a) noted, it is an arduous task to accurately depict such a writhing colony, but Lesueur consummately achieved this in his plate, which is reproduced by Mapstone (2003, fig. 14). *Apolemia uvaria* was much studied in the past, in both the Bay of Villefranche and Messina Harbour, where it was often brought to the surface by upwelling. It was included as an example of a typical physonect in several textbooks, probably because of its large size. In recent years *A. uvaria* has been collected less often, but so far there are no reliable records outside the Mediterranean, where it may be replaced by other species. These include *A. vitiasi* and *A. contorta* from the North Pacific (for a synopsis of distribution see Mapstone 2003) and several other species taken off California and in the northwest Atlantic (Dunn et al. 2005b), as well as giant apolemiids reported by Mackie et al. (1987) that still have not been fully described.

Apolemia contorta (Margulis, 1976)

(Fig. 12)

Tottonia contorta Margulis, 1976: 1246, figs 7–11; 1980b: 342, figs 1a–m, 2a–m; Mackie et al., 1987: 116; Mapstone, 2003: 194, figs 9–13.

Diagnosis

Apolemiid with nectosome having 1 or 2 nectosomal polyps per nectophore; nectophores with axial wings originating close together in distal midline and lateral furrows not meeting in distal midline; upper radial canal following zigzag course on distal nectosac surface; lateral radial canals with shallow

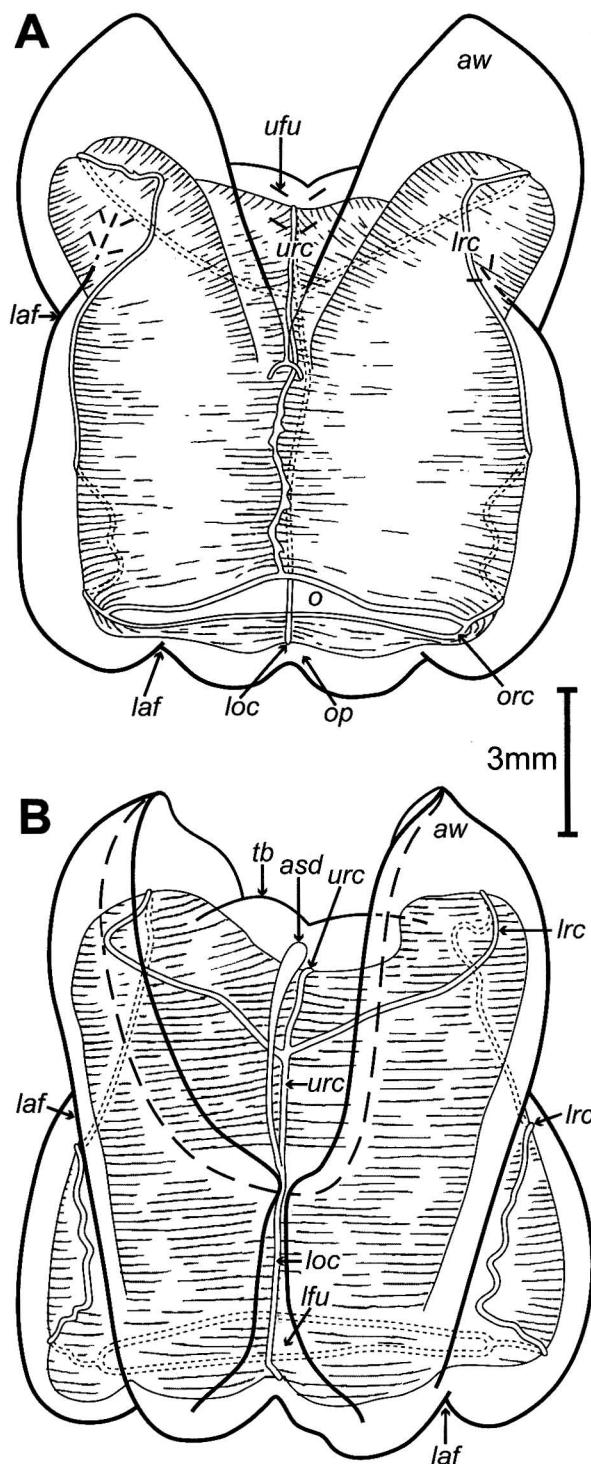


Fig. 12. *Apolemia contorta*: A: nectophore, distal view; B: different nectophore, offset proximal view (asd, ascending surface diverticulum; aw, axial wing; laf, lateral furrow; ifu, lower furrow; loc, lower radial canal; lrc, lateral radial canal; o, ostium; op, ostial process; orc, ostial ring canal; tb, thrust block; urc, upper radial canal).

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

lower loops and typically with undulations in upper and lower loops; ascending surface diverticulum relatively elongate; bracts with many opaque patches on upper surface and bracteal canal remaining close to lower surface throughout.

Material examined

Four nectophores from Canadian Pacific station LC11 (700 m) (Fig. 12) BCPM 996-217-1 (Fig. 11, Table 1). Specimens from the NHM collections: *Apolemia* (as *Tottonia*) *contorta* Registration numbers (Reg. Nos) 2002.787, 12 nectophores, 5 nectosomal polyps, nectosome with 2 attached nectophores, 2 polyps, 1 short siphosomal portion, and 6 long siphosomal portions (34°51'N, 122°45'W); 2002.788, 5 nectophores, nectosome with 2 attached nectophores, 1 polyp, and short siphosomal portion (34°59'N, 123°02'W); 2002.789, 8 nectophores, 1 nectosomal polyp, nectosome with 1 attached nectophore, 1 polyp, and short siphosomal portion (34°51'N, 122°56'W); *A. uvaria* Reg. Nos 1898.5.7.21, 10 nectophores, nectosome with 3 attached nectophores, many polyps, and siphosome with zooids (40°50'N, 14°15'E); 1902.7.29.8, 3 nectophores, nectosome with 7 attached nectophores and many polyps, and siphosome with zooids (40°50'N, 14°15'E); 1952.9.23.94, many bracts (43°48'N, 7°19'E); 1952.9.23.95, 1 nectophore (43°48'N, 7°19'E); 1952.9.23.96, 7 nectophores, nectosome, and siphosomal portion with zooids (43°48'N, 7°19'E); 1952.9.23.86-92, 6 nectophores (43°48'N, 7°19'E); *A. contorta* specimens collected in the vicinity of the Bahamas by the submersibles *Johnson Sea-Link I* and *Johnson Sea-Link II* (JSL I and JSL II). Additional specimens are *Apolemia* (as *Tottonia*) *contorta* holotype, 2 nectophores (07°35'N, 87°54'E), and *Apolemia* (as *Ramosia*) *vitiensis* paratype, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, No. 3/9902, 2 nectophores (53°04'N, 146°11'E), both kindly loaned by S.D. Stepanjants.

Description of material

Nectophores <13 mm along upper-lower axis and <11 mm across right-left axis (Fig. 12); epidermis of distal surface with faint mottling but no red pigment; upper furrow extending distally from thrust block, between axial wings, onto distal nectophore surface, and downwards a short distance towards ostium (between origins of axial wings on distal side of nectophore) (Fig. 12A); lateral furrows originating from lower lateral corners of ostium, passing first proximally, then curving upwards onto

lateral surfaces of nectophore (not illustrated), and terminating distolaterally, somewhat above level of origins of axial wings on distal nectophore surface (Fig. 12A); lower furrow originating between origins of axial wings on proximal surface and at same level as base of ascending surface diverticulum, extending downwards in midline towards lower nectophore surface, turning distally, and terminating at small ostial process below ostium (Fig. 12); ostium broad, but laterally distorted in present material; mesogloea flaccid; thrust block thin and with upper surface slightly bilobed; nectosac with slightly opaque musculature and yellow radial canals; upper and lower radial canals arising from internal pedicular canal (at base of ascending surface diverticulum) on proximal surface of nectosac; upper radial canal passing first upwards, giving off lateral radial canals, and then continuing distally over upper surface of nectosac, onto distal nectosac surface, and following somewhat irregular course downwards to ostium, with small swellings at intervals (Fig. 12A); lower radial canal extending first downwards (Fig. 12B), then onto lower surface of nectosac, and inserting onto ostium on its lower side (Fig. 12A); lateral radial canals each passing first obliquely outwards, then turning upwards and over onto distal nectosac surface (Fig. 12B), passing downwards on this surface as shown in Figure 12A, then curving somewhat onto lateroproximal surfaces of nectosac (Fig. 12B), zigzagging down these surfaces, and turning distally again to insert laterally onto ostial ring canal (Fig. 12A); internal pedicular canal very short, connecting external pedicular canal (not preserved) with junction of upper and lower radial canals of nectosac; ascending surface diverticulum originating from external/internal pedicular canal junction, extending upwards towards thrust block, increasing in diameter towards tip, and terminating on proximal surface of thrust block (Fig. 12A).

Immature nectophores 9–10 mm long, with tips of axial wings relatively close together and radial canals thick, their courses taken to be straight throughout (not illustrated).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see station listed above); northeast Pacific: off Point Conception on California coast (Mapstone 2003). Other records: Sagami Bay, Japan (Lindsay 2006); in the vicinity of the Galapagos Islands (Margulis 1980b); northwest Indian Ocean (Margulis 1976).

Notes

The nectophores from Canadian Pacific waters are smaller than those described by Mapstone (2003) from off Point Conception, California (<28 mm along upper–lower axis), and approximately twice the size of others collected by Margulis (1980b) from the central Pacific and the northwest Indian Ocean (Margulis 1976). This suggests that *Apolemia contorta* has at least two size categories, a feature also recognized in the agalmatid *Nanomia bijuga* (see below) and the pyrostephid genus *Bargmannia* (Pugh 1999a). The nectosomal polyps of *A. contorta* are white to translucent when preserved, and attach to the nectosomal stem either singly or in pairs near the lower end of each nectophoral muscular lamella (Mapstone 2003, fig. 9c). The stem is probably red in life, but the nectophores are likely to be translucent; they can be distinguished from those of *A. uvaria* and *A. vitiazzi* by the covering of closely spaced opaque patches on the distal surface, which also characterizes the upper surfaces of the bracts (Mapstone 2003). These patches are present in the nectophores of *A. contorta* from Canadian Pacific waters, but have been omitted from Figure 12A for clarity. The nectophores of *A. contorta* also differ from those of *A. uvaria* in having lateral radial canals without short diverticula arising from the upper loop, and from those of *A. vitiazzi* in lacking red pigment (Mapstone 2003).

The smaller of two immature nectophores of *Apolemia contorta* collected off Vancouver Island is similar in appearance to that illustrated for this species by Mapstone (2003, fig. 10b), except that the latter is twice as long. Perhaps more food was available to the Point Conception specimens, enabling them to reach a larger size.

No siphosomal zooids are associated with the present *Apolemia contorta* nectophores, but large red gastrozooids and translucent palpons have been described for *A. contorta* specimens collected off California (Mapstone 2003, fig. 12). Bracts up to 11 mm in length are also described from the latter material, together with a number of female gonophores <5 mm in diameter from one specimen (Mapstone 2003, fig. 13). *Apolemia contorta* bracts have a bracteal canal that remains in contact with the lower surface throughout its length, and lacks the small distal extension into the mesogloea found in bracts of *A. uvaria* (Mapstone 2003, compare figs 13a–c with figs 8c–g). This suggests that in *A. contorta* the bracteal lamella may be elongate and attached to the bracteal canal for most of its length (see Section 3.4), whereas in *A. uvaria* it is likely to be somewhat shorter.

Apolemia sp.

(Fig. 13)

Material examined

Twenty-two nectophores from Canadian Pacific stations LB13 (0–700 m), LB14 (0–700 m), LC10 (700 m) (Fig. 13) BCPM 996-216-1, LC10 (500–0, 700–0 m), and A4 (0–500, 500, 0–700, 700–0 m) (Fig. 11, Table 1). Other material referable to this species but not yet described, collected off Point Conception, California, and kindly donated to the author by S.H.D. Haddock. Specimens also referable to this species were collected in the vicinity of the Bahamas by JSL I and JSL II and were made provisionally available to the author by P.R. Pugh.

Description of material

Nectophores <6 mm along upper–lower axis and <5 mm across right–left axis (Fig. 13); nectophores pale brown with epidermis pigmented red between axial wings and along floor of lower furrow (on proximal surface), but without mottling; upper furrow extending distally from thrust block between axial wings onto distal nectophore surface and terminating close to upper nectophore surface (Fig. 13A); lateral furrows each originating lower laterally below ostium and passing first proximally (Fig. 13B), then curving upwards onto lateral nectophore surfaces and curving back onto distal surfaces higher up, continuing across distal nectophore surface as shown in Figure 13A and meeting in distal midline below distal bases (origins) of axial wings; lower furrow originating at origins of axial wings on proximal nectophore surface, below base of ascending surface diverticulum, passing downwards in proximal midline and terminating on proximal side of large ostial process (Fig. 13B); ostium broad, but laterally distorted in present material; mesogloea moderately flaccid; thrust block of moderate thickness and with upper surface typically slightly bilobed (Fig. 13); nectosac brown with thick opaque musculature and prominent orange-pigmented radial canals; upper and lower radial canals arising from internal pedicular canal at lower end of ascending surface diverticulum (its origin), on proximal surface of nectosac (Fig. 13B); upper radial canal passing upwards, giving off two lateral radial canals, continuing onto upper surface of nectosac and over onto distal surface, then passing downwards in distal midline to ostium (Fig. 13A); upper radial canal with smooth walls except for small expansion on distal surface just below junction of two lateral furrows, in all nectophores; lateral radial canals following looped courses typical of apolemiids,

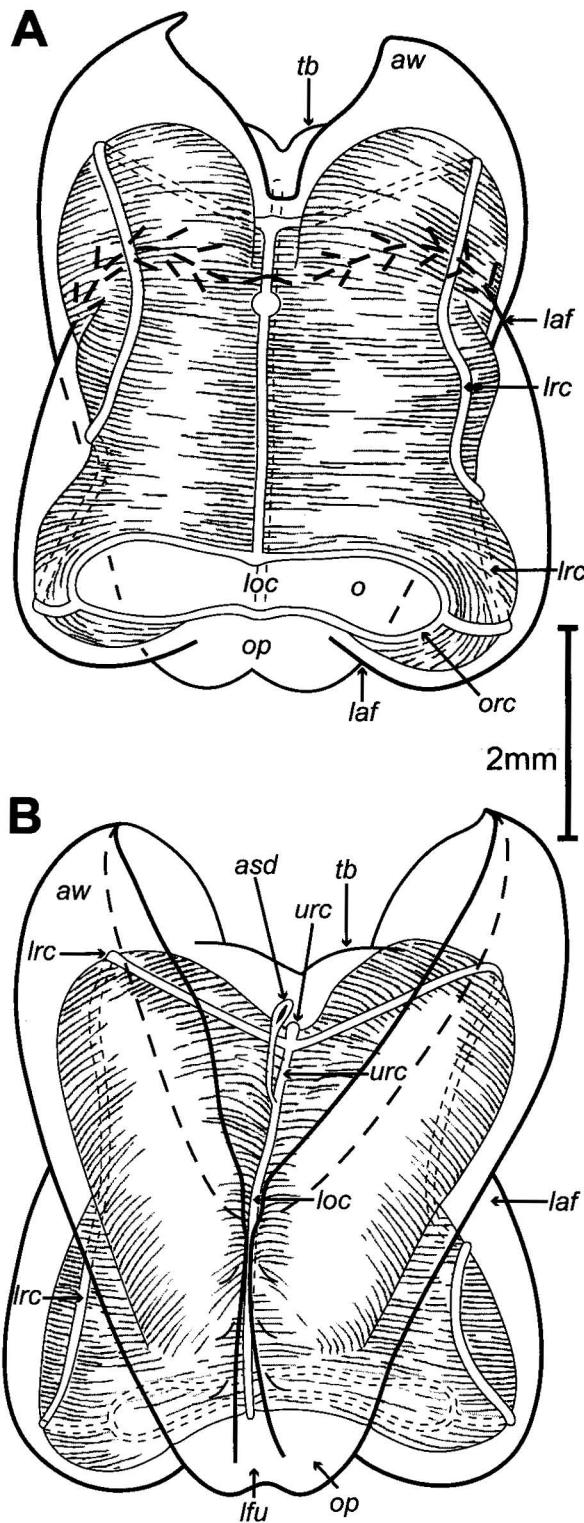


Fig. 13. *Apolenia* sp. nectophore: A: distal view; B: proximal view (asd, ascending surface diverticulum; aw, axial wing; laf, lateral furrow; ifu, lower furrow; loc, lower radial canal; lrc, lateral radial canal; o, ostium; op, ostial process; orc, ostial ring canal; tb, thrust block; urc, upper radial canal).

without undulations; internal pedicular canal very short (not labelled in Fig. 13B), situated at lower end of ascending surface diverticulum, and connecting external pedicular canal (not preserved) with junction of upper and lower radial canals; ascending surface diverticulum short and thin, with slightly swollen tip, passing upwards in proximal midline and terminating on proximal surface of thrust block (Fig. 13B).

Notes

These nectophores are similar to much larger ones collected off Point Conception, California, which measure up to 19 mm in length and are covered in red pigment. Either the pigment forms later during growth or was abraded during collection. The latter nectophores are also similar to those of an as yet unnamed species that was collected by JSL II in the vicinity of the Bahamas (pers. obs.). The present specimens from Canadian Pacific waters are, however, not herein referred to a new species because they lack stems, nectosomal polyps, and bracts; this also applies to the red nectophores from off California. The present apolemiid nectophores are also distorted in the ostial region, the ostial process having bent distally and caused unnatural widening of the ostium. However, other characters correspond closely to those from North Atlantic nectophores, including the merging of the lateral furrows in the distal midline, the straight course of the upper radial canal with the distinct distal swelling below the merged lateral furrows, the position at which the axial wings attach to the nectophore body on both sides of the nectophore (proximal and distal), and the relatively wide ostium and short ascending surface diverticulum.

10.1.2. Family PYROSTEPHIDAE Moser, 1925

Diagnosis

Physonectae with colony linear and having dorsal nectosome, with many similar nectophores but no nectosomal polyps; nectophores with enlarged thrust block, ridges of taxonomic importance, and nectosac with proximal muscle-free zone; nectophores without descending surface diverticulum from pedicular canal on proximal surface; dioecious; gastrozooid tentacles with unicornuate tentilla each having a straight or loosely coiled cnidoband, terminal filament with nematocysts and no involucrum.

Notes

This family was introduced by Moser (1925) for *Pyrostephos vanhoeffeni*, a large and colourful

species with unusual modified palpons on the siphosome, termed oleocysts. It was collected in Antarctica during the German South Polar Expedition. The oleocysts contain oil droplets that are thought to aid flotation of the heavy stem. Totton (1965a) gave a more accurate description and figures of the nectophores and tentilla of *P. vanhoeffeni* than did Moser (1925), and retained her family Pyrostephidae, even though he was unsure of its validity. He also added a second genus, *Bargmannia*, based on nectophores first described in 1954, but made little comment on the characters that his species *B. elongata* shared with *P. vanhoeffeni*. It was another 34 years before the genus *Bargmannia* was reassessed, by Pugh (1999a), who introduced two new species and compared *Bargmannia* with newly collected material of *P. vanhoeffeni*. He concluded that the family Pyrostephidae is valid and the present author concurs.

The family Pyrostephidae is dioecious, as noted above (Section 10.1), and is therefore likely to have more in common with the ancestral siphonophore than genera of the family Agalmatidae *sensu stricto*, since Pugh (2006b) suggests that this ancestor was also probably dioecious. Genera of the family Agalmatidae *sensu stricto* are monoecious (see Section 10.1.3), and are thus treated after the family Pyrostephidae in the present work. Species of both these families, in common with those of all other physonect families except the Apolemiidae, possess tentilla, and these structures are shown diagrammatically for all genera from Canadian Pacific waters in Figure 14. The tentilla of pyrostephids are discussed further below.

Nectophores of pyrostephids are budded from the dorsal side of the nectosome (Pugh 2006b) and have a greatly enlarged thrust block and lower-lateral wings that extend downwards from the lateral surfaces of the nectophore. Most physonect nectophores have axial wings that interdigitate with those of two nectophores that protrude from the opposite side of the stem (Fig. 1A; see Section 10.1). However, in pyrostephids axial wings are absent, and nectophores do not interdigitate, as can be seen from the schematic diagram of a siphonophore colony given by Dunn (2005, fig. 1), which is based on *Bargmannia elongata*. Thus, the lower-lateral wings of pyrostephids flank the nectosac, whereas those of most other long-stemmed physonects arise proximal of it (Fig. 1G) and are equivalent to the lateral wedge-shaped

processes mentioned by Pugh as being reduced or absent in the family Pyrostephidae (1999a, p. 51).

The nectophoral ridges also form a pattern unique to the Pyrostephidae, and have recently been reevaluated by Pugh (2006b). In this family, the vertical-lateral ridges are aligned at an oblique angle to the upper-lower nectophore axis instead of approximately parallel to it, as in most other physonects (for example, see Fig. 1G). This orientation led Pugh (1999a) to rename this ridge the mesolateral ridge, but he has more recently concluded that “because this ridge arises in the proximal half of the nectophore and unites the upper and lower lateral ridges, in the very broadest sense it can be considered as a vertical lateral ridge” (Pugh 2006b, p. 5). Thus, the original name vertical-lateral, as originally used by Totton (1965a), is retained herein, and this ridge is also interpreted here as extending only between the upper-lateral and lower-lateral ridges, not continuing distally towards the ostium as described by Pugh (1999a). The latter portion of Pugh’s mesolateral ridge is herein interpreted as an extension of the lower-lateral ridge (previously infralateral), as in other physonects (see Section 10.1).

Another characteristic of the Pyrostephidae is the greatly enlarged thrust block, which forms the entire proximal end of the nectophore and comprises a plug of mesogloea that pushes into the proximal wall of the nectosac on its lower side. This makes the proximal end of the nectosac appear embayed, or scooped out, in lower view (see Totton 1965a, fig. 41), and results in displacement of the proximal wall upwards so that it comes to lie underneath the upper wall of the nectosac. In this proximal wall the muscles have been lost, producing the muscle-free zone characteristic of pyrostephids (Dunn et al. 2005a; see above). Totton (1965a, fig. 42B) shows well how, in *Pyrostephos vanhoeffeni*, this mesogloal plug (stippled in fig. 42) occludes the proximal part of the nectosac cavity when the nectosac contracts; a similar process must occur in *Bargmannia*, though less of the nectosac must be occluded because it is narrower and longer than that of *P. vanhoeffeni*.

A muscle-free zone is also found in nectophores of the family Erennidae (Pugh 2001), but in these species the nectosac is not deeply embayed proximally, the thrust block is relatively small, and axial wings are developed (Pugh 2001). Nectosacs of the indeterminate agalmatid genus

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

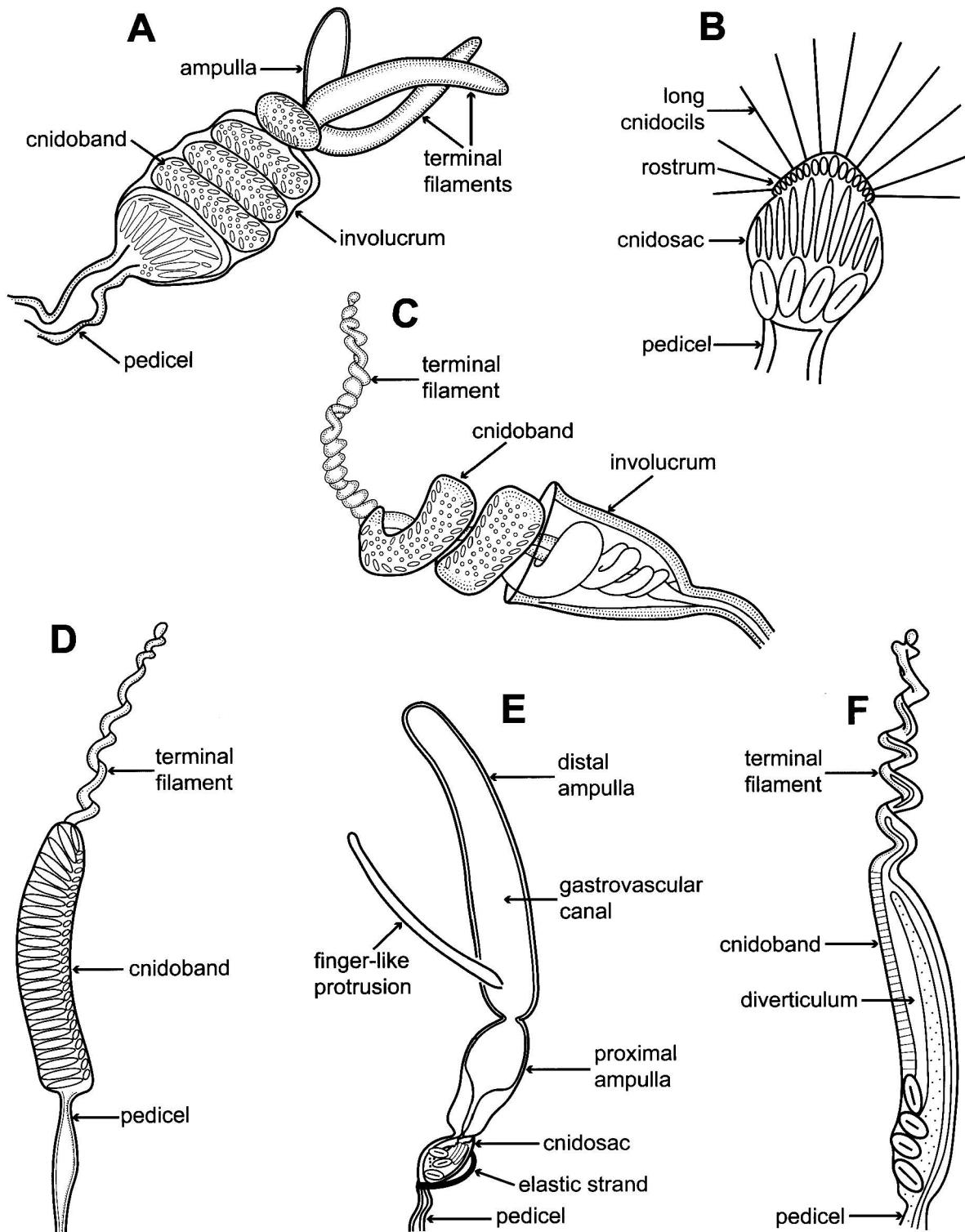


Fig. 14. Tentilla of Canadian Pacific physonects: **A:** *Agalma elegans*; **B:** *Cordagalma ordinata*; **C:** *Nanomia bijuga*; **D:** *Marrus orthocanna*; **E:** *Frillagalma vityazi*; **F:** *Bargmannia elongata*. A is modified from Bigelow (1911b, pl. 18 fig. 10); B is derived from C. Carré (1968a, pl. 3 fig. 7) and Haeckel (1888b, pl. 15 Figs 12, 13); C is modified from Bigelow (1911b, pl. 19 fig. 10); D is partly derived from Kramp (1942, fig. 5b); E is derived from Pugh (1998, fig. 7); and F is derived from Pugh (1999a, fig. 5A). Not drawn to scale.

Marrus also have a muscle-free zone (except for *M. orthocannoides*), but in these species the thrust block is smaller than in pyrostephids, and, like those of erennids, the nectophores have axial wings (see Section 10.1.3). Additionally, in *Marrus* species the tentillum is either straight or loosely coiled and includes a conventional cnidoband with only small nematocysts (Section 10.1.3). The musculature of nectosacs of the nectophores of monoecious physonect families (Agalmatidae *sensu stricto*, Forskaliidae, Physophoridae, and Resomiidae) is, in contrast, complete (see Section 10.1.3).

The tentillum of pyrostephids is unique, and was first figured and described in detail by Totton (1965a) for *Pyrostephos vanhoeffeni*. It was subsequently shown by Pugh (1999a) to be similar in *Bargmannia*. Figure 14F is a schematic illustration of a *B. elongata* tentillum and is derived from a photograph of two tentilla by Pugh (1999a, fig. 5A). It shows a straight cnidoband along one side, formed by the epidermis of a blind-ending diverticular canal, and an extensible region on the other side, formed by the walls of the thin axial canal (Totton 1965a), which extends to the distal tip of the terminal filament. In tentilla with coiled cnidobands, the walls of the axial canal typically form a complex looped elastic band that is responsible for cnidoband extension (Mackie 1999; see Section 4.3).

The cormidia of pyrostephids either include unusual modified palpons called oleocysts (as noted above) that lack palpacles as in *Pyrostephos*, or have none as in *Bargmannia*. In the latter each cormidium bears a unique siphosomal tentacle that carries a row of biserial spherical nematocysts along one side, as described by Pugh (1999a). Dunn (2005) has plotted the exact position of this tentacle in the cormidium of *B. elongata*, and terms it a tentaculozoid. It lies in the ventral midline, and Dunn concludes that it probably represents an atrophied polyp with a single hypertrophied tentacle. Although this tentacle still bears nematocysts, it seems unlikely to be involved in digestion of prey, since the polyp body is absent and the tentacle lacks a lumen. Budding of new cormidia in *B. elongata* is also described by Dunn (2005), and is summarized in the present work in Section 3.2.

Pyrostephids are known to be dioecious (Totton 1965a; Pugh 1999a; Dunn 2005), as noted above, and this character has been linked to a possibly more primitive state in which a descending surface diverticulum is absent (Dunn et al. 2005a, as

descending pallial canal). Perhaps the presence of a muscle-free zone in the nectosac represents another plesiomorphic character, but further gene analysis is needed before this hypothesis can be tested.

Genus *Bargmannia* Totton, 1954

Diagnosis

Pyrostephidae with nectophore having inner branch of upper-lateral ridge reaching ostium, and nectosac with straight lateral radial canals and upper radial canal; cormidia of siphosome without palpons but with unique siphosomal tentacle, typically one per cormidium.

Type species: *Bargmannia elongata* Totton, 1954.

Notes

This genus is reviewed by Pugh (1999a), who includes two previously described species, *Bargmannia elongata* Totton, 1954 and *B. lata* Mapstone, 1998, and introduces two new species, *B. amoena* and *B. gigas*. Although the type species is *B. elongata*, the original material figured by Totton (1954) also includes two figures attributable to *B. lata*, as noted by Mapstone (1998). The latter nectophores came from Discovery Station 1769 and are included in the synonymy of *B. lata* given below. Other nectophores shown in Totton's figure came from Discovery Stations 681 and 699 and have all since been referred by Pugh (1999a) to *B. elongata*. These nectophores, together with other *Bargmannia* material held in the NHM collections and also one specimen of *Pyrostephos vanhoeffeni*, have been examined by the present author (see list below).

Nectophores of *Bargmannia* species and *Pyrostephos vanhoeffeni* both have an upper-lateral ridge (Mapstone 1998, as *apico-lateral ridge*; Pugh 1999a; Totton 1965a) that divides into inner and outer branches distally, and in *Bargmannia* species the inner ridge extends to the ostium. In *P. vanhoeffeni*, however, the inner ridge passes onto an elevated rostrum above the ostium and terminates close to the upper midline, not on the ostial border itself. This rostrum is apparent, although not labelled as such, in the ostial view of a *P. vanhoeffeni* nectophore by Totton (1965a, fig. 40B). In *Bargmannia* the lateral radial canals of the nectosac are taken to be straight in all species because, as Pugh (1999a) points out, they

are approximately straight in preserved nectophores of *B. lata* and *B. gigas*, and only appear undulating in those of *B. elongata* and *B. amoena* because the nectosac becomes distorted at preservation. In *P. vanhoeffeni*, however, the lateral radial canals of the nectosac loop 3 times between their origin from the upper radial canal and their insertion onto the ostial ring canal, and the upper radial canal also follows a sinuous course (Totton 1965a, figs 40, 41).

The size of mature nectophores can vary among individuals of *Bargmannia* species, and a similar trait has also been noted in *Pyrostephos vanhoeffeni* (Pugh 1999a).

Margulis (1982) incorrectly referred *Bargmannia* to the Physophoridae.

***Bargmannia elongata* Totton, 1954**

(Figs 15, 16)

Bargmannia elongata Totton, 1954: 69 (in part), figs 28A–D (not figs 28E and F, = *B. lata*); ?Leloup, 1955: 13; Totton, 1965a: 82, text-figs 45A–D (not text-figs 45E and F, = *B. lata*); Kirkpatrick and Pugh, 1984: 41, figs 11A and B; ?Mackie et al., 1987: fig. 6C; Mapstone, 1998, 141; Pugh, 1999a: 53, figs 1–5; Pugh 1999b: 481, fig. 3.8 (not Gao et al., 2002: 76, fig. 31, = *B. lata*); Dunn, 2005: 838, figs 3–6.

?*Mica micula* Margulis, 1982: 778, figs 2A–EE; Pagès and Gili, 1989: 54, fig. 2; Pugh 1999b: 481.

Diagnosis

Mature nectophores with upper-lateral ridges each having single short ridge directed downwards towards midline at 4/5 nectophore length; outer upper-lateral ridge reaching ostium and without extra branch directed proximally. Bract delicate and foliaceous, rounded distally, and with upper surface having many small patches of rounded ectodermal cells distally, but no semicircular ridge; with or without pair of lateral cusps at midbract.

Material examined

Five hundred and ninety-three nectophores from Canadian Pacific stations LB12 (0–450 m), LB12

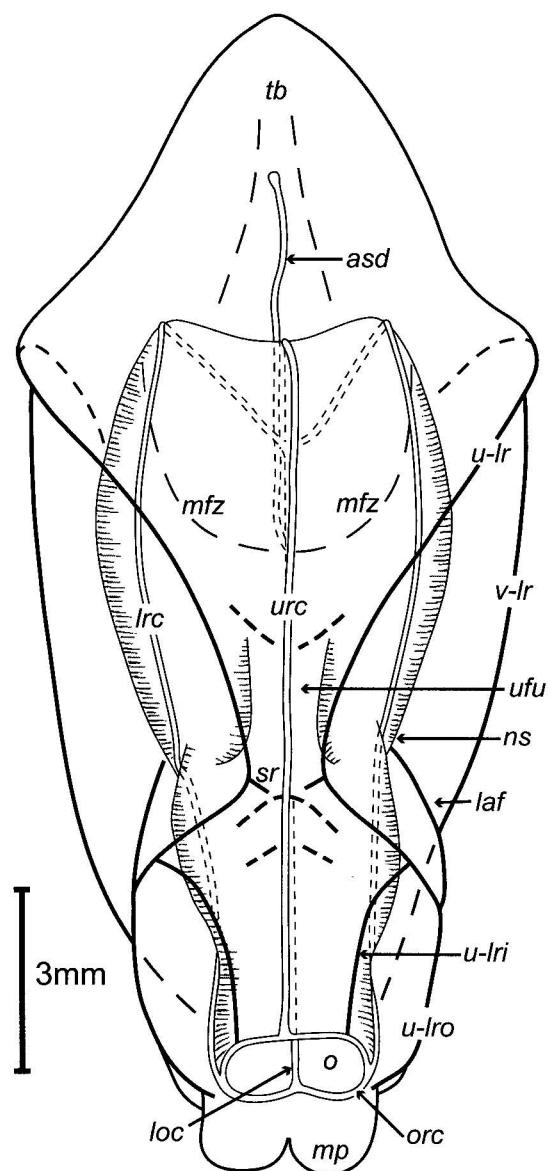


Fig. 15. *Bargmannia elongata*, nectophore, upper view (asd, ascending surface diverticulum; laf, lateral furrow; loc, lower radial canal; lrc, lateral radial canal; mfz, muscle-free zone of nectosac; mp, mouthplate; ns, nectosac; o, ostium; orc, ostial ring canal; sr, short ridge; tb, thrust block; ufu, upper furrow; u-lr, upper-lateral ridge; u-lri, inner upper-lateral ridge; u-lro, outer upper-lateral ridge; urc, upper radial canal; v-lr, vertical-lateral ridge).

(0–450 m), LB13 (0–300, 0–500, 500, 700–0 m), LB14 (500 m), LB16 (0–500, 500, 0–700 m), LB17 (300, 0–500, 500 m), LC9 (300 m), LC10 (300–0, 500–0, 500, 0–575, 575, 700, 700–0 m), LC11 (500 m) (Figs 15, 16 in part) BCPM 996-202-1, LC11 (300, 300–0, 0–500, 500, 0–700, 700–0 m), and A4 (0–500, 500, 700 m) (Fig. 11, Table 1); 15 nectophores from station B-7L (48°43'N, 126°39'W), oblique vertical tow to 1200 m depth

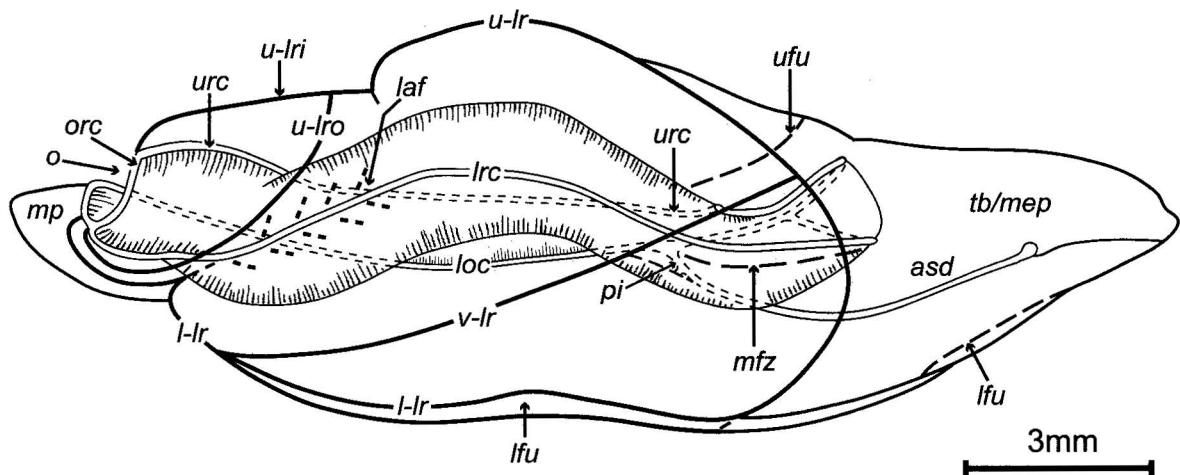


Fig. 16. *Bargmannia elongata*, nectophore, lateral view (asd, ascending surface diverticulum; laf, lateral furrow; ifu, lower furrow; l-rr, lower-lateral ridge; loc, lower radial canal; lrc, lateral radial canal; mfz, muscle-free zone of nectosac; mp, mouthplate; o, ostium; orc, ostial ring canal; pi, internal pedicular canal; tb/mep, thrust block / mesogloal plug; ufu, upper furrow; u-lr, upper-lateral ridge; u-iri, inner upper-lateral ridge; u-iro, outer upper-lateral ridge; u-rc, upper radial canal; v-rr, vertical-lateral ridge).

(used to add morphological details to Figs 15 and 16), collected 27 February 1982 from just outside main study area. Specimens of *Bargmannia elongata* from NHM collections: Reg. Nos 1952.11.19.7, holotype, 1 nectophore (14°27'N, 30°02'W); 1952.11.19.8–25, paratype, 17 nectophores (14°27'N, 30°02'W); 1957.5.15.94, paratype, 5 nectophores (43°03'S, 17°03'E); 1957.5.15.95, paratype, 6 nectophores (21°13'S, 29°55'W); 1998.2163, paratype, 40 nectophores, nectosomal and siphosomal stem portions with zooids, from *Alvin* dive 961 (32°14'N, 117°22'W). Also from NHM collections, specimens of *Bargmannia amoena* Reg. Nos 1998.2164, holotype, 14 nectophores, nectosomal and siphosomal stem portions, and zooids from JSL II dive 1458 (24°01'N, 82°17'W); 1998.2165, paratype, 15 nectophores, siphosomal stem portion, and zooids from JSL I dive 2636 (25°53'N, 77°48'W); *Bargmannia gigas* Reg. Nos 1998.2166, holotype, 1 nectophore (0°00'N, 22°44'W); 1998.2167–2169, paratype, 4 nectophores (0°03'N, 22°44'W); *Pyrostephos vanhoeffeni* Reg. No. 1957.5.15.292, 12 nectophores (55°13'S, 34°59'W).

Description of material

Nectophores elongate, varying from 5 to 24 mm in length along proximal-distal axis, from 4 to 11 mm in width along right-left axis (Fig. 15), and from 2 to 9 mm in depth along upper-lower axis (Fig. 16); mature nectophores 15–24 mm in length, with prominent triangular thrust block forming proximal end of nectophore, typically broadly rounded in upper view (Fig. 15), atypically

slightly asymmetric and with proximal digitiform process (not illustrated); lateral surfaces enlarged into lower-lateral wings; latter extending downwards and flanking lower nectophore surface on each side.

Ridges typically prominent, with upper-lateral, vertical-lateral, and lower-lateral ridges originating together on lateral surfaces of nectophore at junction of thrust block with main body (Figs 15, 16); upper-lateral ridge extending distally over upper surface, passing first diagonally towards upper midline, giving off short ridge (sr), turning abruptly outwards, and then subdividing into inner and outer upper-lateral ridges at 3/10 nectophore length (from ostium) (Fig. 15); short ridge passing downwards towards upper midline; vertical-lateral ridge extending distally diagonally downwards over lateral nectophore surface towards lower border of nectophore; here rejoining lower-lateral ridge near distal end of nectophore (Fig. 16); lower-lateral ridge curving around to lower border of nectophore, joining lower-lateral portion of thrust block in this region, and passing distally along lower edge of lower-lateral wing (of nectophore) to near ostium; slight emargination apparent in lower border at mid-nectophore length, owing to mesogloal bulge on inner lower-lateral wing surface; vertical-lateral ridge rejoining lower-lateral ridge distally, and latter continuing, via indentation at beginning of diagonal lateral furrow, to ostial region (Fig. 16).

Four furrows identifiable on nectophores, including upper furrow, two lateral furrows, and extensive

lower furrow; upper furrow extending distally along upper surface in midline from near distal end of thrust block (Fig. 16) to level of bifurcation of upper-lateral ridge into inner and outer branches (Fig. 15); upper furrow deepest where upper-lateral ridges come close together and short ridges are given off (Fig. 15); lateral furrows extending from notch in lower-lateral ridge near distal end of nectophore diagonally upwards towards proximal end of nectophore for a short distance (Fig. 16); lower furrow extending length of nectophore from proximal point of thrust block to ostium, deep throughout most of length and flanked laterally by inner walls of lower-lateral nectophore wings (Fig. 16); mouthplate bilobed and extending distally from distal border of ostium (Fig. 15).

Mesogloea typically turgid except for flaccid distal ostial region; mesogloea plug of thrust block projecting into proximal end of nectosac and displacing muscle-free wall of nectosac upwards; latter thus lying immediately below upper nectosac wall for most of length (Fig. 16); lateral nectosac walls extending proximally on each side to same level as upper wall and flanking central plug of mesogloea; nectosac tubular, opaque, somewhat flattened in upper-lower plane (between upper and lower surfaces) and with sinuous profile in lateral view (Fig. 16); muscle-free zone of nectosac discernible through upper wall as relatively large U-shaped area at proximal end (Fig. 15, indicated by coarse broken line); nectosac narrower distally than proximally in upper view, and with two upward bulges on each side of upper midline (Fig. 15); lower nectosac surface indented distally in lower midline (Fig. 16), giving inverted U shape to nectosac when viewed from distal end of nectophore (not illustrated); ostial opening directed upper-distally, and velum preserved in some specimens, extending to 1/2 width of velar aperture (not illustrated); upper radial canal originating from internal pedicular canal on lower nectosac surface, passing first proximally over muscle-free zone and turning sharply through 180° onto upper nectosac surface, then following straight course in upper midline to ostium (Figs 15, 16); lateral radial canals originating approximately together from upper radial canal in centre of muscle-free zone, and each following diagonal course to proximolateral edge of nectosac; each lateral radial canal then turning sharply onto upper-lateral nectosac surface and continuing distally along lateral wall of nectosac to ostium; lateral radial canals each lying directly behind lateral furrow in lateral view (Fig. 16); lower radial canal originating from internal pedicular canal and passing distally

straight to ostium; internal pedicular canal short, arising at insertion point of external pedicular canal (not preserved in present material), and passing to junction of upper and lower radial canals; ascending surface diverticulum originating at origin of internal pedicular canal, passing proximally along lower surface of nectophore in midline, and terminating as small swelling just inside mesogloea (Figs 15, 16).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; previously reported in Arai et al. 1993; Mapstone 1998). Northeast Pacific: off San Diego, 32°14'N, 117°22'W, and 33°04'N, 118°16'W (Pugh 1999a). Other regions: the only reliable records are from the North and South Atlantic and are given in Pugh (1999a).

Vertical. This species was found at 300, 500, and 700 m depth in the main study area, and in a sample from 1–1200 m over the hydrothermal-vent plume. Most of the specimens examined by Pugh (1999a) came from at least 500 m.

Notes

A particular nectophore of *Bargmannia elongata* that was illustrated by Totton (1954, figs 28A and B; repeated in 1965a, figs 45A and B) and comes from Discovery Station 699 has been designated by Pugh (1999a) as the holotype.

The nectophores found by Stepanjants (1967) in the North Pacific cannot be reliably identified as *Bargmannia elongata*, since the short ridges arising from the upper-lateral ridges are omitted from her figures. This also applies to the nectophores from the Indian Ocean illustrated by Daniel (1974, 1985) and referred to *B. elongata*, and to those from the Antarctic region that are shown by Alvariño et al. (1990). These references are therefore excluded from the *B. elongata* synonymy given above.

The first full description of a *Bargmannia elongata* colony is given by Pugh (1999a), based on two specimens collected by the remotely operated vehicle *Alvin* off San Diego, California. One of these is deposited in the NHM collections and has been studied by the present author (see above). More recently the siphosomal budding and cormidial organization of *B. elongata* have been analyzed by Dunn (2005) from 19 specimens collected with the

remotely operated vehicle *Tiburon* off Moss Landing, California, as mentioned above and summarized in Section 3.2.

Pugh gives clear figures of the ridge pattern in mature and immature nectophores of *Bargmannia elongata*, and also shows details of the lateral processes that flank the ostium in this species (1999a, figs 2A–C, 3A–C), although these processes could not be distinguished in the nectophores collected from Canadian Pacific waters. Pugh (1999a) also describes the bracts of *B. elongata* for the first time, although no such bracts are associated with the present material. They bear distinctive patches of ectodermal cells on the upper surface, which Pugh (1999a) suggests might represent sites of bioluminescence. He also gives two photographs of live *B. elongata* colonies, and others of preserved tentilla, the siphosomal tentacles unique to *Bargmannia* species, and male gonophores (Pugh 1999a, figs 1A and B, 5A–C).

The zooid composition in a mature physonect cormidium of *Bargmannia elongata* is given by Dunn (2005), based on the first-ever SEM study of young and newly matured cormidia, as discussed in Section 3.2. Dunn (2005) shows that in this species all zooids arise from a single probud on the siphosomal growth zone, or horn, and that the arrangement is precise and directionally asymmetric. The full zooid complement of one cormidium comprises one gastrozooid, one siphosomal tentacle (as tentaculozooid), one gonodendron (as gonozooid, either male or female), two gastrozooid-associated bracts, two left lateral bracts, and two right lateral bracts (Dunn 2005, figs 4, 5). He finds that these zooids arise either in the midventral line or offset to the right or left, and two types of gastrozooid are identified, every 7th or 10th one being larger than the others. The nectosomal growth zone of *B. elongata* was also studied by Dunn (2005), who found a small bud on the posterior side of each developing nectophore, as discussed in Sections 3.2 and 10.1.1.

A small physonect siphonula found several times in the Antarctic Ocean and introduced by Margulies (1982) as *Mica micula* is tentatively referred by Pagès and Gili (1989) to *Bargmannia elongata*, as discussed in Section 3.1. It is therefore included in the synonymy for this species, given above, preceded by a question mark.

Nectophores of *Bargmannia elongata* may be confused with those of *B. amoena*, but in well-preserved material can be distinguished by the

course of the upper-lateral ridge and the presence of the short ridge extending downwards from it, as described above. In *B. amoena* the upper-lateral ridge curves gradually outwards in the distal half of the nectophore (from the upper midline), whereas in *B. elongata* it turns outwards sharply and gives off the short ridge at this point. The bracts of *B. elongata* are also easily distinguishable from those of the other two species, though they are not yet known for *B. gigas*, since they have unique dense spots on the upper surface. The nectophores have a relatively longer thrust block in *B. lata* than in *B. elongata* and *B. amoena*, and the lower-lateral wings are more extensive (Fig. 18). The nectophores are much larger in *B. gigas* than in any other *Bargmannia* species, and bear several extra distinctive ridges.

***Bargmannia lata* Mapstone, 1998**

(Figs 17, 18)

Bargmannia elongata Totton, 1954: figs 28E and F; Totton, 1965a text-figs 45E and F; Gao et al., 2002: 76, fig. 31.

Bargmannia lata Mapstone, 1998: 141, figs 1–3; Pugh, 1999a: 63, figs 12–16.

Diagnosis

Mature nectophores with outer upper-lateral ridges reaching ostium, and without extra branches directed proximally; also without short ridges from main portion of upper-lateral ridge. Bract robust and distally truncate, with semicircular ridge on upper surface; larger bracts with single lateral cusp on outer border at midbract, smaller bracts with pair of lateral cusps at this level.

Material examined

Seventy nectophores and 20 bracts (most designated as holotype and paratypes by Mapstone 1998) from Canadian Pacific stations LC10 (700–0 m), holotype (Figs 17, 18A) BCPM 996-203-1, 1 nectophore and 1 bract; paratype 1 (Fig. 18B) BCPM 996-204-1, 7 nectophores and 7 bracts; paratype 2 BCPM 996-205-1, 6 nectophores and 6 bracts; A4 (500 m), paratype 3 BCPM 996-206-1, 11 nectophores; LB17 (0–700 m), paratype 4 BCPM 996-207-1, 8 nectophores, and LB17 (700 m) paratype 5 NHM 1996.1234–1238, 14 nectophores and 2 bracts; A4

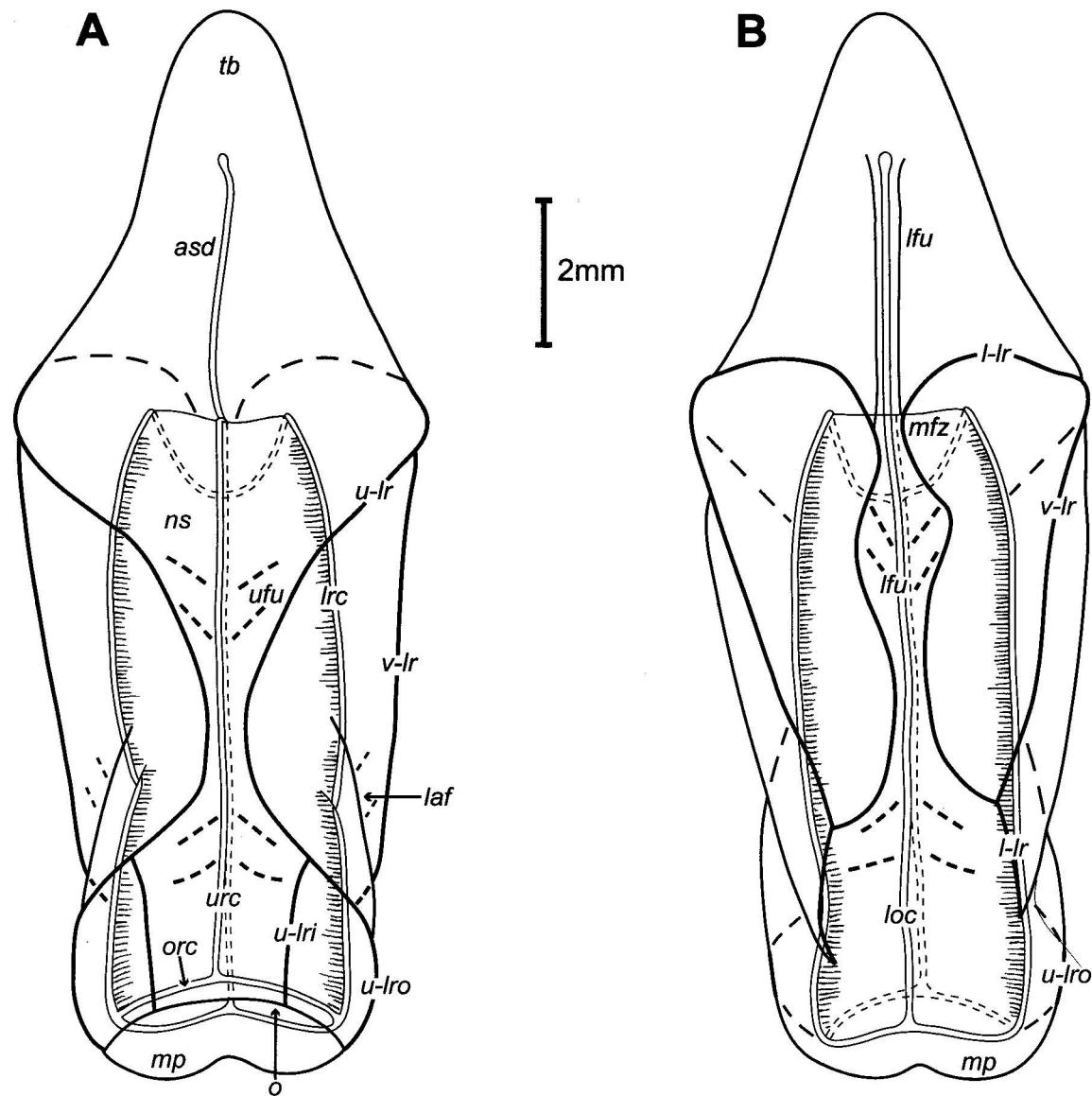


Fig. 17. *Bargmannia lata* holotype, nectophore (derived from Mapstone 1998, fig. 1): A: upper view; B: lower view (asd, ascending surface diverticulum; laf, lateral furrow; lfu, lower furrow; l-lr, lower-lateral ridge; loc, lower radial canal; lrc, lateral radial canal; mfz, muscle-free zone of nectosac; mp, mouthplate; ns, nectosac; o, ostium; orc, ostial ring canal; tb, thrust block; ufu, upper furrow; u-lr, upper-lateral ridge; u-iri, inner upper-lateral ridge; u-iro, outer upper-lateral ridge; urc, upper radial canal; v-lr, vertical-lateral ridge).

(500 m) paratype 6 NHM 1998.1239–1240, 1 bract; LC11 (500–0 m) paratype 7 NHM 1998.1788–1798, 9 nectophores and 2 bracts; station B-7L (48°43'N, 126°39'W, 2 February 1987, 1200 m), paratype 8 NHM 1998.1799–1810, 11 nectophores and 1 bract; LB13 (700 m), 3 nectophores (Fig. 11, Table 1). Other material from the NHM collections now labelled *B. lata* (previously labelled *B. elongata*): Reg. Nos 1949.11.10.378, 4 nectophores (13°06'N, 46°25'E); 1957.5.15.110, 2 nectophores (33°43'S, 8°39'E).

Description of material

Nectophores elongate, varying from 7 to 30 mm in length along proximal-distal axis, from 4 to 12 mm in width along right-left axis (Fig. 17A), and from 5 to 12 mm in depth along upper-lower axis (Fig. 18A); mature nectophores 22–30 mm in length, with holotype 24 mm long, and all having prominent thrust block at proximal end, either narrowly pointed (Fig. 17A) or with tip slightly asymmetric, digitiform and bent over onto lower surface (not illustrated); lateral surfaces enlarged into extensive lower-lateral

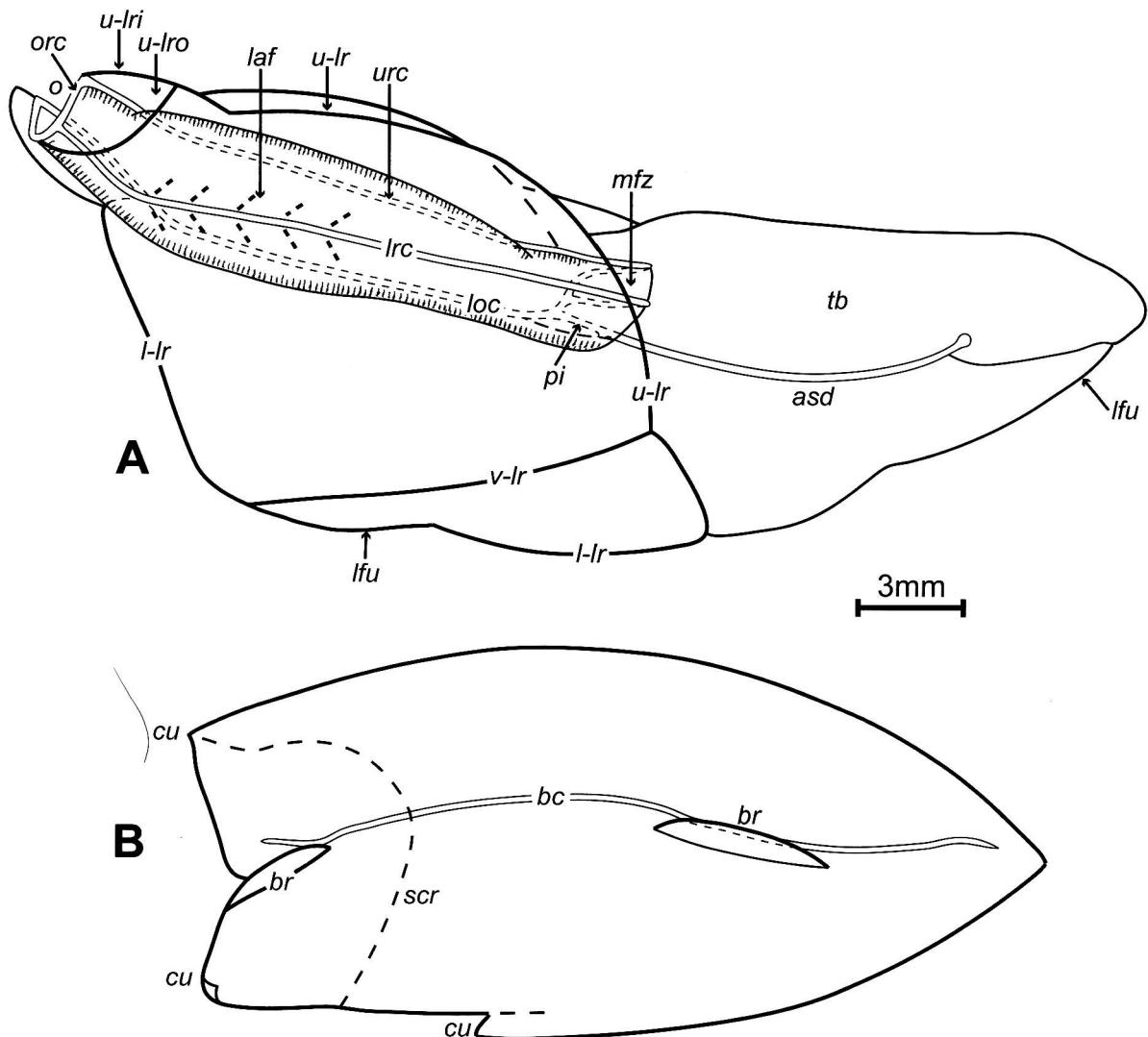


Fig. 18. *Bargmannia lata* holotype: **A:** nectophore, right lateral view; **B:** bract, lower view. A and B are derived from figures 2a and 3, respectively, in Mapstone (1998) (asd, ascending surface diverticulum; bc, bracteal canal; br, bracteal ridge; cu, cusp; laf, lateral furrow; ifu, lower furrow; l-lr, lower-lateral ridge; loc, lower radial canal; lrc, lateral radial canal; mfz, muscle-free zone of nectosac; o, ostium; orc, ostial ring canal; pi, internal pedicular canal; scr, semicircular ridge; tb, thrust block; u-lr, upper-lateral ridge; u-iri, inner upper-lateral ridge; u-lro, outer upper-lateral ridge; urc, upper radial canal; v-lr, vertical-lateral ridge).

wings extending downwards and flanking lower nectophore surface on each side (Fig. 18A).

Proximal junction of upper-lateral, vertical-lateral, and lower-lateral ridges prominent and lying level with proximal end of nectosac in lateral view (Fig. 18A); upper-lateral ridge curving distally onto upper nectophore surface and passing obliquely towards upper midline, lying close to partner in mid-nectophore region (Fig. 17A), then curving

obliquely away from midline and dividing into inner upper-lateral and outer upper-lateral ridges at 1/5 nectophore length (from ostium) (Fig. 17A); vertical-lateral ridge extending diagonally downwards in distal direction over lower-lateral nectophore wing (below level of nectosac in lateral view shown in Fig. 18A) and rejoining lower-lateral ridge on lower nectophore border; lower-lateral ridge curving downwards, first slightly proximally and then curving distally and passing along lower

edge of lower-lateral wing, with slight emargination in mid-nectophore region, towards distal end of nectophore, rejoining lower-lateral, and extending, via indentation marking beginning of lateral furrow, to ostial region (Fig. 18A).

Four furrows identifiable on nectophores, including upper furrow, two lateral furrows, and deep lower furrow; upper furrow extending distally along midline, deepest in midregion of nectophore, where upper-lateral ridges lie relatively close together, and terminating before reaching ostium; lower furrow deep throughout most of length, and extending along length of nectophore in midline, from near proximal end of thrust block to mouthplate region (Fig. 17A); lower furrow flanked laterally by two extensive lower-lateral nectophore wings; mouthplate short, bilobed, and extending distally from distal border of ostium (Fig. 17A).

Mesogloea typically turgid throughout, apart from flaccid distal ostial region; mesogloea plug forming thrust-block region and projecting somewhat into proximal part of nectosac, displacing proximal nectosac wall upwards; nectosac tubular and somewhat translucent, with small invaginated muscle-free proximal end; latter lying immediately underneath muscular upper nectosac wall, discernible in upper view through upper nectosac wall and also in lower view (extent is marked in Fig. 17 by fine broken lines showing courses of lateral radial canals); lateral nectosac walls flanking mesogloea plug proximally on each side (Fig. 18A); nectosac somewhat flattened in upper-lower plane and not undulating in lateral view; distal end of nectosac inverted U shape in distal view (not illustrated); ostial opening directed relatively distally, broad in upper view and without velum preserved; upper and lower radial canals originating from internal pedicular canal on lower nectosac surface, at junction of muscle-free zone and muscular part of lower nectosac wall (Fig. 18A); upper canal extending first proximally over muscle-free zone of nectosac, then turning sharply distad onto upper surface and passing distally to ostium (Fig. 18A); lateral radial canals originating approximately together from upper radial canal in centre of muscle-free zone, extending obliquely towards proximolateral corners of nectosac, then turning onto outer lateral nectosac walls and each continuing distad to ostium (Fig. 18A); lower radial canal extending directly distad to ostial ring canal (Fig. 17B); internal pedicular canal short, passing from insertion point of external pedicular canal (latter canal not preserved) to junction with upper and

lower radial canals, on lower nectosac surface (Fig. 18A); ascending surface diverticulum extending proximally along lower nectophore surface from origin on internal pedicular almost to proximal end of nectophore, with tip penetrating mesogloea just distal of proximal end and swelling slightly (Fig. 18A).

Bracts up to 20 mm long along proximal-distal axis, 9 mm wide across right-left axis, with pointed proximal end and truncate distal end (Fig. 18B); distal end slightly emarginate and flanked by two cusps (relatively inconspicuous in present specimens); lateral cusp also discernible on outer lateral edge of most bracts (Fig. 18B); bracteal canal slightly sinuous and elongate, with two flaps near midline on lower surface (Fig. 18B); other bracts with distal flap only (not illustrated); upper surface with semicircular upper ridge distally, extending from right cusp to left cusp, delimiting distal upper facet.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Mapstone (1998). Northeast Pacific: off San Diego, 33°04'N, 118°16'W (Pugh 1999a). Other regions: North Atlantic (Pugh 1999a), South Atlantic (Totton 1954).

Vertical. This species was found at 500 and 700 m in the main study area and in a sample taken at 1200 m from over the hydrothermal-vent plume. This distribution falls within the vertical range from which one specimen was taken in the northeast Pacific and a number collected in the North Atlantic (Pugh 1999a).

Notes

This species was introduced by Mapstone (1998) for nectophores collected in Canadian Pacific waters. The holotype and four paratypes are held in the British Columbia Provincial Museum and four further paratypes are held in the NHM collections (see list above). The description given by Mapstone (1998) has been modified in the present work to incorporate the new axes described in Section 2.3.1, based on those given by Haddock et al. (2005a).

Bargmannia lata has been redescribed by Pugh (1999a) from a specimen collected by submersible off San Diego. This colony has a pneumatophore,

both immature and mature nectophores, and two types of bracts. The most common bract type is similar to, but longer than (<27 mm), those collected in Canadian Pacific waters, and when the latter bracts were reexamined for the present description, they were found to have two folded-over cusps distally. The gastrozooid and tentacle, siphosomal tentacle, and gonophores of *B. lata* were also described for the first time by Pugh (1999a), although the cormidia of his specimen were too contracted to determine the zooid arrangement within each cormidium. Additional observations made by Pugh include lateral processes flanking the ostium of the nectophore (as *rounded lobes* 1999a, p. 65 and shown in figs 13A and B, 14A and B) and an orange-red colour to the endodermal lining of the siphosome.

The synonymy of *Bargmannia lata* given above also includes two figures of a nectophore referred by Totton (1954, figs 28E and F, reproduced in 1965a as figs 45E and F) to *B. elongata*, as discussed above. These nectophores bear NHM Reg. No. 1957.5.15.110 and were reexamined for the present work together with four others taken during the John Murray Expedition (NHM Reg. No. 1949.11.10.378); all are referable to *B. lata*.

Nectophores of *Bargmannia lata* are distinguishable from those of the other three species in the genus by their lower-lateral wings, which are more extensive than those of *B. elongata* and *B. amoena* and arise more distally from the thrust block than those of *B. gigas*. Nectophores of *B. lata* also lack the short ridge from the upper-lateral ridge found in *B. elongata* and the extra ridges found at various points on nectophores of *B. gigas*. The outer upper-lateral ridge also extends to the distal end of the nectophore in *B. lata*, whereas it terminates short of the ostium in *B. amoena*. The bracts of *B. lata* can be distinguished from those of the other two species for which bracts are known (*B. elongata* and *B. amoena*) by the presence of a distal facet delimited by the semicircular upper ridge (Fig. 18B).

10.1.3. Family AGALMATIDAE (Brandt, 1835)

Diagnosis

Physonectae with colony typically linear and with many similar nectophores, atypically non-linear with few nectophores (*Melophysa*) or none (*Athorybia*); nectosomal polyps absent; nectosome dorsal in all *sensu stricto* genera with nectosomes; nectophores

typically with ridges of taxonomic importance and thrust block not enlarged; nectophores of *sensu stricto* genera also with complete nectosac musculature and descending surface diverticulum from pedicular canal on proximal surface; *sensu stricto* genera monoecious and with gastrozooid tentacles having tentilla either uniciliate with one terminal filament or tricornuate with two terminal filaments and ampulla; cnidoband of *sensu stricto* genera coiled and involucrum partial or complete, with nematocysts on; terminal filament(s).

Notes

The Agalmatidae is the “catch-all” family of the Physonectae and comprises, as Pugh (1999b) points out, all those genera that do not easily fit elsewhere into the suborder. There is, however, a core of genera that form a monophyletic clade, and these have recently been termed the Agalmatidae *sensu stricto* by Dunn et al. (2005b). They include *Nanomia bijuga*, *Halistemma rubrum*, *Agalma clausi*, *A. elegans*, *A. okeni*, and *Athorybia rosacea*, and the clade has recently been redefined by Pugh (2006b) to include all species in these genera, together with another monotypic genus, *Melophysa*. Thus, the two genera *Athorybia* and *Melophysa* previously referred to the short-stemmed family Athorybiidae are now referable to the Agalmatidae *sensu stricto*, and the family Athorybiidae is invalid. Additionally, Pugh has excluded other genera from the Agalmatidae, including *Marrus*, *Stephanomia*, *Cordagalma*, *Frillagalma*, and *Lychnagalma* (Pugh 2006b, fig. 21). The latter “orphaned” genera still require placement somewhere within the systematic framework of the Physonectae, even if only on a temporary basis. So in the present work they are retained as indeterminate genera of the family Agalmatidae, pending further information on their molecular and morphological characters, although the latter characters were excluded from the matrix drawn up to produce the family diagnosis given above.

Agalmatids of the *sensu stricto* group that develop nectophores have a dorsal nectosome, and this character distinguishes them from all indeterminate genera in this family, which have ventral nectosomes (Pugh 2006b, fig. 21). Nectosomal budding has yet to be closely studied in many species, as noted in Section 3.2, but nectophores have been found to be budded from the dorsal side of the nectosome in all those agalmatid *sensu stricto* genera so far investigated that have a nectosome (Pugh 2006b). This now includes

one species of *Halistemma* previously referred by Mapstone (2004) to *H. amphytridis*, the nectophores of which Pugh (2006b) notes are budded from the dorsal side of the nectosome, not from the ventral side as mistakenly shown by Mapstone (2004, fig. 2b). This halistemmid is referred by Pugh (2006b) to *Stephanomia foliacea* Quoy and Gaimard, 1833, not to *H. amphytridis* Lesueur and Petit, 1807, as given by Mapstone (2004), because, as Pugh (2006b) notes on page 42, the bracts of Mapstone's specimen have a "ventral keel" (2004, figs 3d, g, and h, as *vk*) similar to that illustrated and described by Quoy and Gaimard (1833, p. 75, pl. 3 figs 10–12). In bracts of *S. amphytridis* no such keel is present, although its absence is not evident from either the figure of the siphosome by Lesueur and Petit (1807, pl. 29 fig. 5) or the written account of the specimen given by Péron (1807, p. 45). However, since new specimens of the species tentatively referred by Totton (1965a) to *?Halistemma amphytridis* (based on material listed in Totton 1936) have recently been collected and analyzed for two genes by Dunn et al. (2005b), the description and figures published in 1807 by Péron and Lesueur and Petit are herein referred to Totton's *Stephanomia amphytridis*, to agree with Dunn et al. (2005b) and Pugh (2006b).

Species within the Agalmatidae *sensu stricto* that develop nectophores are separated principally on the ridge pattern found in these nectophores and on the tentilla of the tentacles. In most genera, as indeed also in the long-stemmed families Pyrostephidae (Section 10.1.2), Erennidae (Pugh 2001), and Resomiidae (Pugh 2006b), the nectophores bear elongate upper-lateral and lower-lateral ridges, and several also have vertical-lateral and lateral ridges. Within the Agalmatidae *sensu stricto* the upper-lateral ridges are either complete (*Agalma*, *Halistemma*) or incomplete (*Nanomia*) and a pair of lateral ridges is always present (either complete or incomplete), and also a pair of lower-lateral ridges. Upper-lateral and lower-lateral ridges are typically connected by one or more complete vertical-lateral ridges, although in some species of *Halistemma* the latter ridges are incomplete. These ridges are described further below for the species of Agalmatidae *sensu stricto* collected in Canadian Pacific waters. In the *sensu stricto* genus *Melophysa*, up to five nectophores may be developed (Pugh 1999b), but nectophores are less prominent in the colony than bracts, and indeed the nectophores of *Melophysa* are reduced, with only one being functional at a time (Totton 1965a). This nectophore may have some weakly developed ridges, but these are not arranged in the

pattern found in the nectophores of other *sensu stricto* genera. Indeed, Pugh (1999b) comments that the *M. melo* nectophores illustrated by Totton (1965a) are distorted. Nectophores of *M. melo* are best separated from those of *Agalma*, *Halistemma*, and *Nanomia* on the course of the lower radial canal of the nectosac, which is sinuous in *M. melo* and straight in other genera.

The nectosacs of Agalmatidae *sensu stricto* nectophores also have complete musculature, without a proximal muscle-free zone as is found in the Pyrostephidae (Section 10.1.2) and also in the Erennidae and Rhodaliidae, as noted above. Species in the latter three families also lack a descending surface diverticulum on the proximal surface of the nectophore (as also noted above), whereas in all species of the Agalmatidae *sensu stricto* with nectophores, a descending surface diverticulum is present. The thrust blocks of *sensu stricto* nectophores are similar to those of nectophores of the physonect families Erennidae and Resomiidae, but smaller than those found in nectophores of the family Pyrostephidae. As noted above, sex status in physonects is linked to whether or not a descending surface diverticulum develops, and species of the Agalmatidae *sensu stricto* are all monoecious, with a descending surface diverticulum, as are species in the families Forskaliidae, Physophoridae, and Resomiidae (see Pugh 2006b, fig. 21). Monoecy in codonophorans probably evolved only once, as is suggested by the phylogeny of Dunn et al. (2005b), although these authors point out on page 930 that the lack of topological resolution in their data "makes it impossible to rule out the possibility that it arose more than once."

Tentilla can also be used to distinguish genera of the Agalmatidae *sensu stricto*, as mentioned in Section 10.1. The mature tentillum of these species has a cnidoband that is typically tightly coiled around an elastic strand and bears either one terminal filament (unicornuate) or two terminal filaments and an ampulla (tricornuate). Most tentilla of *sensu stricto* genera are also protected by a fold of tissue termed the involucrum, as noted in Section 10.1; this grows up from the base and either partially or completely encloses the cnidoband at maturity (Totton 1965a). Thus, in *Nanomia bijuga* (Fig. 14C) the involucrum is partial and in *Agalma elegans* it is complete (Fig. 14A). In other *sensu stricto* species the involucrum may extend over only a small proximal part of the cnidoband (as in *Halistemma foliacea*; see Mapstone 2004, fig. 3a), or may be so small as to be vestigial (as

in *H. transliratum* (see Pugh and Youngbluth 1988a, fig. 7), *H. rubrum* (see Schneider 1899, pl. 4 fig. 35, as *Agalma rubrum*), and *H. cupulifera* (see Lens and van Riemsdijk 1908, pl. 16 fig. 117)). In some published figures of halistemmid tentilla (for example, Huxley 1859, pl. 6 fig. 8; Mapstone 2004, fig. 3a, of *H. foliacea* as *H. amphyridis*) the cnidoband appears loosely coiled, but this is probably a preservation artefact, since Pugh (1998) comments on page 244 that in core agalmatid genera the tentilla “possess a well developed, tightly coiled cnidoband”.

Tentilla of the short-stemmed *sensu stricto* genera *Athorybia* and *Melophysa* are similar to those found in the genus *Agalma*. In *M. melo* the cnidoband has seven or eight coils, typically enclosed within a complete involucrum, and there are two terminal filaments and an ampulla (tricornuate) (Bigelow 1911b, as *Anthophysa rosea*; Totton 1965a). In *Athorybia* two types of tentilla occur, as described by Bigelow (1911b), Totton (1965a), and Biggs (1978). One type is involucrate, with a complete involucrum enclosing a cnidoband that either consists of two coils (*A. rosacea*) or is folded in half (*A. lucida*), and in the second type is dendritic. Dendritic tentilla are larger and likely to be older. They have a very short involucrum from which projects dendritic structures, either a single pendant-like structure or several branched extensions. The involucrum of these dendritic tentilla does not enclose the cnidoband, and distally there are either two terminal filaments and an ampulla, as in *A. rosacea* (tricornuate), or two filaments that may fuse together when older, and no ampulla, as in *A. lucida*.

Mackie et al. (1987) mention a further four genera introduced into the family Agalmatidae since the review by Totton (1965a). Of these, Pugh (2006b) considers *Sphaeragalma* Margulis, 1976 to be a synonym of *Stephanomia amphyridis* and *Stepanjantsia* Margulis, 1982 to be a synonym of the prayine calycophoran *Rosacea plicata*. The genus *Paragalma* Margulis, 1976 has not been found by any subsequent workers in the field, and although *Rudjakovia* Margulis, 1982 has been collected more recently (Pugh 2006b), there is as yet insufficient evidence to place it firmly within the Agalmatidae *sensu stricto*. Since the present author has not examined the original type material of *Rudjakovia plicata*, its characters are excluded from the generic diagnoses for the Agalmatidae *sensu stricto* given below. Specimens of the other agalmatid genera not found in Canadian Pacific waters, but represented in the NHM collections, have also been examined and

their characters included in a character matrix used to generate the diagnoses of the *sensu stricto* genera given below. The registration numbers for these specimens are given below under *Agalma elegans*.

Family Agalmatidae *sensu stricto*

Genus *Agalma* Eschscholtz, 1825

Diagnosis

Agalmatidae with colony linear and having many ridged nectophores with complete upper-lateral ridges; nectosac of nectophore with straight lower radial canal; tentilla of gastrozooid tentacles tricornuate with complete or incomplete involucrum, two terminal filaments, and ampulla.

Type species: *Agalma okeni* Eschscholtz, 1825.

Notes

Species of *Agalma*, like those of the other core agalmatid genera with nectophores, have sinuous lateral radial canals on the nectosac and are monoecious. The latter character has been shown by Dunn et al. (2005b) to be linked to the presence of a descending surface diverticulum (as *descending pallial canal*) on the nectophore, as noted above.

Species currently assigned to the genus *Agalma* include *A. elegans* (described below), *A. okeni*, and *A. clausi*. The former two are distributed worldwide in tropical and subtropical areas and *A. okeni* has been recorded as far north as Point Conception, California, in the northeast Pacific (Alvariño 1991). However, *A. clausi* has so far only been collected from the Atlantic (Mackie et al. 1987) and the Mediterranean (Mills et al. 1996); it was first described by Bedot in 1888. The 16S and 18S genes of all three *Agalma* species were tested by Dunn et al. (2005b), and the species nested with *Athorybia rosacea* in their consensus tree given as figure 6.

Colonies of *Agalma* vary in rigidity, and in *A. elegans* the stem is long, soft, and retractile, whereas in both *A. okeni* and *A. clausi* it is short, rigid, and non-retractile (Bigelow 1911b). The tentillum of *Agalma* is distinctive, comprising a coiled red cnidoband and two terminal filaments subtended at right angles in life. It has been suggested that this

is an example of aggressive mimicry, since when fishing, the tentilla resemble a swarm of swimming copepods (Purcell 1980) (see also Section 4.3). In *A. elegans* and *A. okeni* the involucrum is thin and membranous and does not cover the ampulla and two terminal filaments (Fig. 14A), whereas in *A. clausi* it is thicker and more cup-like, which allows the cnidoband, ampulla, and terminal filaments to be either withdrawn into it or extended from it, as shown by Bedot (1888, pl. 4 figs 3, 8) and mentioned again by Mills et al. (1996). Another *sensu stricto* agalmatid, *Melophysa melo*, has a similar tentillum to that found in *A. elegans*, with an involucrum that is probably complete in life, as noted above.

***Agalma elegans* (Sars, 1846)**

(Fig. 19)

Agalmopsis elegans Sars, 1846: 36, pl. 5 figs 7, 8 (not 32–35, 37–41, pl. 5 figs 1–6 and pl. 6, = *Nanomia cara*); L. Agassiz, 1862: 369; Haeckel, 1888a: 40; Haeckel, 1888b: 234; Schneider, 1898: 122; Kawamura, 1911: 362, pl. 7 figs 11–17.

Agalmopsis sarsi Kölliker, 1853: 10, pl. 3 figs 1–8; L. Agassiz, 1862: 369; Claus, 1878: 12, pl. 4 fig. 4; Haeckel, 1888a: 40; Haeckel, 1888b: 234.

Agalma punctata Leuckart, 1853: 3, pl. 1 figs 1, 19, 20 and pl. 2, figs 1, 2, 5–7, 23 (not Vogt, 1854: 83, pl. 12 figs 1–8, = *Apolemia uvaria*, or *Agalmopsis punctata* Kölliker, 1853: 15, pl. 4, = *Halistemma rubrum*).

Agalma clavata Leuckart, 1853: 3, pl. 2 fig. 3.

Agalma clavatum: Leuckart, 1854: 337, pl. 13 figs 2–7; Spagnolini, 1870: 652; Haeckel, 1888b: 226 (not Fewkes, 1880a: 137; Fewkes, 1880b: 628, = *Agalma clausi*).

Agalma sarsi: Leuckart, 1854: 331, pl. 12 figs 17 (lower), 21–27 and pl. 13 fig. 1 (note: the legend for plate 12, printed on pages 376 and 377, was incorrectly numbered; figures 4–25 should have been labelled “figures 5–26”. There are two figures numbered 17; the legend for the upper one is given under figure 17, but the legend for the lower one is

given under figure 26); Sars, 1857: 8; Claus, 1860: 316, pl. 26 fig. 27 and pl. 27 figs 32g, 41; Keferstein and Ehlers, 1860: 257; Keferstein and Ehlers, 1861: 9, pl. 1 fig. 20, pl. 2 figs 6–11, and pl. 3 fig. 17; L. Agassiz, 1862: 369; Claus, 1863: 557, pl. 48 figs 37–40; Spagnolini, 1870: 652; Metschnikoff, 1870: 308, pl. 2 figs 14–16; Metschnikoff, 1874: 48, pl. 8 figs 1–13, pl. 9 figs 11–21, and pl. 11 figs 1, 2; Korotneff, 1884: 259, pl. 16 figs 49, 50, pl. 17 figs 55, 69, 74, and pl. 18 figs 76–79; Iwanhoff, 1896: 334, pl. 5 figs 18–22; Woltereck, 1905a: 118, figs 17–21; Woltereck, 1905b: 611, figs 1–11, 20, 21 (not Fewkes, 1880a: 137, pl. 2 fig. 2; Fewkes, 1880b: 628, = *Agalma clausi*).

Agalmopsis clavatum: L. Agassiz, 1862: 369; Spagnolini, 1870: 652.

Agalma elegans Fewkes, 1880a: 141; Fewkes, 1880b: 619, figs 1–6; Fewkes, 1881: 163, pl. 9 figs 1–21 and pl. 10; Fewkes, 1885: 240, pls 1–4; Schneider, 1896: 579, pl. 43 figs 2–4; Bigelow, 1911b: 281, pl. 18 figs 9–13 and pl. 19 figs 1–4; Jacobs, 1937: fig. 7c; Russell, 1939: 356, figs 4a–h; Totton, 1954: 61, frontispiece, fig. 24; Totton, 1955: 239, figs 1–9; Cervigon, 1961: 12, fig. 7; Totton, 1965a: 54, pl. 10 figs 11–17, pl. 11 figs 1, 2, and text-figs 7, 18–20; Biggs, 1977b: 265, fig. 3; Mackie, 1978: 327, fig. 1; Alvariño, 1981: 394, figs 174.3A and B; Purcell, 1984: 318; Pugh, 1999b: 481, figs 3.6, 3.22; Dunn and Wagner, 2006: 747, fig. 4.

Cuneolaria elegans Haeckel, 1888a: 40.

Agalmopsis catena Haeckel, 1888b: 234.

Agalmopsis sarsi: Bedot, 1896: 409.

Agalma sp. Cervigon 1961: figs 8–11.

?*Agalma elegans* Wang and Xu, 1990: 85, figs 1–5.

Diagnosis

Agalma with colony soft and flexible; mature nectophore having upper-lateral ridges with notch and two vertical-lateral ridges; bract foliaceous, with three distal cusps but no red spots on upper surface; tentillum with close-fitting involucrum and non-retractable terminal filaments and ampulla.

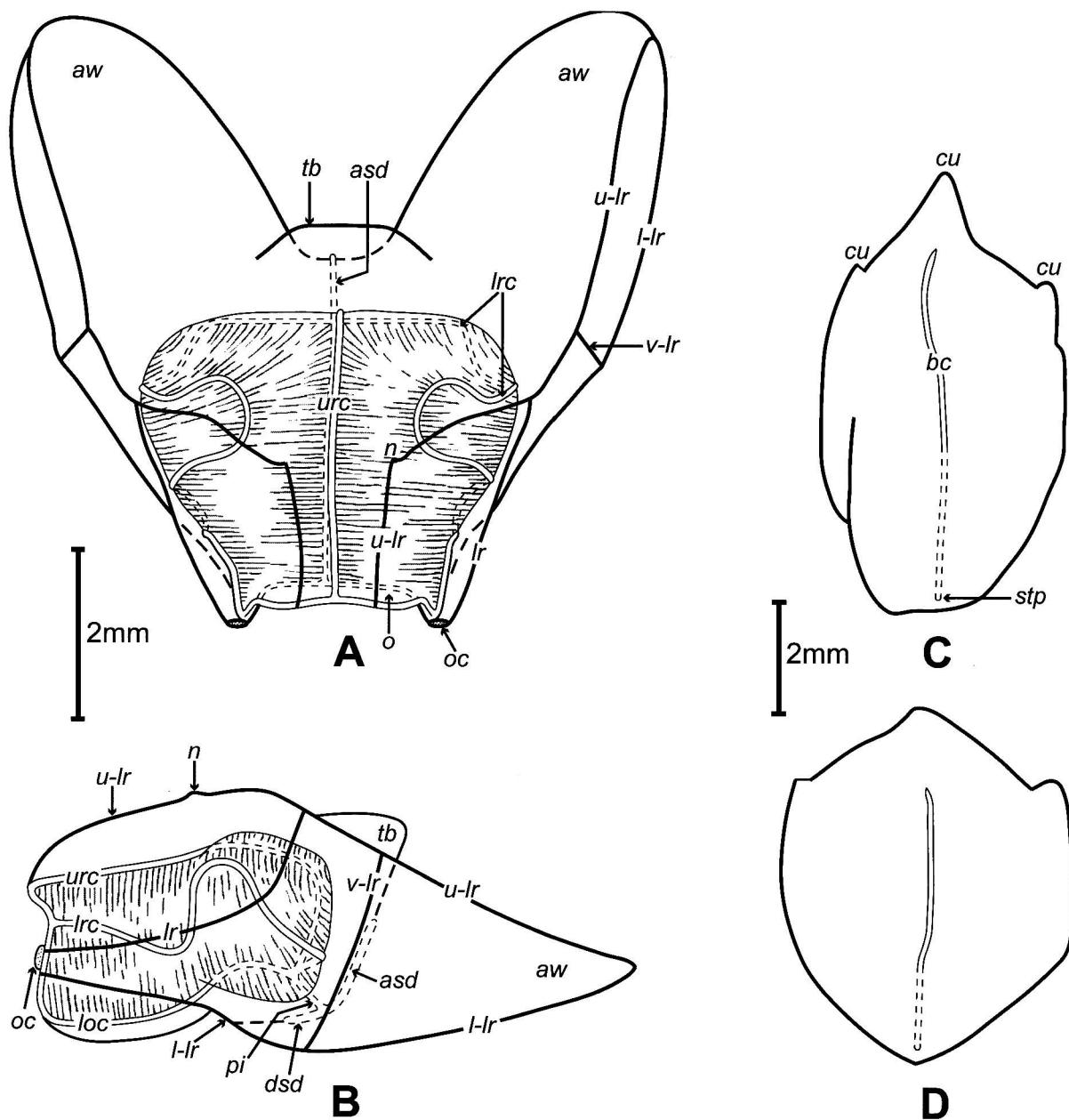


Fig. 19. *Agalma elegans*: A: nectophore, upper view; B: nectophore, lateral view; C and D: bracts, upper view (asd, ascending surface diverticulum; aw, axial wing; bc, bracteal canal; cu, cusp; dsd, descending surface diverticulum; l-lr, lower-lateral ridge; loc, lower radial canal; lr, lateral ridge; lrc, lateral radial canal; n, notch; o, ostium; oc, ostial chromatophore; pi, internal pedicular canal; stp, stem-attachment point; tb, thrust block; u-lr, upper-lateral ridge; urc, upper radial canal; v-lr, vertical-lateral ridge).

Material examined

One hundred and twelve nectophores and 11 bracts from Canadian Pacific stations LB2 (0–28 m), LB2 (28 m) (Figs 19C and D) BCPM 996-199-1, LB4 (88–0 m), LB13 (500–0 m) (Figs 19A and B) BCPM 996-200-1, LB13 (500–0, 700–0 m), LB14 (0–700 m), LB17 (300–0 m), LC6 (0–80

m), LC9 (300–0, 500–0 m), LC10 (300–0, 500–0, 575–0, m), LC11 (500–0, 0–700, 700–0 m), A4 (300–0 m) BCPM 996-201-1, and A4 (300–0 m), 1 nectophore taken in vicinity of thermal vent from tow 2 (1700–0 m) (Fig. 11, Table 1). Specimens from the NHM collections: *Agalma elegans* Reg. Nos 1952.9.23.72, 7 nectophores, 22 bracts, nectosome

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and siphosome with 3 attached nectophores, and circa 15 attached bracts and gonophores ($43^{\circ}48'N$, $7^{\circ}19'E$); 1952.9.23.77, 5 nectophores ($43^{\circ}48'N$, $7^{\circ}19'E$); 1957.3.23.33, 22 nectophores, 38 bracts, and 2 stem portions both including nectosome and siphosome ($13^{\circ}11'S$, $12^{\circ}45'E$); *Agalma okeni* Reg. Nos 1957.4.27.54, 35 nectophores, 3 stem portions including nectosome and siphosome, and many bracts ($1^{\circ}11'S$, $5^{\circ}38'E$); 1957.4.27.1, 6 nectophores, 87 bracts, and 2 stem portions including nectosome and siphosome with more attached bracts ($14^{\circ}42'S$, $42^{\circ}23'E$); *Halistemma rubrum* Reg. Nos 1953.7.2.23, 1 nectophore ($7^{\circ}19'E$, $43^{\circ}48'N$); 1952.9.23.285-294, 21 nectophores, 12 bracts, and 2 stem portions with attached zooids ($43^{\circ}48'N$, $7^{\circ}19'E$); 1952.9.23.304, 12 nectophores, 464 bracts, and stem portion including nectosome and siphosome ($7^{\circ}19'E$, $43^{\circ}48'N$); *H. transliratum* Reg. No. 1987.4.1.1, 7 nectophores of which 3 still attached to young colony ($26^{\circ}24'N$, $77^{\circ}50'W$); *H. striata* Reg. No. 1973.4.26.5, 7 nectophores ($3^{\circ}38'N$, $29^{\circ}14'W$); *Athorybia rosacea* Reg. Nos 1985.12.96, 1 colony with attached gastrozooids and gonophores ($32^{\circ}25.5'N$, $15^{\circ}05.5'W$ to $32^{\circ}29'N$, $15^{\circ}03.75'W$); 1950.9.3.88, 12 bracts ($28^{\circ}44'30''N$, $34^{\circ}38'24''W$); *Melophysa melo* Reg. Nos 1957.8.13, 5 nectophores ($4^{\circ}50'18''S$, $0^{\circ}47'18''W$); 1959.8.10.56, 5 bracts ($08^{\circ}44.65'S$, $41^{\circ}50.3'E$).

Description of material

Nectophores up to 7 mm long, translucent, without mouthplate; axial wings varying in shape from elongate (Fig. 19A) to blunt (not illustrated); ridges discerned only with staining and some absent from smaller nectophores; upper-lateral ridges appearing more prominent proximally, extending from proximal ends of axial wings up and over upper-lateral surfaces of nectophore, converging somewhat towards midline distally and forming slight protruding notch before continuing distally to ostial ring canal (Figs 19A and B); lateral ridge originating from upper-lateral ridge and passing to lateral border of ostium; lower-lateral ridge originating from, and contiguous with, proximal end of upper-lateral ridge, passing along lower-lateral surface of nectophore, and terminating on lower-lateral border of ostium; vertical-lateral ridge passing from upper-lateral ridge orthogonally down to lower-lateral ridge and delimiting two lateral facets; latter somewhat rounded and typically difficult to discern; two lateral ostial chromatophores discernible in some nectophores (Figs 19A and B); shallow

median furrow typically discernible in midline on upper nectophore surface; mesogloea flaccid; thrust block thick, broad-based, and with flat proximal surface in upper view; nectosac broadest proximally (across right-left nectophore axis) and narrower at ostium; latter of varied width in present material, and velum not evident in any specimens; radial canals arising together from internal pedicular canal on proximal nectosac surface (Fig. 19B) with upper and lower radial canals following approximately straight courses to ostial ring canal; lateral radial canals sinuous, each with only slight lower loop after origin from internal pedicular canal (Fig. 19A), followed by larger upward loop onto upper nectosac surface and further smaller loop onto lower surface before insertion onto ostial ring canal (Fig. 19B); internal pedicular canal short, originating from external pedicular canal (not preserved) on lower proximal surface of nectophore in midline (Fig. 19B); ascending surface diverticulum extending upwards from origin of internal pedicular canal and descending surface diverticulum extending downwards from this point.

Bracts up to 7.5 mm long, of varied width and with three distal gelatinous cusps, of which median is largest; upper surface convex and soft, but no distal ridges discernible; mesogloea flaccid; bracteal canal discernible but apparently terminating short of distal end of bract in present material, and proximal section not preserved (Figs 19C and D).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above); $52^{\circ}08'N$, $133^{\circ}26'W$, $53^{\circ}28'N$, $133^{\circ}32'W$ (Berkeley and Berkeley 1960). Northeast Pacific: California region (Margulis and Vereshchaka 1994); off California coast (Alvariño and Kimbrell 1987); off San Francisco (Alvariño and Kimbrell 1987; Alvariño 1991); $53^{\circ}30'N$, $138^{\circ}53'W$, $48^{\circ}00'N$, $133^{\circ}12'W$, $55^{\circ}N$, $150^{\circ}W$, $55^{\circ}N$, $155^{\circ}W$ (Berkeley and Berkeley 1960). Other regions: specimens from elsewhere in the Pacific are mostly from high southern latitudes (Alvariño et al. 1990). *Agalma elegans* has been rated a near-cosmopolitan species (Kirkpatrick and Pugh 1984).

Vertical. Several of the records from off Vancouver Island are from the upper 100 m of the water column, and this is the level preferred by *Agalma elegans* worldwide (Margulis 1984).

Notes

This species was introduced by Sars in 1846, but only his form "B" with tricornuate tentilla is referable to *Agalma elegans*; the remainder is now referred to *Nanomia cara*, including all the figures in his plates 5 and 6 except figures 7 and 8 in plate 5 (Totton 1965a). The species was subsequently introduced by Kölliker (1853) under a different name, *A. sarsi*, and indeed, Sars (1857) later realized his mistake and also referred his form B to *A. sarsi*. As Totton (1965a) points out, this would have been a good name to retain, since Kölliker's account and figures are reasonably accurate, including his interpretation of the arrangement of zooids in the cormidium. However, Haeckel (1888b) chose to ignore this name, and instead restricted the specific name *elegans* to the form with a tricornuate tentillum, and this name has remained in use to the present day.

The most accurate description and figures of *Agalma elegans* so far published are those of Totton (1954, 1965a), who gives an excellent schematic diagram of a young colony with four cormidia (1954 frontispiece, reproduced in 1965a as fig. 7), together with figures of the nectosome, male gonophores, and terminal cormidium. He also gives the first clear account and figures of nectophore morphology, with the courses of the ridges and lateral radial canals accurately shown (1954, figs 24A and B, reproduced in 1965a as figs 18A and B, with upper-lateral ridge given as apico-lateral ridge, and lower-lateral ridge as infralateral ridge). A similar and more recent nectophore figure, unlabelled, is given by Pugh (1999b, fig. 3.6).

Nectophores of *Agalma elegans* may be confused with those of young *A. okeni* specimens because both have only a single vertical-lateral ridge on each side. However, the bracts of *A. okeni* differ considerably from those of *A. elegans* (as shown in Figs 19C and D) because they have a broad distal surface that is divided into four slightly concave facets, as shown by Pugh (1999b, fig. 3.23). The latter author also gives a line drawing of a mature nectophore of *A. okeni* (Pugh 1999b, fig. 3.7), and states in the text that it has no lateral ridge, unlike the nectophore of *A. elegans*. However, a lateral ridge was identified by the present author in nectophores from two specimens of *A. okeni* held in the NHM collections. Possibly this ridge is not always present, but further investigation is needed to resolve this point. Thus, *A. elegans* is distinguishable from *A. okeni* by its looser colony form (see above), its softer non-prismatic mature nectophores with only one vertical-lateral

ridge on each side, and its bracts with only three soft distal cusps.

Both the nectosomal and siphosomal growth zones of *Agalma elegans* were recently studied by Dunn and Wagner (2006), who find that in the former zone an extra small bud is present on the posterior side of each young nectophore bud (see also Section 3.2); whether this small bud is still present beside the nectophore after it has matured is not known. Dunn and Wagner (2006) also show that each cormidium of *A. elegans* extends from one large B-palpon to the next (see Section 3.2), with most cormidial zooids arising from six sub-buds on the probud. Also in this species, more male elements are also budded later, anteriorly from the anteriormost male element, and some bracts also arise later, apparently directly from the stem (Dunn and Wagner 2006).

Genus *Nanomia* Agassiz, 1865

Diagnosis

Agalmatidae with colony linear and having many ridged nectophores with incomplete upper-lateral ridges; nectosac of nectophore with straight lower radial canal; tentilla of gastrozooid tentacles unicornuate, with incomplete involucrum and single terminal filament.

Type species: *Nanomia cara* A. Agassiz, 1865.

Notes

The main characters that distinguish species of *Nanomia* from those of other *sensu stricto* agalmatids are the possession of a partial involucrum on the unicornuate tentillum, together with the arrangement of gonodendra in the cormidium, the extent of the upper-lateral ridges, and the relatively large size of the nectosac. In *Nanomia* species, male and female gonodendra alternate along the length of each cormidium (Totton 1954) but this character is omitted from the present generic diagnosis because it is imperfectly known for most other agalmatids. The upper-lateral ridges are incomplete distally in both *Nanomia* species (Fig. 20A; Totton 1965a, fig. 37B), whereas in other genera where such ridges are present they are complete and terminate at the ostium (*Agalma*, *Halistemma*). Nectosacs of the two *Nanomia* species also fill more of the nectophore than in other *sensu stricto* agalmatids, leaving only a thin layer of surrounding mesogloea, and this makes

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the nectophores particularly soft and the thrust block relatively small and insignificant.

The tentillum of *Nanomia* is well shown for *N. bijuga* by Bigelow (1911b) and diagrammatically reproduced in Figure 14C. For *N. cara* a very similarly shaped tentillum is figured by Fewkes (1888, pl. 2 fig. 9). There may, however, be some variation in both the length of the cnidoband and the relative length of the involucrum in *Nanomia* tentilla. Among the *N. cara* specimens examined from the NHM collections (listed below), the cnidobands of some are composed of more coils than those of others, and are similar to the cnidobands with three or four coils shown by Fewkes for this species; unfortunately, however, no involucra could be discerned in the NHM specimens. Similarly, the cnidobands of one of the two NHM *N. bijuga* specimens with tentilla are longer than those of the specimen shown in Figure 14C, but again the involucrum could not be discerned, whereas in the other specimen the involucrum is identical with that shown in Figure 14C. Kawamura (1911, pl. 7 fig. 9) also shows a slightly longer involucrum for *N. bijuga*. These observations suggest that in some mature tentilla of this species the involucrum may cover more of the cnidoband than in others.

The alternate arrangement of gonodendra in the cormidia of *Nanomia bijuga* was first shown in detail by Totton (1965a, figs 35, 36) and clearly illustrated in figure 5c of Dunn and Wagner (2006). It is also confirmed by the present author in one of the specimens of *N. bijuga* from the NHM collections. Dunn and Wagner (2006) give an elegant description of cormidial formation from a single probud in *N. bijuga*, based on a SEM study. In this species a gastrozooid appears first on the anterior side and then palpons start to form at its base. As these spread out anteriorly along the stem, a bract and then a gonozooid bud laterally from the base of each palpon. The gonozooid subsequently develops into either a group of male gonophores or a gonodendron bearing many female gonophores. This developmental sequence is well shown by Dunn and Wagner (2006) in figures 5d–i. In *N. cara* the same arrangement of male gonophores and female gonodendra can be discerned in two figures of the siphosome by Sars (1846, pl. 5 figs 2, 3, as *Agalmopsis elegans*).

Colonies of *Nanomia bijuga* tend to be smaller than those of *N. cara* and their nectophores are flattened in a different plane, as discussed below, although

giant colonies of *N. bijuga* are known to exist off the west coast of North America (P.R. Pugh, pers. comm., 2006)

The two species of *Nanomia* were introduced over 140 years ago, *N. bijuga* in 1844 and *N. cara* in 1865. However, they were not assigned to the same genus until 1954, by A.K. Totton. Previously the specific name *bijuga* was combined with many generic names, as can be seen from the synonymy given below, whereas the generic name *Nanomia* was combined with the specific name *cara* when first introduced by A. Agassiz (1865). To indicate the correct usage of the specific name *cara* in the synonymy of *N. bijuga* given below, *N. cara* is entered as “not”. It will be noted that the specific name *bijuga* was often combined with the generic name *Stephanomia*, a unicornuate-species name originally introduced for the siphosome of a large physonect, *S. amphyridis* Lesueur and Petit, 1807, the nectosome of which is assumed to have detached and swum away prior to capture. Huxley (1859) later restricted the name *Stephanomia* to this unicornuate species because it has a short involucrum (1859, pl. 6 fig. 8), and introduced a new genus, *Halistemma*, for *H. rubrum*, which has only a vestigial involucrum, as mentioned above. Bigelow (1911b) disagreed with Huxley because he did not consider the involucrum an important character at genus level, and made *Halistemma* a junior synonym of *Stephanomia*, so referring the unicornuate species *bijuga* to the genus *Stephanomia*.

The genus *Stephanomia* was reassessed by Totton (1954), who concluded that the type of involucrum in the tentillum is indeed important for identifying unicornuate species, as is also the course of the lateral radial canals over the nectosac of the nectophore. He therefore referred the two *Stephanomia* species of Bigelow with sinuous lateral radial canals (*S. bijuga* and *S. cara*) to the genus *Nanomia* and introduced a new genus, *Marrus*, for three unicornuate species of agalmatids with unlooped radial canals on the nectosac. However, the genus *Stephanomia* was retained by Totton (1954) for another species, *S. rubrum*, but in his later work he reinstated the genus *Halistemma* for this species “whose cnidobands lack a marked involucrum” (Totton 1965a, p. 56) yet have unicornuate tentilla and sinuous lateral radial canals on the nectosac. Totton (1965a) also referred three further species to the genus *Halistemma*: a new species, *H. striata*, another species, *H. cupulifera* Lens and van Riemsdijk, 1908 described only from the siphosome, and a third species (about which

he had doubts), *H. amphytridis* (Lesueur and Petit, 1807).

More recently, a species outside the family Agalmatidae *sensu stricto* has been referred to the genus *Stephanomia*, namely “*Stephanomia amphytridis*” of Dunn et al. (2005b) and Totton (1936). This species is dioecious and has a ventral nectosome, no descending surface diverticulum on the proximal surface of the nectophore, and a muscle-free zone on the lower proximal surface of the nectosac (Dunn et al. 2005b; Pugh 2006b). It is herein referred to the family Agalmatidae as an indeterminate species, pending further information from molecular characters, as noted above.

***Nanomia bijuga* (delle Chiaje, 1844)**

(Figs 20, 21)

Physsophora bijuga delle Chiaje, 1844: pl. 181 figs 3–6 (not *Agalmopsis elegans* Sars, 1846: 32 (in part), pl. 5 figs 1–6 and pl. 6 figs 1–19, = *Nanomia cara*, or *Nanomia cara* A. Agassiz, 1865: 200, figs 331–350, or Fewkes, 1888: 213, pls 1–3, = *Nanomia cara*).

Anthemodes canariensis Haeckel, 1869a: 18, figs 3–10; Haeckel, 1888a: 40.

Halistemma pictum Metschnikoff, 1870: 306, pl. 2 figs 1–11; Chun, 1888a: 1167.

Stephanomia (Anthemodes) *canariensis*: Metschnikoff, 1874: 36.

Stephanomia pictum Metschnikoff, 1874: 61, pl. 12 figs 1–9 (not *Stephanomia cara* Metschnikoff, 1874: 62, = *Nanomia cara*).

Halistemma tergestina Claus, 1877: 8.

Halistemma tergestinum: Claus, 1878: 1, pl. 1 figs 1–11, pl. 2 figs 1–10 and 12–15, pl. 4, figs 5, 8, 9; Haeckel, 1888a: 40 (not *Halistemma elegans* Claus, 1878: 35, = *Nanomia cara*).

Agalmopsis picta: Fewkes, 1880b: 136, pl. 2 figs 1, 6 (not *Agalmopsis cara* Fewkes, 1880a: 135, = *Nanomia cara*).

Agalmopsis gracile (*lapsus calami*) Fewkes, 1882: 265.

Agalmopsis fragile Fewkes, 1882: 267, pl. 5 fig. 2 and pl. 6 figs 16, 17, 23–25; Fewkes, 1886: 965.

Agalmopsis fragilis: Fewkes, 1883: 844.

Anthemodes canariensis: Haeckel, 1888a: 40; Chun, 1888a: 1170.

Anthemodes picta: Haeckel, 1888a: 40 (not *Anthemodes ordinata* Haeckel, 1888a: 40, = *Cordagalma ordinata*).

Halistemma fragile: Haeckel, 1888a: 40 (not *Halistemma carum* Haeckel, 1888a: 40, = *Nanomia cara*).

Cupulita canariensis: Haeckel, 1888b: 367; Bedot, 1896 (in part).

Cupulita fragilis: Haeckel, 1888b: 367.

Cupulita picta: Haeckel, 1888b: 367; Bedot, 1896: 407 (in part); Kawamura, 1911: 359 (in part), pl. 7 figs 1–10.

Cupulita tergestina: Haeckel, 1888b: 367 (not *Cupulita sarsii* Haeckel, 1888b: 367, = *Nanomia cara*).

Halistemma (Stephanomia) pictum: Chun, 1888b: 13.

Cupulita cara Bedot, 1896: 408 (not *Cupulita cara* Haeckel, 1888b: 367, Römer, 1901: 177 or Vanhöffen, 1906: 27, figs 40–44, = *Nanomia cara*).

Agalmopsis bijuga: Schneider, 1896: 587.

Cupulita (Halistemma) picta: Chun, 1897a: 103; Chun, 1897b: 77, figs 15, 19 (not *Cupulita cara* Chun, 1897a: 103, = *Nanomia cara*).

Cupulita bijuga: Schneider, 1898: 123 (in part).

Anthemodes moseri: A. Agassiz and Mayer, 1902: 167, pl. 12 figs 49–57.

Halistemma (Cupulita) pictum: Woltereck, 1905a: 121.

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Stephanomia bijuga: Bigelow, 1911b: 284, pl. 19 figs 5–11 and pl. 20 figs 1–3; Totton, 1932: 324, figs 6 and 7; Jacobs, 1937: 585, figs 1–3, 7a, 8a; Alvariño, 1980c: 152; 1981: 394 (in part), fig. 174.4 (in part); Palma, 1986: 73, figs 2A–C (not *Stephanomia bijuga* Berrill, 1930: 753, fig. 1, Russell, 1933: 74, Moore, 1937: 51, = *Nanomia cara*) (not *Stephanomia cara* Bigelow, 1911b: 349; Bigelow, 1926: 377, = *Nanomia cara*).

Stephanomia picta: Garstang, 1946: 112.

Nanomia bijuga: Totton, 1954: 52, fig. 19d; Totton, 1955: 241; Daniel and Daniel, 1963: 195, figs III, 2–6; Totton, 1965a: 68 (in part), pl. 10 figs 1–10, pl. 14 fig. 9, and text-figs 32–36; D. Carré, 1969b: 325, figs 1–7, pls 1–4; Daniel, 1974: 51, figs 4a–g; Purcell, 1980: 1045; Purcell, 1984: 318, figs 4k–n; Mapstone and Arai, 1992: 4, figs 3, 4; Pagès and Gili, 1992b: 72, figs 8A and B; Pugh, 1999a: 70; Pugh, 1999b: 483, figs 3.14, 3.28; Bouillon et al., 2004: 212, figs 125A–D; Dunn and Wagner, 2006: 747, fig. 5.

Nanomia cara Mackie, 1962: 689, fig. 1; Mackie, 1963: 335, fig. 24–1; Mackie, 1964: 366, figs 1–9; Mackie, 1985: 758, fig. 3; Mackie and Boag, 1963: 181, figs 2, 4, 6A–D; Totton 1965a: 72, text-figs 37A–C, pl. 14 figs 1–6; Alvariño, 1980c: 152; Freeman, 1983: 591, figs 6, 8A–C, 9A’–E’, 10A and B, 11A and B, 12A–C, 13, 14A–D, 17A–C; Freeman, 1987: 535, figs 1A and B, 2, 3, 4A–C, 5A–D, 6A and B, 7 (not *Nanomia cara* Totton, 1954: 53, figs 19A–C, Totton, 1965a: 72, text-figs 37A–C, pl. 14 figs 1–6, or Kirkpatrick and Pugh, 1984: 38, fig. 10, = *Nanomia cara*).

Diagnosis

A *Nanomia* species with colonies typically small; mature nectophore flattened along proximal–distal axis and with thin thrust block; cormidia with two bract types, including single elongate trifid bract beside gastrozoid and multiple diamond-shaped trifid bracts between gastrozooids.

Material examined

Approximately 29 000 nectophores and 17 pneumatophores from Canadian Pacific stations LB2 (28, 28–0, 30 m), LB4 (88–0, 85–88, 95 m), LB6 (0–70, 70–85, 80, 80–0, 0–90, 90, 90–0 m), LB8 (95–112, 130 m), LB10 (125–0 m), LB12 (0–300, 300, 400–0, 0–450, 450 m), LB13 (0–700 m) BCPM

996–214–1, LB13 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–300, 300, 0–500, 500, 500–0, 0–700, 700 m), LB16 (0–300, 300, 0–500, 500, 500–0, 0–700, 700 m), LB17 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700 m), LC2 (0–60, 60, 90 m), LC6 (70, 70–0, 0–80, 80 m), LC9 (500 m) BCPM 996–215–1, LC9 (0–300, 300, 300–0, 0–500, 500, 500–0 m), LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LD2 (30 m), and LD10 (300 m). Two nectophores collected near thermal vent from tows 2 (0–2200 m) and 3 (1845–2100 m) (Fig. 11, Table 1). Seventy nectophores, 17 pneumatophores, 1 nectophore (Figs 20A–C), and 1 pneumatophore (Fig. 20D) from the Strait of Georgia (for details of the sampling area see Mapstone and Arai 1992). Specimens from the NHM collections: *Nanomia bijuga* Reg. Nos 98.5.7.27, 24 nectophores, nectosome, and siphosome with many attached zooids (40°50'N, 14°15'E); 1953.7.2.47, 1 nectophore (7°19'E, 43°48'N); 1953.9.23.604, 2 nectophores (7°19'E, 43°48'N); 1959.8.10.104, 3 nectophores (01°07'N, 85°36'E); 1973.5.9.4, 12 nectophores, nectosome, and siphosome with many attached zooids (48°27'N, 123°18'W); 1985.12.10.1, 3 nectophores (6°10'S, 39°10'E); *Nanomia cara* Reg. Nos 30.7.28.1, 14 nectophores, nectosome, and siphosome with many attached zooids (51°56'N, 10°17'W); 1934.11.26.1, 48 nectophores (50°11'N, 04°14'W); 1973.5.9.13, 6 nectophores, 18 bracts, nectosome, and siphosome (51°56'N, 10°17'W); unregistered specimen, 7 bracts and siphosome with some attached zooids (51°56'N, 10°17'W).

Description of material

Pneumatophore 3–6 mm long, with red pigment surrounding terminal (apical) pore, pericystic cavity typically containing gas bubble and pneumadenia enclosed by approximately 14 longitudinal septa (Fig. 20D).

Nectophores typically much flattened in plane parallel to stem, measuring 2–6 mm along upper–lower axis and 2–5.5 mm across left–right axis, and most appearing rectangular in proximal and distal views (Figs 20A and B); some nectophores inflated and cubical, measuring <2.5 mm along proximal–distal axis, and appearing rectangular in lateral view (Fig. 20C); opaque, pale brown, and with small mouthplate discernible in some larger nectophores (Fig. 20A); axial wings short, typically folded

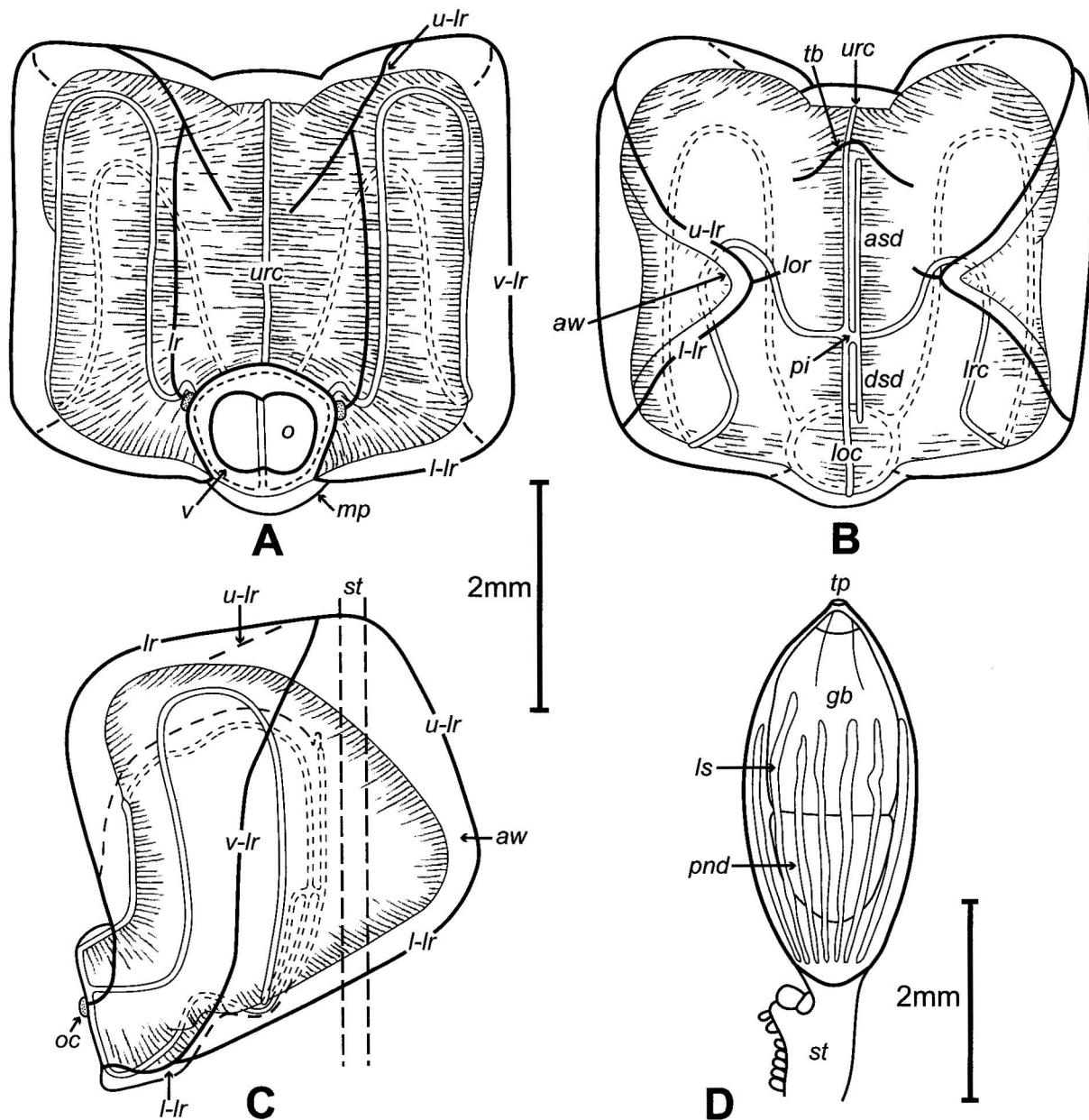


Fig. 20. *Nanomia bijuga*: A: nectophore, distal view; B: nectophore, proximal view; C: nectophore, lateral view; D: pneumatophore, lateral view (modified from Mapstone and Arai 1992) (asd, ascending surface diverticulum; aw, axial wing; dsd, descending surface diverticulum; gb, gas bubble; lr, lateral ridge; l-lr, lower-lateral ridge; lor, lower ridge; lrc, lateral radial canal; ls, longitudinal septum; mp, mouthplate; o, ostium; oc, ostial chromatophore; pi, internal pedicular canal; pnd, pneumadenia (gas gland); st, stem; tb, thrust block; tp, terminal (apical) pore; u-lr, upper-lateral ridge; urc, upper radial canal; v, velum; v-lr, vertical-lateral ridge).

inwards onto proximal surface (Fig. 20B), atypically more extended in inflated nectophores, arising from proximal nectophore surface on right and left sides, and extending towards gap between two nectophores on opposite side of stem (Fig. 20C); ridges easily discernible in larger nectophores and discernible with staining in smaller ones; upper-lateral ridges each

originating at tip of axial wing, passing diagonally upwards onto upper nectophore surface, then downwards and diagonally inwards towards midline on distal surface, terminating close to distal midline at approximately mid-nectophore height (Figs 20A–C), some distance above ostium; lateral ridges typically complete, each arising from upper-lateral ridge on

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upper (Fig. 20C) or distal surface (depending on extent of proximal–distal flattening of nectophore), passing obliquely downwards and inserting onto lateral border of ostium; flattened plaque (for ostial chromatophore) discernible at insertion point onto ostium in best preserved nectophores (Fig. 20A); vertical-lateral ridges each arising from upper-lateral ridge on upper nectophore surface proximal of origin of lateral ridge, passing diagonally down each lateral nectophore surface and inserting onto lower-lateral ridge near ostium (Fig. 20C); lower-lateral ridge originating from, and continuous with, proximal end of upper-lateral ridge, at tip of axial wing; lower-lateral ridges each passing downwards to lower-lateral nectophore edge and turning inwards distally to insert onto lower lateral border of ostium (Figs 20A–C); short lower ridge also discernible on large nectophores, originating from upper-lateral and lower-lateral ridges at tip of axial wing, and extending inwards for short distance towards proximal midline (Fig. 20B); mesogloea flaccid; thrust block thin and narrow-based, forming small protrusion from upper region of proximal surface, discernible in proximal view only (Fig. 20B); nectosac filling nectophore, with short extensions into axial wings (Fig. 20C), and composed of thick brown musculature; radial canals originating together from internal pedicular canal in centre of proximal nectosac surface (Fig. 20B); upper radial canal passing upwards, over upper surface of nectosac and onto distal surface, then downwards to ostial ring canal (Figs 20A and B); lower radial canal passing downwards onto lower nectosac surface, upwards into small pocket, and downwards again to ostial ring canal (Fig. 20C); lateral radial canals passing outwards from internal pedicular canal, then each looping first upwards onto proximolateral surface of nectosac, downwards onto lower lateral surface of nectosac, upwards again onto distal nectosac surface in larger loop, and finally downwards to insert on lateral region of ostial ring canal, close to ostial chromatophore (Fig. 20A); ostium with velum typically present; internal pedicular canal short, originating on proximal surface of nectophore from external pedicular canal (only preserved in one nectophore still attached to portion of nectosome) and inserting onto nectosac in centre of proximal surface (Fig. 20B); ascending surface diverticulum originating from internal pedicular canal on proximal surface of nectophore and extending upwards in proximal midline almost to upper end of thrust block (Fig. 20B), best seen with staining; descending surface diverticulum extending downwards from origin of internal pedicular canal, turning towards lower nectophore

surface, and terminating on slight bulge in lower-proximal surface of nectophore just proximal of small pocket in lower surface (Fig. 20C), also best seen with staining.

Distribution

Geographic. Canadian Pacific waters: Oak Bay (Totton 1965a); central Strait of Georgia (Mackie 1985; Mapstone and Arai 1992); Stuart Channel Howe Sound, Jervis Inlet, Desolation Sound, Toba Inlet, Knight Inlet (Mackie 1985, as *Nanomia cara*); Esperanza Inlet, Nootka Sound, Clayoquot Sound (Mackie 1985, as *Nanomia cara*); off Barkley Sound and Pachena Point, west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993). Northeast Pacific: off California and Baja California (Alvariño 1980c, 1991); off Point Conception (Haddock and Case 1999); Friday Harbor (Mackie 1964, as *Nanomia cara*; see synonymy). Other regions: elsewhere in the Pacific from off Costa Rica (Alvariño 1974), Gulf of California (Totton 1965a), Sagami Bay, Japan (Lindsay 2006), and off Japan (Kubota 1998; Kitamura et al. 2003). *Nanomia bijuga* was once said to be restricted to warmer waters worldwide (Stepanjants 1967, 1977b; Alvariño 1971), but is now known to occur in more temperate waters in the Pacific and South Atlantic (Pugh 1999a), and to have been reliably identified in the North Atlantic up to latitude 32°N (Pugh 1975), with no reliable records farther north except possibly Pugh (1999b).

Vertical. Figure 21 shows that at all but one of the deep-water stations west of Vancouver Island, *Nanomia bijuga* was more abundant at 300 m depth than at 500 or 700 m. In a depth profile from 23 to 345 m in the Strait of Georgia, the species was most abundant at 200 m (Mapstone and Arai 1992). Although more abundant at these depths, *N. bijuga* is also present at much greater depths as shown by both the present records and others worldwide (Margulis 1980b, 1984; Robison et al. 1998). The deepest record from off Vancouver Island was from at least 1845 m in the plume over a thermal vent.

Notes

The nominal species *Nanomia bijuga* was first referred to the genus *Physsophora* delle Chiaje, 1844, and the original illustration of a whole colony of *N. bijuga* by delle Chiaje (1844) was published as a plate numbered 181. The atlas of this work is dated 1841 on the title page, and according to Sherborn

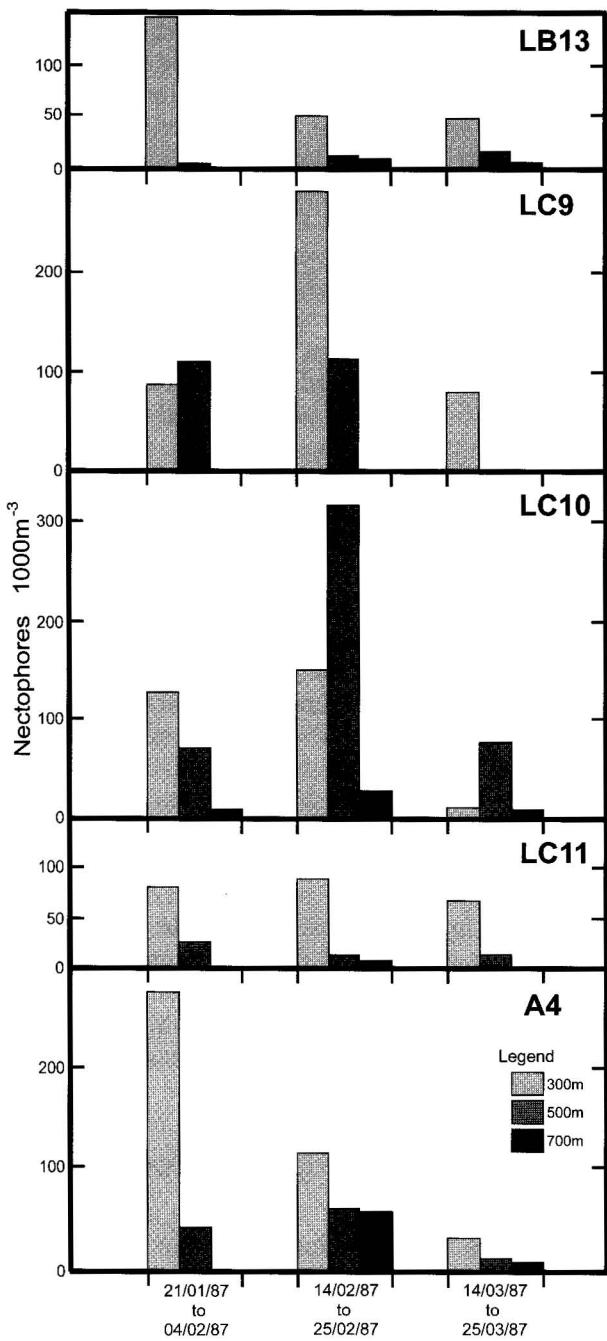


Fig. 21. Winter and spring abundance of *Nanomia bijuga* at five stations during three cruises from 21 January to 4 February 1987, from 14 to 25 February 1987, and from 14 to 25 March 1987.

(1922) this date is correct for plates numbered 1–173. However, plates 174–181 were not published until 1844 (see Sherborn 1922, p. xxxvii, under Chiaje, S. della). The synonymy for *N. bijuga* shows that generic assignment subsequent to delle Chiaje

was complex and resulted in a confusing sequence of binomials. These were partially untangled by Bigelow (1911b), who referred both *N. bijuga* and *N. cara* to *Stephanomia*, as explained above, and then more satisfactorily by Totton (1954, 1965a), who moved both species into the genus *Nanomia*, originally introduced for *N. cara* by Agassiz (1865), as is also mentioned above.

Nanomia bijuga is distinguishable from *N. cara* in the plane of flattening of the nectophores, which is somewhat along the proximal-distal axis in *N. bijuga*. The axial wings of *N. bijuga* are short and appear folded inwards onto the proximal nectophore surface in preserved nectophores, as described above, but are more inflated in life and protrude slightly into the gap between adjacent nectophores on the opposite side of the stem, as shown by Mackie (1964) and Totton (1965a, fig. 32). In *N. cara*, the nectophores are flattened along the upper-lower axis, as in many other physonects (Figs 1A, 12B, *Agalma elegans*), and have longer axial wings (Totton 1954, text-figs 19A and C). In most *N. cara* specimens from the NHM collections the proximal lobes of the nectosac extend farther into each axial wing than is shown in Totton's figures. This may be either a variable character in this species or a preservation artefact caused by dehydration of the thin layer of mesogloea around the nectosac.

Another character used by Totton (1954) to distinguish *Nanomia bijuga* from *N. cara* is the absence of an oil droplet at the base of each palpon. Such a droplet is well shown for *N. cara* by Fewkes (1888, pl. 2 fig. 7), but is also shown by Mackie and Boag (1963) for *Nanomia* specimens from Friday Harbor. These authors refer their material to *N. cara*, but it is now known that oil droplets also occur in the palpons of *N. bijuga* (P.R. Pugh, pers. comm., 2006, and that *N. cara* is found only in the North Atlantic (P.R. Pugh, pers. comm., 2006). Thus, the colonies studied by Mackie and Boag (1963) are referable to *N. bijuga*, as also are all other *Nanomia* specimens collected from Friday Harbor and used for physiological or developmental studies (including Mackie 1962, 1963, 1964; Freeman 1983, 1987). These works are therefore included in the synonymy for *N. bijuga* given above. Colonies of *N. bijuga* in Friday Harbor can unusually be attracted to the surface at night by a light during the summer months, "with fair regularity" according to Mackie (1964, p. 367), whereas most other physonects are restricted to waters farther offshore. The *Nanomia* specimens observed by Mackie (1985) from submersibles at

various sites around Vancouver Island are likewise referable to *N. bijuga* (see also Section 4.1).

In general, colonies of *Nanomia bijuga* are smaller than those of *N. cara*, with specimens in Friday Harbor measuring 11 cm in length when expanded (Mackie and Boag 1963) and a contracted colony from the Bay of Villefranche photographed by Totton (1965a, pl. 14 fig. 9) measuring only 4 cm. However, *N. bijuga* exhibits nectophores of a large size range (Pugh 1999a), like some species of the pyrostephid genus *Bargmannia* (see Section 10.1.2), and giant colonies of *N. bijuga* have been observed off the west coast of North America (P.R. Pugh, pers. comm., 2006). It seems likely that nectophores of *N. bijuga* collected in the Strait of Georgia (east of Vancouver Island) in 1979–1980 and reported by Mapstone and Arai (1992) as being typically 5–6 mm “tall” (though the one shown in fig. 3 is smaller) come from large colonies. Off Vancouver Island both large and small colonies must occur, since the collection includes nectophores of a wide size range, as described above. In contrast, *N. cara* colonies are probably of a similar length to large *N. bijuga* colonies when mature, although the colony figured by A. Agassiz (1865, fig. 332) in the original description of *N. cara* is smaller because it is immature. Mature colonies of *N. cara* observed by Fewkes (1888) in 1881 from a wharf at Grand Manan on the Canada/USA border (at the entrance to the Bay of Fundy) are up to 160 cm long, with the life-sized individual shown in plate 1 measuring 40 cm. Sars (1846) found smaller colonies of *N. cara* (as *Agalmopsis elegans*) up to 50 cm long on the other side of the Atlantic at 61°30'N, off the Norwegian coast, and many small colonies of *N. cara* were reported by Berrill (1930) from Salcombe Harbour on the south coast of the UK.

An extra ridge is often found in nectophores of *Nanomia bijuga*, which Totton (1965a) describes as cutting off the upper outer angles like an ear. He shows such “auriculate” ridges in nectophores from the Mediterranean (1965a, figs 32, 34), and similar ridges are present in figured nectophores from the Benguela Current off the west coast of southern Africa (Pagès and Gili 1992b, fig. 8B) as well as from the South Atlantic generally (Pugh 1999b, fig. 3.14). Some auriculate nectophores are also identified by the present author in nectophores held in the NHM collections and taken off Zanzibar in the Indian Ocean. However, no such ridges occur in any of the *N. bijuga* nectophores collected from Canadian Pacific waters.

Two types of bracts are characteristic of *Nanomia bijuga* (Dunn et al. 2005b, fig. 8), and though none were identified in the present collection, both types have been found in two intact colonies from the NHM collections, as listed above. Bracts are well shown in colonies from Japan by Kawamura (1911, pl. 7), who gives two figures of a long narrow type of bract with three distal cusps attached adjacent to each gastrozooid (figs 5, 6, and see also fig. 10) and two further figures of a shorter and wider diamond-shaped type, of somewhat variable shape, also with three distal cusps. According to Kawamura (1911) bracts of the latter type are apparently attached in four lengthwise rows around the stem, although this does not correlate exactly with the findings of Dunn and Wagner (2006). In the NHM specimens, two long narrow bracts are attached at each gastrozooid, and in the wider type of bract the distal end may sometimes be divided into two facets by faint ridges. These facets are well shown by Pugh (1999b, fig. 3.28) in a bract from the South Atlantic, although this author states that bracts are variable. Bracts of *N. cara* from the NHM collections are mostly longer and blunter distally than the diamond-shaped type so characteristic of *N. bijuga*, and many seem approximately symmetric, although in some there is an asymmetric narrow lobe proximally, one asymmetric lateral cusp distally, and sometimes a second proximolateral cusp on one side. These bracts may well be arranged in enantiomorphic pairs, but a full description of this species, preferably based on specimens collected by submersible, is needed before any firm conclusions can be drawn.

Family Agalmatidae indeterminate

Several genera are retained within the family Agalmatidae in the present work pending further molecular information on their affinities with other physonects, as noted above. They include *Cordagalma*, *Frillagalma*, *Lychnagalma*, *Stephanomia*, and *Marrus*. The first three genera have more characters in common with those of the Agalmatidae *sensu stricto* than do the last two, although all five differ in having a ventral nectosome (Pugh 2006b, fig. 21). *Stephanomia* and *Marrus* also differ in having a muscle-free zone on the nectosac and only an ascending surface diverticulum on the proximal surface of the nectophore. Three of these genera, *Cordagalma*, *Frillagalma*, and *Marrus*, are found in Canadian Pacific waters, with the latter genus represented so far by only one species,

M. orthocanna. Three species are described below, but without generic diagnoses, which are deemed here to be inappropriate for indeterminate genera.

Genus *Cordagalma* Totton, 1932

Type species: *Cordagalma ordinata* (Haeckel, 1888b) by monotypy.

Notes

Cordagalma is a monoecious physonect genus with a descending surface diverticulum on the nectophore and a ventral nectosome. Nectophores lack ridges, and the gastrozooid tentacle bears retained larval tentilla of ovoid form without either a cnidoband or an involucrum (Fig. 14B).

This genus was first introduced by Totton (1932) for a species represented by six small nectophores collected on the Great Barrier Reef and given the name *cordiformis* for their heart shape. Later, C. Carré (1968a) described a number of complete specimens from the Mediterranean, noting that they are small (<30 cm maximum length), can bear up to 40 nectophores per colony, and have unique tentilla (Fig. 14B) that resemble the larval tentilla of other physonects (for example, *Agalma elegans*; Fewkes 1881, pl. 9 fig. 9). He also found that their bracts are distinctive and prismatic and their palpons unusual because they lack palpacles, for which reason he termed them dactylozooids. As C. Carré remarks, these bracts and palpons closely resemble those illustrated by Haeckel (1888b) for *Anthemodes ordinata*, a physonect species only ever found by the Challenger expedition and described in the 1888 Challenger Report.

The tentilla were subsequently studied in more detail by Purcell (1984), and each was found to contain circa 157 nematocysts, with up to 40 adherent anisorhizas for every penetrating stenotele. The prey is apparently trapped by the long cnidocils of the stenoteles, which emerge from the cnidosac as shown in Figure 14B. Further specimens were collected by Mills et al. (1996) in the western Mediterranean, and these authors also remark upon the similarity of the siphosome to that of Haeckel's species *Anthemodes ordinata*. They add (on p. 154) that they "are inclined to adopt the name *Cordagalma ordinata*" for this species,

commenting that the generic name *Anthemodes* cannot be used because it was originally introduced for another agalmatid, *A. canariensis* Haeckel, 1869a, now a junior synonym of *Nanomia bijuga* (delle Chiaje, 1841) (see synonymy above). However, while retaining Totton's generic name *Cordagalma*, they actually alter his specific name *cordiformis* to *cordiforme* to agree with the gender of the generic name, instead of changing it to *ordinata*. Subsequently, the species was listed as *Cordagalma ordinata* for the first time by Bouillon et al. (2004). Indeed, it seems likely that Haeckel (1888b) may have incorrectly linked the siphosome of his specimen with the nectosome of another physonect species, so in the present work the specimen illustrated, and kindly lent by P.R. Pugh, is also referred to *C. ordinata*.

Cordagalma ordinata was found by Pugh (1998) to share some characters with another unusual agalmatid, *Frillagalma vityazi*, that is also found in Canadian Pacific waters and is described below. In particular, both species have dactylozooids that lack palpacles instead of the palpons that are more typical of other physonects, and typically bear palpacles, although in some older cormidia of the latter, the palpacles may be secondarily lost, as reported by Dunn and Wagner (2006). Both species also possess primitive tentilla with only a rudimentary cnidoband or none. However, the referral by Margulis (1993) of a second species, *C. tottoni*, to the genus *Cordagalma* is not in agreement with these characters, since *C. tottoni* is stated in the text to have a cnidoband on the tentillum and palpacles on the palpons, as pointed out by Pugh (1998).

Cordagalma ordinata (Haeckel, 1888b)

(Fig. 22)

Anthemodes ordinata Haeckel, 1888b: 229 (in part), pl. 14 fig. 1 (in part) and pl. 15 figs 1–10, 11–13 (in part), 14, 15.

Cordagalma cordiformis Totton, 1932: 325, figs 8, 9; Totton, 1965a: 61, text-figs 25A–C; Daniel, 1966: 691; C. Carré, 1968a: 79, pls 1–3; D. Carré, 1973: 113, fig. 1, pls 1 and 2; Palma, 1973: 27, pl. 3; Daniel, 1974: 49, figs 3k–n;

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Daniel, 1985: 77, fig. 17; Stepanjants, 1977b: 60, pls 3a and b; Carré and Carré, 1980: 115, fig. 13; Purcell, 1984: 319, figs 4g–i; Mackie, 1985: 758; Pagès and Gili, 1992b: 72, fig. 7; Carré and Carré, 1995: 565, figs 171C, 175B, 181A, 188, 190.

Cordagalma cordiforme: Mills et al., 1996: 154; Pugh, 1998: 244; Pugh, 1999b: 481, figs 3.24, 3.9; Dunn et al., 2005b: 927.

Cordagalma ordinata Bouillon et al., 2004: 211, figs 123A and B.

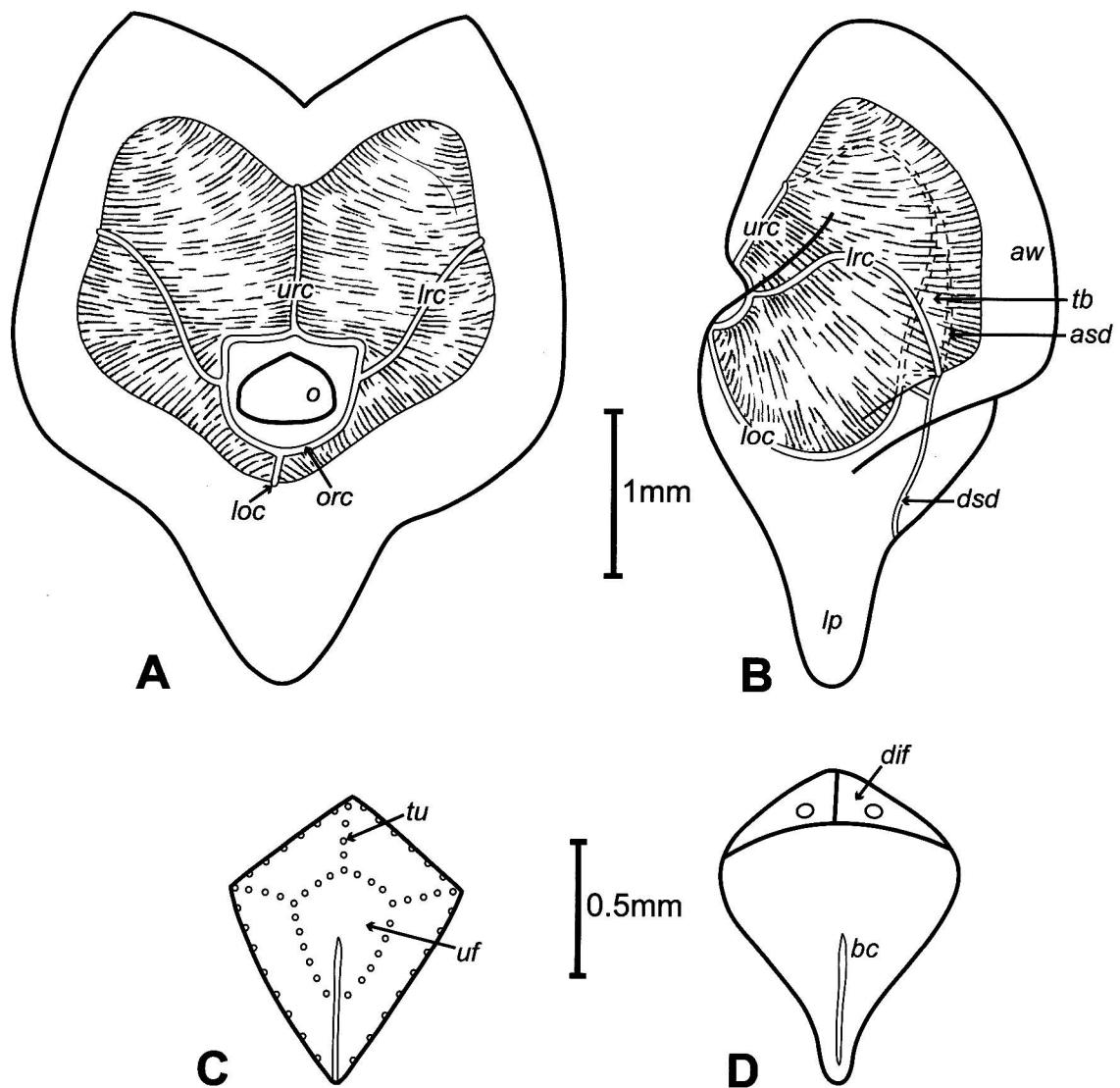


Fig. 22. *Cordagalma ordinata*: A: nectophore, distal view; B: nectophore, lateral view; C and D: bracts, upper view. A, B, and D are from the Mediterranean Sea; C is from the North Atlantic Ocean (asd, ascending surface diverticulum; aw, axial wing; bc, bracteal canal; dif, distal facet; dsd, descending surface diverticulum; loc, lower radial canal; lp, lower process; lrc, lateral radial canal; o, ostium; orc, ostial ring canal; tb, thrust block; tu, tubercle; uf, upper facet; urc, upper radial canal).

Material examined

This species is included because it was previously recorded from Canadian Pacific waters (Mackie 1985, as *C. cordiformis*; see Section 6.1), although no specimens were found in the present samples taken off Vancouver Island, or from others collected in the Strait of Georgia (Mapstone and Arai 1992). The description given below and material illustrated in Figure 22 is based on two good-quality samples kindly loaned by P.R. Pugh from the NOC collection; these come from 36°03'N, 2°48'W (JSL I sample No. 2952-2, 722 m depth) and the North Atlantic (SCUBA sample, 0–30 m depth). A specimen from the NHM collections (Reg. No. 1957.5.15.91, 25 nectophores, 40°16'S, 143°23'E) illustrated by Totton (1965a, fig. 25a) was also examined.

Description of material

Nectophores flattened parallel to stem, measuring up to 2.1 mm along upper-lower axis, 1.4 mm along proximal-distal axis, and 1.6 mm across right-left axis (Fig. 22A); opaque and without mouthplate; axial wings much reduced with only short extensions on either side of stem-attachment region (marked by ascending surface diverticulum in Fig. 22B); prominent triangular lower process from lower nectophore surface (Fig. 22B); ridges not discerned; thrust block thin and only slightly developed (Fig. 22B); mesogloea turgid; nectosac smaller than nectophore and following its outline in distal view; ostium small and located approximately in centre of distal surface (Fig. 22A); radial canals originating together from internal pedicular canal on proximal nectosac wall (Fig. 22B); upper and lower radial canals taken to be straight and lateral radial canals curving only slightly over lateral surfaces of nectosac, lacking distinct loops (Figs 22A and B); internal pedicular canal short, originating from external pedicular canal (not preserved) on proximal surface of nectophore at 2/5 nectophore height and inserting onto nectosac (shown in Fig. 22B but not labelled); ascending surface diverticulum extending upwards over proximal nectophore surface in midline from junction of internal and external pedicular canals (Fig. 22B); descending surface diverticulum elongate and extending downwards from same junction.

Bracts up to 1.5 mm long, kite-shaped, and without distinctive cusps (Figs 22C and D); upper surface prismatic and ridged, lower surface flat; immature bracts with prominent ridges comprising rows

of small tubercles delimiting five facets (Fig. 22C): upper facet, 2 proximolateral facets, and 2 distolateral facets; mature bracts less obviously ridged, with only distolateral facets apparent, each bearing single raised tubercle (Fig. 22D); mesogloea turgid; bracteal canal short and extending only from proximal point of bract to central region (Figs 22C and D).

Distribution

Geographic. Canadian Pacific waters: Howe Sound, Jervis Inlet, Homfray Channel, Pendrell Sound, Waddington Channel, Toba Inlet, Strait of Georgia off Texada Island, Stuart Channel (Mackie 1985, as *Cordagalma cordiformis*). Northeast Pacific: no records. Other regions: a similar number of records from other Pacific locations (for example, Margulis 1987; Kitamura et al. 2003) and a few more from the Atlantic (for example, Totton 1932; Pagès et al. 1996), Mediterranean (for example, Totton 1954; Gili et al. 1987b; Mills et al. 1996), and Indian Ocean (for example, Totton 1954; Daniel 1974, 1985).

Vertical. This species was recorded between 200 and 600 m depth at a number of locations in the Strait of Georgia and neighbouring inlets (Mackie 1985).

Notes

In three of the figures of nectophores from the literature (Palma 1973, pl. 2 fig. 2; Stepanjants 1977b, figs 3A and B; Pugh 1999b, fig. 3.9), the nectophore of *Cordagalma ordinata* is shown with the lower process erroneously directed upwards instead of downwards, as in all other published figures.

Genus *Frillagalma* Daniel, 1966

Type species: *Frillagalma vityazi* Daniel, 1966 by monotypy.

Notes

Frillagalma is the second monoecious physonect genus with a descending surface diverticulum on the proximal surface of the nectophore, and a ventral nectosome, as shown by Pugh (2006b, fig. 21). This species has ridged nectophores arranged in a pattern similar to that found in *sensu stricto* species, but its tentillum is unusual and comprises merely a simple cnidosac (without involucrum) that bears two large sequential ampullae (Fig. 14E).

This genus was introduced by Daniel (1966) for four nectophores with a distinctive pattern of frilled and flared ridges on the upper surface; they came from a small physonect collected in the Indian Ocean. Further nectophores were collected later in the same area (Daniel 1985), but incorrectly associated with bracts of *Agalma okeni*, as noted by Pugh (1998). Meanwhile, Stepanjants (1975) illustrated other *Frillagalma vityazi* nectophores from the North Atlantic and Caribbean, and linked them to a differently shaped bract found in the same samples (shown in her figs 2C and D). This bract appears similar to one illustrated by Totton (1965a, fig. 61), which he concluded might be referable to *Forskalia cuneata*. However, in the first-ever full description of a *F. vityazi* colony (based on 10 specimens collected by submersible off the Bahamas) Pugh (1998) shows that the bract illustrated by Stepanjants and Totton is indeed referable to this species, together with two further types that he describes for the first time.

Colonies of *Frillagalma vityazi* are rigid, like those of the *sensu stricto* agalmatid species *Agalma okeni* and *A. clausi* (see above), but differ from them in having lateral radial canals on the nectosac that are taken to be straight (because they form no obvious loops between their origin from the internal pedicular canal and insertion onto the ostial ring canal). Thus, they resemble those of the other two indeterminate species described in the present work, *Cordagalma ordinata* (see above) and *Marrus orthocanna* (see below). However, the frilled appearance of the nectophore ridges, upon which the specific name is based, is concluded by Pugh (1998) to be a preservation artefact (see his fig. 3). Perhaps in *F. vityazi*, as Pugh (1998) surmises, the crests of the ridges is from the nectophore on relatively narrow processes and this results in them becoming frilled and fluted when dehydrated after preservation in formaldehyde. Nevertheless, frilling seems to be a constant feature of net-caught nectophores (see below), and enables easy identification of *F. vityazi* nectophores when sorting preserved plankton samples.

Another unique character of *Frillagalma* is the tentillum, which, as mentioned above, comprises only a small cnidosac with no more than circa 38 nematocysts (Pugh 1998). This sac is attached to the pedicel by a thick and much-folded elastic strand (in preserved tentilla), as shown by Pugh (1998, fig. 7), through which the gastrovascular canal supplying

the tentillum passes before entering the capsule itself. Pugh also describes how this canal continues on from the capsule into a long swollen proximal ampulla (which he terms a vesicle), and thence typically into a second, longer ampulla (Fig. 14E). He also finds a solid finger-like protrusion typically arising from the second ampulla, as shown in Figure 14E. Pugh (1998) points out that these structures occur in no other siphonophore, and that they differ considerably from the larval-type tentillum of *Cordagalma ordinata*.

In *Frillagalma* the palpons are shorter and more rotund than those of *sensu stricto* agalmatids, and additionally they lack a palpacle; this led Pugh (1998) to term them dactylozooids. Pugh also notes their similarity to the cystons of Haeckel (1888b), which the latter author identified in *Cordagalma ordinata*, as noted above. They are also similar to the dactylozooids of the pyrostephid *Pyrostephos vanhoeffeni*, which are also more swollen distally than adjacent gastrozooids, and lack a palpacle. In the latter species the dactylozooids contain oil droplets for buoyancy, and perhaps the milky white fluid noted by Pugh (1998) in the dactylozooids of *Frillagalma* also aids buoyancy.

***Frillagalma vityazi* Daniel, 1966**

(Figs 23, 24)

Forskalia sp. Totton, 1954: text-fig. 31.

Forskalia cuneata Totton, 1965a: 109 (in part), text-fig. 61 (not *?Forskalia cuneata* Chun 1888a).

Frillagalma vityazi Daniel, 1966: 689, figs 1–6; Daniel, 1985: 86 (in part), figs 19a–c (not fig. 19d, = *Agalma okeni*); Stepanjants, 1975: 97, figs 2a–d; Mackie et al., 1987: 117; Pugh, 1998: 233, figs 1, 2A–C, 3A–D, 4A–D, 5A–E, 6A–D, 7, 8A–C; Pugh, 2003: 1325.

Physonect “C” Pugh, 1974b: 32; Pugh, 1975: 94.

Material examined

Eight pneumatophores, 1113 nectophores, 1089 ventral bracts, and 460 dorsal and lateral bracts from Canadian Pacific stations LB12 (400–0, 0–450, 450 m), LB13 (0–500 m) (Figs 23A–C) BCPM 996-209-1, LB13 (0–300, 300,

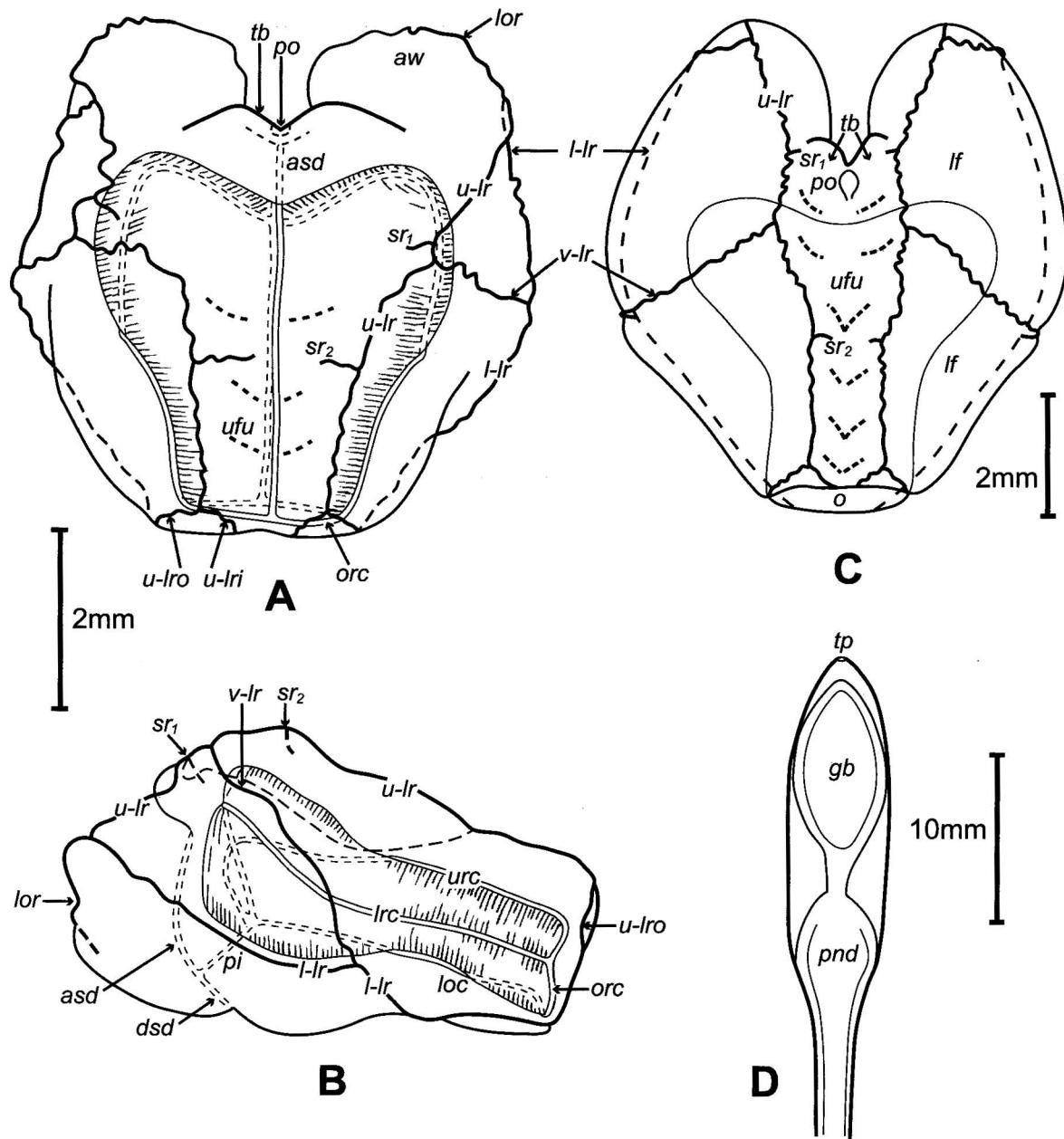


Fig. 23. *Frillagamma vityazi*: **A:** swollen nectophore, upper view; **B:** same nectophore, lateral view; **C:** flatter nectophore, upper view; **D:** pneumatophore, lateral view (*asd*, ascending surface diverticulum; *aw*, axial wing; *dsd*, descending surface diverticulum; *gb*, gas bubble; *if*, lateral facet; *l-lr*, lower-lateral ridge; *lor*, lower ridge; *lrc*, lateral radial canal; *o*, ostium; *orc*, ostial ring canal; *pi*, internal pedicular canal; *pnd*, pneumadenia (gas gland); *po*, pocket; *sr*, short ridge; *tb*, thrust block; *tp*, terminal (apical) pore; *ufu*, upper furrow; *u-lr*, upper-lateral ridge; *u-lri*, inner upper-lateral ridge; *u-lro*, outer upper-lateral ridge; *urc*, upper radial canal; *v-lr*, vertical-lateral ridge).

0–500, 500, 500–0, 0–700, 700–0 m), LB14 (0–300, 300, 0–500, 500, 500–0, 0–700 m), LB16 (0–300, 300, 300–0, 0–500, 500, 0–700, 700 m), LB17 (0–500, 500, 0–700 m), LC9 (500 m) (Figs 24A–D) BCPM 996-210-1, LC9 (300–0, 300, 0–500, 500, 500–0 m), LC10

(300, 300–0, 0–500, 500, 500–0, 0–575, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), A4 (0–700 m) (Fig. 23D) BCPM 996-211-1, and A4 (0–300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m) (Fig. 11, Table 1).

Description of material

Pneumatophores slender, up to 2.5 mm long, brown, with terminal (apical) pore typically discernible; pericystic cavity typically with large intact gas bubble, pneumadenia (gas gland) in lower half (Fig. 23D); longitudinal septa not discernible; portions of nectosomal and siphosomal stem attached to some pneumatophores, typically on elongate stalk and with one or more nectophores still attached by muscular lamellae to nectosomal stem and scattered bracts on siphosomal stem; three gastrozooids collected, all grey and filled with small translucent spherules, but tentacles broken off; some female gonophores attached to siphosomal-stem portions but no dactylozooids found.

Nectophores varying from 2 to 9 mm in length along proximal-distal axis and from 2.5 to 7 mm in width along right-left axis; translucent and compact, with short axial wings (Figs 23A and C); hemispherical and typically half-walnut-shaped, with rounded upper surface and flattened lower surface (Fig. 23B); most mature nectophores large and swollen (Fig. 23A), some flatter and slightly less developed (Fig. 23C); mouthplate absent; ridges prominent and typically frilled and flared; upper-lateral ridges originating on proximal ends of axial wings and extending up and over upper-lateral surfaces, typically remaining far apart proximally and coming closer together distally, on each side of upper furrow (Fig. 23A), atypically closer together throughout (Fig. 23C); upper-lateral ridge bifurcating into inner and outer upper-lateral ridges distally, above ostium, with two inner upper-laterals terminating close together above ostium (Fig. 23C) and two outer upper-laterals terminating on lateral sides of ostium (Fig. 23C); inner and outer upper-lateral ridges delimiting two small triangular facets above ostium (Figs 23A and C); two short ridges, sr_1 and sr_2 , arising from each upper-lateral ridge, as shown in Figures 23A and C, and extending for short distance towards upper midline; ostial chromatophores observed just lateral of ostium in some nectophores (not illustrated); short ridges arising closer to vertical-lateral ridges in swollen nectophores (Fig. 23A) than in less swollen ones (Fig. 23C); sr_1 arising from each upper-lateral near proximal end of axial wings in immature nectophores (not illustrated); lower-lateral ridges contiguous with and originating from upper-lateral ridges on proximal ends of axial wings; lower-lateral ridges each passing along lower lateral surface of nectophore and inserting onto ostium in lower lateral position (Fig. 23B); vertical-lateral ridge passing downwards from upper-lateral ridge

to lower-lateral ridge and delimiting two prominent lateral facets (Fig. 23C); lower ridge arising from junction of upper-lateral ridge with lower-lateral ridge (on proximal end of axial wing), passing short distance towards lower midline, and terminating before reaching latter; upper furrow extending between upper-lateral ridges from thrust block to ostium, broad and U-shaped in swollen nectophores (Fig. 23A), narrow and V-shaped in less swollen nectophores (Fig. 23C); mesogloea turgid; thrust block typically broad, swollen, and with slight median indentation in upper view and small pocket on proximal surface just below indentation (Fig. 23A), atypically more deeply lobed and with pocket lying on upper surface (Fig. 23C); pocket typically lined with epidermis, more readily discerned when stained, but epidermis abraded from remainder of nectophore surface, presumably during capture; nectosac smaller than nectophore, broadest proximally (across right-left nectophore axis) and narrower at ostium; latter of varied width in present material, with velum typically not preserved; radial canals typically originating together from internal pedicular canal (Fig. 23B), with upper and lower radial canals following approximately straight courses to ostial ring canal, and lateral radial canals passing first diagonally outwards to proximolateral corners of nectosac, then along lateral surfaces of nectosac to ostial ring canal as shown in Figure 23B; internal pedicular canal originating from external pedicular canal (not preserved) near lower nectophore surface in midline, and passing to nectosac (Fig. 23B); ascending surface diverticulum extending upwards from origin of internal pedicular canal, terminating below pocket in thrust block; descending surface diverticulum extending downwards from same point (Fig. 23B).

Bracts transparent, prismatic, and detached, with two types typically identifiable in present material, including ventrals and dorsal/laterals; dorsal/laterals up to 4 mm along proximal-distal bracteal axis and of variable width, typically turgid, and either rhomboidal (Fig. 24A) or broader across right-left bracteal axis (Fig. 24B); all dorsal/laterals thickest centrally, with relatively flattened lower surface except for proximal lobe on either right or left side of bract onto which passes faint scar of muscular lamella marking proximal end of bracteal canal (Figs 24A and B); upper surface of dorsal/lateral bracts bearing three prominent and typically frilled ridges; latter delimiting two slightly unequal triangular distal facets and larger more rounded proximal facet (Figs 24A and B); bracteal canal originating

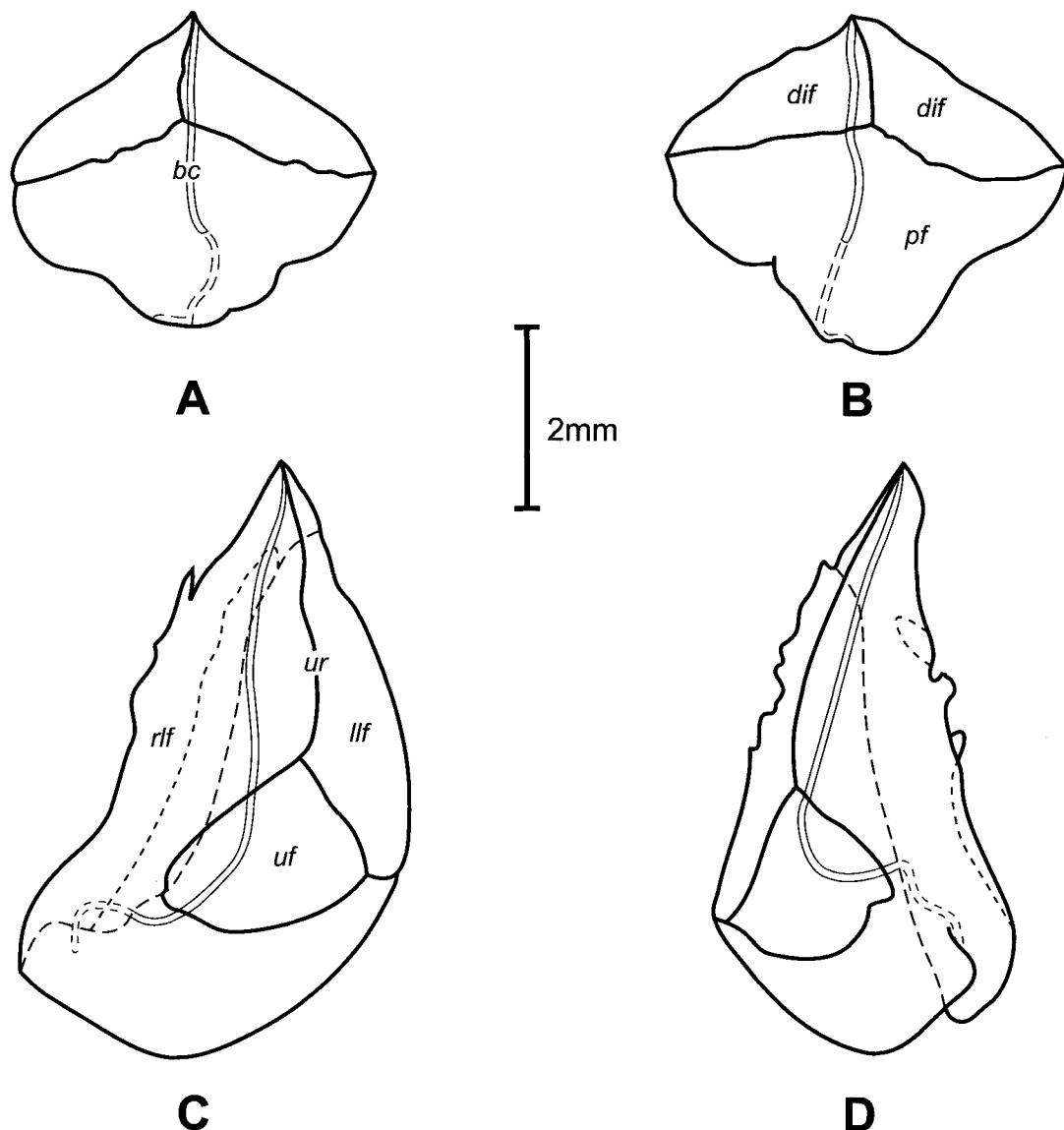


Fig. 24. *Frillagalma vityazi*: A and B: dorsal/lateral bracts, upper view; C and D: ventral bracts, upper view (*bc*, bracteal canal; *dif*, distal facet; *lf*, left lateral facet; *pf*, proximal facet; *rif*, right lateral facet; *uf*, upper facet; *ur*, upper ridge).

as shallow gutter at proximal end of bract, passing onto lower surface of bract for varied distance, then penetrating mesogloea and continuing on straight course to distal tip of bract (Figs 24A and B); bracteal lamellae discerned attached to proximal gutter-like portion of bracteal canal in bracts still attached to portions of siphosome (not illustrated); ventral bracts up to 7 mm along proximal-distal axis, asymmetric, and with rounded proximal and pointed distal ends; mature ventrals thick proximally and in

midregion and broadest at midlength (Fig. 24C); immature ventrals shorter, thinner, and spear-shaped (not illustrated); mature ventrals with small central upper facet offset from upper midline and delimited by three ridges (Fig. 24C); these delimiting ridges present on all bracts and typically short, finely serrated, with serrations not clearly demarcated one from another; upper ridge extending distally from distal side of upper facet, typically serrated, and often with additional very small frills (not shown in

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Figs 24C and D), terminating at distal end of bract and delimiting two lateral facets, right and left (Fig. 24C); each facet with thin lateral margin typically bearing three or more distinct tooth-like cusps (Fig. 24D); cusps omitted from lateral margin of left lateral facet in Figure 24C, where this margin shown as fine broken line; ventral bracts typically flattened along line of upper ridge in present specimens with lower borders of lateral facets lying close together in some bracts (Fig. 24C) and farther apart in others (Fig. 24D); extent of lower bracteal surface indicated by coarse broken line in Figures 24C and D, typically narrow and occluded (Fig. 24C); bracteal canal originating at proximal end of bract on surface of asymmetric swollen process, extending distally along lower bracteal surface as open gutter for short distance, then penetrating mesogloea and continuing to distal tip of bract (Figs 24C and D); bracteal muscular lamella attached to proximal section of bracteal canal, and discerned in bracts still attached to portions of siphosomal stem (not illustrated); bracteal canal bending through 90° angle after penetrating mesogloea in most present ventral bracts (Figs 24C and D), but not in spear-shaped immature ventral bracts (not illustrated).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993). Northeast Pacific: off Point Conception (Haddock and Case 1999). Other regions: no other Pacific records, and few from other oceans (Daniel 1985; Mackie et al. 1987; Pugh 1998). Previously this species was thought to be restricted to warmer waters between the equator and latitude 36°N, but present records show that in the Pacific its range extends farther north.

Vertical. This species was collected at 300, 500, 575, and 700 m in the main study area. Elsewhere it has been reported from 0–2000 m and deeper, most frequently between 600 and 1500 m (Pugh 1998).

Notes

Pneumatophores of *Frillagalma vityazi* from Canadian Pacific waters are typically pigmented light brown, with a terminal (apical) pore, whereas those of colonies collected in the Bahamas lack both pigment and a pore (Pugh 1998). Thus, the present pneumatophores resemble those of *Nanomia bijuga*, which are described above, but are easily distinguishable from

them by the absence of longitudinal septa. The brown coloration is likely to be a preservation artefact.

Nectophores of the present *Frillagalma vityazi* specimens are similar in size to those found by Pugh (1998) from the Bahamas, and almost twice the size of the largest nectophores described by Daniel (1966, 1974) from the Indian Ocean. In contrast, the smallest Canadian Pacific nectophores (2 mm long) are only half the length of the smallest ones found by Daniel. The immature nectophore from Pugh's submersible-collected material, however, is only 0.5 mm long, smaller than any nectophore from the present collection, and it also has a nectosac that is more indented proximally (Pugh 1998, fig. 2A). Pugh (1998) comments that the pattern of ridges on *F. vityazi* nectophores is remarkably constant, and the ridges he describes and figures are also identifiable in all the present nectophores. However, an extra short lower ridge is also herein identified, which extends from the junction of the upper-lateral and lower-lateral ridges around the end of each axial wing tip and inwards towards the proximal midline (Figs 23A and C).

There were no intact whole siphosomes among the *Frillagalma vityazi* nectophores, pneumatophores, and bracts collected off Vancouver Island, but Pugh (1998) found approximately 20 cormidia per colony in his submersible-collected *F. vityazi* material. He also noted that each cormidium comprises three enantiomorphic pairs of bracts, one pair of dactylozooids, and alternating male and female gonophores, all of which are attached to a swollen region of the siphosome lying immediately anterior of each gastrozoid. He distinguishes dorsal, lateral, and ventral bracts (Pugh 1998, figs 4, 5) and describes the dorsal and lateral bracts as being of similar rhomboidal shape, whereas the ventral bracts are more elongate, laterally flattened, and distally pointed. Amongst the present bracts, dorsal and lateral bracts are difficult to separate and are therefore combined in the description given above, but a few lateral bracts could be distinguished from their dorsal counterparts by the asymmetry of their distal facets. These differences are discussed and illustrated in more detail by Pugh (1998). Ventral bracts attach closest to the ventral side of the stem (Pugh 1998) and have a median serrated upper ridge and two long lateral edges that are typically cusped (Figs 24C and D). In life these bracts form an overlapping "carapace" around the siphosomal stem to protect the more delicate gastrozooids, dactylozooids, and gonophores.

Genus *Marrus* Totton, 1954

Type species: *Marrus antarcticus* Totton, 1954.

Notes

Marrus is a physonect genus that lacks a descending surface diverticulum on the proximal surface of the nectophore and has a muscle-free zone on the proximal surface of the nectosac, except for *M. orthocannoides* (Pugh 2006b). The nectosome is ventral and all species except *M. orthocanna* are dioecious. The tentillum, where known, is either loosely coiled or straight (see Dunn et al. 2005a, fig. 7; Fig. 14D) and more similar to the tentilla of *sensu stricto* genera than are the tentilla of *Cordagalma* and *Frillagalma* described above. The ridged nectophore of *Marrus* species differs from that of *sensu stricto* genera in having a mesogloal plug, an associated muscle-free zone on the adjacent wall of the nectosac and straight lateral radial canals on the nectosac.

The genus *Marrus* was erected by Totton (1954) for a group of three long-stemmed physonect species with unlooped radial canals on the nectosac and unicornuate tentilla on the gastrozooid tentacle, as noted above. One of these species had previously been introduced by Kramp (1942) as *Stephanomia orthocanna* from material collected at three stations in the high-Arctic. The specific name *orthocanna* derives from its straight lateral radial canals, and Totton (1954) transferred the species to his new genus on the strength of this character. In the same paper he also introduces two new species, *M. antarcticus* and *M. orthocannoides*. The former comes from the Antarctic Ocean and is described by Totton (1954, p. 60) as the “Antarctic counterpart of *M. orthocanna*”. The latter is placed in the genus because the nectophore is similar to those of the other two species; it has an upper-lateral ridge that divides distally, no vertical-lateral ridge (as oblique ridge), and straight lateral radial canals on the nectosac. In his 1965 monograph, Totton showed that he considered most of these characters to be atypical of the family Agalmatidae because he lists *Marrus* as an indeterminate genus on page 62 (Totton 1965a). More recently, a fourth species, *M. claudanielis*, has been added to the genus by Dunn et al. (2005a), based on two specimens collected off Monterey Bay in the northeast Pacific and in the western North Atlantic. This species also has straight lateral radial canals on the nectophore, a muscle-free zone on the proximal surface of the nectosac, and no vertical-lateral ridges, characters that it shares with *M. orthocanna* and *M. antarcticus* but not necessarily with *M. orthocannoides*, as discussed below.

Marrus orthocanna was redescribed from additional material collected under thick ice in the Fram Basin of the Arctic Ocean northwest of Greenland by Andersen (1981). This author gives good figures of young nectophores, mature nectophores, and bracts from an almost intact colony, and shows a mature nectophore in both upper and lower views (figs 5B, 6B), the coincidence of its outline with that of *M. antarcticus* in figure 7C, and mature bracts with a characteristic diamond shape in figures 8E and F. *Marrus orthocanna* is now known to have a muscle-free zone on the proximal surface of the nectosac (Dunn et al. 2005b), but this character is not mentioned by Andersen (1981). It is interesting to note that in young bracts there is a prominent and thick row of nematocysts (with possible supporting ectodermal cells) at the distal end (Andersen 1981, figs 8C and D, incorrectly labelled *cnidoband*), which in the two mature bracts seems to be abraded. Young tentilla are straight (fig. 9H) but the mature one shown by Andersen (1981) in figure 9I is coiled, although Kramp (1942, fig. 5c) shows a straight tentillum for this species, and Dunn et al. (2005a, table 2) comment that in *M. orthocanna* the cnidoband is “mostly straight”. The tentillum of *M. orthocanna* shown diagrammatically in Figure 14D is derived partly from Kramp’s figure. *Marrus orthocanna* is monoecious, as noted above, and Andersen (1981, fig. 10) includes figures of both male and female gonophores.

The recent paper by Dunn et al. (2005a) that introduces *Marrus claudanielis* includes a colour photograph (fig. 2) of a young bract with a thick line of nematocysts distally (mixed with large granulose ectodermal cells) that is very similar to a young bract figured by Andersen (1981) for *M. orthocanna*. Mature bracts of the two species are also similar in shape (compare fig. 5 in Dunn et al. 2005a with figs 8E and F in Andersen 1981), although their canals follow somewhat different courses. In both species, mature bracts are thickest distally and divided into two distal facets. Nectophores, in contrast, differ somewhat in shape, the axial wings of *M. claudanielis* nectophores being relatively elongate when mature (Dunn et al. 2005a, fig. 4), while in *M. orthocanna* nectophores the wings are blunt (Andersen 1981, figs 5B, 6B); also, in the former species the upper-lateral ridge (as *apico-lateral ridge*) does not divide distally, in contrast to that of *M. orthocanna*. *Marrus claudanielis* also has an extra, if weak, pair of lateral ridges (Dunn et al. 2005a). The nectosac of *M. claudanielis* is broader across the right-left nectophore axis than that of *M.*

orthocanna, although both exhibit a muscle-free zone, and the mature tentillum is apparently longer and more coiled, albeit loosely (Dunn et al. 2005a, fig. 7D). *Marrus claudanielis* also differs from *M. orthocanna* in being dioecious (Dunn et al. 2005a), as noted above.

It seems that *Marrus antarcticus* was introduced by Totton (1954) primarily based on the non-coincidence of collecting areas, and Totton himself notes that the nectophores are very similar to those of *M. orthocanna*, as does Andersen (1981, p. 298). Such differences as can be identified by comparing Totton's figure 20 with Andersen's figures 5B, 6B, and 7A, including the width of the thrust block and degree of rounding of the axial wings, might merely represent differences between two nectophores from the same nectosome. But Totton (1954) associates his nectophores with bracts that are quite different from those of *M. orthocanna*, and describes elongate gonopalpons on the gonodendra, also concluding that *M. antarcticus*, like *M. claudanielis*, is dioecious. A reexamination by the present author of the holotype of *M. antarcticus* and a number of other specimens of this species in the NHM collections (see list below) reveals 13 bracts of the typical *Marrus* type in one of the six jars comprising the holotype (Reg. No. 1957.5.15.154), but no bracts of the type shown by Totton (1954, fig. 21). It is also noteworthy that three of the remaining five holotype jars contain 19 mature and 2 immature nectophores (Reg. Nos 1952.11.19.26, 1957.5.15.142-144, 1957.5.15.145-7); one of these nectophores was illustrated by Totton in his original figure 20 (reproduced as fig. 26 in Totton 1965a), one jar contains only a gastrozooid, and the final, small jar (Reg. No. 1957.5.15.152) contains two vials with two female gonodendra bearing gonopalpons. However, the latter are preserved in benzyl alcohol instead of formaldehyde, and could well be from another physonect. It seems likely, therefore, that the bracts described by Totton (1954) for *M. antarcticus* are referable to a different physonect, and that the holotype specimen, except the two vials of gonodendra, might well be referable to *M. orthocanna*.

Marrus orthocannoides was introduced by Totton (1954) for a single specimen collected in the Indian Ocean but, as noted above, this species has a fully muscular nectosac. It also has differently shaped

bracts and many palpous with palpacles, though no tentilla (Totton 1954). Pugh (1998, 1999a) concludes that *M. orthocannoides* is unlikely to belong to the genus *Marrus*, and the present author agrees. Although the species is not typical of *Marrus*, it cannot be assigned to another physonect genus until more specimens with tentilla are collected.

Species of the family Pyrostephidae also have a muscle-free zone on the nectosac (see Section 10.1.2), while *sensu stricto* agalmatid genera lack such a zone, as noted above. In some other respects, however, *Marrus* more closely resembles other agalmatids, particularly in the structure of its tentillum. A diagrammatic representation of an *M. orthocanna* tentillum is given in Figure 14D and can be seen to differ considerably from that of a typical pyrostephid, as shown in Figure 14F (for *Bargmannia elongata*). Pugh (1999a) notes that the cnidome of *Marrus* includes only heteronemes and haplonemes in the cnidoband, like the cnidomes of other agalmatids (see Section 4.3), whereas in both *Bargmannia* and *Pyrostephos* the cnidome includes large stenoteles at the proximal end of the cnidoband (Pugh 1999a; Fig. 14F). Nectophores of *Marrus* also show more affinities with the Agalmatidae than with the Pyrostephidae because the thrust block is small and flanked by two axial wings when mature (see Section 10.1), whereas in pyrostephids it is greatly enlarged both when immature (see Pugh 1999a, fig. 19B) and when mature (see Section 10.1.2), and there are no axial wings.

Another similarity between *Marrus* and the pyrostephids is the presence of only an ascending surface diverticulum on the proximal surface of the nectophore (Dunn et al. 2005a, table 2, as *ascending pallial canal*). The absence of a descending surface diverticulum in siphonophores has been linked by Dunn et al. (2005b, as *descending pallial canal*) to a dioecious state, as discussed in Section 10.1, but this hypothesis does not fit *Marrus* species, which can be either dioecious or monoecious, as shown by Dunn et al. (2005a, table 2) and discussed by Pugh (2006b). *Marrus* species may therefore represent an intermediate condition between the dioecious pyrostephids and the monoecious agalmatids. It would be interesting in the future to perform a molecular-genetic analysis on some *Marrus* species to ascertain the affinities of this genus with other physonects.

***Marrus orthocanna* (Kramp, 1942)**

(Fig. 25)

Stephanomia orthocanna Kramp, 1942: 17, figs 4, 5.

?*Marrus antarcticus* Totton, 1954: 55, figs 20, 21; Totton, 1965a: 62, text-figs 26A–D, 27A–E; Alvariño, 1981: 395, fig. 174.6; Pugh, 1999a: 70; Pugh, 1999b: 482, figs 3.13, 3.27; Dunn et al., 2005a: 710.

Marrus orthocanna Totton, 1954: 37; Totton and Fraser, 1955e: 3, figs 5a and b; Totton, 1965a: 65, text-figs 30A and B; Stepanjants, 1967: 125, figs 67, 68; Andersen, 1981: 293, figs 1–10; Margulis, 1982: 442 (in part), figs 2A–M; Kirkpatrick and

Pugh, 1984: 36 (in part), figs 9A and ?B; Mackie et al., 1987: 117; Pugh, 1999a: 70; Bouillon et al., 2004: 212 (in part), figs 124E and ?F; Dunn et al., 2005a: 709.

Marrus antarcticus pacifica Stepanjants, 1967: 126, figs 69A and B; Mackie et al., 1987: 117.

Diagnosis

A *Marrus* species with nectophores having truncate axial wings, upper-lateral ridges each with distal bifurcation, and no lateral ridges; nectosac with muscle-free proximal wall; palpons absent and bracts diamond-shaped with two distal facets separated by straight line of nematocysts; tentillum straight or loosely coiled.

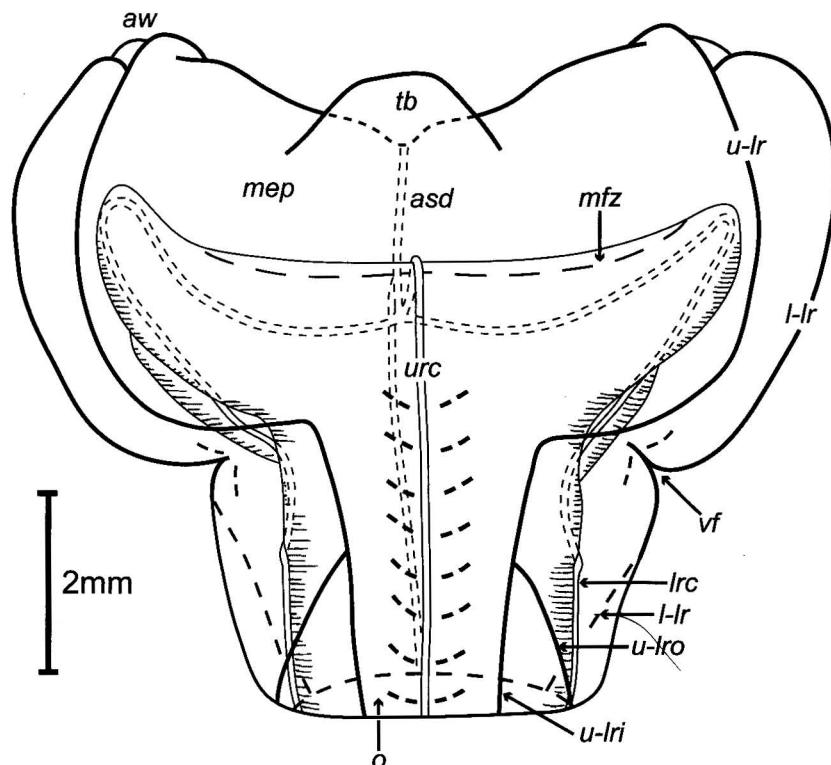


Fig. 25. *Marrus orthocanna*, nectophore, upper view (reconstructed from several specimens) (asd, ascending surface diverticulum; aw, axial wing; l-lr, lower-lateral ridge; lrc, lateral radial canal; mep, mesogloal plug; mfz, muscle-free zone of nectosac; o, ostium; tb, thrust block; u-lr, upper-lateral ridge; u-lri, inner upper-lateral ridge; u-lro, outer upper-lateral ridge; urc, upper radial canal; vf, vertical furrow).

Material examined

Seventy-eight nectophores from Canadian Pacific stations LB13 (0–500 m) BCPM 996-213-1, LB13 (500–0 m) (Fig. 25) BCPM 996-212-1, LB13 (0–500, 500–0, 0–700 m), LB14 (700 m), LB16 (0–700, 700 m), LB17 (0–700 m), LC10 (0–575, 700 m), LC11 (0–500, 0–700 m), and A4 (700–0 m) (Fig. 11, Table 1). One nectophore of *Marrus orthocanna* from JSL I sample No. 2194-4 (823 m) (39°51.3'N, 69°37.2'W) and another of ?*Marrus antarcticus* from Discovery Station 9994 (500–1000 m) (59°1.8'S, 25°48'E), both kindly loaned by P.R. Pugh. Specimens from the NHM collections: *Marrus antarcticus* holotype Reg. Nos 1952.1.19.26, 1957.5.15.142-144, 1957.5.15.145-7, 1957.5.15.148, 1957.5.15.152, and 1957.5.15.154, 22 nectophores, 13 bracts, loose gastrozoooids and gonophores, and 2 gonodendra with palpons (all from 56°57'S, 17°21'W); *M. antarcticus* paratypes: Reg. Nos 1957.5.15.161 and 1957.5.15.169, 8 nectophores and 64 bracts (both from 68°53'S, 13°3'W); 1957.5.15.177, 3 nectophores, many bracts, and gastrozoooids (67°14'S, 0°39'E); 1957.5.15.178, many bracts and elongate gastrozoooids (67°14'S, 0°39'E); 1957.5.15.179 and 1957.5.15.187, siphosomal portions (both from 56°57'S, 17°21'W); 1957.5.116.179 and 1957.5.116.187, many bracts and 9 siphosomal-stem portions bearing female gonophores (68°53'S, 13°3'W).

Description of material

Nectophores up to 9 mm long and 10 mm wide, with typical overall shape shown in Figure 25 reconstructed from several nectophores, both with and without *in situ* nectosacs; axial wings short and broad across left-right nectophore axis, with smooth outline in upper view (Fig. 25); other nectophores less swollen proximally and narrower distally (not illustrated); ridges discernible in all nectophores (with staining), prominent proximally and weaker distally; upper-lateral ridges originating from lower-laterals at proximal ends of axial wings, either just on upper side of axial wings (Fig. 25) or on proximal surfaces of axial wings (not illustrated); these ridges curving around upper lateral borders of nectophore proximally and then either continuing a short distance towards the upper midline before turning sharply through 90° and continuing distally (Fig. 25), or curving more gradually in this region (not illustrated); upper-lateral ridges each bifurcating distally into inner upper-lateral and outer upper-lateral ridges (Fig. 25); inner upper-lateral ridge inserting onto upper border of ostium

and outer upper-lateral ridge inserting onto upper lateral "corners" of ostium; lower-lateral ridges each originating from proximal end of upper-lateral ridge and curving around lower lateral borders of nectophore proximally, then into a vertical furrow in swollen nectophores and continuing distally towards ostium (Fig. 25); lower-lateral ridges less distinctly notched at furrows in other nectophores (not illustrated); lower-lateral ridges inserting onto lower lateral "corners" of ostium in all nectophores (Fig. 25); short lower ridges discerned in many swollen nectophores, each extending inwards from junction of upper-lateral and lower-lateral ridges towards proximal midline and marking proximal edge of each axial wing; furrows identified in some swollen nectophores, including broad shallow upper furrow in distal half of nectophore, in upper midline, and two deeper vertical furrows on lateral nectophore surfaces, each extending from just below 90° angle in upper-lateral ridge to lower-lateral ridge (Fig. 25).

Mesogloea turgid in proximal half of nectophore and flaccid in distal half, with border of ostium particularly flaccid in all nectophores; thrust block arising from upper nectophore surface near proximal end in swollen nectophores (Fig. 25) and from proximal nectophore surface in less swollen nectophores (not illustrated); thrust block with broad base and typically becoming thin and flap-like towards free edge, with rounded profile in upper view, and typically as long as axial wings (Fig. 25), atypically slightly longer or slightly shorter (not illustrated); mesogloea plug lying below thrust block and extending across right-left axis of nectophore, orthogonal to proximal-distal axis (Fig. 25), becoming thinner away from midline; nectosac broad proximally and narrower distally, with distal section appearing thinner than that shown in Figure 25 in some nectophores (not illustrated); broad muscle-free proximal face of nectosac <2 mm deep (along upper-lower nectophore axis), abutting mesogloea plug (Fig. 25); radial canals best discerned in detached nectosacs, with nectosacs intact in most smaller nectophores; upper and lower radial canals originating from junction with internal pedicular canal on proximal border of nectosac in centre of muscle-free face; upper canal passing up proximal face of nectosac and giving off two lateral radial canals after short distance, then continuing up onto upper surface of nectosac, and following straight course to ostium (Fig. 25); lower radial canal passing directly to ostium along lower midline of nectosac (Fig. 25); lateral radial canals each passing

outwards laterally across muscle-free face, then turning onto lateral (muscular) surface of nectosac and each following straight course to lateral border of ostium, via groove in lateral nectosac surface proximally (shown in Fig. 25 but not labelled); ostial ring canal not identified in present specimens because of damage in this region; internal pedicular canal short, passing from origin with external pedicular canal on proximal surface of nectophore (not preserved), through mesogloea, to junction of upper and lower radial canals near lower side of muscle-free zone of nectosac; ascending surface diverticulum extending proximally from pedicular canal junction, then upwards and farther proximally onto thrust block and terminating on lower surface of latter (Fig. 25).

Distribution

Geographic. Canadian Pacific waters: reported only off west coast of Vancouver Island (present collection, see list of stations above). Other regions: *Marrus orthocanna* has been recorded (as *M. orthocanna* and *M. antarcticus pacifica*) from the northwest Pacific, the Bering Sea and Sea of Okhotsk (Stepanjants 1967), Sagami Bay, Japan (Lindsay 2006), the North Atlantic and Arctic regions (Kramp 1942; Andersen 1981; Kirkpatrick and Pugh 1984, as *M. orthocanna*), and the Mediterranean (Bouillon et al. 2004, as *M. orthocanna*).

Notes

The nectophores described above appear most similar to a nectophore figured by Stepanjants (1967, fig. 69) from the North Pacific, Bering Sea, and Sea of Okhotsk, which she referred to *Marrus antarcticus pacifica* because of its similarity to *Marrus antarcticus* Totton, 1954. However, Stepanjants may have been mistaken in her attribution, for two reasons. Firstly, her nectophores come from the Northern rather than the Southern Hemisphere, and are therefore almost certainly referable to *M. orthocanna*, for the reasons given above; secondly, in the future, when better material becomes available, *M. antarcticus* is most likely to be referred to *M. orthocanna*, as also discussed above. The subspecies *M. a. pacifica* is therefore herein referred to *M. orthocanna*.

The present nectophores are also herein referred to *Marrus orthocanna* because they were collected in the Northern Hemisphere. Those shown by

Stepanjants (1967), and mentioned above, appear to be wider than the present nectophores across the right-left axis, but this may be because the former nectophores are distorted in the ostial region. *Marrus* nectophores are very fragile, and Dunn et al. (2005a) report that in *M. claudanielis*, most zooids autotomized while still being approached by the submersible. Nectophores of *M. orthocanna* from Canadian Pacific waters also vary in width across the ostial region, but as described above, most of those with attached nectosacs are narrower than and more similar in proportions to those shown by Andersen (1981, figs 5A, 6A). However, because the ridges in these narrower nectophores were less clear, Figure 25 is a composite based on several broader nectophores.

Marrus orthocanna has only previously been recorded from the North Atlantic and Mediterranean (Bouillon et al. 2004), but the present record extends its range to the northeast Pacific and the records of Stepanjants (1967) to other regions of the North Pacific and adjacent seas. The latter author identifies the species *M. orthocanna* as different from the subspecies *M. a. pacifica*, but the two are herein concluded to be synonyms. Perhaps the nectophores identified as *M. a. pacifica* obtained a richer diet than those identified as *M. orthocanna*. Similar variation is noted for the present *M. orthocanna* nectophores from Canadian Pacific waters. It is to be hoped that better nectophore descriptions for this species, including the range of widths displayed by mature nectophores, will soon be published, based on *M. orthocanna* specimens collected by submersible.

10.2. Suborder CALYCOPHORAE Leuckart, 1854

Diagnosis

Codonophora with nectophores but no pneumatophore; nectophores within colony few (except Hippopodiidae) and typically dissimilar, attached to reduced nectosome; siphosome with discrete cormidia, each comprising gastrozooid with tentacle bearing complex nematocyst batteries on side branches (tentilla), single bract (except Hippopodiidae, Clausophyinae, and *Gymnopraia lapislazula*), and one gonophore or more (monoecious) not on gonodendra, and no palpons (except Stephanophyes).

Notes

Dunn and Wagner (2006) suggested that cormidial paedomorphy and loss of the pneumatophore were major transitions that led to the appearance of the Calycophorae. The former transition indicates that larval cormidia that arise from one point on the siphosome are retained into the adult stage, and palpons and gonodendra do not develop. This makes the cormidia less bulky than those of physonects. Calycophoran cormidia are thus typically discrete, and may or may not be homologous with the discrete cormidia of some physonects (Apolemidae, Rhodaliidae; see Section 10.1).

Historical. The history of families referred to the Calycophorae was reviewed by Bigelow (1911b), who noted that family subdivision was based on either nectophore number alone or on nectophore number and degree of similarity of nectophores. He initially recognized five families, but later reduced these to three (Bigelow and Sears 1937), based upon an interpretation of calycophoran phylogeny by Totton (1932). After further study, Totton (1965a) referred six families to the order, including Prayidae, Hippopodiidae, Diphyidae, Clausophyidae, Sphaeronectidae, and Abylididae, and these are now well established (Carré and Carré 1995).

Relationships. Calycophoran families fall conveniently into two groups, prayomorph and diphyomorph, based on the shape of their nectophores as noted by Mackie et al. (1987). Prayomorph nectophores are similar (homomorphic), rounded, and with a relatively small nectosac and much mesogloea. They are typical of the family Prayidae and are thought to be primitive (Totton 1965a). Diphyomorph nectophores are dissimilar (heteromorphic), except where there is only one, typically angular and streamlined, and strengthened with longitudinal ridges. These nectophores also have a large powerful nectosac with little mesogloea. They are typical of the families Diphyidae, Clausophyidae, and Abylididae. Hippopodiids, despite their angular nectophores, are slow-moving, with a relatively small nectosac and a large volume of mesogloea, and are generally classified as prayomorphs. The Sphaeronectidae is a small family comprising species with a single rounded retained larval nectophore that somewhat resembles the larval nectophore of amphicaryonine prayids, but display other characters that indicate a closer affinity with diphyomorphs (see Section 10.2.5).

Nineteen calycophorans were analyzed by Dunn et al. (2005b) for 16S mitochondrial and 18S ribosomal genes, and the phylogeny derived from these results by Dunn and Wagner (2006, fig. 7) shows a reasonably significant node separating two prayomorph clades from a diphyomorph clade. Amongst the prayomorphs the family Hippopodiidae is monophyletic, and another possible clade comprises the prayine *Praya dubia* and two nectopyramidine prayids, although the node for the latter clade has low maximum-likelihood (ML) bootstrap and parsimony bootstrap values (Dunn et al. 2005b, fig. 6). Other prayines tested have poorly supported nodes, suggesting that the family Prayidae is paraphyletic. All diphyomorph families are monophyletic, with the exception of the Clausophyidae (represented by three species) for which two nodes have low ML bootstrap and parsimony bootstrap values or none. The remaining seven diphyomorphs tested constitute a monophyletic clade for the family Sphaeronectidae (represented by one species) and another clade, which is also well supported, for the more closely related families Diphyidae and Abylididae (represented by six species). Within the latter clade, *Abylopsis tetragona*, the only abylid tested, is possibly more closely related to *Chelophyses appendiculata* and *Diphyes dispar* than to *Muggiaeaa atlantica*, *Lensia conoidea*, and *Sulculeolaria quadrivalvis*, although the node separating these two clades also has low or no ML bootstrap and parsimony bootstrap values (see Dunn et al. 2005b, fig. 6). The abylid *A. tetragona* is nested within the family Diphyidae (represented by five species), indicating that the family Abylididae may have evolved from the diphynine Diphyidae, although more evidence is needed to confirm this hypothesis; so far, genes from only 1 of 10 probably valid abylid species have been analyzed.

Only five of the six valid calycophoran families are represented in the present collection from Canadian Pacific waters, and no abyliids have been found. However, the latter family may be present, since unidentified abylid species have been observed on the Endeavour Ridge (Burd and Thompson 2000), although none were found in earlier samples included in the present collection, which were taken in the same area. Abyliids typically comprise a small angular prismatic anterior nectophore (with a somatocyst) linearly aligned with, or superimposed upon, a larger posterior nectophore (without a somatocyst). The family occurs in warmer waters,

and species of the genera *Abyla*, *Abylopsis*, *Bassia*, and *Ceratocymba* have been recorded off California (Alvariño 1967b, 1980c, 1991; Cairns et al. 2002). Many marine species are known to be extending their ranges northward.

Characters used to distinguish zooids of the suborder Calycophorae from those of the suborder Physonectae (see Section 10.1) are reviewed below, followed by analyses of the calycophoran families, genera, and species found in Canadian Pacific waters.

Nectophores. Calycophorans typically bear two ectophores, as discussed above, although in some groups one ectophore may be secondarily lost, as discussed by Dunn et al. (2005b). The mature colony of one prayomorph genus is atypical and bears up to four mature ectophores (see Section 10.2.1.2).

The axes of typical prayomorph and diphyomorph calycophoran ectophores are shown in Figures 2B and C and 3A and B, and most were extrapolated by the present author from the axes defined by Haddock et al. (2005a); they are explained in Section 2.3.1. In typical prayomorphs the proximal–distal axis is shorter than the upper–lower axis, and in typical diphyomorph posterior ectophores the proximal–distal axis is longer than the upper–lower axis. However, in the diphyomorph anterior ectophore the proximal–distal axis is very short, and the main axis is herein identified as the anterior–posterior axis of the colony. Other prayomorph and diphyomorph axes, shown in Figures 2G and 3G, are more derived, and are discussed further in Sections 10.2.2 and 10.2.5.

Axial wings and a thrust block are not developed in calycophoran ectophores. Instead the proximal or lower surface is hollowed out to form a hydroecium (proximal surface in prayids, lower surface in posterior diphyomorph ectophores). In apposed prayomorph colonies this cavity, combined with the hydroecium of its partner, together form a chamber into which the stem can be withdrawn for protection during swimming. In linearly aligned diphyomorph colonies the stem is only withdrawn into the hydroecium of the posterior ectophore, the proximal end of which fits tightly into the hydroecium of the anterior ectophore to form a rigid swimming unit (Fig. 3A). Muscular lamellae hold the two calycophoran ectophores together, and are clearly identifiable in most prayomorphs from Canadian Pacific waters; they are also herein identified in some diphyomorph colonies, although in smaller colonies of both types they are difficult to discern.

Ridges are present in the ectophores of most diphyomorph species, and these are typically aligned along the anterior–posterior axis of the colony. Earlier names used by Totton for these ridges do not accord well with the new ectophore axes identified here (see Section 2.3.1), and are therefore replaced by names that relate better to the upper–lower and left–right axes of these ectophores. These ridges are discussed in more detail in Section 10.2.3.

The pedicular canal connects each calycophoran ectophore to the stem and can be direct or disjunct, as discussed in Section 2.3.2. It can also develop blind-ending diverticula that either pass along the surface, penetrate the mesogloea, or both. Any penetrating diverticulum is herein termed a somatocyst, and this structure can be limited to a single diverticulum per ectophore as in most diphyomorphs, or include several diverticula per ectophore as in some prayomorphs. These variations are discussed in Section 2.3.2 and a selection of typical diverticula shown schematically in Figure 6.

Siphosomal elements. Calycophoran cormidia are discrete, formed from a probud (Dunn and Wagner 2006), and separated by internodes in mature colonies similar to those found in some apolemiid physonects (see Sections 10.1 and 10.1.1). In calycophorans, however, these cormidia typically detach at maturity from the end of the stem to form free-swimming eudoxids, except in some prayids, in hippopodiids, in dipyrids of the subfamily Sulculeolariniae, and in clausophyids of the subfamily Clausophyinae (see Section 10.2.4.3). Each cormidium typically comprises a complex bract, a single gastrozooid with a tentacle bearing complex nematocyst batteries, or tentilla, and gonophores. Palpons are absent (except possibly in *Stephanophyes*, although these are atypical).

Gastrozooids of calycophorans are borne on a short pedicel, with a tentacle arising from the base that bears tentilla of one type. However, calycophoran tentilla are not of taxonomic importance because those of different species are very similar in structure.

Gonophores are present in all mature calycophoran cormidia, and all calycophorans are monoecious (Dunn et al. 2005b, fig. 7). In diphyomorphs such as *Lensia achilles*, *L. conoidea*, *Dimophyes arctica*, *Muggiae atlantica*, and *Chelophyes appendiculata*, these gonophores are dispersed by the eudoxid phase (see Section 3.1; Figs 3F, 7B), and each eudoxid

produces a succession of gonophores, with only the initial one developing from the original probud of the cormidium. In more primitive diphyomorphs (such as *Sulculeolaria quadrivalvis*) only a single gonophore develops per cormidium, as discussed in Section 10.2.3.1. Prayomorphs may or may not release eudoxids; this is summarized in Section 3.1 and discussed in more detail in Section 10.2.1.

Bracts are developed in most calycophorans; the exceptions are the prayomorph prayine *Gymnopraia lapislazula* (Haddock et al. 2005a), the hippopodiids (see Section 10.2.2), and clausophyne clausophyids (see Section 10.2.4.3). Calycophoran bracts are complex and display a diversity of shapes. They contain either a branching system of bracteal canals as in prayomorphs, or a single swollen canal, known as a phyllocyst, as in most diphyomorphs. At present, the function of the phyllocyst is unknown, and further investigation is needed. It may contain oil droplets to provide additional buoyancy, accumulate lipophilic toxins to discourage predation, or act a food store for the eudoxid during its existence in the plankton, where it can live independently for several weeks (Fig. 8B). Calycophoran bracts typically wrap around the stem like a cloak, as shown in Figures 2D and 3C, and are attached to it by a small bracteal lamella, or pedicel, at the proximal end. Atypically, they connect to the stem via a longer lamella that arises from the lower bracteal surface, as in the prayine prayid *Lilyopsis fluoracantha* (Haddock et al. 2005a, figs 5B and C).

10.2.1. Family PRAYIDAE Kölliker, 1853

Diagnosis

Calycophorae with similar, apposed nectophores, typically two, atypically one or four; nectophores without mouthplate, typically smooth and with weak ridges or none, atypically angular with more prominent ridges; somatocyst present or absent in definitive nectophores, simple or complexly divided; cormidia with bracts (except *Gymnopraia*) typically having six bracteal canals but no discrete phyllocyst.

Notes

This family, although diverse, includes species that are considered to form a natural group (Totton 1965a). The molecular analysis of Dunn et al. (2005b), summarized in figure 7 of Dunn and Wagner (2006), suggests that prayids are paraphyletic and probably gave rise to the more advanced

diphyomorph calycophorans. Within the family are three subfamilies, the Amphicaryoninae, Prayinae, and Nectopyramidinae.

Prayomorph relationships. Prayines form the largest and probably most primitive group of prayids, and their nectophores are typically larger than those of amphicaryonines and nectopyramidines. Amphicaryonines are probably derived from prayines by a reduction in the size of the definitive nectophore and the bracts, and retention of the larval nectophore as the larger nectophore of the pair, although no molecular evidence is yet available to support this hypothesis. Nectopyramidines are another small and possibly derived group (Dunn and Wagner 2006, fig. 7) in which one nectophore has been lost, probably secondarily; the single definitive nectophore is angular and ridged (Pugh 1992a).

Nectophores. Prayid colonies are slow-moving, owing to the extensive development of mesogloea, and in most genera the nectosac is smaller relative to the nectophore than is the case in diphyomorph nectophores, as noted in Section 10.2 and shown in Figures 2A and B. In prayid nectophores the upper-lower axis tends to be longer than the proximal-distal axis, with much of the extensive mesogloea lying in the upper region of the nectophore, above the nectosac. This is particularly noticeable in the prayine prayids collected from Canadian Pacific waters, and allows the identification of an outer surface (Fig. 2B) in addition to proximal, upper, and merged lower/distal surfaces of prayids in general. These surfaces are described for individual species below.

Most prayid colonies comprise a pair of apposed nectophores each connected to the stem by an external pedicular canal, and this canal link is strengthened by a triangular muscular lamella that encloses the canal and extends from the colony stem to the proximal midline of the nectophore. Such a lamella is shown in Figures 5B–D, and is also clearly illustrated (though not always labelled) in a number of figures of complete prayid colonies by Bigelow (1911b, pl. 2 fig. 1 and pl. 4 figs 1, 3), Kawamura (1915b, pl. 7 figs 4, 6), and Mapstone (2005, fig. 1). This lamella is attached to the nectophore in a line along each side of one or more diverticula from the pedicular canal, herein termed the ascending and descending surface diverticula, as discussed in Section 2.3.2. These diverticula form part of an autotomy joint between nectophore and stem, as described by Mackie et

al. (1987), which probably facilitates loss of the nectophore during nectophore replacement (see Sections 2.3.2 and 3.3). They also possibly bring nutrients to the lamellae from the siphosome for muscular contraction (see Section 2.3.2), and remove wastes.

Another diverticulum that arises either from the pedicular canal or from its ascending surface diverticulum is the somatocyst. The term somatocyst is limited here to distinct diverticula that penetrate the mesogloea, as noted in Section 2.3.2; thus, as is apparent from the family diagnosis given above, a somatocyst is not present in all prayids. Amphicaryonines lack such a “true” somatocyst, as do the prayine genera *Rosacea*, *Craseoa*, and *Prayola*, but in other prayines and in nectopyramidines a “true” somatocyst is present. It originates in one of the following ways: directly from the external/internal pedicular canal junction as in the prayines *Lilyopsis* and *Gymnopraria*; from the tip of the ascending surface diverticulum and (or) one or more points along its length as in the prayines *Praya*, *Desmophyes*, *Mistoprayina*, *Stephanophyses*, and the nectopyramidines *Nectopyramis natans*, *Nectadamas diomedae*, and *N. richardi*; from both the tip of the ascending surface diverticulum and two unique lateral surface diverticula as in the nectopyramidine *Nectopyramis thetis*. In general, canals forming the prayid somatocyst are thin, except for a prominent swollen tip to the somatocyst of *Desmophyses annectens* (Kirkpatrick and Pugh 1984, fig. 21A), but may contain small oil droplets. Thus, the prayid somatocyst might act as a food-storage reservoir, in the same way as in diphyomorph calycophorans, or give additional buoyancy to the colony; alternatively, it may have a circulatory function as suggested by Totton (1954). Another possibility is that the diverse shapes of prayid somatocysts are examples of neutral evolution (as defined by Lincoln et al. 1982).

In general, prayid siphonophores are infrequently collected with nets, and few samples include larval nectophores, except in the case of species in which a larval nectophore is retained as one nectophore of the pair in mature colonies (see Sections 3 and 10.2.1.1). Most diagnoses are therefore restricted to characters of definitive nectophores and bracts.

Bracts. Bracts occur in cormidia, and in mature prayine prayid colonies cormidia remain attached to the stem throughout life, whereas in amphicaryonine prayids (Bigelow 1911b) and nectopyramidine

prayids (Pugh 1992a) they are released as free-swimming eudoxids. In prayines, the bract lies athwart the stem and is thickened “above” it, tapering to a relatively solid lateral lobe on one side and a slightly hollowed out hydroecial lobe (of anterior and posterior sublobes) on the other. It typically contains six bracteal canals. A very short canal from the stem inserts onto the paired longitudinal canals, which lie parallel to the stem axis, and from these arise a pair of hydroecial canals supplying the hydroecial lobe, a lateral canal supplying the lateral lobe (previously “ventral” canal), and an upper canal that passes to the upper surface (previously “dorsal” canal). In the bracts of amphicaryonines there is no lateral lobe, and the canals are reduced to a single pair; in nectopyramidine bracts both lobes occur and all six canals can be present, although more often they are reduced in number. Gonophores develop inside the bracteal hydroecial cavity, and in most prayids grow to fill it completely (and extend beyond it), although in the prayine genera *Lilyopsis* and *Stephanophyses* and the nectopyramidine genus *Nectopyramis* they remain very small, and the cavity becomes filled with an additional, larger cormidal bell (special nectophore) instead.

A swollen globular or ovoid structure known as the central organ is found associated with the stem-attachment point of the bracts and larval nectophores of some prayid species, and also in the hydroecium of definitive nectophores of some nectopyramidine prayids (Pugh 1992a). It may serve as a food-storage reservoir (Totton 1954), but is of uncertain origin in definitive nectophores of nectopyramidines. It may represent a fragment of the siphosomal stem of the colony in prayine and nectopyramidine bracts and eudoxids (Totton 1965a).

Prayid subfamilies. In their molecular analysis, Dunn et al. (2005b) did not test any amphicaryonines. Therefore, the subfamilies included in the Prayidae are treated below in the order followed by Totton (1965a) and Pugh (1999b).

10.2.1.1. Subfamily Amphicaryoninae Chun, 1888a

Diagnosis

Prayidae with two apposed nectophores of unequal sizes, larger representing retained larval nectophore, smaller representing first definitive nectophore; surface without distinct ridges and furrows; disjunct pedicular canal present (where discernible), always with ascending surface diverticulum, with or without

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

descending surface diverticulum; somatocyst absent. Bract with canals reduced to two hydroecials (representing longitudinals and hydroecials merged); free-swimming eudoxid released.

Notes

The probable origin of the two nectophores, as given in the diagnosis, is discussed by Totton (1954, 1965a), who is the first to distinguish the two genera based on the type of nectosac found in the smaller nectophore. In *Maresearsia* this nectosac is functional, whereas in *Amphicaryon* it is not.

In the smaller definitive nectophore of amphicaryonines and the larger retained larval nectophore of *Maresearsia*, the long axis of the nectosac and ostial opening lies at an obtuse angle to the anterior-posterior axis of the colony. However, in the larval nectophore of *Amphicaryon* the nectosac bends through 90°, so for most of its length it lies parallel to the colony axis, and the ostium opens towards the posterior end of the colony. As a result the upper surface of this nectophore is extensive, while the lower surface is reduced. In the small shield-like definitive nectophore of *Amphicaryon*, both upper and lower surfaces are reduced, and in *A. acaule* they are represented by edges only, as described below.

A. acaule the nectosac is in contact with the outer nectophore surface and has four radial canals. In *A. ernesti* the nectosac has lost contact with the outer surface (though connected to it by a fine strand of tissue; see Totton 1954), only two radial canals are present, and one of these forms a rete (branching network). In *A. peltifera* the nectosac is lost, and Totton (1954, p. 96) notes that the radial canals are reduced to a "characteristic three-branched canal". Examination of this canal in a complete colony of *A. peltifera* from the NHM collections (listed below) shows that one of these branches is the descending surface diverticulum, while the other two are more lateral and probably represent two reduced radial canals. This agrees with Totton's figure of *A. peltifera* (1965a, fig. 62) in which an elongate ascending surface diverticulum is shown connecting the smaller definitive nectophore to the stem (by a muscular lamella), with three finger-like projections extending downwards (towards the lower nectophore edge) from its proximal end.

Both *Amphicaryon ernesti* and *A. peltifera* are known from the tropical Pacific (Alvariño 1991), and the former has been recorded as far north as southern California (Alvariño 1967b).

Genus *Amphicaryon* Chun, 1888a

Diagnosis

Amphicaryoninae with nectosac functional in larger larval nectophore only; larval nectophore having internal pedicular canal that varies in length, and ascending and descending surface diverticula; definitive nectophore with ascending surface diverticulum, and descending surface diverticulum present or absent; bract with canals approximately straight.

Type species: *Amphicaryon acaule* Chun, 1888a.

Notes

This genus currently comprises three species, two of which were described in 1888 by Haeckel (1888b) and Chun (1888a) (*Amphicaryon peltifera* and *A. acaule*) and a third was added by Totton in 1954 (*A. ernesti*). All were briefly redescribed and figured by Pugh (1999b, figs 3.31–3.33, 3.44). Species differences are based mainly on the smaller definitive nectophore, in which the nectosac and radial canals have become progressively reduced. In

Amphicaryon acaule Chun, 1888a

(Fig. 26)

Amphicaryon acaule Chun, 1888a: 1162; Bigelow, 1911b: 195, pl. 4 figs 1–8; Moser, 1912c: 529, fig. 9; Moser, 1915a: 209; Moser, 1925: 399; Totton, 1936: 231; Totton, 1954: 95; Stepanjants, 1967: 152, figs 96, 97; Palma, 1973: 30, pl. 4; Daniel, 1974: 76, figs 6a–e; Daniel, 1985: 120, figs 29a–e; Xu and Zhang, 1978: 36, fig. 27; Alvariño, 1981: 400, fig. 174.14; Kirkpatrick and Pugh, 1984: 50, fig. 15; Pagès and Gili, 1992b: 75 (in part), fig. 12; Pugh, 1999b: 485, figs 3.31, 3.44 (not Bigelow, 1918: 403, = *A. ernesti*).

Diplodoxia acaulis: Chun, 1888a: 1162.

Amphicaryon acaula: Moser, 1913a: 146.

?*Eudoxia tottoni* Leloup, 1934: 13, fig. 5.

Amphycarion acaule (*lapsus calami*) Pagès et al., 2006: 365.

Diagnosis

Both nectophores with very short internal pedicular canal; nectosac of smaller definitive nectophore with four radial canals and ostium in contact with nectophore surface.

Material examined

Thirty-one complete colonies, 6 detached small definitive nectophores with 6 associated larger larval nectophores, 3 detached larval nectophores, 7 complete eudoxids, 54 loose bracts, and 22 loose gonophores from Canadian Pacific stations LB4 (95 m), LB6 (0–90, 90–0 m), LB12 (300 m), LB13

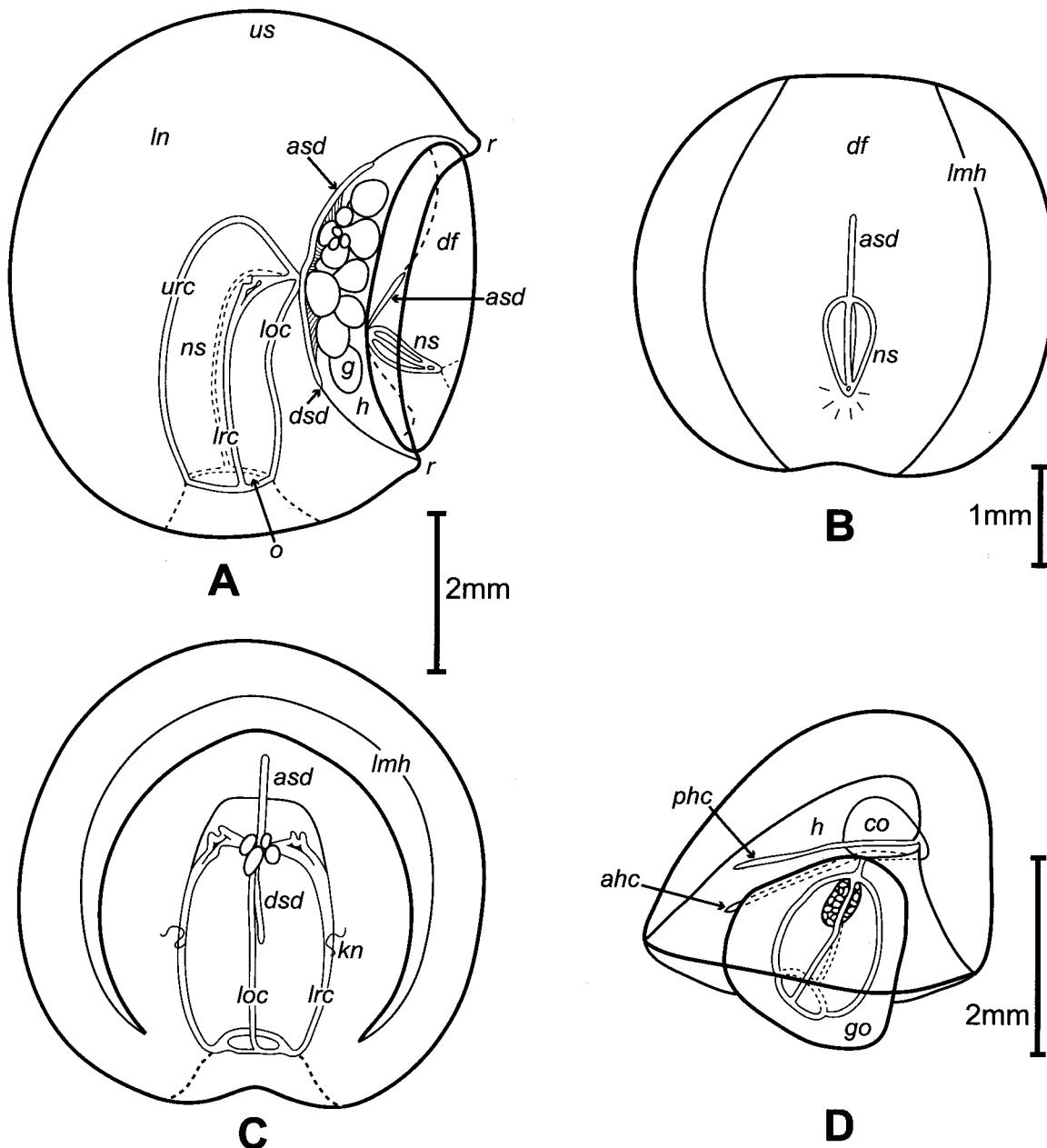


Fig. 26. *Amphicaryon acaule*: A: colony, lateral view; B: definitive nectophore, proximal view; C: larval nectophore, proximal view; D: eudoxid, right lateral view (*ahc*, anterior hydroecial canal (bract); *asd*, ascending surface diverticulum; *co*, central organ; *df*, definitive nectophore; *dsd*, descending surface diverticulum; *g*, gastrozooid(s); *go*, gonophore; *h*, hydroecium; *kn*, knob; *lmh*, limit of hydroecium; *ln*, larval nectophore; *loc*, lower radial canal; *lrc*, lateral radial canal; *ns*, nectosac; *o*, ostium; *phc*, posterior hydroecial canal (bract); *r*, rim, on larval nectophore; *urc*, upper radial canal; *us*, upper surface).

(0–300, 0–500, 500–0, 700–0 m), LB14 (500–0 m), LB17 (0–300, 300–0 m), LC2 (90 m), LC6 (95 m) (Figs 26B–D) BCPM 996-218-1, LC9 (300–0, 500–0 m), LC10 (0–300, 300–0, 500–0, 500, 0–575, 575–0, 700–0 m), LC11 (500–0 m), A4 (0–700 m) (Fig. 26A) BCPM 996-219-1, and A4 (300–0, 0–500, 500–0, 700–0 m) (Fig. 11, Table 1). Specimens from NHM collections: *Amphicaryon acaule* Reg. Nos 1957.8.25.14, 1 pair of joined larval and definitive nectophores ($33^{\circ}40.5'S$, $16^{\circ}55.25'E$); 1957.8.25.59, 2 pairs of joined larval and definitive nectophores ($00^{\circ}06'S$, $49^{\circ}45'E$); 1957.8.25.60, 1 pair of joined larval and definitive nectophores ($00^{\circ}06'S$, $49^{\circ}45'E$); 1957.8.25.61, 1 pair of joined larval and definitive nectophores ($02^{\circ}39'N$, $50^{\circ}46'E$); 1957.8.25.62, 1 pair of joined larval and definitive nectophores and 1 detached larval nectophore ($02^{\circ}39'N$, $50^{\circ}46'E$); *A. ernesti* Reg. Nos 1952.11.19.5 (holotype), 1 pair of joined larval and definitive nectophores ($10^{\circ}30'N$, $18^{\circ}46'W$); 1973.5.17.7, 1 pair of joined larval and definitive nectophores and 11 detached definitive nectophores ($3^{\circ}48'S$, $10^{\circ}08'E$); *A. peltifera* Reg. Nos 1957.8.25.70, 1 pair of joined larval and definitive nectophores ($07^{\circ}42'S$, $44^{\circ}14'E$); 1959.10.23.61, 1 pair of joined larval and definitive nectophores ($35^{\circ}08'S$, $17^{\circ}47'E$).

Description of material

Larger larval nectophores hemispherical, up to 8 mm in diameter, with proximal–distal axis (between siphosomal zooids and ostium) at approximately 35° to colony axis (Fig. 26A); brown, typically rough, crumpled, but probably smooth in life; upper surface rounded and extensive, lower surface (between hydroecium and ostial aperture) short, distal surface with ostial opening, and proximal surface comprising hydroecium; latter with bordering rim partially enclosing smaller nectophore, deepest in stem-attachment region, shallow laterally, with two small knobs at lower lateral corners of deeper region (Fig. 26C); mesogloea flaccid; pedicular canal comprising short external portion (hidden by stem components in Fig. 26A), short disjunct pedicular canal, and very short internal pedicular canal (not labelled in Fig. 26A); ascending surface diverticulum and descending surface diverticulum both prominent (Figs 26A and C), with muscular lamella connecting each to stem in best preserved specimens; nectosac with 90° bend close to upper end, and distal ostium opening into small depression (Figs 26A and C); radial canals originating together from proximal end of nectosac, with upper radial canal longer than lower radial canal, and lateral

radial canals typically each with small rete proximally (Figs 26A and C).

Smaller definitive nectophores up to 5 mm in diameter, approximately circular in proximal view (Fig. 26B), with short proximal–distal axis (Fig. 26A); distal surface flat except for small depression leading to ostium of reduced nectosac; proximal surface smooth and slightly concave, with shallow hydroecium; limit of latter indicated by two thin lines in Figure 26B; mesogloea firm; pedicular canal comprising short external and disjunct portions (occluded by stem components in Fig. 26A), and internal portion too short to be illustrated; latter inserting onto reduced pear-shaped nectosac; ascending surface diverticulum present, but no descending diverticulum (Figs 26A and B); four radial canals, short, originating from proximal end of nectosac and passing directly to distal end; ostial ring canal not developed.

Bracts up to 4 mm along proximal–distal axis, either hemispherical in lateral view (Fig. 26D) or with shorter upper–lower axis and more elongate proximal–distal axis (not illustrated); colour and surface texture as in larval nectophore; mesogloea flaccid; hydroecium shallow with broad opening; bracteal canals comprising elongate straight anterior and posterior hydroecial canals (Fig. 26D), more prominent in larger bracts.

Gonophore up to 3 mm long, surface texture and colour as in larval nectophore; asymmetric; nectosac subspherical (Fig. 26D) with four radial canals; short internal pedicular canal from radial canals to proximal end of gonophore; two short mantle canals identified on gonophore surface in one detached gonophore (not illustrated), arising from pedicular canal; hydroecium not evident.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: off Baja California to mid-California (Alvariño 1980c, 1991); off San Diego (Alvariño 1967b). Other regions: a number of records from other Pacific locations (for example, Margulis and Vereshchaka 1994; Gao et al. 2002), including many from southern latitudes (for example, Alvariño et al. 1990; Palma and Rosales 1995; Pagès et al. 2001). A near-cosmopolitan species most frequently recorded in warm waters (Kirkpatrick and Pugh 1984).

Vertical. This species was collected from between 90 and 500 m depth in the present study. It was recorded only in the epipelagic layer in the northeast Atlantic and central Pacific by Casanova (1980) and Margulis and Vereshchaka (1994), and was also noted in the epipelagic zone in other studies (Pagès and Gili 1991b; Pagès et al. 2001, 2006). However, it occasionally occurs in deeper layers and has been recorded down to at least 950 m (Pugh 1974b).

Notes

The three species of *Amphicaryon* can be most easily distinguished by the degree of reduction of the nectosac in the smaller definitive nectophore, as noted above. However, the internal pedicular canal in the larger larval nectophore is always shorter in *A. acaule* than in either *A. ernesti* or *A. peltifera*, and in Canadian Pacific *A. acaule* specimens it is typically so small as to appear absent. This is also true of some larval nectophores of *A. acaule* from the NHM collections (Reg. No. 1957.8.25.14), although in others the internal pedicular canal is slightly longer (Reg. No. 1957.8.25.59-63), and it appears to be similar in a colony from the South Atlantic figured by Pugh (1999b, fig. 3.31). However, in none of these larval nectophores is the internal pedicular canal as long as in those of *A. ernesti* and *A. peltifera* from the NHM collections (*A. ernesti*: Reg. Nos 1952.11.19.5, 1957.8. 25.48-51, 1959.8.10.85, 1959.10.23.61; *A. peltifera*: Reg. Nos 1957.8.25.70, 1959.10.23.61). The internal pedicular canal is well shown, though not labelled, in Totton's figures of the *A. ernesti* holotype (1965a, fig. 63B) and *A. peltifera* (1965a, fig. 62), and in two figures by Pugh (1999b, figs 3.32, 33).

Another variation among *Amphicaryon* species is the degree to which the smaller definitive nectophore is clasped by the larger larval nectophore. The closest union occurs in *A. acaule*, where, in the best preserved colonies, the thin circular edge of the smaller nectophore fits under a hydroecial rim (described above) in the larval nectophore. This is shown in Figure 26A for a Canadian Pacific colony, and is also well illustrated by Pagès and Gili (1992b, fig. 12). It contrasts with the looser connection between the two nectophores in *A. ernesti* and *A. peltifera*, which lack a rim, as is well shown for *A. ernesti* by Pagès and Gili (1992b, fig. 13) and for *A. peltifera* by Pugh (1999b, fig. 3.33).

In the subfamily Amphicaryoninae, a rete often forms on the radial canals of the nectosac, although it is never present in *Amphicaryon peltifera* from the South Atlantic (Pugh 1999b), and was also not found in any of the NHM *A. peltifera* specimens examined. Some branching occurs on the lateral radial canals of many, but not all, larval nectophores of *A. acaule* from Canadian Pacific waters, as shown in Figures 26A and C, and is also reported for larval nectophores of *A. acaule* from the South Atlantic (Pugh 1999b). In larval nectophores of *A. ernesti*, expansions of the lateral radial canals are more pronounced, and in the smaller definitive nectophore the lower radial canal of the nectosac (lateral radial canals are absent) is similarly expanded, as noted by Pugh (1999b), and in the NHM *A. ernesti* specimens examined by the present author. Such branching is greatest, however, in both nectophores of *Maresearsia praecleara*, where, as Pugh (1999b, p. 485) points out, "The radial canals on the nectosac of the larval nectophore are highly branched near their bases [proximally], and those of the definitive one also show some branching."

Similarities among the three *Amphicaryon* species include the presence of two knobs on the proximal surface of the larger larval nectophore. They are shown for a Canadian Pacific *A. acaule* nectophore in Figure 26C, and also occur in larval nectophores of *A. ernesti* and *A. peltifera* from the NHM collections. Such knobs probably serve to prevent collapse of the hydroecium during contraction of the nectosac during swimming.

Diverticula from the pedicular canal are variously developed in amphicaryonines, and ascending and descending surface diverticula are present in the larval nectophore of *Amphicaryon* species. In the definitive nectophores of *A. acaule* and *A. ernesti* there is only an ascending diverticulum, whereas in definitive nectophores of *A. peltifera* a short descending diverticulum is also present (see above). Muscular lamellae connect these diverticula to the stem, as noted above, and this is clearly illustrated in *A. acaule* by Bigelow (1911b, pl. 4 figs 1, 3), who also shows a short disjunct pedicular canal in this species. Such a canal is identified in some well-preserved *A. acaule* specimens from Canadian Pacific waters and one from the NHM collections (Reg. No. 1957.8.25.59).

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Pugh (1999b) considers that the bracts of the three species of *Amphicaryon* found in the South Atlantic are indistinguishable, but the eudoxids found in Canadian Pacific waters are all herein referred to *Amphicaryon acaule* because they are present in the same samples as the polygastric stage, and no other *Amphicaryon* species were identified in the area. The bract of *Eodoxia tottoni*, which was described and figured by Leloup (1934), has a similar appearance to that of *A. acaule*, and has been tentatively referred to *A. acaule* in the synonymy, following Totton (1954).

Genus *Maresearsia* Totton, 1954

Diagnosis

Amphicaryoninae with nectosac functional in both nectophores, and each nectophore with short internal pedicular canal and ascending surface diverticulum but no descending surface diverticulum; bract with long curving bracteal canals.

Type species: *Maresearsia praeclara* Totton, 1954 by monotypy.

Notes

Only one species has so far been referred to the genus *Maresearsia*, and mature colonies of this species are larger than those of *Amphicaryon acaule*, as are the bracts. Larval nectophores of *M. praeclara* reach a maximum diameter of 22 mm, whereas those of *A. acaule* reach only 8 mm.

Mature colonies of *Maresearsia praeclara* also differ from those of *Amphicaryon* species in the size and shape of the nectosac and radial canals, as noted above. In specimens of *M. praeclara* from the NHM collections the ascending surface diverticulum is swollen for much of its length, whereas in *Amphicaryon* it remains a simple narrow tube. There may also be a short protuberance, containing a black pigment spot, from its end into the mesogloea in the larval nectophore of *M. praeclara*, and a similar one from the upper surface of the ascending diverticulum in the definitive nectophore. The spot in the larval nectophore appears to be at the origin of a broken line to the label "somatocyst" in Totton's figure of a whole colony (1954, fig. 46), but is situated at the tip of a short protuberance into the mesogloea from the ascending diverticulum in one NHM specimen (Reg. No. 1982.11.30.317). In the smaller

definitive nectophore of the same colony there is a slight protuberance, containing a black spot, from the upper surface of the ascending diverticulum, but neither of these protuberances is a true somatocyst as defined above because they do not deeply penetrate the mesogloea; they seem, therefore, to be analogous to the short protuberance into a mesogloal pad in some nectophores of *Rosacea plicata* (Pugh and Harbison 1987).

Nectophores of *Maresearsia praeclara* resemble those of *Amphicaryon* species in having two knobs on the proximal surface of one of the nectophores, possibly to prevent damage to the stem in the restricted hydroecium, as noted above. However, whereas in *A. acaule* they occur on the larger larval nectophore (Fig. 26C), in the NHM *M. praeclara* material (Reg. No. 1982.11.30.27) examined for the present work these knobs are situated on the smaller definitive nectophore. They are shown, though not labelled, in Totton's anterior view of a *M. praeclara* colony (1954, fig. 47). They may protect the stem from damage by holding the hydroecium open during swimming, and could be of greater importance in *Maresearsia* than in *Amphicaryon* because in the former genus both nectosacs are functional.

Maresearsia praeclara Totton, 1954

(Fig. 27)

Maresearsia praeclara Totton, 1954: 97, figs 46–48, pls 6, 7; Phillips, 1972: 170, figs 39–41 (in part); Daniel, 1974: 80, fig. 6i; Pugh, 1974b: 37; Alvariño, 1981: 401, fig. 174.17; Kirkpatrick and Pugh, 1984: 52, fig. 16; Pugh 1999b: 485, figs 3.34, 3.45.

Maresearsia sphaera Stepanjants, 1967: 153, fig. 98.

Maresearsia sp. Daniel, 1974: 81, fig. 6j.

Amphicaryon intermedia Daniel, 1970: 147, fig. 1a; Daniel 1974: 77, figs 6f–h.

Material examined

Three bracts from Canadian Pacific stations LB13 (0–300 m) (Fig. 27) BCPM 996-220-1, LB14 (0–700 m), and LC11 (0–500 m) (Fig. 11, Table 1). Specimens from NHM collections: Reg. Nos 1952.11.19.6 (holotype), 1 larval nectophore (08°27'N, 05°59'E);

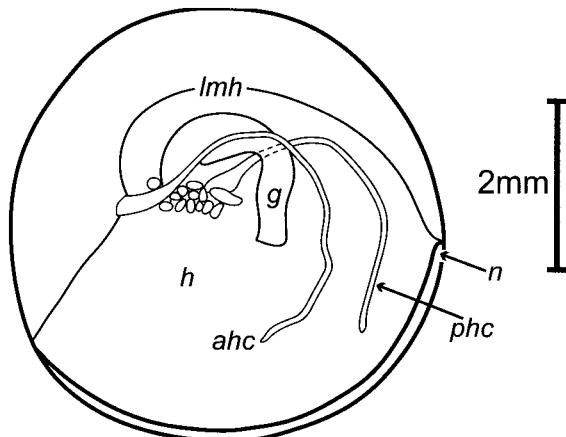


Fig. 27. *Maresearsia praecleara*, eudoxid, left lateral view (ahc, anterior hydroecial canal (bract); g, gastrozooid; h, hydroecium; lmh, limit of hydroecium; n, notch; phc, posterior hydroecial canal (bract)).

1957.8.25.74, 1 larval nectophore (02°53'S, 04°22'E); 1958.1.1.11, 1 pair of joined larval and definitive nectophores (07°28'N, 30°01'W); 1982.11.30.317, 1 larval nectophore and 1 definitive nectophore (32°33'N, 17°01'W to 32°33'N, 16°49'W).

Description of material

Bracts up to 6 mm in diameter, circular in lateral view (Fig. 27), with proximal-distal and upper-lower axes of approximately similar lengths; bract with short right-left bracteal axis, and some thickening of mesogloea in lateral walls; transparent, with smooth surface; bracteal hydroecium large, with opening a narrow slit on lower surface (Fig. 27); mesogloea turgid; anterior and posterior hydroecial canals following slightly different semicircular courses, and each with thickened proximal end (Fig. 27); large gastrozooid in hydroecia of two specimens. No gonophores found.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: off southern California (Widder et al. 1983); off Point Conception (Haddock and Case 1999). Other regions: few other Pacific records (Stepanjants 1967, 1977b; Pagès et al. 2001); Indian Ocean (Totton 1954; Daniel 1970); a few records from South Atlantic (Alvarino 1981), and from North Atlantic (see Kirkpatrick and Pugh 1984). A rare species found in all tropical and temperate ocean regions.

Vertical. In the South Atlantic, this species was recorded between 400 and 700 m depth (Pugh 1999b).

Notes

The nominal species *Maresearsia sphaera* Stepanjants, 1967 (type specimen 1/9221, Zoological Institute of the Russian Academy of Sciences, St. Petersburg; Savitskaja 1977) was based on nectophores collected from the Sea of Okhotsk. These nectophores are identical with those of *M. praecleara* as first described by Totton (1954) except that they are much smaller. Pugh (1974b, 1999b) therefore relegated *M. sphaera* to a junior synonym of *M. praecleara* and the present author concurs. The nominal species *Amphicaryon intermedia* Daniel, 1970 was originally referred to the genus *Amphicaryon* because the nectophores had undivided radial canals, but should be referred to *Maresearsia* because both nectophores have functional nectosacs, as was also concluded by Pugh (1999b).

An extensive muscular lamella is attached around the perimeter of the swollen ascending surface diverticulum in NHM *Maresearsia praecleara* nectophores, and in one specimen (Reg. No. 1957.8.25.74) an external pedicular canal connecting to a short internal pedicular canal via a short disjunct pedicular canal is discernible. However, in this specimen this region is not perfectly preserved, so further material is needed to confirm this observation. A short internal pedicular canal occurs in the smaller definitive nectophore, but an external pedicular canal could not be identified in any of the NHM specimens. There is no descending surface diverticulum in any of the NHM *M. praecleara* nectophores examined.

Immature bracts of *Maresearsia praecleara* have a lateral notch in the bracteal margin when they are still attached to the stem (Totton 1954), and this is illustrated, though not labelled, in Totton's text-figure 48A. However, this notch is lateral because at this immature stage the two sides of the bract are asymmetric. Once the eudoxid has detached from the stem, the notch comes to lie at the extreme distal end of the bract, as shown Figure 27 and also in the figure of a slightly smaller bract from the South Atlantic by Pugh (1999b, fig. 3.45). In bracts still attached to the stem the thickened ribbon-like proximal ends of the two bracteal canals extend from the proximal border of the bract, as shown by Totton (1954, fig. 48A, as eudoxid). However, once the bract detaches to become a eudoxid, this region appears to undergo

differential growth, so by the time the eudoxid matures, the proximal ends of the bracteal canals lie well inside the bracteal hydroecium, as shown in the mature eudoxid from Canadian Pacific waters in Figure 27.

10.2.1.2. Subfamily Prayinae Chun, 1897a

Diagnosis

Prayidae typically with two apposed definitive nectophores (except *Stephanophyes*) of similar sizes; surface typically smooth; larval nectophore, where known, large and caducous; definitive nectophore with direct or disjunct pedicular canal, with or without ascending and descending surface diverticula; somatocyst present or absent. Bract (except *Gymnopraia*) with canals, typically six: two longitudinal canals, two hydroecial canals, lateral canal, and upper canal (absent in *Prayola*); free-swimming eudoxid not released but stem fragments bearing cormidia sometimes separating from colony.

Notes

Prayne characters were reviewed by Pugh and Harbison (1987), who recognized nine genera, *Praya*, *Rosacea*, *Desmophyes*, *Prayoides*, *Prayola*, *Lilyopsis*, *Stephanophyes*, *Craseoa*, and *Mistoprayina*, and listed characters of their representative species in their table 1. The same genera were also recognized by Carré and Carré (1995), although Pugh (1992c) had meanwhile referred *Prayoides* to the genus *Praya*. A newly considered list of characters for this subfamily is given by Haddock et al. (2005a, table 3), and these authors also introduce a new genus, *Gymnopraia*. This brings the total number of recognized prayine genera again to nine, and adds two new species to the subfamily.

In prayine nectophores the proximal-distal axis lies at an obtuse angle to the anterior-posterior axis of the colony, and the upper-lower nectophore axis is typically extended, giving an additional outer surface to most nectophores, as noted in Section 10.2.1 and shown in Figure 2B. As a result, the upper ends of the two nectophores form the anterior end of the colony, and these ends tend to be smoothly rounded in most genera, although in *Praya* the upper surfaces are sculptured (see below). The upper-lower nectophore axis is particularly elongate in nectophores with small nectosacs (*Praya*, *Rosacea*, and *Craseoa*) because of their extensive mesogloea, but is also longer than the proximal-distal axis in nectophores with less mesogloea and larger nectosacs (*Prayola*,

Mistoprayina, *Stephanophyes*, and *Lilyopsis*) and in nectophores with intermediate-sized nectosacs (*Desmophyes* and *Gymnopraia*).

Pugh and Harbison (1987) considered differences in nectosac size to be of generic importance in the subfamily Prayinae, but this character is now thought to be of less significance than variation in the course of the pedicular canal and its diverticula (Haddock et al. 2005a). As the terminology of the latter authors is herein revised for diverticula from the pedicular canal (see Section 2.3.2), distinguishing characters of the subfamily Prayinae suggested by Haddock et al. (2005a) can be summarized as follows: the course of the pedicular canal from the stem to the nectosac, the presence or absence of an ascending surface diverticulum (as *somatocyst along the hydroecium*), the presence or absence of a descending surface diverticulum (as *descending branch*) and a penetrating somatocyst (as *ascending somatocyst branch*), and the course of the lateral radial canals over the nectosac.

Following the new interpretation of the somatocyst given in Section 2.3.2, it is herein concluded that a somatocyst is not developed in the prayine genera *Rosacea*, *Craseoa* and *Prayola* because species of these genera lack a penetrating diverticulum from the pedicular canal (Haddock et al. 2005a, table 3, as *ascending branch*). Similarly, species of the prayine genus *Prayola* may also lack an ascending surface diverticulum, although such a diverticulum is developed in *Rosacea* and *Craseoa* (Haddock et al. 2005a, as *somatocyst along the hydroecium*). In contrast, prayine species of the genera *Praya*, *Desmophyes*, *Mistoprayina*, *Gymnopraia*, *Stephanophyes*, and *Lilyopsis* display a somatocyst in the definitive nectophore, and this diverticulum may be short (*Desmophyes*, *Mistoprayina*), long (*Gymnopraia*), or subdivided (*Praya* and *Stephanophyes*) (Haddock et al. 2005a, as *ascending branch*). Larval nectophores of prayines, however, vary in their pedicular canal diverticula and somatocyst, and may or may not have a penetrating somatocyst. In the larval nectophores of the two *Praya* species (Pugh 1992c, figs 5A, 6A), only an ascending surface diverticulum is present, while in the larval nectophore of *Lilyopsis rosea* (labelled N₁ in fig. 1 of C. Carré 1969) there is a true somatocyst but it lacks the bifid tip characteristic of the first definitive nectophore (Haddock et al. 2005a).

In definitive nectophores of *Rosacea plicata* and *R. flaccida* a very short extension from the tip of

the ascending surface diverticulum may penetrate a small mesogloal protuberance on the wall of the hydroecium (Pugh and Harbison 1987); a similar short extension occurs in *R. repanda* and a smaller one in *R. limbata* (Pugh and Youngbluth 1988b). But as Pugh and Harbison (1987) conclude, this extension is not a true somatocyst because it does not deeply penetrate the mesogloea, as it does in *Desmophyes annectens*, *D. villafrancae*, and *Praya, Lilyopsis*, and *Gymnopraia* species. In *D. haematogaster* and the N₂ of *Mistopravina fragosa* this penetrating branch is short, but it nevertheless passes farther into the mesogloea than the extension found in *Rosacea* species, and so is herein considered a “true” somatocyst, following Haddock et al. (2005a). In *R. plicata* the short extension into the mesogloal pocket is not consistently present (Pugh and Harbison 1987), and has not yet been found in any *R. plicata* specimens from Canadian Pacific waters.

So far the only prayine nectophores collected from Canadian Pacific waters are those of species of *Praya* and *Rosacea*, but *Lilyopsis fluoracantha*, *L. rosea*, *Gymnopraia lapislazula*, and *Desmophyes annectens* have all been reported from farther south, off California (Alvariño 1980c, 1991; Haddock et al. 2005a).

Genus *Praya* Quoy and Gaimard, *in de Blainville*, 1834

Diagnosis

Prayinae with definitive nectophore having disjunct pedicular canal, ascending and descending surface diverticula, and divided somatocyst; nectosac with more than four radial canals, branching and subbranching. Bract present, crescent-shaped and flattened in plane approximately orthogonal to anterior–posterior colony axis; bracteal canals six, with lateral bracteal canal arising midway between hydroecial canals, and longitudinal canals reduced to spurs; gonophore with three mantle canals and nectosac 1/2 bell height; no cormidial bell.

Type species: *Praya dubia* (Quoy and Gaimard, *in de Blainville*, 1830).

Notes

The genus *Praya* was introduced by de Blainville (1830, p. 125, as *Praia*) for a specimen collected by Quoy and Gaimard during the voyage of the *Astrolabe* near Kangaroo Island, off the coast of South Australia. In 1830 this species was described and figured in manuscript form only, but a full description was subsequently published on page 104 of Quoy and Gaimard (1833). These authors named their specimen *Diphyes dubia*, although both they and de Blainville were doubtful about its affinity with the family Diphylidae, hence the choice of the specific name *dubia*. De Blainville referred the species to a newly proposed genus because *Diphyes* had priority for *D. dispar* Chamisso and Eysenhardt, 1821. Quoy and Gaimard (1833) referred the species to “notre genre *Praya*” on page 105, indicating their preference for the latinized name, but de Blainville introduced it as the French name *Praia*. De Blainville’s text was first published in the *Dictionnaire des Sciences Naturelles* in 1830, whereas the figure was published in the *Manuel d’Actinologie ou de Zoophytologie* in 1834 (pl. 6 fig. 4) with differently paginated text. As Totton (1965a) pointed out, and according to the current Rules of Zoological Nomenclature (Article 23.9.1.1), the junior synonym *Praya* has priority over *Praia* because the latter has not been used as a valid name since 1899.

Quoy and Gaimard (1833, p. 106) collected a second closely related species, *Diphyes prayensis*, which they found in the natural harbour of Praia, São Tiago, in the Cape Verde Islands. This species is conspecific with *Rosacea cymbiformis* (see below). *Praya dubia* itself was not recorded again in the literature for approximately 75 years, during which time the name *Praya* was applied to species now referred to the genus *Rosacea*. When *Praya* specimens were collected on the *Albatross* Expedition (Bigelow 1911b) they differed considerably from *Praya* as it was then known, prompting Bigelow to refer his two species (one new) to a newly proposed genus, *Nectodroma*. He later realized, however, that *Praya* should have priority and reverted to this generic name in his 1931 paper.

All authors since Bigelow (1931) have used *Praya*, except Alvariño, who refers the species to *Nectodroma* because of “original misspellings” of earlier generic names (Alvariño et al. 1990, p. 4).

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Pugh (1992c) describes larval nectophores of *Praya* species for the first time, and Pugh (1999b) notes that extra reserve bells are often present in mature *Praya* colonies, while Totton (1965a) notes that extra reserve bells may also occur in *Rosacea*. Nectophores are probably produced continually throughout life in prayids (Mackie et al. 1987; see Section 3.3).

***Praya dubia* (Quoy and Gaimard, *in de Blainville*, 1830)**

(Fig. 28)

Praia dubia de Blainville, 1830: 125; de Blainville, 1834: 137, pl. 6 fig. 4.

Diphyes dubia: Quoy and Gaimard, 1833: 104, pl. 5 figs 34–36.

Rosacea dubia: Schneider, 1898: 79 (in part); Schneider, 1899: 24 (in part).

Nectodroma dubia: Bigelow, 1911b: 204 (in part), pl. 3 figs 8, 9; Moser, 1925: 381, text-fig. 55; Alvariño, 1967b: 478; Alvariño, 1971: 28; Alvariño, 1980c: 152; Alvariño, 1981: 402, fig. 174.19.

Praya dubia: Bigelow, 1931: 531; Totton, 1965a: 122, pl. 23 figs 6, 7 (not text-figs 70A and B, 74H, = *P. reticulata*); Stepanjants, 1967, 149: fig. 94; Palma, 1973: 36, pl. 11 figs 1, 2 (?pl. 11 fig. 3); Daniel, 1974: 87 figs 7a and b; Kirkpatrick and Pugh, 1984: 58, figs 19A–C; Daniel, 1985: 138, figs 34a–e (in part); Pugh and Harbison, 1987: 87; Pugh, 1992c: 896, figs 2, 4b, 5, 7, 9; Pugh, 1999b: 485, figs 3.36, 3.47 (not Schneider, 1896: 79, = *Stephanophyes superba*, or Pagès and Gili, 1991a: 359, = *P. reticulata*).

?*Rosacea (Prayoides) intermedia* Leloup, 1934: 11, fig. 4; Totton, 1954: 89.

?*Prayoides intermedia*: Totton, 1965a: 125; Daniel, 1974: 89, fig. 7D; Kirkpatrick and Pugh, 1984: 60, fig. 20; Pugh, 1984: 466; Daniel, 1985: 142, figs 36a–e; Pugh and Harbison, 1987: 87; Pugh, 1992c: 908.

Nectocarmen antonioi Alvariño, 1983: 339, figs 1–5; 1991: 4; Alvariño and Kimbrell, 1987: 15.

Diagnosis

Definitive nectophore with ascending surface diverticulum lacking lateral branches; somatocyst comprising one to six median ascending branches and right and left lateral ascending branches, subdividing or not; radial canals of nectosac typically with few anastomoses or none. Bract with upper canal not discernibly curved; anterior hydroecial canal not curving distally.

Material examined

Three definitive nectophores (one with reserve bell) from Canadian Pacific stations A4 (0–700 m) and LC11 (0–300 m) (Figs 28A–D) BCPM 996-221-1 (Fig. 11, Table 1). Specimens of *Praya dubia* and other prayine genera from NHM collections: Reg. Nos 1957.11.5.1 *Praya dubia*, 5 definitive nectophores (12°08'N, 20°53'W); 1957.9.14.169 *Stephanophyes superba*, 4 detached bracts and 2 stem portions with attached zooids (05°54'S, 11°19'E); 1986.6.1.2 *Craseoa lathetica* holotype, N₁ and N₂ with stem, and 4 detached cormidia (25°23'N, 77°55'W); 1986.6.1.2 *Mistoprayina fragosa* holotype, N₁ and N₂ and detached cormidia (25°23'N, 77°55'W); 1986.6.1.3 *Prayola urinatrix* holotype, 2 definitive nectophores with stem and attached gastrozooids, 5 detached bracts, and 12 detached partial cormidia (25°22'N, 77°54'W)

Description of material

Description based mainly on best preserved Canadian Pacific nectophore collected, a N₂, shown in Figure 28 (second nectophore of pair not collected); an associated N₁–N₂ pair, 37 and 33 mm long, respectively, also collected but not used for most of description given below, owing to poorer internal preservation. Small reserve bell attached inside hydroecium of figured N₂, but omitted from Figure 28A for clarity.

Best definitive N₂, 79 mm tall and 53 mm wide, elongate, flattened between proximal and outer surfaces and across upper surface, latter appearing broad in outer view (Fig. 28A), and with transverse upper furrow and ridge in upper view (Fig. 28C); outer surface smooth (Fig. 28B), and lateral surfaces each with marginal longitudinal ridge (Figs 28A and B); proximal surface comprising elongate hydroecial chamber and inner surfaces of hydroecial wings; wings arising on upper surface relatively close together (Fig. 28C), extending entire length of nectophore and forming narrow hydroecial opening

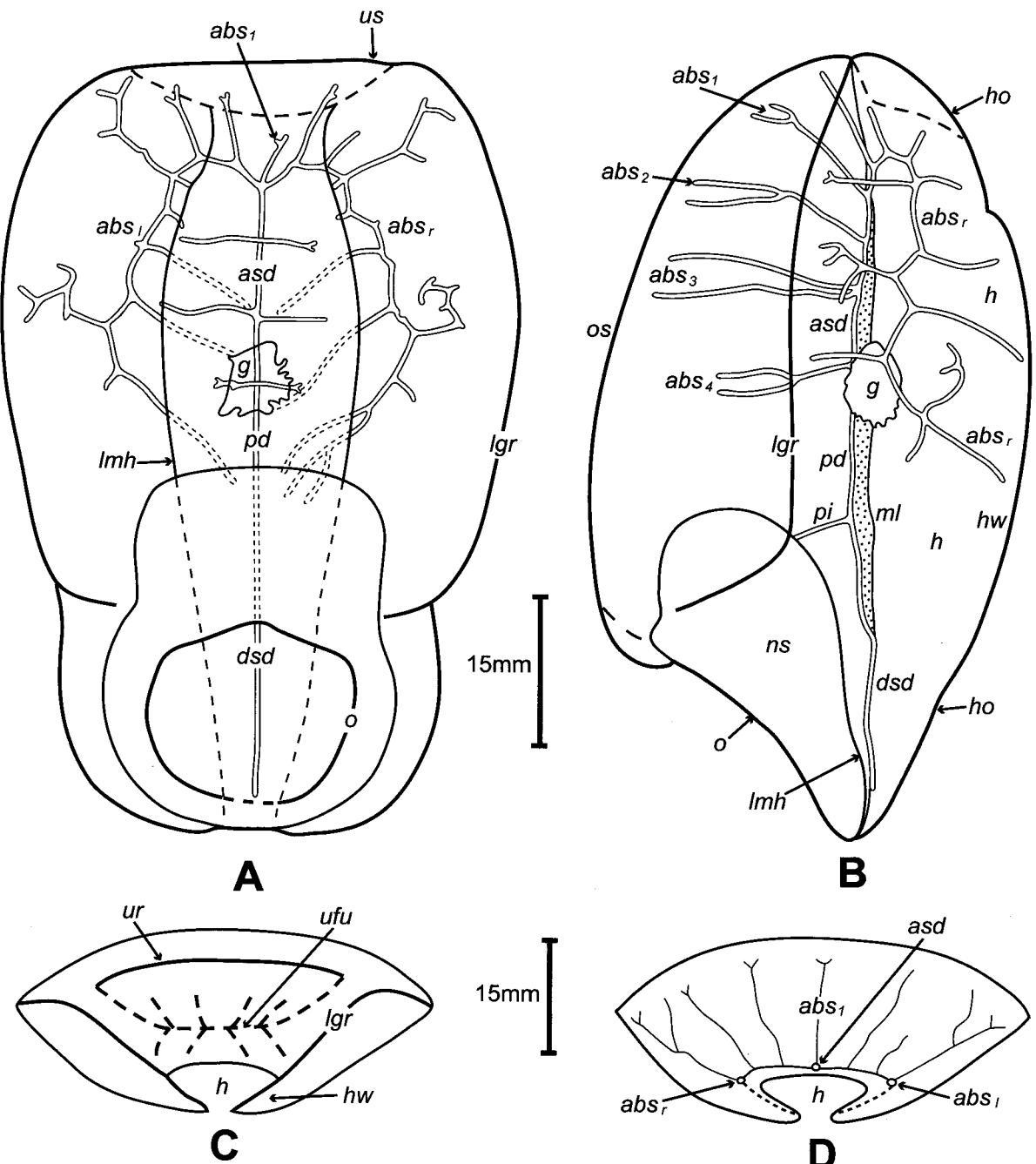


Fig. 28. *Praya dubia*: A: N₂ definitive nectophore, outer view; B: N₂ definitive nectophore, lateral view (*abs*₁ not shown); C: N₂ definitive nectophore, upper view, illustrating surface features; D: same as C, illustrating somatocyst canals (*abs*, ascending branch of somatocyst; *asd*, ascending surface diverticulum; *dsd*, descending surface diverticulum; *g*, gastrozooid(s); *h*, hydroecium; *ho*, hydroecial opening; *hw*, hydroecial wing; *lgr*, longitudinal ridge; *lmh*, limit of hydroecium; *ml*, muscular lamella; *ns*, nectosac; *o*, ostium; *os*, outer surface; *pd*, disjunct pedicular canal; *pi*, internal pedicular canal; *ufu*, upper furrow; *ur*, upper ridge; *us*, upper surface).

(Fig. 28B) approximately touching throughout; longitudinal ridges each extending along length of nectophore on lateral surface, originating on upper surface of nectophore and bending towards outer

nectophore surface at lower end, terminating at approximately 1/4 nectophore length (Fig. 28B); mesogloea turgid; hydroecium extending laterally for 1/3 of total nectophore width (Fig. 28A).

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Pedicular canal comprising external, disjunct, and internal portions, with external portion passing from anterior end of stem, through N_2 nectophoral muscular lamella to hydroecial wall in nectophore proximal midline (inside hydroecial cavity), inserting a short distance posterior of fourth ascending branch of somatocyst Fig. 28B, abs_4 ; insertion hidden by stem mass in Figure 28A (labelled g); latter comprising coiled-up anterior portion of stem only (posterior portion lost), many attached gastrozooids, and muscular lamella of N_1 ; disjunct pedicular canal extending from insertion point of external pedicular canal on hydroecial midline towards lower end of nectophore to origin of internal pedicular canal (Fig. 28B); latter penetrating mesogloea and inserting onto nectosac a short distance below its upper end (Fig. 28B).

Nectophoral muscular lamella contracted in best N_2 , and comprising two portions (shown in Fig. 28B but individual portions not labelled): upper portion extending from external pedicular canal to junction of ascending surface diverticulum and two lateral somatocyst branches; lower portion extending from external pedicular canal to point approximately halfway down descending surface diverticulum.

Diverticula from pedicular canal comprising ascending surface diverticulum extending from upper end of disjunct pedicular canal in midline almost to upper end of hydroecium; descending surface diverticulum extending from lower end of disjunct pedicular canal to point just above lower edge of ostium (Figs 28A and B).

Somatocyst comprising four median ascending somatocyst branches (abs_{1-4}) and right and left lateral ascending somatocyst branches (abs_{1-4}); first median ascending somatocyst branch and right and left lateral somatocyst branches arising approximately together from upper end of ascending surface diverticulum, second to fourth median ascending somatocyst branches (abs_{2-4}) arising from ascending surface diverticulum below first ascending branch (Figs 28A and B), and originating from ascending surface diverticulum either as single branch subdividing once (abs_1 , abs_2 , abs_4) or as two separate branches (abs_3) (Fig. 28B); right and left lateral somatocyst branches penetrating mesogloea immediately after dividing from ascending surface diverticulum, and each extending first laterally, then turning approximately towards lower end of nectophore, terminating near edges of hydroecial wings at approximately 1/2 nectophore length; many sub-branches arising from each lateral somatocyst branch, either subdividing

further or not, and directed towards upper, lateral, or outer surfaces, or towards inner hydroecial surface of nectophore (Figs 28A, B, and D).

Somatocyst of N_2 from stn LC11 comprising six ascending branches from ascending surface diverticulum (not illustrated).

Nectosac extending from almost 1/2 nectophore length to lower end of nectophore, with ostium opening onto upper/distal surface of nectophore at 45° to long nectophore axis (Fig. 28B); many radial canals arising from distal end of internal pedicular canal and branching dichotomously over upper part of nectosac, but poorly preserved and incomplete distally in present specimen, and therefore omitted from Figures 28A and B.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: 32°36'N, 117°30'-31'W, off Baja California (Totton 1965a); from Baja California to San Francisco (Alvariño 1980c, 1991); California coastal waters (Alvariño and Kimbrell 1987); off San Diego (Alvariño 1967b); San Pedro Channel, off California (Alvariño 1983); off Point Conception (Alvariño 1971; Haddock and Case 1999); Monterey Submarine Canyon (Widder et al. 1989); 39°13'N, 123°14'W, Californian Sonoma coast (Hobson and Chess 1988); 40°01'N, 127°39'W, off northern California coast (Stepanjants 1967); off Oregon (Pearcy 1972). Other regions: a number of records from other Pacific locations (for example, Moser 1925; Bigelow 1931; Totton 1965a; Alvariño et al. 1990; Lin and Chang 1991; Lin 1993; Lindsay 2006). *Praya dubia* has been recorded in the Atlantic, Antarctic, and Indian oceans but not so far in the Mediterranean (Kirkpatrick and Pugh 1984) or the Arctic Ocean.

Vertical. The two samples collected in the present study were within the depth ranges recorded off California (Alvariño 1991, table 1, between 0 and 475 m).

Notes

The large *Praya dubia* N_2 described above is here distinguished from a smaller *P. dubia* N_1 , also collected but not illustrated, by more turgid mesogloea, a narrower hydroecium, and hydroecial wings that meet in the proximal midline and originate closer together at the upper end of the nectophore. In the N_1 , these

wings remain open so that they can partially enclose the N₂ in life, as also occurs in *Rosacea cymbiformis* (Mapstone 2005). The somatocyst of the present N₂ (and that from stn LC11, see above) comprises more ascending branches from the ascending surface diverticulum, and more sub-branches from the two main lateral branches of the somatocyst than are shown in two *P. dubia* nectophores from the eastern tropical Pacific by Bigelow (1911b, pl. 3 figs 8, 9), in *P. dubia* nectophores from British waters by Kirkpatrick and Pugh (1984, fig. 19), and in a young *P. dubia* definitive nectophore from the Bahamas by Pugh (1992c, fig. 9). All the latter nectophores have only one ascending branch to the somatocyst, and fewer sub-branches from the lateral somatocyst branches than the Canadian Pacific N₂ nectophore. However, the ascending branches of the present somatocyst are similar to those illustrated by Quoy and Gaimard (1833) for a *P. dubia* specimen collected off South Australia, another described by Moser (1925) taken off Valparaiso, and two further *P. dubia* nectophores described from the northeast Pacific (Stepanjants 1967). Thus, it seems likely that the nectophores described by Bigelow (1911b) and Kirkpatrick and Pugh (1984) are less mature than the present N₂, though more mature than the very young definitive nectophore described by Pugh (1992c). It is also apparent that initially the somatocyst appears to comprise only a single ascending branch followed by further branches that appear during subsequent growth of the colony, and also more sub-branches from the lateral branches of the somatocyst.

Three regularly spaced median ascending somatocyst branches are also shown by Moser (1925, text-fig. 55), although her figure was probably modified from that of Quoy and Gaimard (1833), and four such branches are also shown by Stepanjants (1967, fig. 94). This suggests that the number of median ascending somatocyst branches in *Praya dubia* is variable. In contrast, the descending surface diverticulum is unbranched in all Canadian Pacific definitive nectophores examined, as well as in all earlier figures by other authors, with the exception of Moser's figure, in which two elongate side branches are shown. It seems likely that Moser's figure is an anomaly, and that the descending surface diverticulum of *P. dubia* is always unbranched.

Nectosacs of the present specimens extend to the lower end of the nectophore and are longer than the nectosac shown by Bigelow (1911b) but similar to that shown by Kirkpatrick and Pugh (1984). The nectosac is delicate and its lower part may have been lost in Bigelow's material. The present nectosacs are

large, considerably larger than those of the present *Praya reticulata* specimens (see below).

No bracts of *Praya dubia* were found in the present collection, and none are held in the NHM collections. Bracts of this species are more difficult to distinguish from those of *P. reticulata* than are the mature definitive nectophores, but despite this, accurate bract descriptions for the two species are given for the first time by Pugh (1992c). He separates the bracts of *P. dubia* from those of *P. reticulata* in both this paper (Pugh 1992c) and a later one (Pugh 1999b), as follows: marginal ridge not distinct (except in the youngest bracts); lateral (as *ventral*) lobe typically larger than hydrocial lobe, and two sublobes (as *flaps*) of hydrocial lobe of similar size; no distinct upper furrow (as *dorsal furrow*), and upper canal without long distal extension into hydrocial lobe (present in some mature *P. reticulata* bracts, including those from Canadian Pacific waters; see below); lateral (as *ventral*) canal with relatively short distal section extending into the mesogloea.

Pugh (1992c) also notes that the nominal species *Rosacea (Prayoides) intermedia* Leloup, 1934 is based on characters of larval and immature definitive nectophores of a species referable to *Praya*, probably *P. dubia*. *Nectocarmen antonioi* Alvariño, 1983, described from a single specimen with a stem bearing typical *P. dubia* bracts, is considered by both Pugh (1992c) and the present author to be conspecific with *P. dubia*.

***Praya reticulata* (Bigelow, 1911b)**

(Figs 29, 30, 31)

Nectodroma reticulata Bigelow, 1911b: 206, pl. 1 figs 7, 8 and pl. 3 figs 1–7; Bigelow, 1913: 65; Boone, 1933: 35; Alvariño, 1967b: 478; Alvariño, 1980c: 152; Alvariño, 1981: 402; Alvariño, 1991: 11.

Praya reticulata: Bigelow, 1931: 532, figs 185–189; Totton, 1965a: 123, pl. 23 figs 1–4 and text-fig. 74G; Stepanjants, 1967: 151, figs 95a and b; ?Daniel, 1974: 88, fig. 7c; Pugh and Harbison 1987: 87; Pagès and Gili, 1992b: 77, fig. 16; Pugh, 1992c: 896, figs 1b and c, 3, 4a, 6a–d, 8a and b; Pugh 1999b: 486, figs 3.37, 3.48.

Praya dubia Totton, 1965a: pl. 23, figs 1–4 and text-figs 70A and B, 74H (not p. 122, pl. 23 figs 6, 7, = *P. dubia*); Pagès and Gili, 1991a: 359.

Diagnosis

Definitive nectophore with ascending surface diverticulum having many short lateral branches; somatocyst consisting of single median ascending branch only, typically subdividing many times; radial canals of nectosac typically with many anastomoses. Bract typically having long upper canal curving in direction of hydroecial lobe; anterior hydroecial canal long, curving distally.

Material examined

Three pairs of definitive nectophores (2 with portions of stem attached, 1 with reserve bell) from Canadian Pacific stations A4 (500 m), A4 (0–300 m) (Figs 29, 30) BCPM 996-222-1, and LC10 (500–0 m); 422 bracts from stations LB12 (0–300 m) (Fig. 31) BCPM 996-223-1, LB13 (0–500, 700 m), LB14 (0–500 m), LB16 (0–500 m), LC9 (0–300 m), LC10 (500–0 m), A4 (0–300, 0–500 m), LD10 (300 m), and LD12 (0–500) (Fig. 11, Table 1). Specimens of *Praya reticulata* from the NHM collections: Reg.

Nos 1957.9.14.220, N₁ and N₂ (10°19'S, 09°37'E); 1957.11.5.24, N₁ and N₂ (51°39'S, 146°35'E).

Description of material

Description based mainly on best preserved pair of definitive nectophores collected, as shown in Figures 29 and 30; N₂ shorter than N₁ (Figs 29A and B), with nectophore upper surface and subdivision of ascending branch of somatocyst differing in N₁ and N₂ (Figs 30B and C); other features similar.

Definitive N₁ up to 102 mm tall and 47 mm wide, elongate, turgid, with extensive hydroecial wings (Fig. 29B); wings originating close together on upper nectophore surface, proximal of median upper protuberance, and extending to lower end of nectophore; median upper protuberance narrow, containing median portion of fine and much-branched ascending branch of somatocyst, flanked laterally by two deep upper furrows (Fig. 30D); upper furrows coalescing on outer side of median upper

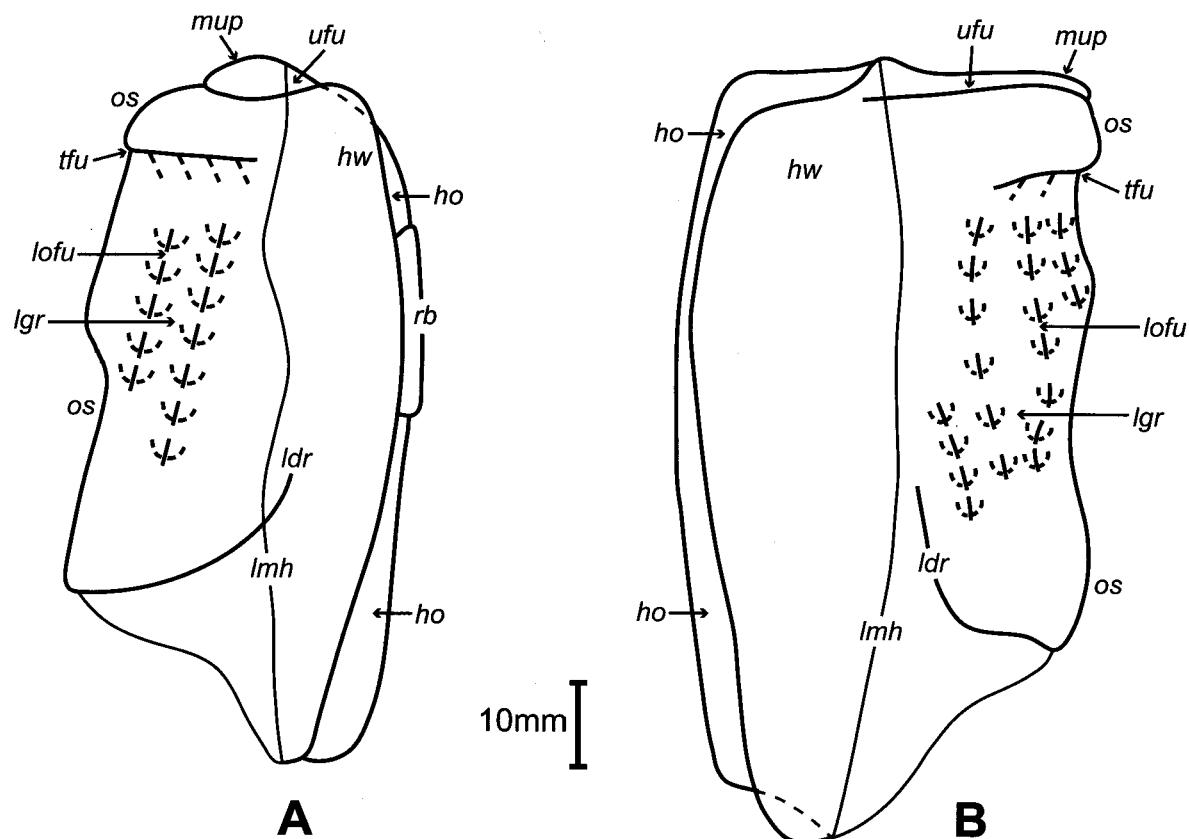


Fig. 29. *Praya reticulata*: A: N₁, definitive nectophore, right lateral view; B: N₁, definitive nectophore, left lateral view (ho, hydroecial opening; hw, hydroecial wing; ldr, laterodistal ridge; lgr, longitudinal ridge; lmh, limit of hydroecium; lofu, longitudinal furrow; mup, median upper protuberance; os, outer surface; rb, reserve bell; tfu, transverse furrow; ufu, upper furrow).

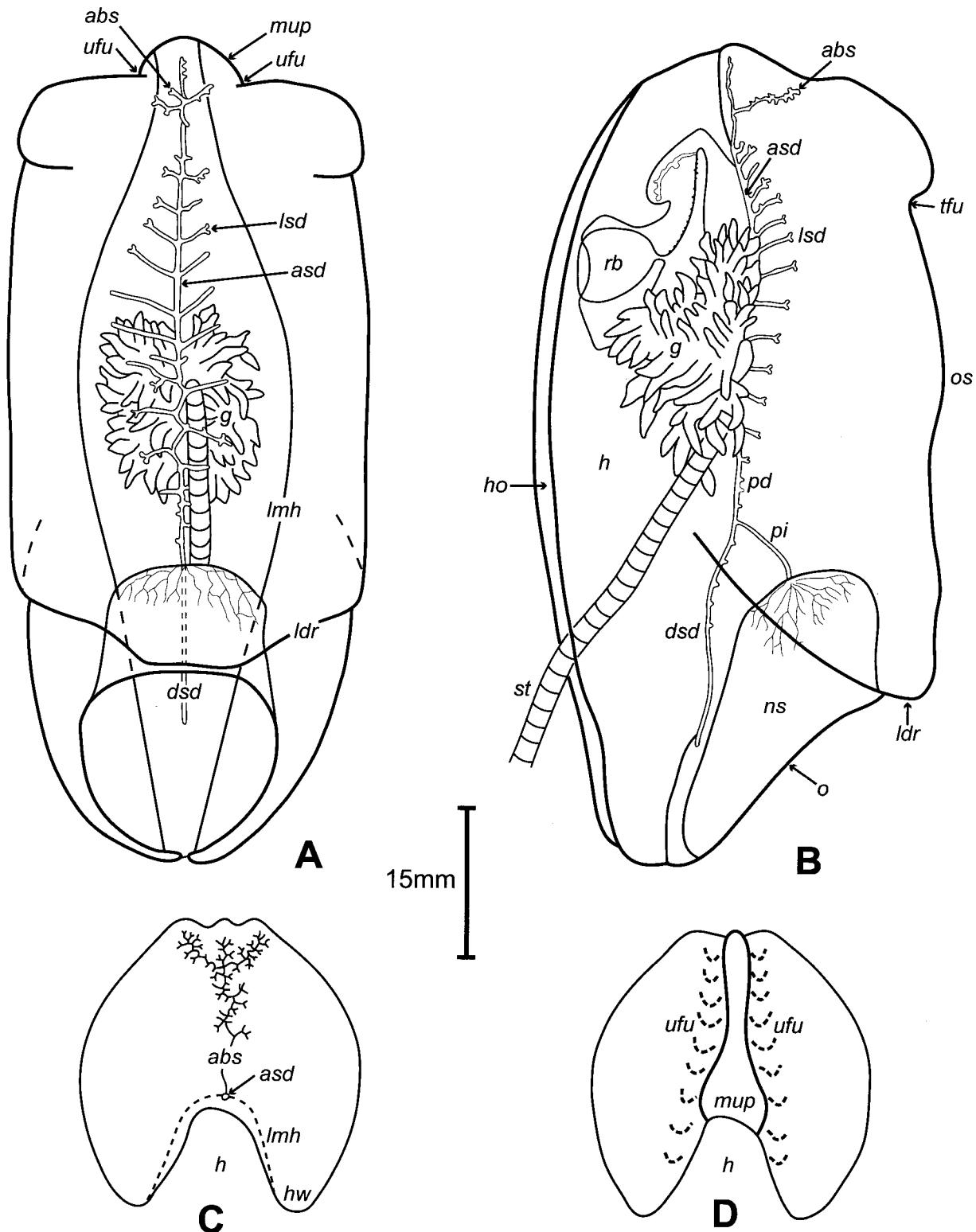


Fig. 30. *Praya reticulata*: A: N_2 definitive ectophore, upper view; B: N_2 definitive ectophore, left lateral view; C: N_1 definitive ectophore, upper view, illustrating somatocyst canals; D: same as C, illustrating surface features (abs, ascending branch of somatocyst; asd, ascending surface diverticulum; dsd, descending surface diverticulum; g, gastrozooid(s); h, hydroecium; ho, hydroecial opening; hw, hydroecial wing; ldr, laterodistal ridge; lmh, limit of hydroecium; lsd, lateral surface diverticulum; mup, median upper protuberance; ns, nectosac; o, ostium; os, outer surface; pd, disjunct pedicular canal; pi, internal pedicular canal; rb, reserve bell; tfu, transverse furrow; ufu, upper furrow).

protuberance (not illustrated); two lateral swellings of main nectophore body flanking lateral furrow coalescence and containing two fine much-branched lateral portions of ascending branch of somatocyst (Fig. 30C); outer nectophore surface with transverse furrow below upper end and several longitudinal furrows on main outer surface (Fig. 29B).

Definitive N_2 up to 82 mm tall and 47 mm wide, cylindrical, and turgid; hydroecial wings extensive but less deep than those of N_1 , enclosing stem and reserve bell (Fig. 29A); wings also originating together on upper nectophore surface, proximal of median upper protuberance, and extending to lower end of nectophore; median upper protuberance broad, projecting upwards 7 mm from main nectophore body, farther than in N_1 , and containing single ascending branch of somatocyst; median upper protuberance flanked by two shallow upper furrows (Fig. 29A); upper furrows coalescing on outer side of median upper protuberance (not illustrated); outer nectophore surface with transverse furrow and some longitudinal furrows (Fig. 29A).

Both nectophores with weak laterodistal ridges on lateral surfaces (Figs 29, 30A and B) delimiting outer surface from ostial region and fusing in outer midline (Fig. 30A); longitudinal ridges on main outer surface (Figs 29) between longitudinal furrows.

Pedicular canal extending from stem to nectosac and comprising external pedicular canal from stem, through nectophoral muscular lamella to proximal midline on wall of hydroecium; long disjunct pedicular canal extending along proximal midline from ascending surface diverticulum to descending surface diverticulum; relatively elongate internal pedicular canal from disjunct canal, through mesogloea to nectosac (Fig. 30B); only disjunct and internal pedicular canals identifiable in nectophores detached from stem (not illustrated).

Nectophoral muscular lamella extending along proximal midline of nectophore from upper end of ascending surface diverticulum to partway along descending surface diverticulum, divisible into upper and lower portions, and connecting nectophore to stem (identified in three nectophores); lamella folded over and omitted from Figure 30B for clarity.

Ascending and descending surface diverticula extending from disjunct pedicular canal towards upper and lower ends of nectophore in all nectophores collected, as shown in Figures 30A and

B; many short lateral surface diverticula arising from ascending diverticulum and disjunct pedicular canal, and extending out laterally close to hydroecial wall, as shown in Figures 30A and B, typically bifurcating distally; short lateral diverticula also arising from upper end of descending surface diverticulum, but absent from extreme lower end of latter.

Somatocyst consisting of single median ascending branch originating from ascending surface diverticulum near upper end of nectophore (Fig. 30B); ascending branch penetrating mesoglea and passing towards outer nectophore surface; this ascending branch with many very short side branches in N_2 (Fig. 30B) and many more subdivided side branches and two slightly longer and more prominent lateral side branches in N_1 (Fig. 30C); two short lateral surface diverticula also originating from upper end of ascending surface diverticulum at junction with ascending branch of somatocyst, and extending laterally in both nectophores (shown for N_2 in Fig. 30A, not illustrated for N_1); short upper extension of ascending surface diverticulum continuing upwards from origin of ascending branch of somatocyst to extreme upper end of nectophore (shown but not labelled in Figs 30A and B for N_2 , not illustrated for N_1).

Nectosac extending from 1/3 nectophore length to near lower end of nectophore, with ostium at approximately 45° to upper-lower axis of nectophore (in lateral view; Fig. 30B, N_2); radial canals ramified with many dichotomous branches and some anastomoses, incompletely preserved at lower end in all nectophores (Fig. 30B).

Small reserve bell in hydroecium of best preserved N_2 (Figs 29A, 30B), absent from hydroecium of other definitive nectophores; bell 26 mm long, with relatively short thick ascending surface diverticulum and relatively elongate thin ascending branch of somatocyst (Fig. 30B).

Bracts large, up to 21–33 mm across right-left bracteal axis and 16–25 mm along proximal-distal bracteal axis, with short upper-lower axis, convex upper surface, and concave lower surface; bilobed in anterior view, with median indentation marking region of bract attachment to stem in life (Fig. 31); right-left bracteal axis passing across bract from right side (left side in Fig. 31) to left side (right side in Fig. 31) at level of median indentation (within body of bract); lower surface of hydroecial lobe hollowed out to form major part of bracteal hydroecial cavity

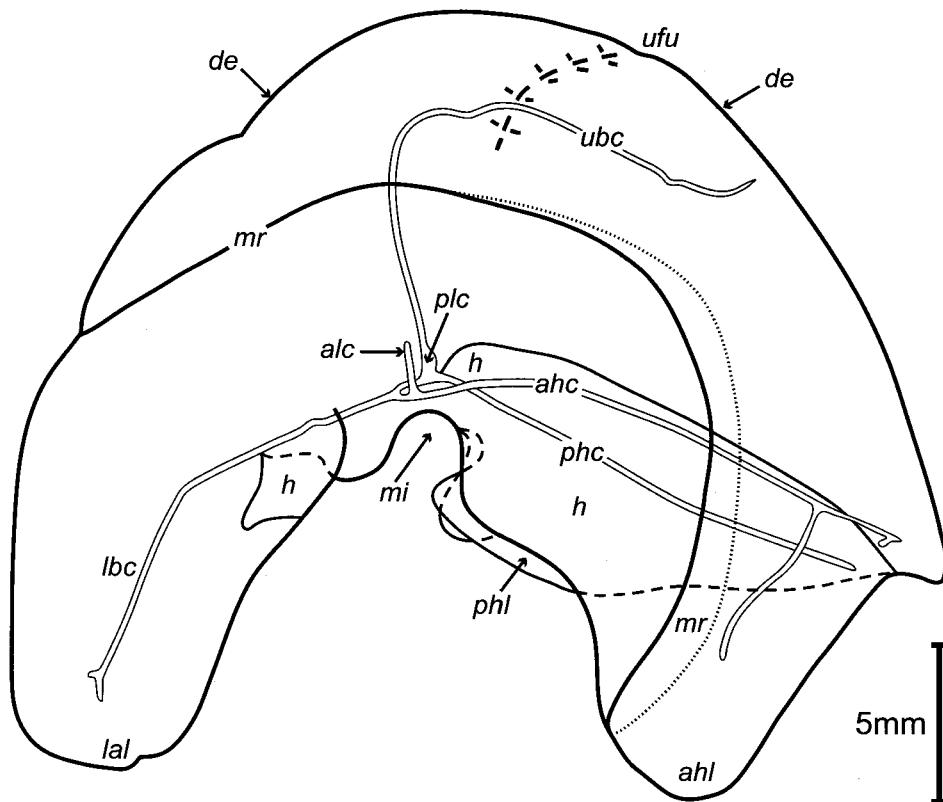


Fig. 31. *Praya reticulata*, bract, upper/anterior view (*ahc*, anterior hydroecial canal (bract); *ahl*, anterior hydroecial lobe (bract); *alc*, anterior longitudinal canal (bract); *de*, distal edge; *h*, hydroecium; *lal*, lateral lobe (bract); *lbc*, lateral bracteal canal; *mi*, median indentation; *mr*, marginal ridge; *phc*, posterior hydroecial canal (bract); *pfl*, posterior hydroecial lobe (bract); *plc*, posterior longitudinal canal (bract); *ubc*, upper bracteal canal; *ufu*, upper furrow).

(housing gastrozoid and tentacle), and consisting of partially fused anterior and posterior hydroecial lobes (Fig. 31); anterior surface of bract with upper furrow, passing towards outer distal edge of bract (but not extending onto lower surface), and more proximal prominent marginal ridge (Fig. 31); marginal ridge thicker and crested over hydroecial lobe, thinner over lateral lobe; posterior hydroecial lobe smaller than anterior hydroecial lobe, subdividing into two sublobes close to stem indentation (Fig. 31); lateral lobe elongate, with small hollowed-out portion of hydroecial cavity on proximal surface (Fig. 31).

Bracteal mesogloea firm in small bracts, softer in large bracts; central organ not identified; bracteal canals with tips typically swollen and comprising longitudinals aligned parallel to stem axis and reduced to two spurs beyond point of origin of hydroecials, with blind-ending anterior spur (*alc*) and posterior spur (*plc*); latter spur giving rise to upper canal, typically from its tip, atypically subterminally; upper canal (*ubc*) typically thinner proximally than other canals, initially passing outwards and then

curving round as shown in Figure 31 (in all bracts); additional short sub-branch arising from upper canal directly below upper furrow in some bracts (not illustrated), with second sub-branch arising distal to first in others; upper canal swollen to variable extent just proximal of first branch in some small bracts (not illustrated); anterior hydroecial canal (*ahc*) longer than posterior hydroecial canal (*phc*) and typically with branch at point where canal turns into anterior hydroecial lobe (Fig. 31); this branch with or without bifurcate tip; posterior hydroecial canal typically without branching tip (Fig. 31), sometimes swollen or bifurcate; lateral canal (*lbc*) elongate, with distal portion (more than 1/3 of total length) inflected into mesogloea, typically thin throughout (Fig. 31), atypically appearing thicker proximally, owing to attachment of elongate muscular lamella along canal itself, with small diverticulum typically present at distal end of lamella, also atypically with short branch halfway along length of lamella (atypical variations not illustrated); canals thicker in immature bracts. Many bracts with gastrozoid attached.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993). Northeast Pacific: off Baja California to mid-California (Alvariño 1980c, 1991); off San Diego (Alvariño 1967b); Monterey Bay, as *Nectodroma reticulata* (Bigelow and Leslie 1930); Monterey Bay (Bigelow 1931); off Oregon (Pearcy 1972); 40°20'N, 144°04'W; 44°58'N, 128°50'W; 46°52'N, 135°49'W, northeast Pacific (Stepanjants 1967); Friday Harbor (Mills 1981); Puget Sound (Bigelow 1931). Other regions: few records from elsewhere in Pacific (for example, Bigelow 1911b, 1931; Boone 1933; Totton 1965a; Zhang and Xu 1980), with few also from other oceans (for example, Totton 1965a; Pugh 1974b, 1984; Margulis 1979; Pagès and Gili 1992b; Gibbons and Thibault-Botha 2002; Pagès et al. 2006).

Vertical. *Praya reticulata* was collected at 300, 500, and 700 m depth, extending the known range for the northeast Pacific noted by Alvariño (1991).

Notes

Bigelow (1911b) was the first author to note that the hydroecial wings (or flaps as he called them) of *Praya reticulata* (as *Nectodroma reticulata*) differed in the two nectophores of the colony, commenting on page 206 that “the flaps are widely separate” in one, probably the older, nectophore, and “partially enclosed the other”, younger nectophore. This difference is well displayed in the best preserved pair of nectophores from Canadian Pacific waters (described above), and other differences are also apparent that are not mentioned by Bigelow. These include a differently shaped upper end in the N_1 and N_2 , and a varied amount of branching of the ascending branch of the somatocyst. In the Canadian Pacific N_1 the upper end is generally flattened in lateral view (Fig. 29B), while in the N_2 there is a prominent median upper protuberance (Fig. 29A). In this respect the N_2 protuberance closely resembles that of a newly formed definitive nectophore still attached to the larval nectophore and figured by Pugh (1992c, fig. 6B) from a specimen taken in the vicinity of the Bahamas. Thus, in *P. reticulata*, as noted in Section 3.3 for the prayine *Rosacea cymbiformis* (Mapstone 2005) and for prayines in general, the two definitive nectophores develop sequentially, with the first definitive nectophore initially having a projecting median upper protuberance similar to that of the mature N_2 described above. This protuberance

later sinks down into the nectophore and becomes partially circumscribed by a deeper upper furrow. The nectophore is now a N_1 and encloses a newly developing N_2 within its hydroecium. This type of nectophore replacement is thought to occur continuously in prayines, and is explained in more detail in Section 3.3.

The reserve nectophore attached to the best N_2 from Canadian Pacific waters is 10 mm longer than the young nectophore figured by Bigelow from the eastern tropical Pacific (1911b, pl. 1 figs 7, 8), but the two nectophores appear similar in all features. This suggests that Bigelow’s nectophore could have become detached from the parent nectophore at capture, and was in life attached to a N_2 . In these reserve bells the ascending somatocyst is precociously developed in comparison with the ascending surface diverticulum, and the outer nectophore surface is not yet fully extended.

In both definitive nectophores of *Praya reticulata* the hydroecial wings originate close together at the upper end of the nectophore, whereas in the N_1 of *P. dubia*, as in the N_1 of *Rosacea cymbiformis*, they originate farther apart. The latter two species have a N_1 with a flatter and broader upper end, particularly in *P. dubia*, and both species lack the distinctive median upper protuberance found in nectophores of *P. reticulata*. In *P. reticulata*, the N_1 can also be distinguished from the N_2 by the extent to which the ascending branch of the somatocyst is subdivided, whereas in *P. dubia* there is no obvious correlation between the number of ascending somatocyst branches and the type of nectophore, at least in the few specimens examined by the present author.

The ascending somatocyst of a definitive nectophore of *Praya reticulata* illustrated by Bigelow (1911b, pl. 3, figs 1–3, 5) is only slightly more complex than that of a *P. reticulata* N_2 from Canadian Pacific waters shown in Figure 27B, and indeed, is similar to the branched ascending somatocysts of two other N_2 ’s also from Canadian Pacific waters but not illustrated. The sub-branching in all four of these nectophores is simpler than that found in the ascending branches of the three N_1 ’s taken from Canadian Pacific waters, which is not fully shown in Figure 30C because this figure is partly diagrammatic. It therefore seems likely that Bigelow’s two figures 7 and 8 (pl. 1) represent a N_2 , and that he did not illustrate a N_1 if, indeed, he collected one. The descending surface diverticulum of the nectophore shown by Bigelow (as *descending branch*) terminates below the ostial opening of the

nectosac, but in more recent figures by Pugh (1992c, figs 8A and B) this diverticulum terminates short of the lower end of the ostial opening, as in all the Canadian Pacific nectophores collected. It is here concluded that Bigelow's representation of both the nectosac and the descending surface diverticulum in *P. reticulata* is somewhat diagrammatic.

The bracts collected from Canadian Pacific waters are typically twice the size of those described by Pugh (1992c) from the Atlantic. The marginal ridge was first illustrated as a "vertical fold" over the hydroecial lobe by Totton (1965a, fig. 70b) and is discernible throughout its course in all present bracts; it was also noted in Atlantic material by Pugh (1992c, fig. 3). The upper furrow is shallow in all present bracts, whereas in bracts from the Atlantic it is described as deep (Pugh 1992c, as *dorsal furrow*). The swelling noted in the upper canal of a number of smaller Canadian Pacific bracts has not been previously described. In some present bracts the upper canal has a branch to the upper/outer surface and in all bracts the distal end of the upper canal is long and similar to that of a bract figured by Bigelow, also from the northeast Pacific (1911b, pl. 3 fig. 6) and in some from the Atlantic (Pugh 1992c, fig. 3E). However, in another bract from Monterey Bay (Bigelow 1931, fig. 185) the distal end of the upper canal is shorter, and similar to the condition noted in other bracts described by Pugh (1992c, fig. 3A).

Gonophores of the two *Praya* species have a characteristic three-branched mantle canal at their apices, in contrast to those of other prayines, which typically have only two branches (Pugh and Harbison 1987).

Genus *Rosacea* Quoy and Gaimard, 1827

Diagnosis

Prayinae with definitive nectophore having disjunct pedicular canal and ascending and descending surface diverticula, but no somatocyst; nectosac with four radial canals, laterals sigmoid. Bract present, globular or kidney-shaped and somewhat flattened in plane approximately orthogonal to anterior-posterior colony axis (except in *R. flaccida*); six bracteal canals, with lateral bracteal canal arising midway between hydroecial canals, and longitudinal

canals typically reduced to spurs; gonophore with two mantle canals or none, and nectosac 1/2 bell height or more; no cormidial bell.

Type species: *Rosacea plicata* Bigelow, 1911a.

Notes

The genus *Rosacea* was founded by Quoy and Gaimard (1827) for two new species, *R. ceutensis* and *R. plicata*, which they collected in the Strait of Gibraltar. However, as the former has never been found again and the name has remained unused since 1899, it is a *nomen oblitum*. Bigelow (1911a and b) referred a number of specimens from the Bay of Biscay and eastern tropical Pacific to *R. plicata* Quoy and Gaimard, 1827 because he thought they had identical "somatocysts". However, the "pallial canal" of Bigelow's nectophores (herein termed the *ascending surface diverticulum*, but previously considered to be a part of the somatocyst; see Pugh and Harbison 1987, p. 88) clearly differs from the somatocyst illustrated by Quoy and Gaimard (1827, pl. 4b fig. 4) because it lacks a swollen tip (Bigelow 1911b, pl. 2 figs 7–9). Bigelow's species *plicata* was subsequently found by many workers, who also incorrectly attributed their material to Quoy and Gaimard's species. Only Kawamura (1915b) described and illustrated two specimens with swollen somatocysts that were taken off Misaki, Japan, and hence correctly referred them to Quoy and Gaimard's species. Totton (1965a) recognized Bigelow's error and gave his own species the name *Rosacea plicata sensu* Bigelow, 1911 to distinguish it from that of Quoy and Gaimard. However, this name is invalid under Article 57.2 of the International Code of Zoological Nomenclature, and the case for conserving the name *R. plicata* for Bigelow's species was accordingly submitted to the International Commission on Zoological Nomenclature by Mapstone and Pugh (2004). This has been accepted (see Opinion 2157 in *Bulletin of Zoological Nomenclature*, volume 63 number 3; International Commission on Zoological Nomenclature 1999, 2006), so Bigelow's species is now the type species of the genus.

Desmophyes annectens Haeckel, 1888b was first inferred by Totton (1954, 1965a) and subsequently considered by Pugh and Harbison (1987) to be an almost certain synonym of Quoy and Gaimard's species *Rosacea plicata*, although they noted that it cannot be verified because Haeckel's original specimen is lost. Kawamura's figure of *R. plicata* (1915b, pl. 7 fig. 6) shows a colony of *D. annectens*. As a result, in making the case mentioned above

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

(Mapstone and Pugh 2004), it was additionally requested that the names *Desmophyes* Haeckel, 1888a and *Desmophyes annectens* Haeckel, 1888b be placed in the Official Lists of Generic and Specific Names in Zoology, together with *Rosacea* Quoy and Gaimard, 1827 type species by designation *Rosacea plicata* Bigelow, 1911, and that the specific name *plicata* Quoy and Gaimard, 1827 be placed on the Official Index of Rejected and Invalid Specific Names in Zoology. This has now been done.

Four further species have been added to the genus *Rosacea* since Bigelow introduced *R. plicata* in 1911. These include *R. flaccida* Biggs et al., 1978, *R. repanda*, *R. limbata* Pugh and Youngbluth, 1988, and, more recently, *R. arabiana* Pugh, 2002. The oldest species, *R. cymbiformis*, has also recently been redescribed by Mapstone (2005) and the characters that differentiate it from the five other known *Rosacea* species discussed. In the descriptions given below, the new terminology of Haddock et al. (2005a), as extended by the present author and explained in Section 2.3, is applied. The specific diagnoses for *R. cymbiformis* and *R. plicata* given below are also changed from those of Mapstone (2005) as follows: the ostial angle is omitted from the *R. cymbiformis* diagnosis, since this may be influenced by changes at preservation (Biggs et al. 1978); “basal sill”, given in the diagnosis of *R. plicata* by Mapstone (2005), is herein changed to “lower sill”, which better accords with the upper-lower nectophore axis now identified in *Rosacea* nectophores (Fig. 2A; see Section 2.3.1).

Rosacea cymbiformis (delle Chiaje, 1830)

(Fig. 32)

Physalia cymbiformis delle Chiaje, 1830: pl. 76 fig. 1; delle Chiaje, 1841: 134: pl. 33 fig. 1.

Diphyes prayensis Quoy and Gaimard, 1833: 106, pl. 5 figs 37, 38.

Praya diphyses Lesson, 1843: 144; Gegenbaur, 1853: 300; Vogt, 1854: 99 (in part), pl. 16 fig. 3; Huxley, 1859: 52, pl. 3 fig. 3; ?Fewkes, 1883: fig. 6 (not *P. diphyses* Kölliker, 1853: 33, pl. 9, Vogt, 1854: 99 (in part), pl. 16 figs 1, 2 and pl. 17; Fewkes, 1883: 841, fig. 5: all these = *Desmophyes annectens*;

not *P. diphyses* Graeffe, 1860: 12, pl. 1 figs 1–3, = *Lilyopsis rosea*).

Praya cymbiformis: Leuckart, 1853: 2, pl. 1 figs 4, 8–10, 13–15 and pl. 2 fig. 4; Leuckart, 1854: 286, pl. 11 figs 18–24; ?Huxley, 1859: 30; Sars, 1857: 11; Keferstein and Ehlers, 1861: 20, pl. 1 fig. 28; ?Fewkes, 1883: 841, fig. 6; Haeckel, 1888b: 146; Iwanzoff, 1896: 334, pl. 5 figs 34–37; Schneider, 1896: 621, pl. 44 figs 11–14 and pl. 45 fig. 32; Chun, 1897b: 66, text-fig. 8; Bigelow, 1911b: 200 (in part), pl. 2 figs 1–6; Moser, 1912c: 529, fig. 10; Kawamura, 1915b: 318 (in part), pl. 7 figs 4, 5; Moser, 1915b: 653 (in part); Moser, 1917: 705 (in part); Moser, 1924a: 14, pl. 1 figs 1–3; Moser, 1925: 374 (in part); Fraser, 1950: 95 (not Browne, 1926: 60, = *Rosacea plicata*).

Praya maxima Gegenbaur, 1853: 301, pl. 17 figs 1–6; Gegenbaur, 1854: 450; Huxley, 1859: 30, pl. 12 figs 2, 3; Chun, 1885: 522, figs 9, 10, 14, 15; Haeckel, 1888b: 146.

Praya galea Haeckel, 1888b: 146, pl. 31.

Eudoxella galea: Haeckel, 1888b: 108 (in part), pl. 32 figs 8–13, 15 (?pl. 32 fig. 14).

Rosacea cymbiformis: Schneider, 1898: 79; Schneider, 1899: 13, figs 14–17; Leloup, 1933: 8; Bigelow and Sears, 1937: 10 (in part), figs 6–8; Totton, 1954: 88, pl. 4 figs 6, 7; ?Leloup, 1955: 5, fig. 3; Totton, 1965a: 118, pl. 21 fig. 1, pl. 22 figs 1–3, and text-figs 68, 69; Patriti, 1970b: 289, fig. 2; Palma, 1973: 32 (in part), pls 5, 26, 7; Daniel, 1974: 85 (in part), ?figs 6k, 1, and p; Biggs et al., 1978: 216; Kirkpatrick and Pugh, 1984: 56, fig. 18; Daniel, 1985: 134, figs 33a–f; Pugh and Harbison, 1987: 87, figs 13d and e; Bonnemains and Carré, 1991: 58, fig. 15 (reproduction of an unpublished drawing by Lesueur); Pagès and Gili, 1992b: 76, fig. 15 (in part); Pugh, 1999b: 486 (in part), figs 3.38, 3.49; Gamulin and Kršinic, 2000: 32, fig. 9 (in part); Bouillon et al., 2004: 229, figs 140e and f, 141a; Mapstone and Pugh, 2004: 151; Mapstone, 2005: 709, figs 1–5.

Praya californica Gravier, 1899: 87, figs 1–4.

Praya cimbiformis (*lapsus calami*) Neppi, 1921: 224.

Praia prayensis Stechow, 1922: 152.

Rosacea (Rosacea) cymbiformis: Leloup, 1934: 10.

Rosacea cymbiformes: Kinzer, 1965: 248.

Neorosacea cymbiformis: Margulies, 1994: 26, pl. 3 figs m, n.

Diagnosis

Definitive nectophores with surface smooth; hydroecium with elongate opening extending full length of nectophore, lack lower sill, broad in N_1 and narrow in N_2 ; radial canals arising together from internal pedicular canal, with lateral canals following complex S-shaped courses, each comprising three loops but no cross-branch; mesogloea flaccid. Bract with upper bracteal canal originating from posterior longitudinal canal between origins of lateral bracteal canal and posterior hydroecial bracteal canal; lateral bracteal canal and anterior hydroecial canals not question-mark-shaped.

Material examined

Sixty-eight bracts from Canadian Pacific stations LB6 (80–0 m), LB8 (?–0 m), LB14 (300 m), LC9 (300–0 m), LC10 (700–0 m) (Fig. 32) BCPM 996-224-1, LC10 (700–0 m), and A4 (0–500 m) (Fig. 11, Table 1). Specimens of *Rosacea cymbiformis* from the NHM collections, from the Bay of Villefranche,

at the surface: Reg. Nos 1952.9.23.175, detached N_1 and N_2 ; 1952.9.23.177, detached N_1 and N_2 ; 1952.9.23.179–181, detached N_1 and N_2 ; 1952.9.23.191, detached N_1 and N_2 ; 1952.9.23.192, 2 each detached N_1 's and N_2 's; 1952.9.23.194, 2 N_2 's, each with stem attached; 1952.9.23.198, detached N_1 , 2 detached N_2 's, and 1 N_2 with stem; 1952.9.23.200, detached N_1 and N_2 ; 1952.9.23.201, 5 detached N_1 's and 5 detached N_2 's, 1 N_2 with attached stem; 1952.9.23.202, detached N_1 and N_2 ; 1952.9.23.203, 4 detached N_1 's and 5 detached N_2 's; 1973.5.15.53, detached N_1 and N_2 ; 1973.5.15.54, N_1 and N_2 with attached stem. *Rosacea arabiana* holotype from the NHM collections: Reg. No. 2001.6920, joined N_1 and N_2 , detached N_1 and N_2 , 3 bracts, and 2 gonophores ($24^{\circ}13'N$, $58^{\circ}36'E$).

Description of material

Bracts up to 13 mm across right-left bracteal axis, 9 mm along proximal-distal bracteal axis, with thin upper-lower axis and median indentation proximally where bract attached to stem in life; surface without distinct ridges and furrows and divided into rounded lateral and hydroecial bracteal lobes in anterior view (Fig. 32); latter subdivided into anterior and posterior hydroecial lobes with posterior lobe of two sublobes, having flap on inner surface of larger posterior sublobe in best preserved material (Fig. 32); hydroecium narrow in region of stem attachment (at

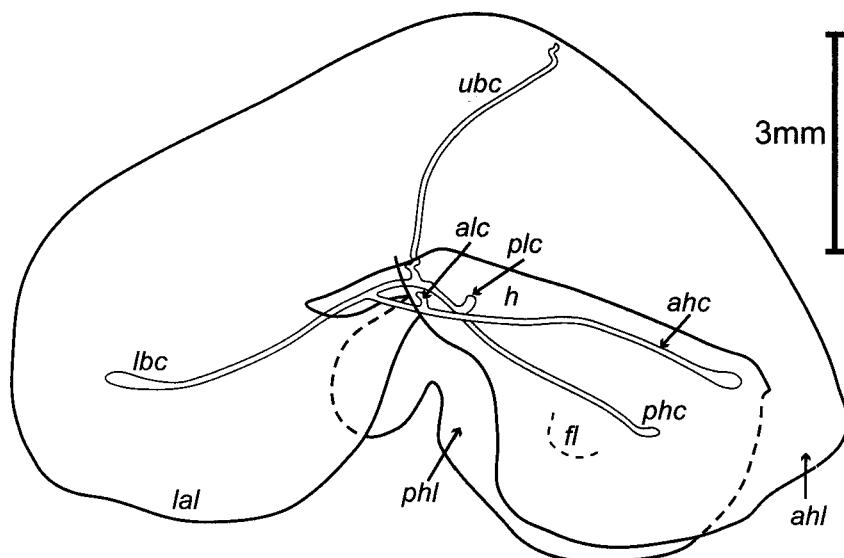


Fig. 32. *Rosacea cymbiformis*, bract, upper/anterior view (ahc, anterior hydroecial canal (bract); ahl, anterior hydroecial lobe (bract); alc, anterior longitudinal canal (bract); fl, flap; h, hydroecium; lal, lateral lobe (bract); lbc, lateral bracteal canal; phc, posterior hydroecial canal (bract); phl, posterior hydroecial lobe (bract); plc, posterior longitudinal canal (bract); ubc, upper bracteal canal).

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junction of lateral canal with longitudinal canals), broadening into discrete cavity on lower left side of bract (on right in Fig. 32), between two hydroecial lobes; central organ not identified; bracteal canals (Fig. 32) with tips typically swollen and comprising two short longitudinal canals aligned approximately parallel to stem axis and terminating as two blind-ending spurs (*alc* and *plc*), with additional atypical short “spur-like” canal arising between posterior spur and origin of upper canal in some bracts (not illustrated); upper canal thinner than other bracteal canals, tip not swollen, course typically sinuous distally, atypically sinuous throughout, and terminating close to upper/outer bracteal surface; anterior and posterior hydroecial canals unbranched, straight, remaining close to hydroecium throughout, posterior longer than anterior. Gonophores not identified.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Although bracts were found in the present collection, no definitive nectophores were identified, and because, historically, they have been difficult to distinguish from those of *Rosacea plicata* (see Pugh 1999b) — though more recently they have been redescribed by Mapstone (2005) — many records are unreliable. Northeast Pacific: off Baja California to mid-California (Gravier 1899; Alvariño 1980c, 1991; Alvariño and Kimbrell 1987). Other regions: few reliable records from remainder of Pacific (for example, Bigelow 1911b; Kawamura 1915b, 1954; Purcell 1980, 1981a and b; Margulis 1987; Gasca and Suárez 1992a). *Rosacea cymbiformis* has been reported from widely distributed locations in the Atlantic and Indian oceans.

Vertical. Bracts were collected mostly in surface waters down to 300 m. Off California, *Rosacea cymbiformis* was reported between 0 and 475 m (Alvariño 1991). In the Atlantic, *R. cymbiformis* stem groups remain in deep water during the day, and colonies migrate upwards into the 240–260 m layer at night (Roe 1974).

Notes

A brief history of names previously applied to the prayine species *Rosacea cymbiformis* is given by Mapstone (2005), but herein a full synonymy is included. It is long and complex, with many papers published during the 19th century. Many new species

of prayids were named, but were later shown to be synonyms of earlier species. *Rosacea cymbiformis* was originally introduced by delle Chiaje under the name *Physalia cymbiformis* in a plate dated 1830, although the description accompanying it was not published until 1841. Subsequently, the species was described under five different names until the binomen used today was introduced by Schneider in 1898. Three early authors used the name *Praya diphyses* for *R. cymbiformis*, but other usages of *P. diphyses* refer to *Desmophyes annectens* Haeckel, 1888b and one to the rare prayine species *Lilyopsis rosea* (see above).

In the past, nectophores of *Rosacea cymbiformis* have often been confused with the N₁ of the widely distributed species *R. plicata* Bigelow, 1911a (see description below). Recently, Mapstone (2005) examined a large number of specimens of *R. cymbiformis* from the NHM collections and compared them with NHM specimens of *R. plicata*. She found that in nectophores of *R. cymbiformis* the hydroecial opening always extended the full length of the nectophore, whereas in the *R. plicata* N₁ it was typically found to be somewhat shorter, and the lower end was always marked by a distinct “sill” formed by a thickening of the mesogloea between the nectosac and the descending surface diverticulum. This sill is absent in *R. cymbiformis*, giving a smoother contour to the proximal wall of the hydroecium in this species.

***Rosacea plicata* Bigelow, 1911a**

(Figs 33, 34)

Rosacea plicata Bigelow, 1911a: 341 (in part); Bigelow, 1911b: 201 (in part), pl. 2 figs 7–9; Bigelow, 1913: 64 (in part), pl. 5 figs 10, 11; Leloup, 1933: 8 (in part); Bigelow and Sears, 1937: 11 (in part), figs 9–14; Totton, 1954: 89 (in part), fig. 41-3 and text-fig. 32; Leloup, 1955: 6 (in part); Stepanjants, 1967: 145 (in part), figs 92, 93; Palma, 1973: 34 (in part), pls 8, ?9, 10; Xu and Zhang, 1978: 36 (in part), fig. 24 (not figs 25, 26, indet.); Alvariño, 1981: 401 (in part), fig. 174.18; Alvariño et al., 1990: 14 (in part), fig. 20; Gao et al., 2002: 86 (in part), figs 37A and B; Mapstone and Pugh, 2004: 149; Bouillon et al., 2004: 229, figs 141B and C; Mapstone, 2005: 709; ICZN Opinion 2157, 2006: 207 (not

Kawamura, 1915b: pl. 7 figs 6–8, ?Kawamura 1954: 102, and Margulis, 1994: 20, figs 1c–j, 2, = *Desmophyes annectens* Haeckel 1888b).

Hippopodius hippopus Bigelow, 1911a: 350.

Praya cymbiformis Moser, 1915b: 653 (in part); Moser, 1920: 174 (in part); Browne, 1926: 60 (in part, not *P. cymbiformis* Leuckart 1853).

Praya diphyses Moser, 1925: 377 (in part).

Rosacea (Rosacea) plicata: Leloup, 1934: 11 (in part).

Rosacea plicata sensu Bigelow, 1911a: Totton, 1965a: 116 (in part), text-figs 65–67; Daniel, 1974: 84 (in part), (not figs 6m–o, indet.); Biggs et al., 1978: 207; Kirkpatrick and Pugh, 1984: 54, fig. 17; Daniel, 1985: 130 (in part), fig. 32; Pugh and Harbison, 1987: 86, figs 13f and g; Pagès and Gili, 1992b: 76 (in part), fig. 14; Pagès et al., 1994: 877; Pugh, 1999b: 486 (in part), figs 3.39, 3.50; Pugh, 2002: 171.

Neorosacea bigelowi Margulis, 1994: 24, pl. 3a–l.

Diagnosis

Definitive nectophores with surface smooth, or if with protuberances then not in upper-lateral position; hydroecial opening delimited by lower sill, being elongate and broad in N_1 , shorter, narrower, and slit-like in N_2 ; radial canals arising together from internal pedicular canal, with lateral canals following complex S-shaped courses, each comprising two loops but no cross-branch. Bract with upper bracteal canal originating from posterior hydroecial canal; lateral bracteal canal and anterior hydroecial canals not question-mark-shaped.

Material examined

Nine detached definitive nectophores from Canadian Pacific stations LB13 (700–0 m) (N_2), LB16 (500 m) (N_1 and N_2) (Fig. 34A) BCPM 996-225-1, LC9 (0–500 m) (N_1 and N_2), LC11 (500 m) (N_1 and N_2) (Figs 33A and B) BCPM 996-226-1, LD10 (300 m) (N_2), and A4 (300–0 m) (N_2); 11 bracts from stations LB17 (0–500 m), LC10 (700–0 m), and LC11 (0–500 m) (Fig. 34B) BCPM 996-227-1 (Fig. 11, Table 1). Specimens of *Rosacea plicata* from the NHM collections: Reg. Nos 1939.6.10.1, lectotype, N_1 and N_2 (Bay

of Biscay); 1939.6.10.2–5, 2 N_1 's and 2 N_2 's (Bay of Biscay); 1957.9.14.70, 11 N_1 's and 12 N_2 's (48°49'S, 109°16'E); 1957.9.14.71, N_1 and N_2 (41°41'N, 14°34'W); 1959.6.25.1, N_1 and N_2 and 24 bracts (51°48'S, 107°50'E); 1982.11.30.314, N_1 and N_2 (41°54'N, 41°54'W); 1985.12.9.9, 44 N_1 's and 50 N_2 's (41°05'N, 14°38'W); 1985.12.9.10–16, attached N_1 and N_2 pair (41°31'N, 14°21'W), 3 N_1 's and 2 N_2 's (45°54'N, 09°39'W) and 3 N_1 and 7 N_2 nectophores (40°15'N, 10°15'W).

Description of material

Definitive N_1 10–24 mm tall (Fig. 34A), definitive N_2 nectophores 9–29 mm tall (Figs 33A and B); N_1 taller than N_2 in samples with a pair of definitive nectophores; both nectophores cylindrical, with rounded upper and outer surfaces and somewhat slit-like hydroecial opening on proximal surface, hydroecium delimited at lower end of nectophore by lower sill; longer and slightly broader overall in N_1 (Fig. 34A) than in N_2 (Fig. 33B); proximal surface typically flattened across right-left nectophore axis below hydroecial opening in N_2 ; borders of hydroecial wings undulating in lateral view (Fig. 33A); protuberances discernible lower-laterally on outer surface close to borders of hydroecial opening in some N_2 nectophores (Fig. 33B); hydroecium deep in lateral view in both N_1 and N_2 (Fig. 33A), and occupying 1/2 nectophore width in proximal view at widest point (Figs 33B, 34A), narrowing rapidly towards upper end in both nectophores and also narrowing at lower end to sill; sill at lower level in N_1 than in N_2 (not shown in proximal view in Fig. 34A).

Pedicular canal extending from stem to nectosac in N_2 shown in Figure 33, and from hydroecial wall to nectosac in N_1 shown in Figure 34A; pedicular canal in N_2 comprising short external pedicular canal from stem through nectophoral muscular lamella to proximal midline of hydroecium (hidden by contracted stem mass in Fig. 33), long disjunct pedicular canal along hydroecial midline to upper end of descending surface diverticulum, and relatively elongate internal pedicular canal from lower end of disjunct canal to nectosac.

Nectophoral muscular lamella intact in one specimen and comprising upper portion extending upwards from insertion point of external pedicular canal, and lower portion extending downwards to origin of internal pedicular canal (the two portions shown but not labelled in Fig. 33A).

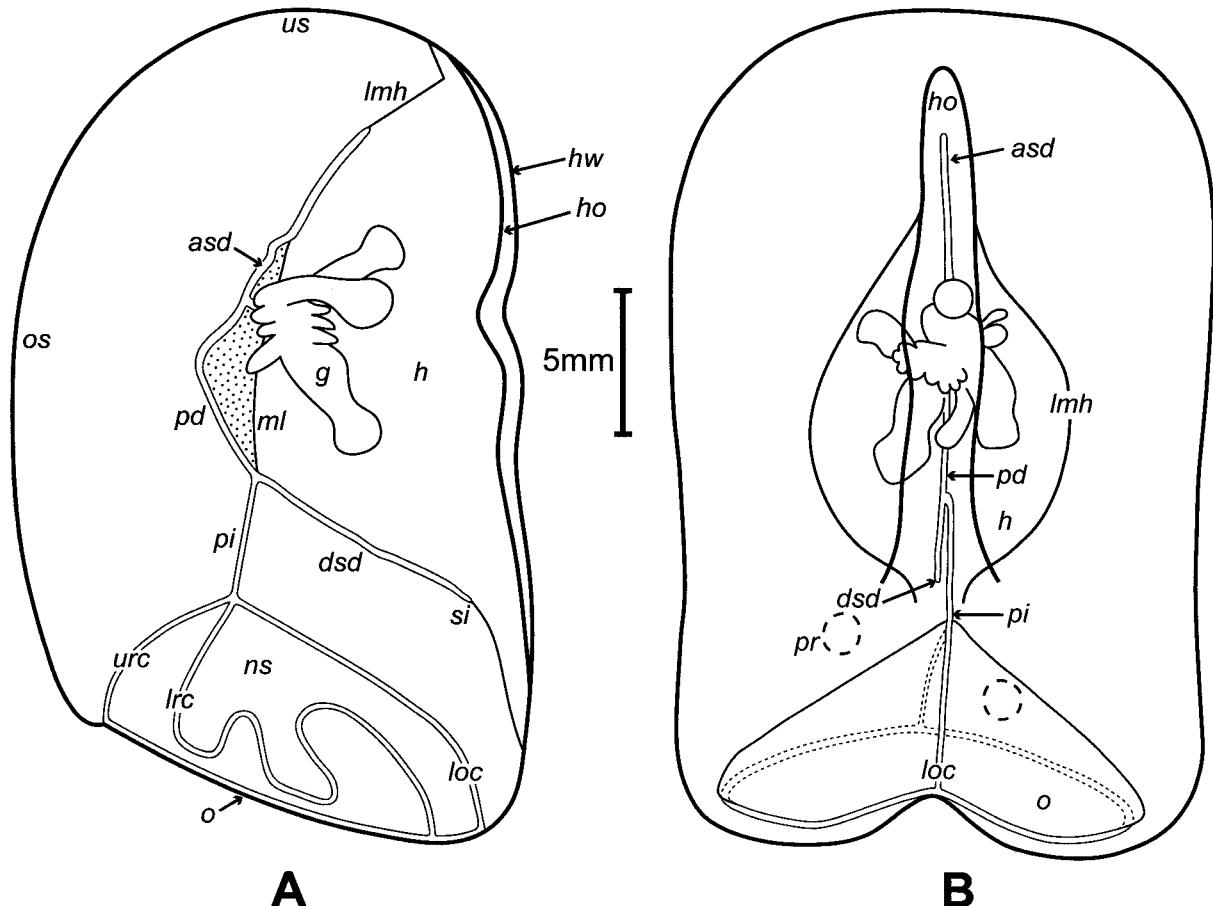


Fig. 33. *Rosacea plicata*: A: N₂ definitive nectophore, right lateral view; B: N₂ definitive nectophore, proximal view (asd, ascending surface diverticulum; dsd, descending surface diverticulum; g, gastrozooid(s); h, hydroecium; ho, hydroecial opening; hw, hydroecial wing; lmh, limit of hydroecium; loc, lower radial canal; lrc, lateral radial canal; ml, muscular lamella; ns, nectosac; o, ostium; os, outer surface; pd, disjunct pedicular canal; pi, internal pedicular canal; pr, protuberance; si, sill; urc, upper radial canal; us, upper surface).

Diverticula from pedicular canal comprising ascending surface diverticulum extending upwards along hydroecial (proximal) midline and terminating before reaching upper end of hydroecium (Fig. 33A); this diverticulum without short extension from tip into mesogloea in any nectophore; descending surface diverticulum extending downwards in hydroecial midline from disjunct pedicular canal to hydroecial sill, measuring up to 6 mm in largest nectophores.

Nectosac with broad ostium, but full course of lateral radial canals discerned only in best preserved N₂ (Fig. 33A).

Bracts compact and up to 11 mm across right-left bracteal axis, 9 mm along proximal-distal axis, with median indentation on proximal side for stem offset to one side in Figure 34B; surface without distinct

ridges and furrows; posterior hydroecial lobe with flap on inner surface (Fig. 34B), but sublobes of this lobe not discernible in present material; mesogloea firm; hydroecium broadest between two hydroecial lobes; central organ prominent in one specimen (Fig. 34B); bracteal canals with tips typically not swollen and comprising two short longitudinal canals aligned approximately parallel to stem axis and terminating as two short spurs, both blind-ending (alc and plc); upper canal thinner than other canals, tip not swollen, typically not undulating, and arising from posterior hydroecial canal closer to origin of latter from posterior longitudinal canal than to tip of posterior hydroecial canal (Fig. 34B); hydroecial canals unbranched, remaining close to hydroecium, typically straight, atypically sinuous distally (not illustrated), with anterior hydroecial canal approximately twice length of posterior hydroecial canal (Fig. 34B). Gonophores not identified.

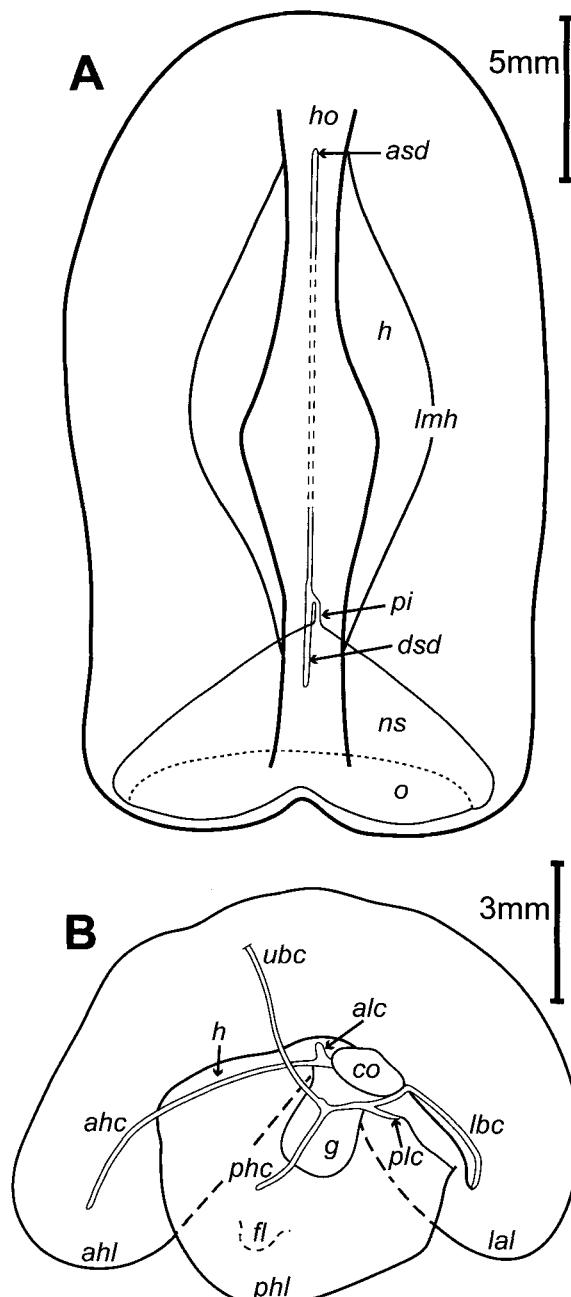


Fig. 34. *Rosacea plicata*: A: N, definitive nectophore, proximal view; B: bract, lower/posterior view (ahc, anterior hydroecial canal (bract); ahl, anterior hydroecial lobe (bract); alc, anterior longitudinal canal (bract); asd, ascending surface diverticulum; co, central organ; dsc, descending surface diverticulum; fl, flap; g, gastrozooid; h, hydroecium; ho, hydroecial opening; lal, lateral lobe (bract); lbc, lateral bracteal canal; lmh, limit of hydroecium; ns, nectosac; o, ostium; pi, internal pedicular canal; phc, posterior hydroecial canal (bract); phl, posterior hydroecial lobe (bract); plc, posterior longitudinal canal (bract); ubc, upper bracteal canal).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: $30^{\circ}30'N$, $120^{\circ}00'W$ (Alvariño 1967b); $30^{\circ}35'N$, $117^{\circ}23'W$ (Bigelow 1911b); off Point Conception (Haddock and Case 1999). Other regions: few other reliable records from Pacific, cosmopolitan from the Bering Sea to the Antarctic, including the tropics (Bigelow 1911b, 1913; Palma 1977; Alvariño et al. 1990). Also widely distributed in the Atlantic, Indian, and Antarctic oceans.

Vertical. This species was recorded at 300 and 500 m off Vancouver Island, similar to depths at which it was found off California (Alvariño 1991). Elsewhere *Rosacea plicata* is thought to inhabit deeper water layers than *R. cymbiformis* (see Kirkpatrick and Pugh 1984). In the Atlantic *R. plicata* occurred in the mesopelagic depth-band between 300 and 500 m (Pugh 1984, 1990; Pagès et al. 1994).

Notes

The name *Neorosacea bigelowi* was introduced by Margulies (1994) for Bigelow's species *Rosacea plicata* and is therefore included in the synonymy list given above. However, it is now invalid because Case 3309 submitted by Mapstone and Pugh (2004) proposed conservation of usage of *Rosacea plicata* Bigelow, 1911, which name is now conserved (see ICZN Opinion 2157). The published opinion gives priority to the name *Rosacea plicata* Bigelow, 1911 over the name *Rosacea plicata* Quoy and Gaimard, 1827. However, incorrect referral of *Rosacea plicata* by almost all authors since 1911 to Quoy and Gaimard's species has necessitated the addition of "in part" to most entries in the synonymy given above.

Bigelow's original figures of definitive nectophores of *Rosacea plicata* from the eastern tropical Pacific (1911b, pl. 2 figs 7–9) show the ascending surface diverticulum remaining close to the wall of the hydroecium throughout its length, though in the text (p. 202) he mentions that in some of his Biscayan nectophores the "upper end of the somatocyst [= ascending surface diverticulum] turns dorsally [= towards outer surface], away from the . . . hydroecium . . . and its terminal region is slightly thickened". He adds, however, that this condition is so variable that he doubts whether there is any discontinuity between the two. Pugh and Harbison (1987) reexamined Bigelow's material, together

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with other *R. plicata* nectophores from the Discovery Collections, and also concluded (p. 88) that this variation is “a true, but inconsistent, morphological characteristic of this species.”

In the definitive nectophores of *Rosacea plicata* from Canadian Pacific waters, the ascending surface diverticulum lacks a short extension from the tip into a mesogloal pad, as discussed above, and in this respect resembles Bigelow’s illustrated nectophores from the eastern tropical Pacific. Small protuberances noted on the lower lateral surfaces of some definitive nectophores from the present collection are similar to those described in *R. limbata* (Pugh and Youngbluth 1988b), except that in the latter they are situated much closer to the upper end of the nectophore.

The present diagnosis for definitive nectophores of *Rosacea plicata* omits the angle of ostial opening, for the reason given above. However, most earlier authors, including Mapstone (2005), consider it of diagnostic importance, and indeed, the ostium is directed “basally” (towards the posterior end of the colony) in many published figures of large mature nectophores, such as the N₁ and N₂ illustrated by Bigelow from the eastern tropical Pacific (1911b, pl. 2 figs 7–9), 21 and 19 mm long, respectively, Totton’s (1965a) figure 65C of a 30 mm long *R. plicata* N₁ (not a N₂ as erroneously stated in the figure caption), and Pugh’s (1999b) figure 3.39 of a *R. plicata* nectophore that is 33 mm long. It is also characteristic of an associated pair of *R. plicata* nectophores in the NHM collections (Reg. No. 1959.6.25.1; see the list above), which both measure 24 mm in length. In contrast, the ostium opens at approximately 45° to the long axis of some smaller preserved nectophores figured by Bigelow and Sears (1937, fig. 9, the younger, left nectophore of the pair) and Pagès and Gili (1992b, fig. 14, nectophore type not given); this may be due to distortion because in younger nectophores the mesogloea is more flaccid (maximum turgidity is not attained until a larger size is reached), or indeed to artificial displacement of the ostium by a thicker layer of mesogloea between the hydroecium of the nectophore and the lower proximal wall of the nectosac at preservation, as is found in *R. flaccida* (Biggs et al. 1978).

The origin of the upper bracteal canal in *Rosacea plicata* was erroneously stated by Mapstone (2005, p. 720, as *dorsal canal*) to originate from the right (now posterior) longitudinal canal instead of from the right (now posterior) hydroecial canal. The upper canal clearly originates from the posterior hydroecial canal

in this species, as can be seen from Figure 34B above and is stated in the species diagnosis given above.

10.2.1.3. Subfamily *Nectopyramidinae* Bigelow, 1911b

Diagnosis

Prayidae with single asymmetric definitive nectophore, typically ridged, replacing smaller ridged larval nectophore; definitive nectophore with disjunct pedicular canal, ascending surface diverticulum, and somatocyst, and with or without descending surface diverticulum and lateral surface diverticula. Bract with canals typically reduced to four and comprising two hydroecial canals (merged or not merged with two longitudinals), lateral canal, and upper canal; free-swimming eudoxid released.

Notes

The subfamily *Nectopyramidinae* was comprehensively reviewed and revised by Pugh (1992a), who gave a good historical account and introduced a new genus and species based on the shape of the hydroecium, the course of the pedicular canal, branching of the somatocyst, and the presence or absence of a cormidial bell in the eudoxid. Previously, the family had been considered monogeneric for *Nectopyramis* (Totton 1965a), but Pugh moved the species *N. diomedae* into a new genus, *Nectadamas*, and added a second species, *Nectadamas richardi*. He retained *Nectopyramis* for *N. thetis* and *N. natans*. Species descriptions in Pugh’s paper follow the terminology conventions of 1992, but the names used in describing the present Canadian Pacific specimens are based on the names of axes and canals introduced by Haddock et al. (2005a) for two prayine prayids, interpreted and extended to the *Nectopyramidinae* by the present author. Names used for the somatocyst are slightly different to those of Haddock et al. (2005a), and follow the definitions given in Section 2.3.2. Surface portions of Pugh’s pallial canal are herein identified as ascending and descending diverticula and a disjunct portion of the pedicular canal; penetrating portions are defined as median or lateral ascending branches of the somatocyst.

Nectopyramidines are a small group of atypical prayids in which one definitive nectophore has been lost, as noted above. Pugh (1992a) showed

that during growth these species produce a larval nectophore that is later replaced by a definitive one. Both nectophores typically have a ridged surface, much mesogloea, a small nectosac, and a short proximal–distal axis between the stem-attachment point (close to the wall of the hydroecium) and the ostium (of the nectosac). A longer upper–lower axis is herein identified, extending from the short (and often pointed) lower surface or angle of the nectophore (between the ostium and the hydroecial opening) to its uppermost point (angle) or surface (see Figs 35C, 36A, and 37C below of the definitive and larval nectophores). The latter axis is herein determined to align approximately parallel with the opening of the hydroecium, and at an acute angle to the proximal–distal nectophore axis in definitive nectophores of the two *Nectadamas* species and the larval nectophore of *Nectopyramis thetis*. However, in definitive nectophores of the two *Nectopyramis* species, the hydroecial opening extends the whole length of the nectophore, and as a result, the long upper–lower axis lies almost parallel to the short proximal–distal axis. As in prayines and amphicaryonines, the upper end of a nectopyramidine nectophore represents the anterior end of the colony, and the posterior end of the colony is marked by the terminal cormidium of the siphosome.

Mature eudoxids of nectopyramidines comprise a large bract, a gastrozooid, and gonophore(s), with or without an additional cormidial bell (Pugh 1992a, as “special nectophore”); each eudoxid represents a terminal cormidium that has detached from the siphosome. The proportions of the bract change after detachment: the bracteal lobes enlarge and the original point of attachment to the stem, where the gastrozooid is also attached to the longitudinal bracteal canals, comes to lie deep within the bracteal hydroecium, above the cormidial bell (when present). The axes of nectopyramidine bracts are therefore most easily determined in immature bracts, including those of *Nectopyramis thetis* shown by Bigelow (1911a, pl. 28 fig. 3) and *Nectadamas diomedaeae* shown by Bigelow (1911b, text-fig. A, as *Nectopyramis diomedaeae*), and then extrapolated to mature bracts. Thus, a proximal–distal bracteal axis can be identified that extends from the original stem-attachment point at the origin of the bracteal canals, along the hydroecium between the anterior and posterior hydroecial canals, to a distal point where these canals terminate. In the bract of *N. thetis*

this point is herein termed the distal angle (see Fig. 36B of a *N. thetis* bract below), whereas in that of *N. diomedaeae* it is herein interpreted as lying at the tip of the hydroecial lobe, and in that of *N. richardi* as lying at the point where this lobe would protrude if developed (see descriptions and Figs 38B and 39B, C of *Nectadamas* bracts below). Additionally, in the mature bract of *N. thetis* the proximal–distal axis is herein extrapolated backwards to an elongate proximal ridge, which comes to lie at an acute angle to a diamond-shaped upper facet in this species, as is explained below. The upper–lower axis in a *N. thetis* bract thus extends from the bracteal hydroecium to this upper facet, and is longer than the equivalent axis in the prayine bracts described above (Section 10.2.1.2). In bracts of *N. natans*, however, this axis is shorter because the bract has little depth and is more elongate. In bracts of *Nectadamas* species there is no upper facet; instead, the upper–lower axis extends from an upper point (*N. diomedaeae*) or rounded surface (*N. richardi*) to the hydroecium. Names used in the descriptions of nectopyramidine bracts given below are derived from these axes.

Nectopyramis thetis and both the species referable to *Nectadamas* occur in Canadian Pacific waters. *Nectopyramis natans* has also been reported from the northeast Pacific as far north as off Point Conception, California (Alvarino 1991; Haddock and Case 1999).

Genus *Nectopyramis* Bigelow, 1911a

Diagnosis

Nectopyramidinae with definitive nectophore not laterally flattened, hydroecium extensive, with elongate opening on proximal surface; pedicular canal with very short external portion, relatively elongate disjunct portion from which radial canals of nectosac originate separately and directly, and no internal portion; ascending and descending surface diverticula present. Larval nectophore with spinose ridges, and pedicular canal similar to that of definitive nectophore. Bract of varied shape but not laterally flattened, with cormidial bell.

Type species: *Nectopyramis thetis* Bigelow, 1911a.

***Nectopyramis thetis* Bigelow, 1911a**

(Figs 35, 36)

Nectopyramis thetis Bigelow, 1911a: 338, pl. 28 figs 1–4; Leloup, 1932a: 1, figs 1–5; Leloup, 1933: 10, figs 11–15; Bigelow and Sears, 1937: 5, figs 2–5; Totton, 1954: 78, figs 35–37; Totton, 1965a: 135, text-figs 76, 77; Stepanjants, 1967: 141, fig. 88; Alvariño, 1981: 404, fig. 174.24; Kirkpatrick and Pugh, 1984: 66, figs 23A and B; Alvariño et al., 1990: 56, fig. 86; Pugh, 1992a: 284, figs 2–8.

Nectopyramis spinosa Sears, 1952: 3 (in part), fig. B; Totton, 1954: 86 (in part), pl. 5 fig. 1 and text-figs 40a and b (not fig. 40c); Totton, 1965a: 137 (in part), pl. 27 fig. 2 and text-figs 79A and B (not text-fig. 79C or text-figs 80A and B); Daniel, 1974: 91, figs 7e and f; Alvariño, 1981: 404 (in part), figs 174.23B and C (not fig. 174.23A, = *Nectopyramis natans*; not fig. 174.23D, = *N. richardi*); Kirkpatrick and Pugh, 1984: 68 (in part), fig. 24; Alvariño et al., 1990: 17 (in part), figs 24B and C (not figs 25A and D).

Diagnosis

Definitive nectophore pyramidal, triangular facets delimited by weak ridges; lateral surface diverticula from pedicular canal; somatocyst with median ascending branch arising from ascending surface diverticulum and two lateral ascending branches arising from lateral surface diverticula. Larval nectophore with nonfunctional nectosac and typically only two radial canals. Bract pyramidal with six bracteal canals, including lateral bracteal canal.

Material examined

Two definitive nectophores from Canadian Pacific stations LC10 (500 m) and LC11 (500 m) (Fig. 35C) BCPM 996-228-1; 3 larval nectophores from stations LB12 (300 m), LB14 (0–300 m), and A4 (500–0 m) (Fig. 36A) BCPM 996-229-1; 12 eudoxids from stations LB13 (0–500, 500–0 m), LB17 (500 m) (Fig. 36B) BCPM 996-228-2, LB17 (0–500, 700 m), A4 (0–700, 700 m), LC10 (500, 575, 700 m), and LC11 (500, 700 m); 2 bracts collected near thermal vent from tow 1 (1900–0 m) (Fig. 11, Table 1). Specimens of *Nectopyramis* species from the NHM collections: Reg. Nos 1930.5.20.8, *N. thetis* holotype, 1 definitive nectophore (47°03'N, 7°55'W);

1982.11.30.326, *N. thetis*, 1 eudoxid (40°17'N, 12°45'W); 1957.9.14.182, *N. natans*, 1 definitive nectophore (33°50'–34°13'S, 16°04'–15°49'E); 1957.9.14.184, *N. natans*, 1 eudoxid (02°49.5'S, 09°26'W).

Description of material

Definitive nectophores up to 16 mm along upper-lower axis and 10 mm from lateral angle to proximal edge; pyramidal, comprising four triangles, with slit-like hydrocial opening along proximal edge; four facets: upper facet, distal facet (with ostial opening), and left and right lateral facets (Figs 35A and B); ridges discernible between upper and lateral facets, but edges rounded between upper and distal facets and between distal and lateral facets in present nectophores; mesogloea turgid; hydroecium elongate, extending almost whole length of upper-lower nectophore axis, swollen in midregion, and containing central organ and several gastrozooids attached to contracted siphosomal stem (obscured in Fig. 35C); pedicular canal with very short external portion and elongate disjunct portion Fig. 35C, pd); upper end of latter giving rise to median ascending surface diverticulum (with some short side branches) and left and right lateral ascending surface diverticula; left diverticulum extending farther than right in both nectophores, and with small side branches at lower end; descending surface diverticulum arising from lower end of disjunct pedicular canal, turning to right near tip, and with short side branches (too small to be included in Fig. 35C), remaining close to hydroecium throughout; somatocyst comprising median ascending branch from upper end of ascending surface diverticulum and left and right ascending branches from left and right surface diverticula, respectively; median ascending branch with short side branches, lateral ascending branches without side branches; nectosac small and shallow, with ostium opening onto distal facet, and upper, lateral, and lower radial canals arising separately from disjunct pedicular canal (Fig. 35C).

Larval nectophores up to 4 mm high, approximately ovoid, with slightly hollowed-out distal surface adjacent to nectosac and elongate rounded proximal surface marked by hydrocial opening (Fig. 36A, ho); ridges with conspicuous cusps, each with 2–5 points; upper ridge without cusps in some regions, paired upper lateral ridges with many cusps, and these ridges together forming characteristic "figure of eight" in upper view, half of which is visible in

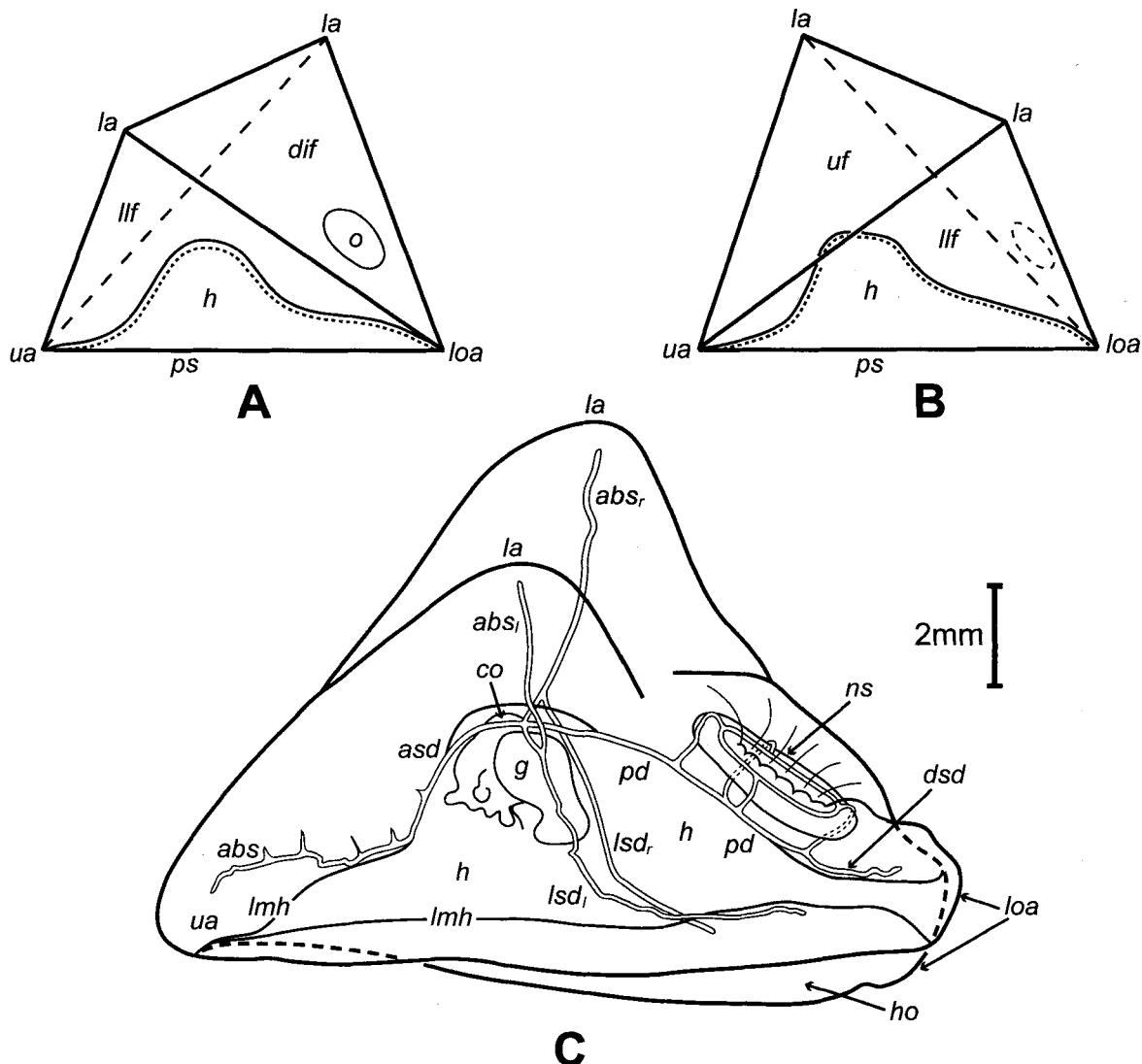


Fig. 35. *Nectopyramis thetis*: A and B: diagrammatic representations of definitive nectophore from left side, showing facets (A, laterodistal view; B, upper-lateral view); C: definitive nectophore, left lateral view (*abs*, ascending branch of somatocyst; *asd*, ascending surface diverticulum; *co*, central organ; *dif*, distal facet; *dsd*, descending surface diverticulum; *g*, gastrozooid(s); *h*, hydroecium; *ho*, hydroecial opening; *la*, lateral angle; *llf*, left lateral facet; *lmh*, limit of hydroecium; *loa*, lower angle; *lsd*, lateral surface diverticulum; *ns*, nectosac; *o*, ostium; *pd*, disjunct pedicular canal; *ps*, proximal surface; *ua*, upper angle; *uf*, upper facet).

Figure 36A; lateral ridge arising from each upper lateral, curving towards proximal surface (with hydroecial opening), then towards upper surface, and terminating just short of upper ridge (Fig. 36A); lower lateral ridge arising from each lateral in two nectophores (Fig. 36A, *lwr*) and from just below in a third, passing downwards, then bending distally and terminating below nectosac (Fig. 36A); paired perihydroecial ridges enclosing proximal hydroecial opening, lying close together centrally, and flaring outwards more towards upper end than lower end in present specimens (Fig. 36A, *phr*); mesogloea turgid;

hydroecium deep, with slit-like opening, extending to almost 1/2 circumference of nectophore (Fig. 36A, *h*), containing gastrozooid and small central organ; pedicular canal with thickened disjunct portion and ascending and descending surface diverticula, curving around wall of hydroecium as shown in Figure 36A; nectosac small, spherical, with two short radial canals arising from disjunct pedicular canal (Fig. 36A).

Bracts up to 12 mm tall between upper and lower proximal angles, 13 mm between lower proximal

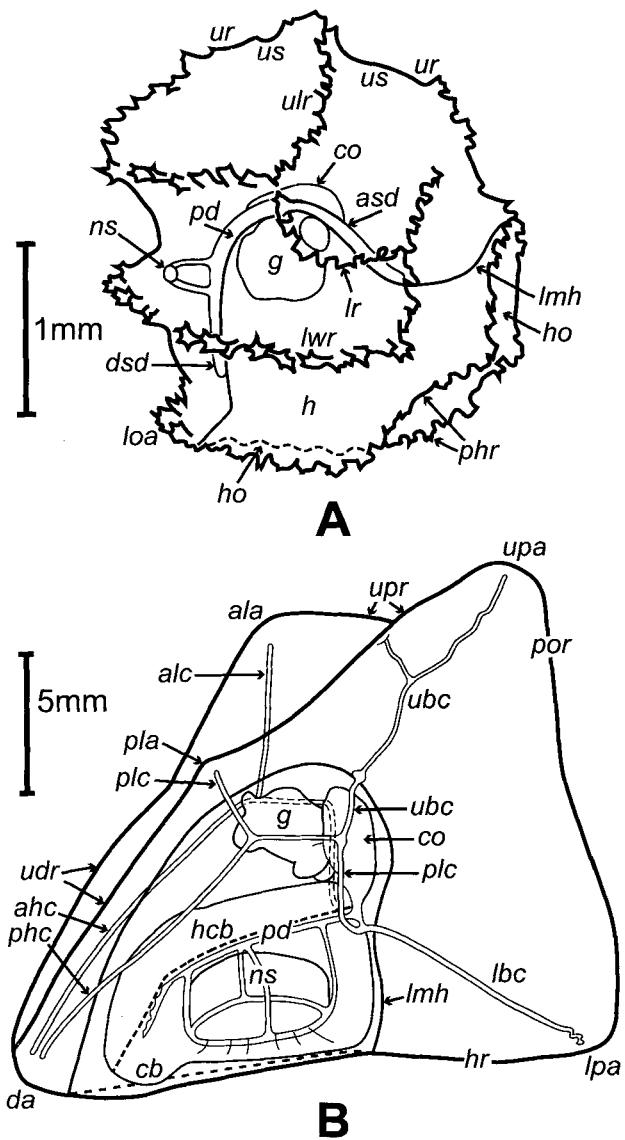


Fig. 36. *Nectopyramis thetis*: A: larval nectophore, lateral view; B: eudoxid bract with cormidial bell, lower/posterior view (*ahc*, anterior hydroecial canal (bract); *ala*, anterior lateral angle; *alc*, anterior longitudinal canal (bract); *asd*, ascending surface diverticulum; *cb*, cormidial bell; *co*, central organ; *da*, distal angle; *dsd*, descending surface diverticulum; *g*, gastrozooid(s); *h*, hydroecium; *hcb*, hydroecium of cormidial bell; *ho*, hydroecial opening; *hr*, hydroecial ridge; *lbc*, lateral bracteal canal; *lmh*, limit of hydroecium; *loa*, lower angle; *lpa*, lower proximal angle; *lr*, lateral ridge; *lwr*, lower lateral ridge; *ns*, nectosac; *pd*, disjunct pedicular canal; *phc*, posterior hydroecial canal (bract); *phr*, perihydroecial ridge; *pla*, posterior lateral angle; *plc*, posterior longitudinal canal (bract); *por*, proximal ridge; *ubc*, upper bracteal canal; *ldr*, upper distal ridge; *ulr*, upper lateral ridge; *upa*, upper proximal angle; *upr*, upper proximal ridge; *ur*, upper ridge; *us*, upper surface).

and distal angles (Fig. 36B); four-sided inverted pyramid with quadrangular "base" forming upper facet, four triangles forming two proximolateral and two distolateral facets (not labelled in Fig. 36B; see notes below); ridges between facets prominent, except ridges dividing two lateral facets on each side; latter not clearly demarcated in present material; upper facet extending laterally into two lateral angles with left typically smaller than right; two prominent upper proximal ridges, each passing from upper proximal angle to lateral angle; two prominent upper distal ridges, each passing from lateral angle to distal angle (Fig. 36B); proximal ridge passing from upper proximal angle to lower proximal angle; mesogloea turgid in most specimens, flaccid in some; hydroecium deep, with somewhat slit-like opening, typically containing single gastrozooid and cormidial bell (Fig. 36B); central organ prominent in some specimens, and with three lateral connections to longitudinal canals in best preserved bracts; six bracteal canals (Fig. 36B): (i) anterior longitudinal canal arising from junction of central organ with lateral bracteal canal (gastrozooid also originating here, but obscured in Fig. 36B), passing upwards around anterior (left) side of central organ (indicated by fine broken lines in Fig. 36B), turning sharply towards distal end of bract, and then turning sharply again after short distance to continue as anterior longitudinal canal into anterior lateral angle (Fig. 36B, *alc*); (ii) posterior longitudinal canal also originating from junction of central organ with lateral canal and passing up posterior (right) side of central organ, giving off upper bracteal canal (*ubc*), and then turning sharply towards distal end of bract and after short distance turning sharply again and continuing into posterior lateral angle (Fig. 36B, *plc*); (iii) anterior hydroecial canal extending from origin on second sharp bend in anterior longitudinal canal towards distal end of bract, lying close to hydroecium throughout (Fig. 36B, *ahc*); (iv) posterior hydroecial canal extending from origin on second sharp bend of posterior longitudinal canal towards distal end of bract, lying close to hydroecium throughout (Fig. 36B, *phc*); hydroecial canals typically with many small branches to hydroecial wall (not illustrated) and with fused tips in 50% of bracts; (v) upper bracteal canal passing from junction with posterior longitudinal canal upwards to hydroecial wall and then penetrating mesogloea to pass into upper proximal angle, typically with short branch arising halfway along its course and passing to upper facet (Fig. 36B, *ubc*); (vi) lateral bracteal canal from origin of longitudinal canals and central organ (marking stem-attachment point) to lower

proximal angle of bract (Fig. 36B, *lbc*); cormidial bell (special nectophore; Fig. 36B, *cb*) up to 8 mm long, still attached in most bracts, connecting to base of central organ via disjunct pedicular canal; latter passing along hydroecial wall of bell, giving off upper, two lateral, and lower radial canals to cormidial-bell nectosac, then continuing beyond it as short descending surface diverticulum (Fig. 36B); lateral radial canals of bell originating from disjunct pedicular canal either together or separately (not illustrated). Two small gonophores noted in one specimen, both female.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: off Baja California to mid-California (Alvariño 1980c, 1991); off San Diego (Alvariño 1967b). Other regions: few records from elsewhere in the Pacific (Pugh 1992a); this species is better known from other oceans, particularly the North Atlantic (Pugh 1992a, table 2).

Vertical. Specimens were collected from 300, 500, and 700 m depth in the present study. In the Atlantic, *Nectopyramis thetis* was most frequently reported from 300–700 m (within a depth range from near the surface to 4000 m), being most abundant in samples from between latitudes 30° and 50°N and inhabiting shallower depths at higher latitudes (Pugh 1992a).

Notes

The concept of the species *Nectopyramis spinosa* originally described by Sears (1952) was finally dispelled by Pugh (1992a), who examined 391 nectophores with nonfunctional nectosacs and showed that a number contained immature definitive nectophores of *N. thetis* and must therefore be larval nectophores of the latter species. A further 45 of these nectophores, however, had functional nectosacs, of which 8 contained immature nectophores of *N. natans*, indicating that they were larval nectophores of *N. natans*. Larval nectophores of the latter species also have a different ridge pattern, but none were collected in Canadian Pacific waters. The eudoxid that Totton (1954) ascribed to *N. spinosa* was shown by Pugh (1992a) to belong to *Nectadamas richardi*; this species occurs off Vancouver Island and is described below.

The larger of the two definitive nectophores of *Nectopyramis thetis* collected in Canadian Pacific waters is longer (16 mm) than the largest recorded

by Pugh (1992a) (12 mm), but other features of these two nectophores, and the bracts collected, fall within the range noted by Pugh. However, the central organ of the bract is smaller than that described by Pugh (1992a) in all present specimens except one. Patches of ectodermal cells described by Pugh (1992a) on the hydroecial walls of the bract and cormidial bell (as *special nectophore*), and thought to be responsible for bioluminescence, are not discernible in any of the Canadian Pacific specimens.

Nectophores of *Nectopyramis thetis*, as well shown by Pugh (1992a, fig. 10), can be distinguished from those of *N. natans* by their pyramidal shape. Definitive nectophores of *N. natans* are elongate and bow-shaped, with a relatively longer hydroecial opening and ascending surface diverticulum / branch of the somatocyst (together labelled the *somatocyst* by Pugh 1992a). In *N. natans* there are no upper and lower facets as described above for *N. thetis*, and the ridges are weakly defined (Pugh 1992a). Additionally, *N. natans* lacks the left and right ascending branches of the somatocyst and left and right surface diverticula as described above for *N. thetis*. The larval nectophore of *N. natans* has a functional nectosac with two radial canals (Pugh 1992a). The bract is arrow-shaped like the definitive nectophore, with only an upper canal ("dorsal" of Pugh 1992a) and two lateral/longitudinal canals.

Similarities in somatocyst structure between the definitive nectophores of *Nectopyramis thetis* and those of the prayine *Praya dubia* suggest that *N. thetis* may be more closely related to *P. dubia* than is *Nectadamas diomedae* (described below). In *Nectopyramis thetis* the somatocyst comprises an ascending median branch and two ascending lateral branches, and similar branches are present in *P. dubia*. In the latter species, however, all three branches arise together from the upper end of the ascending surface diverticulum, whereas in *N. thetis* only the median ascending branch arises from this point, with the lateral ascending branches arising separately from the two lateral surface diverticula. Also, the somatocyst branches of *N. thetis* do not subdivide extensively as they do in *P. dubia*.

The angles and facets displayed by bracts of *Nectopyramis thetis* and mentioned in the species description above are well shown in diagrammatic form by Pugh (1992a, fig. 6d). Thus, Figures 35A and B, which show the facets and angles of a typical definitive nectophore of this species, complement the figure given by Pugh for the bract.

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

Cormidial bells have so far been identified in the cormidia of only five prayid species: two *Nectopyramis* species, two *Lilyopsis* species (C. Carré 1969; Haddock et al. 2005a), and *Stephanophyses superba* (Chun 1891). These bells seem slightly larger in relation to the bract in the three prayine species than in the two nectopyramidines, but in all species they must provide locomotion or buoyancy for the cormidium, whether “free-swimming” or not.

Diagnosis

Definitive nectophore large and rhomboidal; pedicular canal with descending surface diverticulum; somatocyst of three median ascending branches; lower radial canal of nectosac extending into lower nectophore angle. Bract with distinctive lateral and hydrocial lobes on distal surface and bracteal canals dividing and subdividing.

Material examined

Two definitive nectophores from Canadian Pacific stations LB17 (0–500 m) and LC10 (0–575 m) (Fig. 37) BCPM 996-230-1; 47 eudoxids from stations LB12 (300, 0–450 m), LB13 (300, 0–500, 500–0, 700–0 m), LB14 (0–500 m), LB17 (0–300, 0–500, 500, 0–700 m), LC9 (300–0, 0–500, 500, 500–0 m), LC10 (300–0, 0–500, 500–0, 575–0, 700–0 m), LC11 (0–500, 500, 500–0 m), A4 (300 m) (Fig. 38) BCPM 996-231-1, A4 (0–500 m) BCPM 996-232-1, and A4 (300–0, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m); 2 eudoxids collected near thermal vent from tows 1 (1750–0 m) and 2 (0–2200 m) (Fig. 11, Table 1). Specimens of *Nectadamas diomedae* from the NHM collections: Reg. Nos 1985.12.918, 1 eudoxid (45°54'N, 09°39'W); 1957.8.13.129, 1 eudoxid (43°03'S, 17°03'E).

Description of material

Definitive nectophores measuring up to 31 mm from upper angle to lower angle, 21 mm from distal angle to proximal surface; rhomboidal; left lateral surface with distinctive ridge pattern and left lateral ridge dividing complexly (Fig. 37A); right lateral surface with longer lateral ridge and fewer branches (Fig. 37B); circumferential ridge discernible, passing onto right surface and dividing to delimit narrow proximal facet with slit-like hydrocial opening (Fig. 37B); ostial opening also displaced onto right surface, opening distolaterally (Fig. 37B); mesogloea turgid; hydroecium asymmetric, deep, with narrow opening, and containing several large gastrozooids attached to contracted siphosomal stem (Fig. 37C, stem obscured); pedicular canal comprising very short external portion, short disjunct portion, and elongate internal portion; ascending surface diverticulum extending from upper end of disjunct pedicular canal (at insertion point of external pedicular canal) and giving off third and second median ascending branches of somatocyst (Fig. 37C, abs_3 and abs_2); ascending surface diverticulum then dividing into left ascending surface diverticulum and first median

Genus *Nectadamas* Pugh, 1992a

Diagnosis

Nectopyramidinae with definitive nectophore laterally flattened, hydroecium discrete and pouch-shaped, with short opening on proximal surface; pedicular canal with very short external portion, short disjunct portion, and internal portion from which all radial canals of nectosac originate together; median ascending surface diverticulum always present, descending diverticulum present or absent. Larval nectophore, where known, with smooth ridges and pedicular canal similar to that of definitive nectophore. Bract triangular, laterally flattened, and without cormidial bell.

Type species: *Nectadamas diomedae* (Bigelow, 1911b).

Nectadamas diomedae (Bigelow, 1911b)

(Figs 37, 38)

Nectopyramis diomedae Bigelow, 1911b: 191, pl. 1 figs 1–6; Bigelow, 1931: 528; Totton, 1954: 83, pl. 5 figs 2, 3 and text-fig. 39; Totton, 1965a: 131, pl. 23 fig. 5 and text-figs 74B and C, 75; Leung, 1970: 20, fig. 3; Phillips, 1972: 174, fig. 42; Alvarino, 1981: 403, figs 174.21A and B.

Nectopyramis diomedea (lapsus calami) Moser, 1925: 116; Fraser, 1961: 37; Stepanjants, 1963: 1886, fig. 1; Stepanjants, 1967: 142, fig. 89; Stepanjants, 1989: 418.

Nectopyramis sp. nov. Totton, 1936: 232.

Nectadamas diomedae: Pugh, 1992a: 310, figs 21–27.

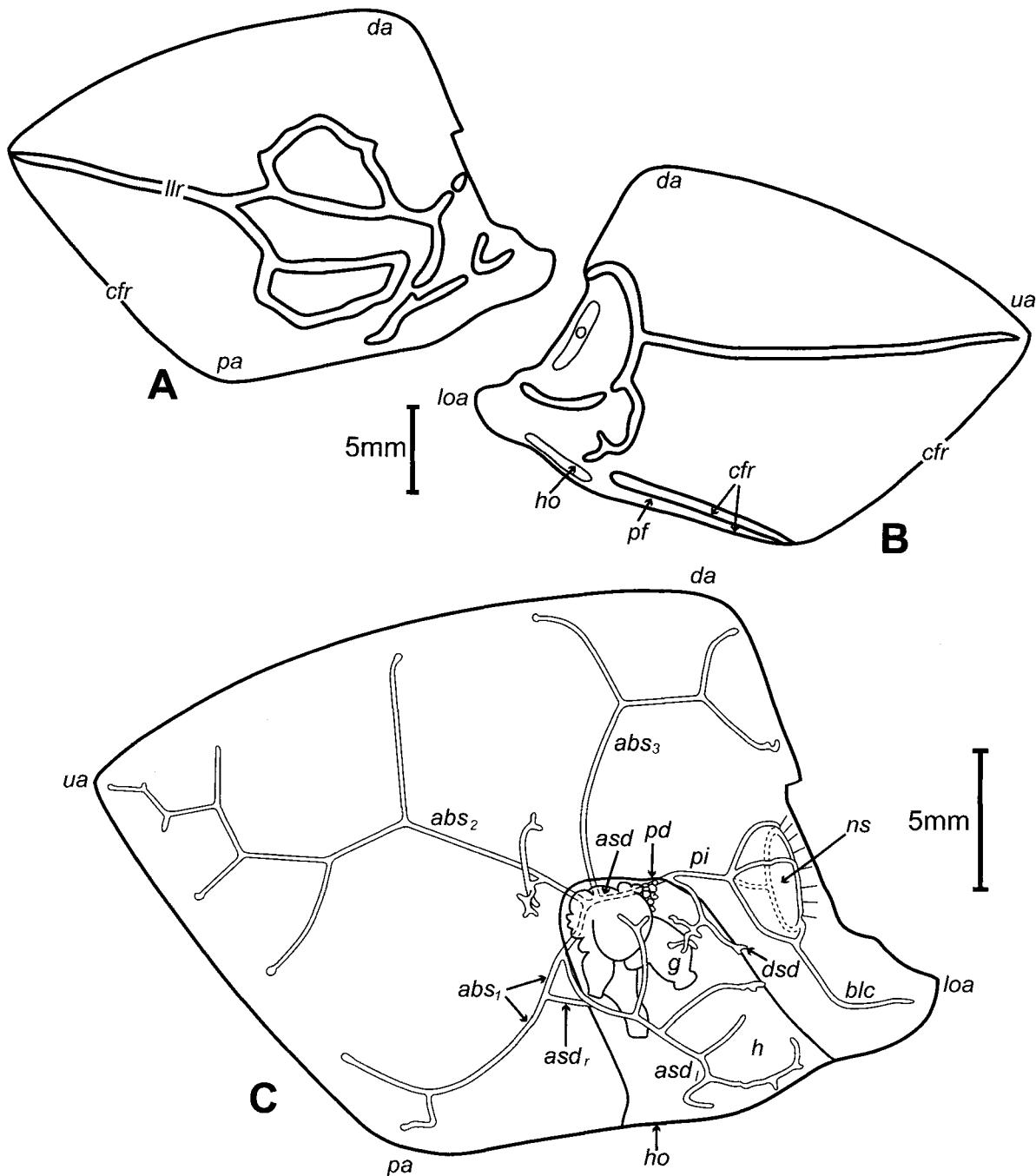


Fig. 37. *Nectadamas diomedaeae*: A and B: definitive ectophore, left and right lateral views showing surface ridges; C: definitive ectophore, left lateral view (*abs*, ascending branch of somatocyst; *asd*, ascending surface diverticulum; *blc*, branch of lower radial canal; *cfr*, circumferential ridge; *da*, distal angle; *dsd*, descending surface diverticulum; *g*, gastrozooid(s); *h*, hydroecium; *ho*, hydroecial opening; *loa*, lower angle; *llr*, left lateral ridge; *ns*, nectosac; *o*, ostium; *pa*, proximal angle; *pd*, disjunct pedicular canal; *pf*, proximal facet; *pi*, internal pedicular canal; *ua*, upper angle).

ascending somatocyst branch (Fig. 37C, *asd*, and *abs*); first ascending somatocyst branch penetrating mesogloea, almost immediately giving off right ascending surface diverticulum (Fig. 37C, *asd*) and then continuing towards proximal angle;

left ascending surface diverticulum continuing along upper hydroecial wall, onto left hydroecial wall, and branching as shown in Figure 37C; right ascending surface diverticulum passing to right hydroecial wall and branching several times

(not illustrated); descending surface diverticulum originating from disjunct pedicular canal and passing along distal wall of hydroecium onto left side (Fig. 37C, *dsd*), with one or more branches; somatocyst comprising three median ascending branches, all sub-branching as shown in Figure 37C: *abs*₃ to distal angle, *abs*₂ to upper angle, and *abs*₁ to proximal angle; last one giving rise to right ascending surface diverticulum, as mentioned above; nectosac small, laterally flattened, reaching 1/10 nectophore length (along upper-lower axis), with radial canals straight, and with branch of lower canal into lower process, either undivided (Fig. 37C) or with two short diverticula (not illustrated).

Bracts large, up to 36 mm tall, 22 mm in maximum width, flat laterally, resembling isosceles triangle with slightly convex longer sides, and hydroecial and lateral bracteal lobes forming “base”; bracteal lobes typically similar in size (Fig. 38, *lal* and *hl*), atypically with one lobe larger than other (not illustrated); ridges comprising circumferential ridge and three longitudinal ridges on left lateral surface (= upper/anterior view, Fig. 38A); ridges not discernible on right lateral surface; hydroecial opening slit-like (Fig. 38A); central organ absent; bracteal canals with degree of branching varied and unrelated to bract size, comprising two merged longitudinal/hydroecial canals originating at junction of gastrozooid and lateral canal and passing, as anterior and posterior hydroecial canals, into hydroecial lobe (Fig. 38B, *hl*), each typically branching once (Fig. 38B, *ahc* (anterior hydroecial canal)) or several times (not illustrated); upper canal extending upwards from origin with longitudinal/hydroecial canals into upper angle of bract and branching as shown in Figure 38B, atypically with either more or fewer branches (not illustrated); lateral canal passing from origin from longitudinals, along hydroecial wall towards lateral lobe of bract (Fig. 38B, *lal*), and penetrating mesogloea, typically branching once, atypically twice, and terminating in lateral lobe.

Gonophores present in hydroecium of most bracts, asymmetric, with hydroecium elongate, (Fig. 38B), ripe manubrium atypically present.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above); 53°05'N, 138°31'W, edge of shelf, B. C. waters (Bigelow 1913). Northeast Pacific: off San Diego (Alvariño 1967b); off Baja California to California (Alvariño 1991); off Point Conception

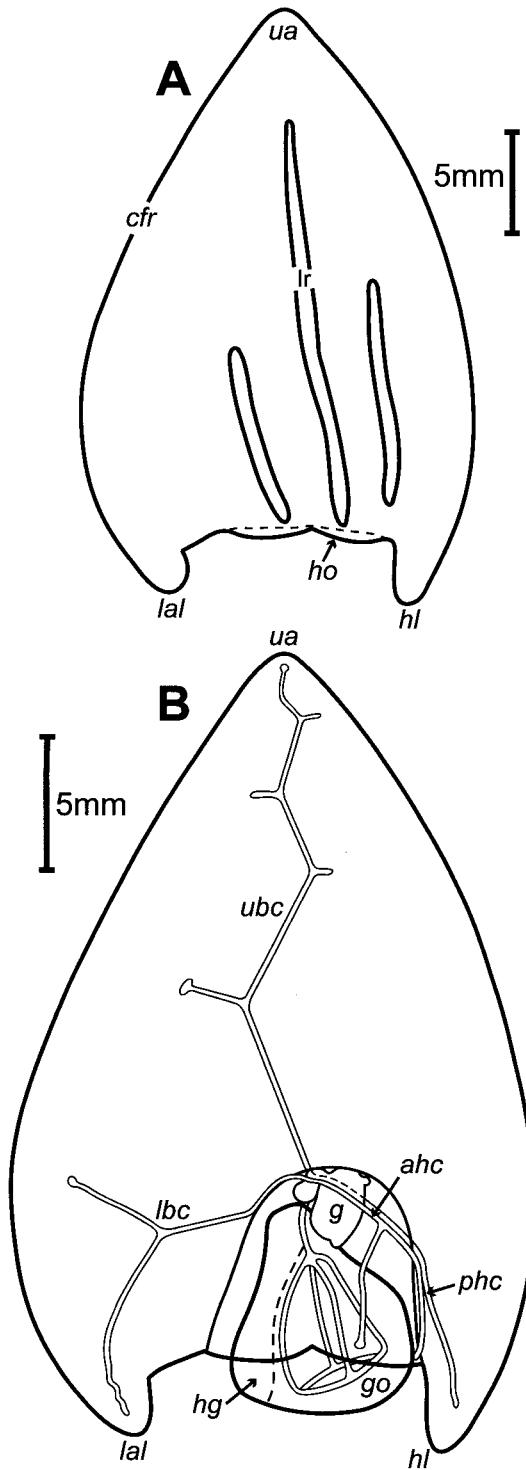


Fig. 38. *Nectadamas diomedae*: A: eudoxid bract, upper/anterior view of surface ridges; B: eudoxid bract with gonophore, upper/anterior view (*ahc*, anterior hydroecial canal (bract); *cfr*, circumferential ridge; *g*, gastrozooid(s); *go*, gonophore; *hg*, hydroecium of gonophore; *hl*, hydroecial lobe (bract); *ho*, hydroecial opening; *lal*, lateral lobe (bract); *lbc*, lateral bracteal canal; *lr*, lateral ridge; *phc*, posterior hydroecial canal (bract); *ua*, upper angle; *ubc*, upper bracteal canal).

(Haddock and Case 1999). Other regions: few records from remainder of Pacific (Pugh 1992a), except from high southern latitudes (Alvariño et al. 1990). Cosmopolitan species with widespread distribution in other oceans (Pugh 1992a, table 7).

Vertical. The records given above, together with unpublished observations, indicate that *Nectadamas diomedaeae* occurs throughout the depth range sampled. It was found from 25 to 475 m off California (Alvariño 1991), and similar depth ranges have been noted in the North Atlantic: 650–750 m (Pugh 1974b), 500–650 m (Casanova 1980), 450 and 600 m (Pugh 1984), and 300–800 m (Pugh 1992a).

Notes

The holotypes of this species are housed in the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts (Catalog No. 1595).

Pugh (1992a) gave detailed descriptions of nectophores and bracts of *Nectadamas diomedaeae* from 45 definitive nectophores, 3 larval nectophores, and approximately 300 eudoxids. In the present work only 2 definitive nectophores were found, together with 47 eudoxids (but no larval nectophores), and the canal systems of the definitive nectophore and bract are interpreted differently, as noted above. However, the branching patterns of the ascending branches of the somatocyst (Pugh 1992a, as *pallial canal branches 1–3*) and those of the right and left ascending surface diverticula (Pugh 1992a, as *left and right hydroecial canals*) in the two Canadian Pacific definitive nectophores fall within the range described by Pugh (1992a) for specimens from the central and North Atlantic.

In the present work the ascending branches of the somatocyst in the definitive nectophore of *Nectadamas diomedaeae* are numbered from the end of the ascending surface diverticulum to the origin of the latter from the disjunct pedicular canal in order to correlate with those of *Praya dubia*, as described above. However, whether these branches are homologous is uncertain, and indeed, Pugh (1992a) considered it unlikely. The “left and right hydroecial canals” of Pugh (in the definitive nectophore) are herein interpreted as the left and right ascending surface diverticula from the pedicular canal, following the terminology explained in Section 2.3.2, even though in *N. diomedaeae* the right ascending surface diverticulum originates from the first ascending branch of the somatocyst (*abs.*) rather

than from the common ascending surface canal, as in *P. dubia* (see Fig. 28A).

Pugh (1992a) shows that once the left ascending surface diverticulum passes onto the left wall of the hydroecium it subdivides more than the right ascending surface diverticulum. This can be seen by comparing Figure 37C with figures showing these diverticula by Pugh (1992a, figs 21–24, labelled only as *right* and *left hydroecial canals* in fig. 22). Pugh (1992a) also reports that in most definitive nectophores of *Nectadamas diomedaeae* there is only a single descending surface diverticulum (as *descending branch of the pallial canal*), and that this diverticulum passes to the left wall of the hydroecium as in the two Canadian Pacific definitive nectophores described above. However, in one of Pugh’s specimens a second diverticulum that passed onto the right wall of the hydroecium was found.

Nectadamas richardi Pugh, 1992a

(Fig. 39)

Nectopyramis spinosa eudoxid Totton, 1965a: 137 (in part), text-figs 74D, 80B; Daniel, 1985: fig. 99b; Pugh, 1974b: 41 (in part); Alvariño, 1981: 404 (in part), fig. 174.23D; Alvariño et al., 1990: fig. 24D (not *N. spinosa* Sears, 1952).

Nectopyramis sp. nov. Pugh, 1990: 31.

Nectadamas richardi Pugh, 1992a: 304, figs 16–19.

Diagnosis

Definitive nectophore small and approximately rounded; pedicular canal without descending surface diverticulum; somatocyst of two median ascending branches; lower radial canal not extending into lower nectophore angle. Bract with truncate distal surface, lacking distinct bracteal lobes, and bracteal canals typically not subdividing.

Material examined

One definitive nectophore with (originally) 3 attached eudoxids from Canadian Pacific station LB13 (0–500 m) (Figs 39A and B) BCPM 996-233-1; 6 free-swimming eudoxids from stations LB17 (0–500, 0–700, m); LB17 (0–300 m) (Fig. 39C) BCPM 996-234-1, and A4 (300, 0–500, 500–0, 0–700 m)

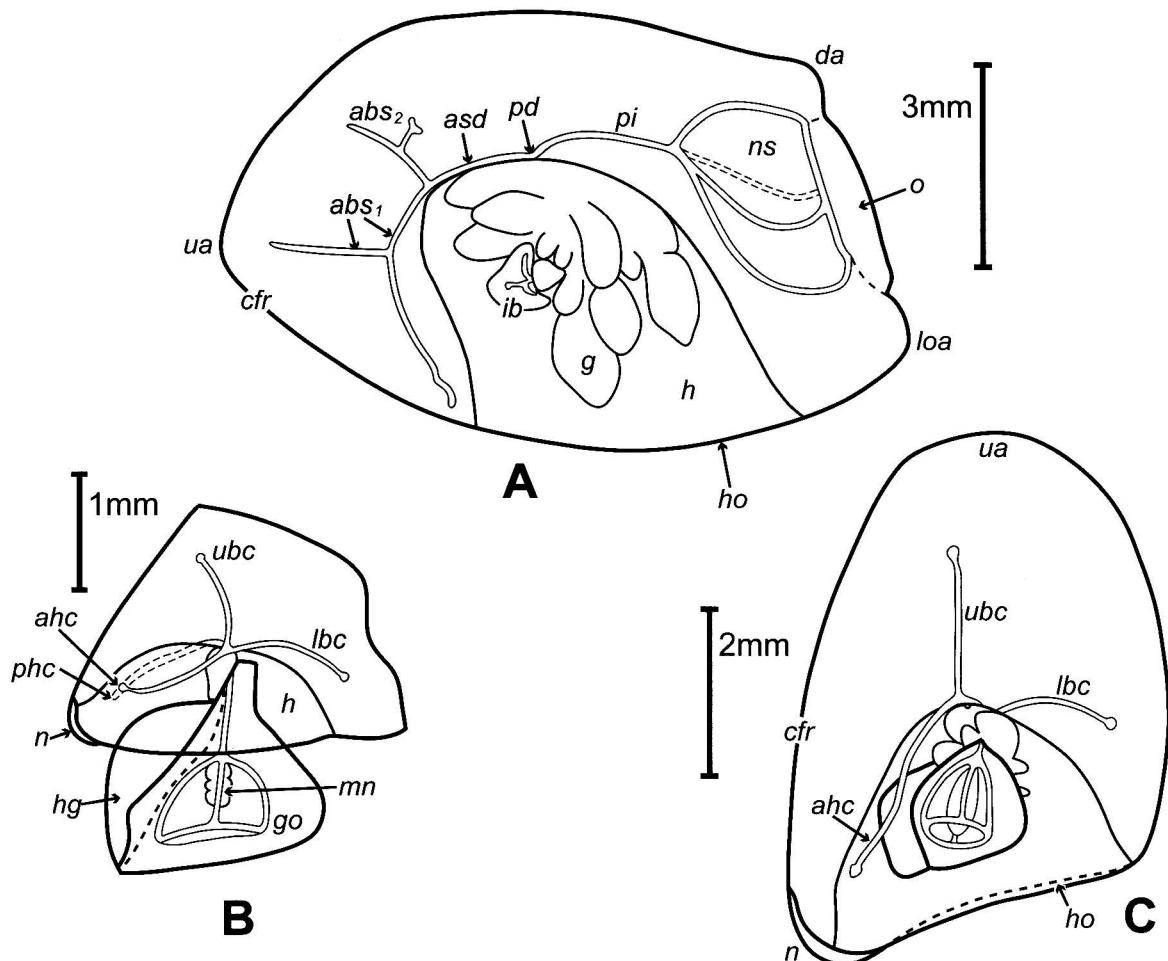


Fig. 39. *Nectadamas richardi*: A: definitive nectophore, left lateral view; B: young eudoxid bract, upper/anterior view; C: older eudoxid bract, upper/anterior view (*abs*, ascending branch of somatocyst; *asd*, ascending surface diverticulum; *ahc*, anterior hydroecial canal (bract); *cfr*, circumferential ridge; *da*, distal angle; *g*, gastrozooid(s); *go*, gonophore; *h*, hydroecium; *hg*, hydroecium of gonophore; *ho*, hydroecial opening; *ib*, immature bract; *lbc*, lateral bracteal canal; *mn*, manubrium (gonophore); *n*, notch; *ns*, nectosac; *o*, ostium; *pd*, disjunct pedicular canal; *phc*, posterior hydroecial canal (bract); *pi*, internal pedicular canal; *ua*, upper angle; *ubc*, upper bracteal canal).

(Fig. 11, Table 1). Specimen of *Nectadamas richardi* from the NHM collections: Reg. No. 1991.11.8.1, holotype, 1 definitive nectophore and 2 eudoxids (45°38'N, 14°07'W).

Description of material

Definitive nectophore measuring 10 mm from rounded upper angle to distal surface, ovate, with truncate distal surface between distal angle and lower angle (Fig. 39A); circumferential ridge discernible, but no other ridges; mesogloea turgid; hydroecium asymmetric, deep, with narrow opening large relative to size of nectophore, and containing several large gastrozooids and immature bract (Fig. 39A); pedicular canal with external portion not discernible (but concluded to be immediately

to left of very short disjunct pedicular canal; Fig. 39A, *pd*), probable short disjunct portion, and elongate internal portion; short ascending surface diverticulum from disjunct pedicular canal to point of origin of somatocyst; somatocyst comprising two ascending branches: *abs*₁ extending from ascending surface diverticulum into mesogloea and dividing once, as shown in Figure 39A, and *abs*₂ shorter and with small sub-branch; radial canals of nectosac originating together from internal pedicular canal; ostium broad, opening onto distal surface in slight depression (Fig. 39A).

Bracts up to 6.5 mm tall, flattened laterally, with upper angle rounded (Fig. 39C), but pointed in immature bract (Fig. 39B); without bracteal lobes flanking hydroecial opening; circumferential

ridge (Fig. 39C), but no other ridges, discerned; hydroecium deep, with broad opening extending distally as small notch (Figs 39B and C); central organ absent; four bracteal canals: unbranched upper canal extending to 3/4 bract height, unbranched lateral canal, and two short longitudinal canals (not labelled in Figs 39B and C) merged with two hydroecial canals; anterior and posterior hydroecial canals unbranched and all bracteal canals with swollen tips.

Gonophores up to 4.5 mm tall; asymmetric, with flaps enclosing gutter-like hydroecium; four radial canals, taken to be straight, originating together from pedicular canal; ripe gonads present on manubrium (Figs 39B and C).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection). Northeast Pacific: off Baja California (Totton 1965a). Other regions: many specimens from the northeast Atlantic (Pugh 1992a).

Vertical. Specimens were found at 300 m and between 1 and 700 m. Since Pugh (1992a) found most at 600–1000 m in the North Atlantic, with populations deeper at high latitudes, it is not surprising that so few specimens were recorded in the present study area.

Notes

Nectadamas richardi was introduced by Pugh (1992a) and first described from a collection of 83 nectophores and 634 bracts taken in the North Atlantic. The eudoxid was originally referred by Totton (1965a) to *Nectopyramis spinosa* (see synonymy). The pedicular canal and somatocyst of *N. richardi* are herein described differently to Pugh (1992a), following the rationale given in the notes for *N. diomedaeae* above, and also in Section 2.3.2. The *pallial canal branches* 2 and 3 of Pugh (1992a) are here interpreted as sub-branches of the first ascending branch of the somatocyst in *N. richardi* because their junction lies within the mesogloea.

10.2.2. Family HIPPOPODIIDAE Kölliker, 1853

Diagnosis

Calycophorae with nectophores similar and numbering six or more in mature colony; nectophores spirally arranged on elongate “nectosome”, without

mouthplate, and either smooth or angular with ridges and cusps; simple thin somatocyst in all definitive nectophores; cormidia without bracts.

Notes

Colonies of this family are globular or cylindrical and nectophores are closely stacked, so the ostia of younger and more anterior nectophores are occluded by larger and more posterior nectophores, as shown in Figure 2E and well illustrated by Mackie (1965, fig. 3) and Chun (1897b, fig. 11). Nectosacs function only in the two posteriomost nectophores (Bigelow 1911b; Mackie 1973). Hippopodiids resemble prayids in having a large amount of mesogloea and a relatively small nectosac, and Totton (1954, 1965a) considered the two families closely related, as mentioned above (Section 10.2). The molecular phylogeny of Dunn et al. (2005b) shows them to be a monophyletic clade within the Codonophora, possibly related to a clade comprising a prayine and two nectopyramidine prayids.

Although the nectophores of hippopodiid colonies appear at first glance to arise from a common nectosomal stem, as in long-stemmed physonects (see Figs 2E, 1A), in hippopodiids each nectophore buds from the pedicel of its predecessor, so only the youngest nectophore is attached to the stem itself. Thus, the budding zones for nectophores and siphosomal cormidia remain close together in hippopodiids as in other calycophorans (see Section 3.2), and the youngest nectophores are budded off from the apex, or anterior end, of the colony. The “nectosome” spirals downwards (posteriorly) from this point, with nectophores becoming progressively older towards the “base”. The siphosome hangs down inside the chamber enclosed by the nectophores, as is well illustrated by Pugh (1983, fig. 44b), and is withdrawn into it for locomotion. Bracts are absent from hippopodiids, and in the *Vogtia* colony shown in Figure 2E the bractless cormidia are extended posteriorly below the “nectosome” for feeding. The first nectophore to develop, the larval one (see Section 3.1), is particularly large and buoyant to support the developing definitive nectophores.

The nectophore of a typical hippopodiid has a relatively short proximal-distal axis and a relatively elongate upper-lower axis (Figs 2F and G). The upper-lower axes of the youngest nectophores are aligned similarly to those of prayine prayids, with their upper surfaces forming the anterior end of the colony. As nectophores mature, they move down

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

and around the central chamber and rotate through 90°, and their upper surfaces come to face outwards, with the ostia of the two oldest nectophores directed posteriorly (Fig. 2E). This allows efficient propulsion of the colony in an anterior direction. Nectosacs of preserved hippopodiids appear shallow (Figs 2E and G), giving the impression that they can eject only a small amount of water per contraction, but this belies their movements in life. As Totton (1954, p. 99) comments for *Hippopodius hippocampus*, the “oral [distal] side of the nectosac . . . takes part in a scooping action (as it fills with water) reminiscent of a movement of the appendages of a cirripede”. He also explains that the upper wall of the nectosac gains freedom of movement because it is very thin, and this is apparent from the much-inrolled borders of the upper sides of the nectosacs in preserved nectophores from Canadian Pacific waters.

Definitive nectophores of hippopodiids are connected by a number of muscular lamellae that form the false “nectosome” mentioned above. In preserved material these lamellae arise alternately, one below another, from a common “stem”, and there is a canal in this stem that must be contiguous with the stem canal of the siphosome. An external pedicular canal for each nectophore arises from this canal and passes via the lamella to insert onto the proximal surface of the nectophore in the midline. It gives rise to an ascending surface diverticulum that extends towards the upper end of the nectophore, and a shorter disjunct pedicular canal that extends towards the lower end. The latter then penetrates the mesogloea as the internal pedicular canal. In hippopodiids there is no descending surface diverticulum (Fig. 5F), and as Totton (1965a) notes, this shows the close affinity of the family with the Prayidae, since larval nectophores of the latter family also lack a descending surface diverticulum (p. 139, as *downward prolongation of the pallial canal*). However, this applies only to the known larval nectophores of prayine prayids, since a descending diverticulum is present in the retained larval nectophores of all amphicaryonine species except *Maresearsia praeclara* (see Section 10.2.1.1), and also in one of the two genera of the prayid subfamily Nectopyramidinae, *Nectopyramis* (see Section 10.2.1.3). Additionally, Haddock et al. (2005a) show that a descending surface diverticulum (as *descending branch* of the somatocyst; table 3) is absent from definitive nectophores of six prayine genera, although it is developed in definitive nectophores of the two prayine genera from Canadian Pacific waters (see Section 10.2.1.2). In hippopodiids the nectophoral

muscular lamella is prominent and is connected along the entire length of the ascending diverticulum and disjunct pedicular canal; it can reach 3.5 mm in length in large nectophores.

A somatocyst arises from the upper end of the ascending surface diverticulum in hippopodiids, and this junction is clearly discernible in all preserved nectophores examined from Canadian Pacific waters, including detached ones. In the latter, the diverticulum leaves a gutter-shaped scar along the proximal midline that terminates abruptly at the base (or proximal end) of the somatocyst. The somatocyst then extends towards the upper end of the nectophore in the mesogloea, just below the hydroecial surface, becoming more “penetrating” towards its tip as the hydroecial wall rises to meet the proximal angle. Such a somatocyst occurs in *Vogtia pentacantha* and *V. spinosa*, but in *V. serrata*, *V. glabra*, and *Hippopodius hippocampus* it remains close to the hydroecial wall throughout. These species have a more extensive hydroecium and, also, all have nectophores with either few cusps or none at all, leading Totton (1954) to surmise that *H. hippocampus* and *V. glabra* may have lost their cusps (his *teeth*) secondarily, after evolving from the more spinous species.

The genus *Vogtia* was originally distinguished from *Hippopodius* by the structure of the juvenile tentillum (Kölliker 1853). The latter is coiled in *Vogtia* but not in *Hippopodius* (Totton 1965a). However, as Totton points out, this is a minor difference that may not be of generic importance. It arises because the cnidobands of *Hippopodius* are too short to form a coil before they take on their mature form. Whilst Schneider (1898) and Moser (1925) both referred *Vogtia* (Kölliker, 1853) to *Hippopodius* (Quoy and Gaimard, 1827), Totton (1965a) chose to retain both genera to maintain nomenclatural stability. Pugh (1999b) followed Totton, and the present author concurs with the latter two authors.

The species presently referred to the Hippopodiidae are *Hippopodius hippocampus* (Forskål, 1776) and five *Vogtia* species (see below), three of which have been identified from Canadian Pacific waters. *Hippopodius hippocampus* has been recorded in the northeast Pacific off California (Alvariño 1980c; Margulis and Vereshchaka 1984; Haddock and Case 1999) and the definitive nectophores clearly differ from those of the three Canadian Pacific *Vogtia* species in being horseshoe-shaped rather than angular.

Genus *Vogtia* Kölliker, 1853

Diagnosis

Hippopodiidae with cnidoband of juvenile tentillum long and coiled, straightening out at maturity; definitive nectophore either angular with ridges and facets, or rounded.

Type species: *Vogtia pentacantha* Kölliker, 1853.

Notes

The three *Vogtia* species from Canadian Pacific waters, *V. pentacantha*, *V. serrata*, and *V. spinosa*, all have angular nectophores, on each of which eight main surfaces can be identified: two large and approximately parallel proximal and distal surfaces (the former hollowed out into a shallow hydroecial cavity, the latter flattened and punctuated by a large ostium) and six approximately triangular facets. The latter occur in pairs and form the lateral surfaces of the nectophore. Most of them are difficult to discern in distal view because they tend to be aligned orthogonal to the distal surface, but are apparent in the lateral view of a *V. pentacantha* nectophore described below (Fig. 40B), where the lateral angle is foreshortened. These triangular facets approximately resemble isosceles triangles, and three make up each lateral nectophore surface. Two lie on their sides, with narrow bases and elongate apices and the base of the third, which has a short apex, forms part of the proximal surface of the nectophore. The apices of all three facets meet at the lateral angle on the distal edge of the nectophore. The upper and lateral borders of the hydroecial cavity (on the proximal side of the nectophore) are formed by the proximal edges of the two upper facets and the bases of the two proximolateral facets (Figs 40A, 41A, 43). The bases of the two upper facets together form the upper angle of the nectophore, here identified as comprising a distal and a proximal angle connected by a short upper ridge (Fig. 40B). The bases of the two lower facets form the “vertical” lower lateral borders of the nectophore, between its distal and proximal surfaces, except in *V. serrata*. There are also two small ostial facets at the lower end of the nectophore on the distal side. These are attached to the lower end of the nectosac, and are typically separated from the remainder of the distal surface by two short ridges (Fig. 40A).

Another angular species, *Vogtiakuruae*, was described by Alvariño (1967a) from off California, but is

interpreted as a synonym of *V. serrata*, as discussed below. The other two species referable to *Vogtia* are *V. glabra* Bigelow, 1918 and *V. microsticella* Zhang and Lin, 1990. Both have rounded nectophores but neither has yet been recorded from the northeast Pacific. The latter was only described from material collected in the East and South China seas.

Vogtia pentacantha Kölliker, 1853

(Fig. 40)

Vogtia pentacantha Kölliker, 1853: 31, pl. 8 figs 1–8; Keferstein and Ehlers, 1861: 23, pl. 3 figs 13–16 and pl. 5 figs 12–15; Spagnolini, 1870: 627; Chun, 1897a: 35, pl. 1 figs 11–14; Bigelow, 1911a: 351 (in part); Bigelow, 1913: 66 (in part); Bigelow, 1918: 406, pl. 4 fig. 1; Browne, 1926: 61; Totton, 1954: 100; Totton and Fraser, 1955d: 3, fig. 4; Rengarajan, 1973: 147, fig. 12b; Daniel, 1974: 99, figs 8c and d; Alvariño, 1981: fig. 174.28; Kirkpatrick and Pugh, 1984: 74, fig. 27; Daniel, 1985: 153, figs 40a and b; Pugh, 1999b: 487, fig. 3.57; Gamulin and Kršinic, 2000: 40 (in part), not fig. 14, indet.; Gao et al., 2002: 93 (in part), ?fig. 42; Bouillon et al., 2004: 226, fig. 137G; Thibault-Botha and Gibbons, 2005: 133, fig. 5 (not Moser, 1912a: 329, = *Vogtia serrata*; Bigelow 1913, pl. 5 figs 7–9 and pl. 6 fig. 6, = *Vogtia serrata*).

Hippopodius pentacanthus: Claus, 1863: 551, pl. 47 figs 23–26; Schneider, 1898: 84 (in part); ?Moser, 1917: 736, pl. 4 figs 4, 5; Moser, 1920: 183 (in part); Moser, 1924a: 43, pl. 2 figs 1–6; Moser, 1925: 416.

Hippopodius (Vogtia) pentacanthus: Moser, 1915b: 653.

Diagnosis

Definitive nectophore pentagonal, with upper and proximolateral facets bearing a few scattered cusps or none; without deep furrow and flap between lower and ostial facets.

Material examined

Fifteen definitive nectophores from Canadian Pacific stations LC9 (300–0 m) (Fig. 40B) BCPM 996-236-1, LC10 (500–0 m) (Fig. 40A) BCPM

996-235-1, LC11 (500 m), and A4 (300 m) (Fig. 11, Table 1). Specimens from the NHM collections: Reg. Nos 1982.11.30.320 *Hippopodius hippopus*, 2 detached definitive nectophores ($40^{\circ}17'N$, $12^{\circ}45'W$); 1957.10.28.72 *H. hippopus*, 6 definitive nectophores attached to stem ($35^{\circ}9.5'S$, $47^{\circ}00'W$); 1957.11.9.24 *Vogtia glabra*, 8 definitive nectophores ($05^{\circ}54'S$, $11^{\circ}19'E$); 1982.11.30.323 *V. glabra*, 1 definitive nectophore ($40^{\circ}17'N$, $12^{\circ}45'W$); 1985.12.9.30 *V. pentacantha*, 7 detached definitive nectophores and 7 definitive nectophores attached to stem ($41^{\circ}5'N$, $14^{\circ}38'W$).

Description of material

Four nectophores attached to single stem portion in one sample, all other nectophores detached; definitive nectophores pentagonal, 4–9 mm “tall” along upper-lower axis (from upper ridge / distal angle to lower midline, between ostial facets), 5–12 mm wide across broad right-left axis (between right and left lateral angles; Fig. 40A, *lla* and *rla*) and with much shorter proximal-distal axis (Fig. 40B, between *pa* and *da*); ridges typically cusped; nectophore with prominent upper angle comprising proximal and distal angles connected by upper ridge (Fig. 40B, *ur*), right and left

lateral angles, and two lower angles (Fig. 40A, *loa*); lateral surfaces comprising two upper facets (left and right), large, concave, with one to three cusps or none, with surfaces directed outwards upper-laterally from colony, and resembling two elongate isosceles triangles lying on their sides with bases forming short cusped upper ridge and apices contributing to lateral angles on distal nectophore surface (right upper facet shown in Fig. 40B, *ruf*); long sides of upper facets consisting of ridges with variable number of cusps, and proximal side curving distally towards lateral angle, with or without cusps at upper end (latter not illustrated); distal side typically cusped throughout; two proximolateral facets, with or without one to three cusps, resembling two isosceles triangles with apices at lateral angles, bases forming lateral walls of hydroecium on proximal surface, and two sides with cusped ridges separating them from upper and lower facets (right proximolateral facet shown in Fig. 40B, *rpf*); two lower facets, slightly concave, approximately triangular with apex at lateral angle, base smooth and free, and sides consisting of cusped ridges abutting proximolateral facet (foreshortened in Fig. 40B), and cusped/smooth ridge abutting distal nectophore surface, indented centrally

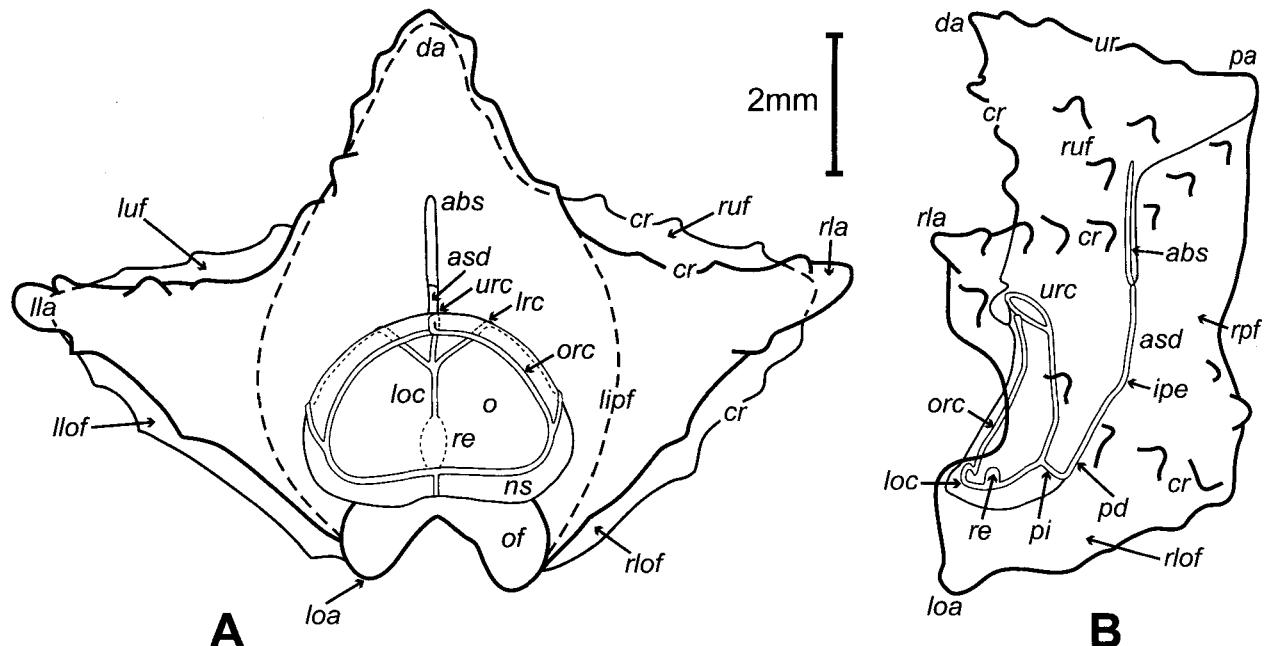


Fig. 40. *Vogtia pentacantha*: A: definitive nectophore, distal view; B: definitive nectophore, right lateral view (drawn from a different nectophore) (abs, ascending branch of somatocyst; asd, ascending surface diverticulum; cr, cusped ridge; da, distal angle; ipe, insertion point of external pedicular canal; lipf, limit of proximolateral facet; lla, left lateral angle; llof, left lower facet; loa, lower angle; loc, lower radial canal; lrc, lateral radial canal; luf, left upper facet; ns, nectosac; o, ostium; of, ostial facet; orc, ostial ring canal; pa, proximal angle; pd, disjunct pedicular canal; pi, internal pedicular canal; re, rete mirabile; rla, right lateral angle; rlof, right lower facet; rpf, right proximolateral facet; ruf, right upper facet; ur, upper ridge; urc, upper radial canal).

(Fig. 40B, *rlof*); two ostial facets, small, arising from distal corner of base of lower facet and lower edge of nectophore adjacent to nectosac (Fig. 40A, *of*), with short ridge separating them from distal surface of nectophore; mesogloea turgid; hydroecium on proximal surface (indicated by coarse broken line in Fig. 40A), thinnest at upper end and thickest over ostial facets; pedicular canal comprising elongate external portion through muscular lamella from “stem canal” to proximal nectophore surface, inserting onto nectophore at arrow labelled *ipe* in Figure 40B, short disjunct portion, and short internal portion to nectosac (Fig. 40B, *pi*); ascending surface diverticulum elongate, extending upwards from disjunct pedicular canal to base of somatocyst at 1/2 nectophore height (from lower border of ostium), and present as gutter in detached nectophores (Fig. 40); somatocyst thin, consisting of single ascending branch, and extending towards upper surface as shown in Figure 40; nectosac shallow (Fig. 40B) with distinctive flange-like velum around ostium (omitted from Fig. 40A for clarity); upper and lower radial canals originating together from internal pedicular canal and lateral canals originating from upper canal only, either together (Fig. 40A) or staggered, curving over nectosac, and inserting laterally onto ostial ring canal; lower radial canal shorter than upper, expanded as bilobed rete mirabile in most nectophores, with rete narrow in large nectophores (Fig. 40A) and broad in small nectophores (not illustrated).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: off San Francisco and San Diego (Alvariño 1991); Monterey Bay (Bigelow and Leslie 1930). Other regions: *Vogtia pentacantha* has been infrequently collected elsewhere in Pacific from such widely scattered locations as the Antarctic Ocean and off Chile (Alvariño et al. 1990; Palma and Rosales 1997), off Costa Rica (Gasca and Suárez 1992a), and in the South China Sea (Lin 1993). Range also includes all other oceans.

Vertical. In the present study *Vogtia pentacantha* was collected from 500 and 300 m and in the water column from between these depths and the surface. This range is similar to that recorded off

California (Alvariño 1991). In the North Atlantic, at latitude 11°N, it was found down to 750 m, with maximum abundance recorded in the top 200 m (Pugh 1991).

Notes

Nectophores of *Vogtia pentacantha* have prominent upper facets that are directed outwards from the colony, and a relatively narrow lower region facing the central chamber. These facets all have cusped ridges, but a few cusps may also occur on the upper facets. In most nectophores from the present collection, one to three cusps were identified near the upper angle, and cusps (as spines) were noted in a similar position by Totton (1965a). Other facets are smooth.

Vogtia serrata (Moser, 1925)

(Figs 41, 42)

Vogtia pentacantha laevigatus Günther, 1903: 429.

Vogtia pentacantha Bigelow, 1913: 66 (in part), pl. 5 figs 7–9 and pl. 6 fig. 6; Moser, 1912a: 329; Bigelow and Leslie, 1930: 560; Naumov, 1955: 62, pl. 10 fig. 1 (not Kölliker, 1853: 31, = *V. pentacantha*).

Vogtia serrata Moser, 1913a: 149; Bigelow, 1918: 405; Bigelow, 1931: 538, fig. 190; Bigelow and Sears, 1937: 19; Totton and Fraser, 1955d: 3, fig. 5; Totton, 1965a: 142, pl. 27 fig. 3 and text-fig. 81.5; Stepanjants, 1967: 136, figs 81–87; Alvariño, 1971: 27; Alvariño, 1981: 406, fig. 174.29; Zhang, 1984: 56, fig. 1; Kirkpatrick and Pugh, 1984: 74, fig. 28; Daniel, 1985: 151; Pugh, 1999b: 487, fig. 3.59; Gao et al., 2000: 91 (in part), not fig. 40, indet.; Bouillon et al., 2004: 226, fig. 137H.

Hippopodius serratus: Moser, 1915a: 212; Moser, 1915b: 653; Moser, 1920: 172; Moser, 1925: 420, pl. 27 figs 6–8 and pl. 28 figs 4–9; Hardy and Günther, 1935: 106.

Vogtia kuruae Alvariño, 1967a: 236, figs 1, 2; Alvariño, 1971: 27; Alvariño, 1981: 406, fig. 174.27; Alvariño and Ambros, 1986: 85; Gao et al., 2002: 94, fig. 43.

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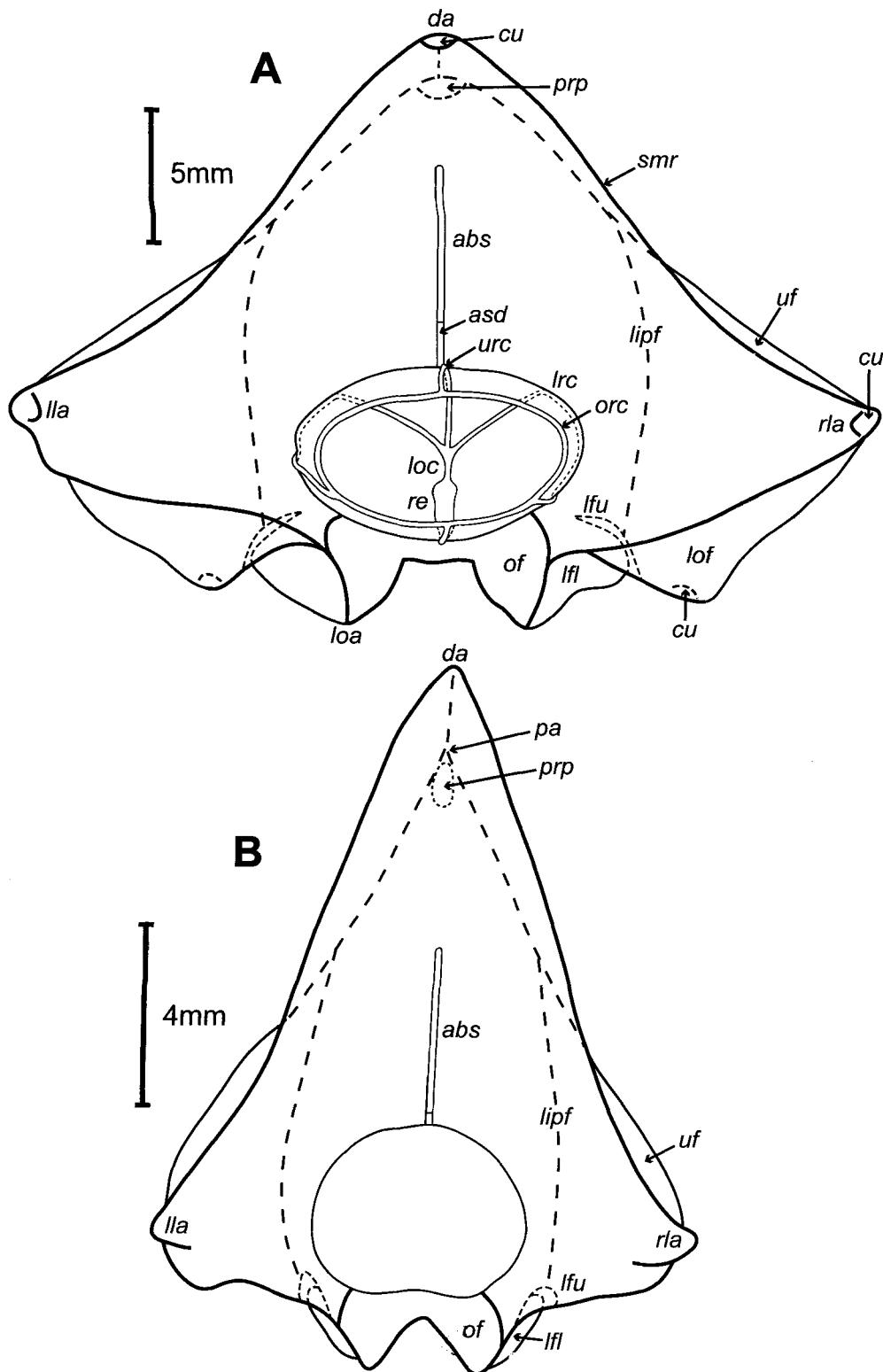


Fig. 41. *Vogtia serrata*: A: definitive nectophore, distal view; B: elongate definitive nectophore, distal view (*abs*, ascending branch of somatocyst; *asd*, ascending surface diverticulum; *cu*, cusp; *da*, distal angle; *ifl*, lower flap; *lfu*, lower furrow; *lrf*, limit of proximolateral facet; *lla*, left lateral angle; *loa*, lower angle; *loc*, lower radial canal; *lof*, lower facet; *lrc*, lateral radial canal; *of*, ostial facet; *orc*, ostial ring canal; *pa*, proximal angle; *prp*, proximal protuberance; *re*, rete mirabile; *rla*, right lateral angle; *smr*, smooth ridge; *uf*, upper facet; *urc*, upper radial canal).

Diagnosis

Definitive nectophore pentagonal or triangular, without cusps on any facets; deep (lower) furrow and flap between lower and ostial facets.

Material examined

One thousand, one hundred and eighty-four definitive nectophores from Canadian Pacific stations LB12 (0–300, 300, 400–0 m), LB13 (0–500 m) (Fig. 41B) BCPM 996-237-1, LB13 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–300, 300, 0–500, 500, 0–700, 700 m), LB16 (0–500, 500, 0–700 m), LB17 (0–300, 300, 300–0, 0–500, 500, 0–700 m), LC9 (0–300, 300, 300–0, 0–500, 500, 500–0 m), LC10 (500–0 m) (Fig. 41A) BCPM 996-238-1, LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–575, 575–0, 700–0 m), LC11 (0–300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m); 106 larval nectophores from stations LB12 (0–300, 300, 450 m), LB13 (0–300, 0–500, 500, 500–0 m), LB14 (0–300, 300, 0–500 m), LB17 (300 m) (Figs 42A and B) BCPM 996-239-1 (0–300, 300, 500, 0–700, 700 m), LC9 (300, 500, 500–0 m), LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 575–0, 700–0 m), LC11 (700–0 m) (Figs 42C and D) BCPM 996-240-1 (0–300, 500, 500–0, 700–0 m), and A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 700–0 m); 22 nectophores collected from near thermal vent in tows 1 (1750–0, 1900–0 m) and 2 (0–2200, 1700–0 m) (Fig. 11, Table 1). Specimens of *Vogtia serrata* from the NHM collections: Reg. Nos 1957.11.9.176, 5 detached definitive nectophores, 1 attached to stem portion (47°23'S, 56°20'E); 1957.11.9.170, 2 definitive nectophores joined to stem portion (23°39'S, 10°54'E).

Description of material

Up to five nectophores attached to 12 stem portions in nine samples, other nectophores detached; definitive nectophores up to 12 mm "tall", 13 mm wide, and pentagonal (Fig. 41A), or 21 mm "tall", 15 mm wide, and triangular (Fig. 41B); nectophores with elongate or exceptionally elongate upper-lower axis, broad right-left axis, and shorter proximal-distal axis; ridges smooth in all except smallest nectophores; one or two of latter with serrated ridges; nectophore with upper angle comprising proximal and distal angles connected by upper ridge, prominent in elongate nectophores (Fig. 41B), less prominent in pentagonal nectophores (Fig. 41A), right and left lateral angles, and two lower angles; cusps or larger

protuberances at some angles, but none along lengths of ridges; proximal angle with either protuberance (Fig. 41), small cusp, or no swelling (not illustrated), and distal angle with either large protuberance (Fig. 41B), small cusp (Fig. 41A), or no swelling (not illustrated); lateral surfaces comprising six facets, with upper and proximolateral facets typically larger than lower facets (Fig. 41A), upper facets atypically much larger than proximolateral and lower facets (Fig. 41B); two upper facets, variably concave, directed outwards upper-laterally (Fig. 41A) or more laterally (Fig. 41B) from colony, resembling two elongate isosceles triangles lying on their sides with bases forming smooth upper ridge and apices forming lateral angles; distal sides slightly longer than proximal sides, and with small irregularity in centre (not discernible in distal view shown in Fig. 41); proximal sides curving distally towards lateral angle; two proximolateral facets (extent indicated by coarse broken lines in Fig. 41), typically slightly concave, resembling isosceles triangle (except in elongate nectophores) with apex at lateral angle, base free and forming edge of hydroecium (on proximal surface), two sides abutting upper and lower facets, typically with cusp at lower end of ridge shared with lower facet (Fig. 41A), atypically without cusp (Fig. 41B); two lower facets, slightly convex with apex at lateral angle, sides abutting proximolateral facet and distal surface, and base extending from distal nectophore surface over deep lower furrow (Fig. 41A) to lower end of proximolateral facet (at cusp in Fig. 41A); lower facets of elongate nectophores lying immediately below pentagonal distal surface, so not discernible in distal view (Fig. 41B); two ostial facets, small, triangular, arising from lower distal surface of nectophore adjacent to lower border of ostium, and from lower flap (Fig. 41); lower flap between proximal and distal nectophore surfaces, lying closer to midline than proximolateral and lower facets and adjacent to deep lower furrow (Fig. 41A, *ifū*); flap measuring up to 4.5 mm long by 2 mm deep, and appearing largest in turgid nectophores (Fig. 41A, *ifū*), folded and less easy to discern in flaccid nectophores (Fig. 41B); mesogloea moderately turgid to flaccid; hydroecium on proximal surface (indicated by coarse broken lines in Fig. 41), shallowest at upper end, deepest over ostial facets, with extra slight hollow between bases of proximolateral facets and proximal end of lower flap (not illustrated); hydroecium atypically forming elongate channel (Fig. 41B); pedicular canal comprising external portion through muscular lamella from "stem" canal to proximal nectophore surface, short disjunct portion between external and internal portions, and short internal portion to nectosac (not

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

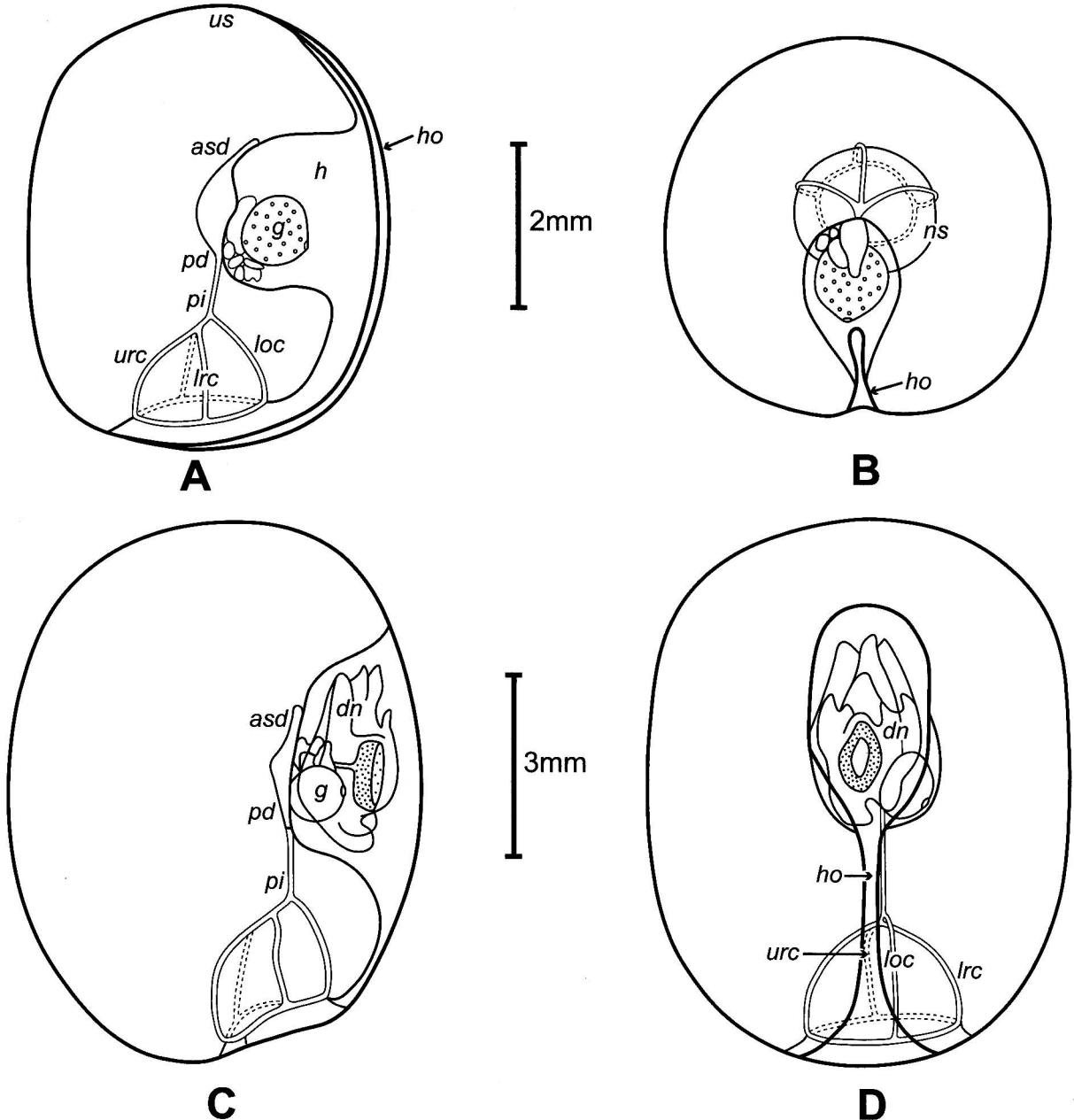


Fig. 42. *Vogtia serrata*: **A:** young larval nectophore, right lateral view; **B:** young larval nectophore, upper view; **C:** older larval nectophore, right lateral view; **D:** older larval nectophore, proximal view (*asd*, ascending surface diverticulum; *dn*, developing definitive nectophore; *g*, gastrozooid(s); *h*, hydroecium; *ho*, hydroecial opening; *loc*, lower radial canal; *lrc*, lateral radial canal; *ns*, nectosac; *pd*, disjunct pedicular canal; *pi*, internal pedicular canal; *urc*, upper radial canal; *us*, upper surface).

illustrated); ascending surface diverticulum elongate, extending upwards from disjunct pedicular canal to base of somatocyst (Fig. 41A), typically at just over 1/3 nectophore height, atypically at 1/2 nectophore height, and present as gutter in detached nectophores; somatocyst thin, consisting of single ascending branch, and extending to 3/4–4/5 nectophore height; nectosac shallow, with prominent ostium and velum

(latter typically damaged in present specimens and omitted from Fig. 41); upper and lower radial canals originating from internal pedicular canal, and lateral radial canals, where discerned, arising from upper radial canal either together or staggered; lower canal typically developing small rete mirabile (Fig. 41A), broad in smaller nectophores but absent in most larger nectophores.

Larval nectophores 3.5–10 mm tall, hemispherical, with extensive rounded upper surface and narrow slit-like hydroecial opening on proximal surface, extending down to distal surface (Fig. 42); distal surface with ostium slightly indented and lower surface not identifiable; hydroecium of larger larval nectophores with developing definitive nectophore (Figs 42C and D); external pedicular canal short (obscured by gastrozooid in Fig. 42), inserting onto junction of disjunct pedicular canal and ascending surface diverticulum; latter two canals, typically swollen and atypically not swollen, merged with (Figs 42A and C); central organ discernible between latter two merged canals and gastrozooid in some young nectophores (shown in Fig. 42A but not labelled); muscular lamellae not discernible; internal pedicular canal extending from lower end of disjunct pedicular canal to nectosac, relatively elongate; nectosac with upper and lower radial canals arising from internal pedicular canal, lateral radial canals arising from upper radial canal (Figs 42A and C); all radial canals relatively straight; large gastrozooid in many nectophores.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993); 47°50'–48°56'N, 128°22'–129°54'W, over Endeavour Ridge (Burd and Thompson 2000). Northeast Pacific: off California and Baja California (Alvariño 1980c, 1991); 29°01'N, 132°09'W; 29°11'N, 131°41'W; 30°47'N, 125°25'W; 30°59'N, 124°53'W, east of Baja California (Alvariño 1967a); off San Diego (Alvariño 1967b); off Point Conception (Haddock and Case 1999); Monterey Bay (Bigelow and Leslie 1930). Other regions: many records from remainder of Pacific (for example, Bigelow 1913; Alvariño 1967a; Alvariño et al. 1990; Palma and Rosales 1997; Lindsay 2006) and from other oceans (for example, Musaeva 1976; Alvariño 1981; Pugh 1991).

Vertical. Off Vancouver Island *Vogtia serrata* was collected from 300–700 m, within the vertical distribution recorded at other Pacific locations (Alvariño 1967a, 1991; Stepanjants 1970), but may also have been present from the surface to greater depths. In the North Atlantic *V. serrata* was recorded at all depths from the surface to 5425 m (summarized in Pagès et al. 1994). In spite of worldwide reports of very deep records, this species has a mainly lower epipelagic and upper mesopelagic distribution (Margulis 1980b, 1984; Pagès et al. 1994; Pugh et al. 1997).

Notes

The specific name derives from the serrated ridges observed in juvenile nectophores (Moser 1925), but such ridges were found in only a few very small nectophores from the present collection, the ridges being smooth in all other immature nectophores and all mature nectophores. Similar smooth ridges occur in nectophores from the South Atlantic (Pugh 1999b) and Indian Ocean (Daniel 1985).

The present definitive nectophores vary in shape, with the upper angle lying much farther from the nectosac in some nectophores than in others. Similar elongate nectophores have been collected elsewhere in the Pacific and are illustrated by Stepanjants (1967, fig. 85a) and Bigelow (1931, fig. 190). However, elongate nectophores have not yet been recorded from the South Atlantic (Pugh 1999b) or from waters around the British Isles (Kirkpatrick and Pugh 1984). The degree of development of the proximal protuberance on the upper end of the nectophore also varies: in elongate nectophores it is typically large, whereas in pentagonal nectophores it is smaller. Small cusps may also develop on the distal side of the upper and lateral angles and at the lower junction of the proximolateral and lower facets in pentagonal nectophores, but in many nectophores these regions are flat or occasionally humped. Such gelatinous cusps have not been described in *Vogtia serrata* by previous authors, although they are indicated by Moser (1925, pl. 28 fig. 9) and Kirkpatrick and Pugh (1984, fig. 28). However, Totton (1965a) comments that all hippopodiids possess either protuberances or cusps (as spines) at some stage during their growth, although these tend to be less conspicuous in older nectophores. Thus, the large protuberances in a number of mature nectophores of *V. serrata* suggest a closer affinity of this species with *V. glabra* and *H. hippocampus*, whose definitive nectophores have two and four protuberances, respectively, than with *V. pentacantha* and *V. spinosa*.

Nectophores with prominent upper and lateral angles and smooth facets and ridges were referred by Alvariño (1967a) to the nominal species *Vogtia kuruae*. However, nectophores of *V. serrata* show a considerable range of form, and serrated ridges occur only in the smallest nectophores, so the nectophores of *V. kuruae* resemble those of *V. serrata*. Alvariño (1967a) also showed furrows or hollows beneath the “lateral” processes in her two illustrations, though without commenting upon them in the text. In the present work, therefore, *V. kuruae* is considered conspecific with *V. serrata*, in agreement with Daniel

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(1985) and Pugh (1999b).

Larval nectophores of *Vogtia serrata* are easily confused with those of *Rosacea plicata* because, as Totton (1954) points out, both are hemispherical with a pocket-shaped hydroecium that opens onto the proximal surface ("ventral" surface of Totton) as a narrow slit. However, they can be distinguished by the "somatocyst" (merged ascending surface diverticulum and disjunct pedicular canal in the above description), which is elongate and relatively straight in *V. serrata* but ovate or globular with a pronounced angle over the dorsal (= proximal) wall in *R. plicata* (Totton 1954). In the present larval nectophores of *V. serrata*, the ascending surface diverticulum / disjunct pedicular canal is straight (Fig. 42C) or at only a slight angle (Fig. 42A), whereas in *R. plicata* Totton shows it curving sharply around the central organ (1954, fig. 43B). He adds that the central organ is absent in older larval nectophores, and indeed, it could not be identified in any of the larger larval nectophores of *V. serrata* collected from Canadian Pacific waters. It may have been absorbed into the stalk canal, as

Totton suggests. The ascending surface diverticulum / disjunct pedicular canal is elongate in all the present larval nectophores of *V. serrata*, but is also swollen in several of them, including those shown in Figures 42A and B. Perhaps this is attributable to a more abundant supply of food in Canadian Pacific waters than at the Antarctic ice edge, where Totton's nectophores were collected.

Original figures of larval nectophores of *Vogtia serrata* by Moser (1924a, pl. 3 fig. 4; 1925, pl. 28 figs 4–7) may not be referable to this species because, as Totton (1954) points out, the definitive nectophore shown within its hydroecium cannot be positively identified as that of *V. serrata*. It does, however, seem likely that Moser's two other figures of a larval nectophore of *V. serrata* (1925, pl. 28 figs 5, 6) are indeed of a hippopodiid because they have a straight ascending surface diverticulum / disjunct pedicular canal (*somatocyst* of Moser). However, it is unclear whether they are referable to *Vogtia* or *Hippopodius* because no radial canals are shown on the nectosac. In larval nectophores of *Vogtia*, all four radial canals are present (Figs 42A and B; Kirkpatrick and Pugh

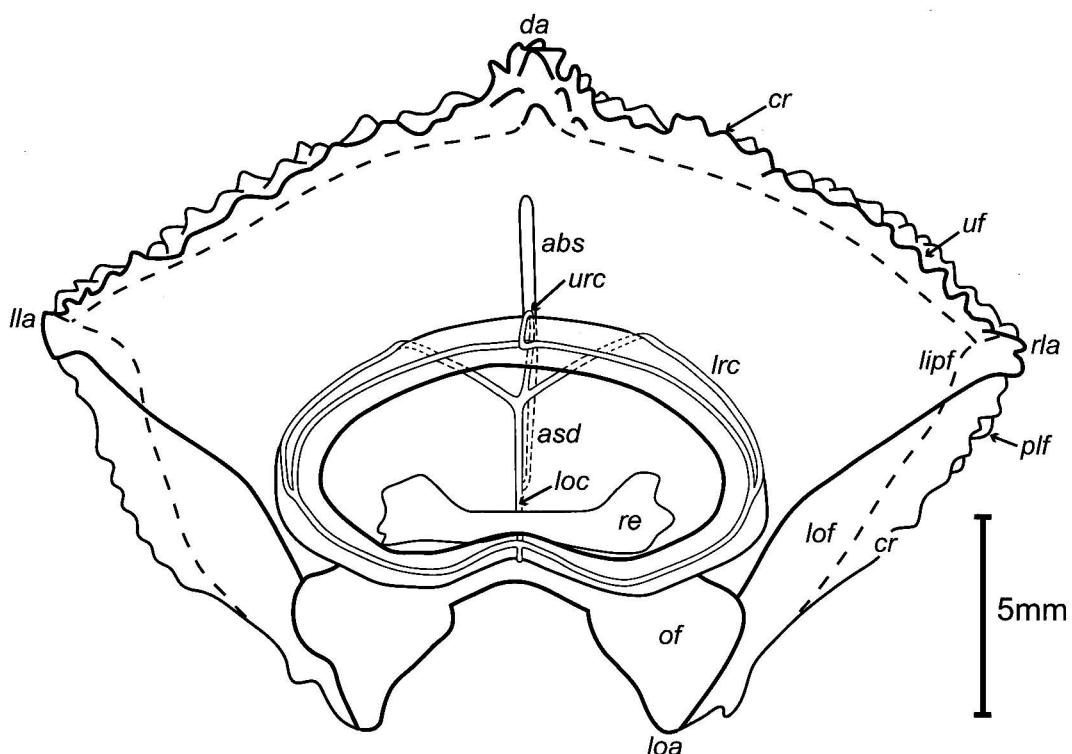


Fig. 43. *Vogtia spinosa*, definitive nectophore, distal view (abs, ascending branch of somatocyst; asd, ascending surface diverticulum; cr, cusped ridge; da, distal angle; lla, left lateral angle; loa, lower angle; loc, lower radial canal; lof, lower facet; lrc, lateral radial canal; of, ostial facet; plf, proximolateral facet; re, rete mirabile; rla, right lateral angle; uf, upper facet; urc, upper radial canal).

1984), whereas those of *Hippopodius* have only an upper (as "dorsal") and a lower (as "ventral") radial canal (D. Carré 1968).

***Vogtia spinosa* Keferstein and Ehlers, 1861**

(Fig. 43)

Vogtia spinosa Keferstein and Ehlers, 1861: 24, pl. 5 figs 16, 17; Haeckel, 1888b: 364; Chun, 1897a: 35; Bigelow, 1911a: 351; Bigelow, 1911b: 210, pl. 15 figs 5–12; Bigelow, 1913: 67, text-fig. 1; Bigelow, 1931: 537; Stepanjants, 1967: 136, fig. 80; Rengarajan, 1973: 148, fig. 12c; Daniel, 1974: 98, figs 8a and b; Daniel, 1985: 151, figs 39a–d; Totton in Pugh 1974a: fig. 1; Xu and Zhang, 1978: 37, fig. 33; Alvariño, 1981: 406, fig. 174.30; Kirkpatrick and Pugh, 1984: 74, fig. 26; Pagès and Gili, 1992b: 78, fig. 18; Pugh, 1999b: 487, fig. 3.58.

Vogtia köllikeri Haeckel, 1888b: 182, pl. 29 figs 9–14.

Hippopodius pentacanthus Schneider, 1898: 84 (in part).

Vogtia pentacantha Bigelow, 1918: pl. 4 fig. 1 (not Kölliker 1853: 31, = *V. pentacantha*).

Hippopodius spinosus: Moser, 1925: 419.

Diagnosis

Definitive nectophore pentagonal, with upper and proximolateral facets bearing many closely spaced cusps; without deep furrow and flap between lower and ostial facets.

Material examined

Forty-two definitive nectophores from Canadian Pacific stations LB12 (300 m) (Fig. 43) BCPM 996-241-1, LB12 (0–300 m), LC9 (500–0 m) BCPM 996-242-1, LC11 (700 m), and A4 (0–700 m) (Fig. 11, Table 1). Specimens of *Vogtia spinosa* from the NHM collections: Reg. Nos 1985.12.9.28, 23 detached definitive nectophores and 1 definitive nectophore with attached stem portion (41°5'N, 14°38'W); 1985.12.9.29, 13 detached nectophores (45°54'N, 09°39'W).

Description of material

Six nectophores attached to stem portion in one sample, three in another, all other nectophores detached; definitive nectophores 7–21 mm "tall", 9–26 mm wide, pentagonal with elongate upper–lower axis, broad right–left axis (Fig. 43), and short proximal–distal axis; ridges and facets typically cusped; nectophore with prominent upper angle, comprising proximal and distal angles and upper ridge (Fig. 43, da), right and left lateral angles, and two lower angles; lateral surfaces comprising six triangular facets: two upper facets, slightly convex and with dense covering of small cusps, directed outwards upper-laterally from colony, resembling two elongate isosceles triangles with bases forming short cusped upper ridge and apices forming lateral angles (on distal nectophore surface); long sides of upper facets cusped, with double row of cusps on distal side and shallow indentation in centre, proximal side slightly shorter and approximately straight; two proximolateral facets, slightly concave, directed either laterally or lateroproximally, slightly deeper than upper facets, triangular with bases smooth and forming lateral walls of hydroecium (shown by coarse broken lines in Fig. 43), two sides, both cusped, meeting at lateral angle; two lower facets, concave, directed slightly proximolaterally in mature nectophores, laterally in immature nectophores, larger than proximolateral facets and deeper along proximal–distal axis, approximately triangular with apex at lateral angle, base free, smooth, somewhat curved, and extending from distal surface at lower nectophore angle to proximal surface of nectophore; ridge abutting proximolateral facet cusped, ridge abutting distal nectophore surface only cusped near lateral angle, smooth and slightly concave towards lower angle, with ostial facet attached at lower end; two ostial facets, small, typically with distinctive triangular shape, atypically rounded, and separated from distal nectophore surface by short ridge, also connecting to lower end of lower facet; mesogloea turgid; hydroecium on proximal surface (indicated by broken line in Fig. 43) shallowest at upper end and deepest between bases of ostial facets; pedicular canal comprising elongate external portion passing through muscular lamella from "stem" canal to proximal nectophore surface, short disjunct portion between external and internal portions, and short internal portion reaching nectosac (not illustrated); ascending surface diverticulum elongate, extending upwards from disjunct pedicular canal to base of somatocyst, at 3/5 nectophore height, present as gutter in detached nectophores (Fig. 43); somatocyst thin, consisting of single ascending branch extending

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to 4/5 nectophore height; nectosac broad, reaching 1/2 nectophore width, shallow, with prominent velum, typically rolled up (Fig. 43); radial canals simple and, where intact, with upper and lower radial canals arising from internal pedicular canal, and lateral canals arising from upper canal a short distance from insertion of pedicular canal, either together or staggered; lower radial canal with well-developed rete mirabile; in juvenile nectophores, rete covering almost entire proximal surface of nectosac (not illustrated), and in mature nectophores, typically bilobed, broad, and prominent (Fig. 43, *re*) and atypically reduced to two thin lateral extensions (not illustrated).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: off San Francisco (Alvariño 1980c, 1991); off Oregon (Pearcy 1972); 40°N, 127°39'W, northeast Pacific (Stepanjants 1967). Other regions: other Pacific records few and widely scattered in such locations as the Antarctic Ocean and off Chile (Alvariño et al. 1990; Palma 1994; Palma and Rosales 1995), off the Galápagos Islands (Alvariño and Ambros 1986), and in the South China Sea (Lin 1993). Also widely distributed in other oceans.

Vertical. *Vogtia spinosa* was collected at 700 and 300 m and between 0 and 700 m, extending a further 200 m below the deepest record for a population off California (Alvariño 1991). In the North Atlantic *V. spinosa* occurred mainly between 100 and 450 m and extended down to 950 m (Pugh 1974b, 1984, 1990, 1991).

Notes

The portions of “stem” found in two of the present samples consist of a “nectosome” with pedicels and muscular lamellae for up to 11 nectophores, and a length of true siphosome that extends from the posterior end of the budding zone. This relationship is well illustrated in a specimen of *Vogtia spinosa* collected during the *Albatross* Expedition by Bigelow (1913, text-fig. 1).

In descriptions of *Vogtia spinosa* given by Pagès and Gili (1992b) and Bouillon et al. (2004), the colony is described as comprising two parallel rows of nectophores attached obliquely to a central stem. However, the arrangement of nectophores on the

nectosomal “stem” is thought to be more complex than this, as discussed above. The authors of both papers note that a single colony is composed of up to 19 nectophores, more than are found in the present specimens (maximum of 12 nectophores per sample) and more than previously illustrated (Bigelow 1911b, pl. 15 fig. 5).

The upper facets of *Vogtia spinosa* nectophores from the present collection, even the smallest nectophores, all have a dense covering of cusps, which clearly distinguishes them from some nectophores of *V. pentacantha* in which up to four cusps are scattered over the otherwise smooth surfaces of the upper facets. Additionally, the long distal ridge separating the upper facets from the distal surface of the nectophore is covered with a double row of cusps in *V. spinosa*, whereas it has only a single row in *V. pentacantha*.

Large nectophores of *Vogtia spinosa* taken from Canadian Pacific waters also differ from those of *V. serrata* and *V. pentacantha* in having less prominent upper and lateral angles. This is because the upper facets are convex and the lower facets, which are typically directed outwards at 45° from the upper-lower nectophore axis, are separated by a broader nectosac than those of *V. serrata* and *V. pentacantha*. The upper and lateral angles of *V. spinosa* nectophores illustrated by Totton (1965a, fig. 81.3), Bigelow (1911b, pl. 15 fig. 9), and Stepanjants (1967, fig. 80) are more prominent than those of the Canadian Pacific specimens. The latter more closely resemble those shown by Pugh (1999b, fig. 3.58) from the South Atlantic and by Kirkpatrick and Pugh (1984, fig. 26) from shallow waters around the British Isles.

A photograph taken by C. Carré of a discharged mastigophore nematocyst from a *Vogtia spinosa* tentillum was published posthumously in A.K. Totton’s last paper (included in Pugh 1974a).

10.2.3. Family DIPHYIDAE Quoy and Gaimard, 1827

Diagnosis

Calycophorae with dissimilar nectophores, typically two, with conical anterior one linearly adjoined to elongate posterior one, atypically only anterior one developed; nectophore(s) with mouthplate and typically with longitudinal ridges; facets between ridges typically elongate (except in *Giliinae* and *Lensia quadriculata*); somatocyst in anterior nectophore only, typically simple and swollen, not

reaching anterior end; cormidia with bracts; latter with phyllocyst typically globular or elongate but without bracteal canals (except Giliinae).

Notes

Several of the most successful siphonophore species are included within the Diphyidae, which is the largest of the 16 families composing the Siphonophora (see Section 2.1). Although this family includes a diversity of species, the molecular analysis by Dunn et al. (2005b), as interpreted by Dunn and Wagner (2006, fig. 7), suggests that it is monophyletic, as discussed in Section 10.2. The present diagnosis is based on the familial characters of Pugh and Pagès (1995) and Pugh (1999b), modified after the new terminology of Haddock et al. (2005a) as here applied to diphymorph calycophorans and discussed in Sections 2.3, 2.3.1, 2.3.2, and 10.2.

Diphyomorph relationships. The Diphyidae is closely related to the Clausophyidae and Abylidiae and several possible interrelationships have been postulated for these three families. Mackie et al. (1987, p. 131) point out that “Most authors have suggested that the presence of a somatocyst in the posteriornectophore of clausophyid species, ... absent from such nectophores in the other two families, is a primitive character since such a structure is present in all prayomorph nectophores”, or almost all, according to the new definition of the somatocyst given in the present work. These authors go on to summarize the views of Totton and Leloup as follows: “Totton (1954, 1965a) considered that the evolutionary pathways of the diphymorphs diverged early, with one branch leading to the Diphyidae and the other by way of the Clausophyidae to the Abylidiae. Leloup (1954), however, placed the clausophyids . . . at the base of his diphymorph genealogy, with the Abylidiae considered as the most advanced forms.” The new molecular analysis of Dunn et al. (2005b), as summarized by Dunn and Wagner (2006, fig. 7), lends support to the latter theory, since the single abylid sampled is nested within the Diphyidae, and the clade comprising the diphids, abyldids, and sphaeronectids is sister to the clade that includes two of the three clausophyids.

Larval nectophores are known for so few species of Diphyidae and Clausophyidae that their features cannot be included in the present family diagnoses. However, both families are thought to develop first a larval nectophore with a somatocyst, followed later by one or two definitive nectophores. The larval nectophore of diphyids is, in general, shed

and replaced by anterior and posterior definitive nectophores (Pugh and Pagès 1995). This has been conclusively shown for the diphyine diphyid *Lensia conoidea* by D. Carré (1967), who reared fertilized eggs in the laboratory to the late calyconula stage (see Section 3.1). However, Totton (1965a) suspected that in *Diphyes* species the larval nectophore is retained to become the anterior nectophore, although he never published the evidence. He also concluded that the anterior nectophore of abyldids represents the retained larval nectophore, as was soon shown to be the case by C. Carré (1967) for *Abylopsis tetragona*. However, it is unclear from the molecular phylogeny of Dunn et al. (2005b) whether such a character is plesiomorphic or apomorphic.

Nectophores. When two nectophores are present in diphymorphs, they are dissimilar, or heteromorphic (see Section 10.2), and a proximal-distal nectophore axis is only important in the posterior nectophore. In the anterior nectophore the main axis lies anterior-posterior and is aligned with the anterior-posterior axis of the colony (Fig. 3A). These axes are explained in Section 2.3.1. In the descriptions of anterior nectophores given below, the pointed end is termed the anterior end (previously *apex*) and the opposite, truncate end the posterior end (previously *base*). The latter is here subdivided into a “distal” portion around the ostium, including the cusps and mouthplate, and a “posterior”, hydrocial portion in the region of the stem-attachment point and hydrocial opening (Figs 3A and D). In diphyids the stem-attachment point is not carried on a median mesogloea protuberance (except in sulculeolariines; see Section 10.2.3.1) as in most nectophores of the family Clausophyidae (see Section 10.2.4). The proximal end of the posterior nectophore fits into the “posterior” hydrocial region of the anterior nectophore as described above, and where the hydroecium is very shallow, a posterior facet (previously *basal facet*) can be identified in the anterior nectophore, which effectively constitutes the anterior wall of the hydroecium (*Lensia achilles* and *L. conoidea*; see below). Some of the anterior nectophores from Canadian Pacific waters have a short proximal-distal axis (*Muggiae atlantica* and *Chelophys appendiculata*; see below), while others have none (*L. achilles* and *L. conoidea*; see below). In contrast, a longer proximal-distal axis is evident in the anterior nectophore of the tropical species *Diphyes dispar* (see Haeckel 1888b, pl. 33 fig. 1, as *Diphyopsis compressa*) and in anterior nectophores of various clausophyids collected in Canadian Pacific waters. This axis is discussed further for clausophyids in Section 10.2.4.

An upper-lower axis lies orthogonal to the long anterior-posterior axis in the diphyomorph anterior nectophore (Figs 3A and D), but is not orthogonal to the much shorter proximal-distal nectophore axis, as explained in Section 2.3.1. However, in the diphyomorph posterior nectophore the upper-lower axis is orthogonal to the proximal-distal axis (Fig. 3E), and in this respect somewhat resembles the upper-lower axis of physonect nectophores (Fig. 1B). The upper-lower axis in diphyomorph nectophores also differs somewhat from that in a typical prayomorph *Rosacea*-type nectophore (Fig. 2A), where it forms the long axis of the nectophore, as it does in nectophores of hippopodiids (Fig. 2G). However, these differences are of little significance, since the siphonophore axes designated by Haddock et al. (2005a, p. 695) "refer to absolute axes". A right-left nectophore axis lies orthogonal to the upper-lower axis in all diphyomorph nectophores, and can be identified when the upper surface is viewed from outside the colony (following Haddock et al. 2005a). Where ridges are developed in diphyomorph nectophores, their names relate to these two axes, as described below. It is interesting to note that in complete diphynine colonies (and those of ridged clausophyids), the right lateral ridge(s) of the anterior nectophore align(s) with the left lateral ridge(s) of the posterior nectophore and vice versa (Fig. 3A). This is because the upper surface of the anterior nectophore lies adjacent to the lower surface of the posterior nectophore (Fig. 3A), probably as a result of the posterior nectophore migrating to a position immediately behind (posterior of) the anterior nectophore during evolution (see Section 2.3.1; Fig. 4).

The posterior diphyomorph nectophore, when developed, varies in size relative to the anterior nectophore, and in the Diphyidae it is typically smaller. However, in the Clausophyidae it is typically slightly larger and in the Abylididae it is typically much larger. Loss of the posterior nectophore (monophyly) is apparent within each family, indicating that it is a character of generic rather than family importance. Examples include *Muggiaeae* species within the Diphyidae and *Heteropyramis* species within the Clausophyidae (see below), and *Enneagonum* species within the Abylididae (see Pugh 1999b, fig. 3.132). Considerable reduction in the size of the posterior nectophore is atypical amongst diphyomorphs, but is apparent in *Dimophyes* species within the Diphyidae (see below).

The nectosac (of the nectophore) is larger relative to the nectophore in diphyids than in either

clausophyids or abyliids, and thus diphyids are the most efficient swimmers. An increase in turgidity of the mesogloea and development of longitudinal ridges have increased the rigidity of nectophores in this group, and the two diphyid nectophores together form the most streamlined swimming unit of any siphonophore. This is exemplified by the extremely successful diphyid *Chelophyses appendiculata*. The physiology of locomotion in this species is discussed in Section 4.2.

New names are given here to the longitudinal ridges and facets of the ridged diphyomorph species described below, as noted above, and these are based on the upper-lower and right-left nectophore axes defined in Sections 2.3.1 and 10.2. Thus, all nectophores have an upper ridge (Totton's "dorsal"), two lower ridges (Totton's "ventral"), and a variable number of intervening lateral ridges, with the lower ridges typically delimiting a narrow and elongate triangular lower facet in the anterior nectophore and bordering an elongate hydroecial opening in the posterior nectophore. An additional ostial ridge is identified in the present work that borders the ostium on its upper and lateral sides and extends distally onto each side of the mouthplate to the distolateral borders of the nectophore.

A mouthplate is present in most diphyomorph nectophores and has been termed a basal lamella by previous authors. Kirkpatrick and Pugh (1984) and Pugh (1999b) define it as a thin extension of the nectophore below the ostium. In the present work it is termed a distal lamella because it abuts the ostium (which is distal), and the name distal lamella is restricted here to the thin extension that is aligned across the right-left axis of the nectophore and extends distally beyond the ostial cusps (when developed). It may be entire (as in posterior nectophores of *Lensia achilles*, *Dimophyes arctica*, and *Clausophyes moserae*; see below), notched or emarginate (as in posterior nectophores of *Sulculeolaria quadrivalvis*, *L. conoidea*, *Chelophyses appendiculata*, *Chuniphyes multidentata*, and *C. moserae*; see below), or completely divided into two separate and often overlapping lobes or lappets (as in anterior nectophores of *S. quadrivalvis*, *L. achilles*, *L. conoidea*, *L. havock*, *L. multicristata*, *L. hostile*, *Muggiaeae atlantica*, *C. appendiculata*, and *Gilia reticulata*; see below). Lappets occur only in the anterior nectophores of diphyids, and this term is used here in the same sense as in Pagès and Gili (1992b).

Bracts. Diphyomorph calycophorans typically release a eudoxid into the plankton (Section 2.3), and this first develops on the siphosome as a cormidium. At maturity it detaches from the posterior end of the siphosomal stem, as shown for *Chelophyses appendiculata* by Mackie et al. (1987, fig. 36). Eudoxids may live in the plankton for several weeks and release sexual products (gonophores) for species dispersal. In diphyids of the subfamily Sulculeolariinae (Section 10.2.3.1), prayids of the subfamily Prayinae (Section 10.2.1.2), and clausophyines of the family Clausophyidae (Section 10.2.4.3), eudoxids are not released from the siphosomal stem, and gonophores must separate from attached cormidia. In contrast, eudoxids are released from the siphosomal stem of species in the subfamilies Amphicaryoninae and Nectopyramidinae, as discussed above (see Sections 10.2.1 and 10.2.1.3). Each diphyomorph eudoxid comprises a bract and a gonophore, with buds for more gonophores situated at the point where the gonophore and gastrozooid attach to the bract. The only exception is the clausophyid *Crystallophyes amygdalina*, which has a unique “fuseudoxid” comprising a bract and gonophore fused together (Pagès and Pugh 2002).

Bracts of free-living diphyomorph eudoxids are typically helmet-shaped, with a conical head-piece and a flange-like neck-shield that varies in length. The terms head-piece and neck-shield are taken from Totton (1932, p. 318), who considered them to be “good points of reference” for eudoxid descriptions, and based them on two German terms introduced earlier by Moser (1925); they are used throughout the present work wherever appropriate. The proximal–distal bracteal axis extends from the proximal rounded or pointed end of the head-piece, where the bract was originally attached to the stem, to the distal border of the neck-shield. The head-piece contains a phyllocyst which originates from a portion of the colony stem that swells and becomes parenchymatous prior to detachment, as is well shown for *Chelophyses appendiculata* by Mackie et al. (1987, fig. 36). However, in figures of some other diphyomorphs (*Diphyes dispar* (as *Diphyopsis compressa*) by Haeckel 1888b, pl. 34 fig. 9; *Kephyses* (as *Diphyes*) *ovata* by Keferstein and Ehlers 1861, pl. 5 fig. 2) the phyllocyst appears to develop as a separate bud. In shape this structure tends to resemble the somatocyst of the anterior nectophore (Pugh and Pagès 1995). In diphyids the phyllocyst is typically discrete and lacks branches (*Lensia achilles* and *L. conoidea*; see below), except for one species, *Dimophyes arctica* (see below),

that has unusual thin proximal and distal branches, as noted by Pugh and Pagès (1995). In the single giliine diphyid species, *Gilia reticulata* (see Pugh and Pagès 1995, fig. 2) and in those clausophyid species that develop bracts (see Sections 10.2.4.1 and 10.2.4.2), two bracteal canals arising from the base of the phyllocyst and pass into the neck-shield on each side. Pugh and Pagès (1995) note the similarity of these branches to the bracteal hydrocial canals of prayids. In the present work the term phyllocyst is restricted to the swollen organ characteristic of free-living diphyomorph eudoxids, and is not applied to the slight swellings of the bracteal canals found in some prayomorph eudoxids (amphicaryonine prayid bracts, for example). The phyllocyst may act as a food store for the eudoxid or perform another function (see Section 10.2).

Diphyid subfamilies. Totton (1965a) referred two subfamilies, Sulculeolariinae and Diphyniae, to the Diphyidae, and more recently a third subfamily, Giliinae, was added by Pugh and Pagès (1995). The latter is monotypic for *Gilia reticulata*, which shows affinities with both diphynine diphyids and clausophyid diphyomorphs. The sulculeolariines are a small primitive group (Mackie et al. 1987). The Diphyniae is the largest and most diverse subfamily within the Siphonophora.

10.2.3.1. Subfamily Sulculeolariinae Totton, 1954

Diagnosis

Diphyidae with nectophores typically replaced up to 4 times if lost; nectophores having smooth surfaces; anterior nectophore similar in size to, or smaller than, posterior nectophore, with rounded anterior end and typically with commissural canals between lateral radial canals and upper canal (on lower side of nectosac). Bract smooth and cloak-like, with two reduced bracteal canals; cormidia not separating from stem, with each cormidium releasing only one free-swimming gonophore.

Notes

Several features of the species in this subfamily set them apart from other diphyids: they are typically larger, are less streamlined, retain the ability to regenerate nectophores if these are lost (see Section 3.3), and have a stem that is relatively longer than that of other diphyids. The long stem has developed to accommodate the large number of cormidia needed for adequate gamete production, since in this subfamily the cormidia are retained on the

stem, and each produces only a single gonophore (C. Carré 1979). These characters suggest that the sulculeolariines are closer to the ancestral diphyid stock than are the other two diphyid subfamilies (Mackie et al. 1987), but the findings of Dunn et al. (2005b) appear not to support this conclusion. The latter authors find that for the two genes they tested, *Sulculeolaria quadrivalvis* is nested within a clade that includes two diphynine diphyids, *Lensia conoidea* and *Muggiae atlantica*. Furthermore, this clade is sister to another that comprises two more diphynine diphyids and an abylid (Dunn et al. 2005b, fig. 6).

Monotypic for *Sulculeolaria* de Blainville, 1830.

Genus *Sulculeolaria* de Blainville, 1830

Diagnosis

With the characters of the subfamily.

Type species: *Sulculeolaria quadrivalvis* de Blainville, 1830.

Notes

The genus *Sulculeolaria* was reviewed by C. Carré (1979), who recognized six species: *S. biloba*, *S. chuni*, *S. monoica*, *S. pacifica*, *S. quadrivalvis*, and *S. turgida*. Of these, all except *S. pacifica* and *S. turgida* have been recorded in the northeast Pacific (Alvariño 1991; Purcell 1980, 1981b). *Sulculeolaria quadrivalvis* is described below, and species other than *S. pacifica* can be identified using Pagès and Gili (1992b) or Pugh (1999b). The characters of *S. pacifica* are summarized by C. Carré (1979, tables 2, 3), and figures of the nectophores are given by Stepanjants (1973, pl. 2 figs 11–13). A seventh species, *S. brintoni* (Alvariño, 1968b), is considered by C. Carré (1979) to represent a third or fourth regenerated anterior nectophore of *S. quadrivalvis* and is therefore a synonym of *S. quadrivalvis* (see below).

Sulculeolaria quadrivalvis, *S. chuni*, and *S. turgida* were successfully reared in the laboratory by C. Carré (1979), who found that the nectophores are regenerated up to 4 times, as discussed in Section 3.3. He also published good figures of their bracts (C. Carré 1979, figs 4a–c), and noted an extra pair of cusps (as teeth) on the distal margin of the bracts of *S. turgida* (fig. 4c). Pugh (1999b)

comments that the bracts of *Sulculeolaria* species are indistinguishable. No conclusion can be drawn here about this disparity of views, since no *Sulculeolaria* bracts were found in the present collection. C. Carré's bract figures also show a thin canal arising from the pedicel of the gastrozooid and entering the bract; in *S. quadrivalvis* (fig. 4a) this canal clearly divides into two branches, one of which passes round to the opposite side of the pedicel. It seems likely that these canals are equivalent to the bracteal canals of *Gilia reticulata* and clausophyid species (Pugh and Pagès 1995), and probably also, as these authors suggest, to the longitudinal/hydroecial canals of prayid bracts.

Sulculeolaria quadrivalvis de Blainville, 1830

(Fig. 44)

Sulculeolaria quadrivalvis de Blainville, 1830: 126; de Blainville, 1834: 138, pl. 6 fig. 6; Totton, 1932: 341, text-fig. 19; Leloup, 1933: 26; Bigelow and Sears, 1937: 32; Totton, 1954: 109; Patriti, 1964: 210; Totton, 1965a: 143, pl. 29 fig. 4, pl. 30 figs 1–4, pl. 31 figs 1–3 and text-fig. 82; Alvariño, 1968b: 343, fig. 4f; Palma, 1973: 38, pls 12, 13; Stepanjants, 1973: 657, pl. 3 figs 1–4; Daniel, 1974: 104, text-figs 9a, b, and k; C. Carré, 1979: 28, fig. 1, pl. 1; Kirkpatrick and Pugh, 1984: 80, fig. 30; Pagès and Gili, 1992b: 82, figs 22A and B; Gamulin and Kršinic, 2000: 44, figs 16a and b.

Galeolaria quadridentata Quoy and Gaimard, 1833: 45, pl. 5 figs 32, 33; Bigelow, 1918: 417, pl. 8 figs 1, 2; Browne, 1926: 67.

?*Abila trigona* delle Chiaje, 1841: pl. 145 fig. 4.

Epibulium aurantiaca Vogt, 1852: 524, pl. 14 figs 1, 2; Metschnikoff, 1874: 39, pl. 6 figs 1–10 and pl. 7 figs 11–15; Fewkes, 1880c: 322, pl. 3 figs 3–6.

Diphyes quadrivalvis: Gegenbaur, 1853: 315, pl. 16 figs 8–11; Gegenbaur, 1854: 453; Sars, 1859: 12; Keferstein and Ehlers, 1861: 18; Spagnolini, 1870: 621; Schneider, 1896: 620, pl. 45 figs 31, 37; Schneider, 1898: 87; Schneider, 1899: 17, fig. 31.

Epibulium filiformis Leuckart, 1853: 2, pl. 1 fig. 12 and pl. 2 figs 8, 9, 17 (not Eschscholtz, 1829: 148 = *Rhizophysa filiformis*).

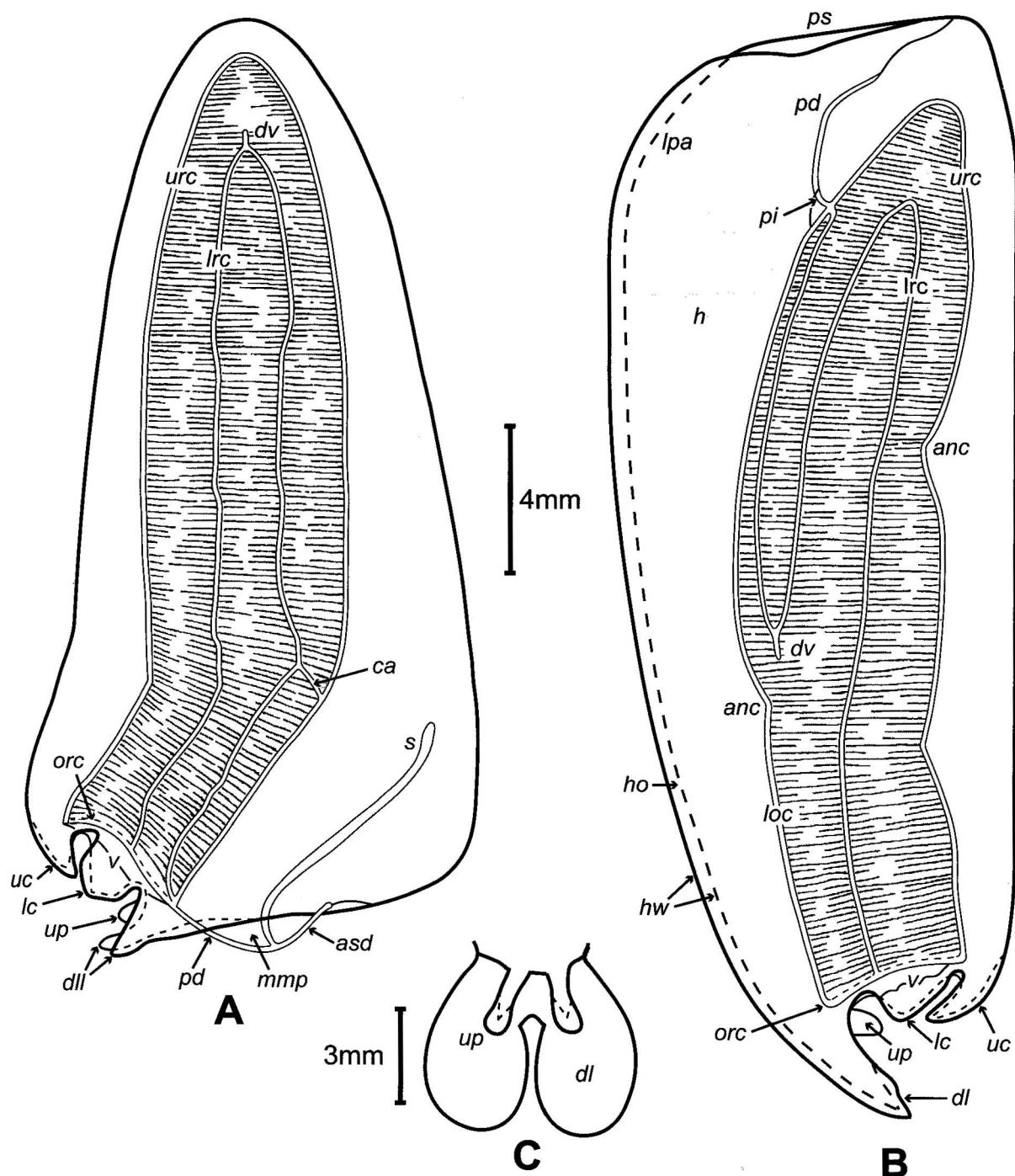


Fig. 44. *Sulculeolaria quadrivalvis*: A: anterior nectophore, right lateral view; B: posterior nectophore, left lateral view; C: distal lamella of posterior nectophore, upper view (anc, annular constriction; asd, ascending surface diverticulum; ca, commissure; dl(l), distal lamella (lappets); dv, diverticulum; h, hydroecium; ho, hydroecial opening; hw, hydroecial wing; lc, lateral cusp; lpa, lower proximal angle; lrc, lateral radial canal; mmp, median mesogloea protuberance; orc, ostial ring canal; pd, disjunct pedicular canal; pi, internal pedicular canal; ps, proximal surface; s, somatocyst; uc, upper cusp; up, upper pad; urc, upper radial canal; v, velum).

Galeolaria filiformis: Leuckart, 1854: 280, pl. 11 figs 14a and b; Huxley, 1859: 38 (in part), pl. 12 fig 1; Sars, 1859: 11.

Galeolaria aurantiaca: Vogt, 1854: 110, pls 18, 19, pl. 20 figs 1–5, and pl. 21 ?fig. 2 (not fig. 1); Weismann, 1883: 199, pl. 21 figs 1–8; Korotneff,

1884: pl. 16 fig. 52; Lochmann, 1914: 262, pl. 7 figs 1–3 and text-figs 1, 2.

Diphyia (Galeolaria) quadrivalvis: A. Costa, 1862: 90, pl. 3 figs 1–9.

Epibulium quadrivalvis: Korotneff, 1884: 279, text-figs 7–9.

Epibulium aurantiaca var. *canariensis* Chun, 1888a: 1158.

Galeolaria quadrivalvis: Chun, 1897a: 17; Lens and van Riemsdijk, 1908: 58, pl. 9 fig. 74; Bigelow, 1911b: 237, pl. 5 figs 1–7 and pl. 6; Bigelow, 1918: 416; Moser, 1925: 139; Browne, 1926: 66; Leloup, 1932b: 4.

Galette quadrivalvis: Stechow, 1921: 261; Bigelow, 1931: 549, figs 195–200.

Galette quadridentata Bigelow, 1931: 556, figs 201–203.

Sulculeolaria quadridentata: Bigelow and Sears, 1937: 31.

Sulculeolaria brintoni Alvariño, 1968b: 343, fig. 3.

Diagnosis

Sulculeolariinae with anterior nectophore having distal ostial cusps comprising two upper cusps and two lateral cusps, and mouthplate of two lappets, each with upper pad; somatocyst elongate and sinuous, reaching 1/3–2/5 nectophore length; posterior nectophore having distal cusps comprising two upper cusps and two lateral cusps, deeply emarginate mouthplate with two upper pads, and nectosac with two annular constrictions.

Material examined

Two anterior nectophores and 2 posterior nectophores from Canadian Pacific stations LB12 (300 m) (Fig. 44) BCPM 996-243-1, and LC9 (300–0 m) (Fig. 11, Table 1). Specimens of *Sulculeolaria quadrivalvis* from the NHM collections: Reg. Nos 1959.10.23.206, 8 anterior nectophores and 23 posterior nectophores (15°8'N, 42°1'E); 1986.5.14.1, 1 anterior nectophore (0°32'S, 126°11'E).

Description of material

Number and size of distal cusps around ostium, and presence of pads on distal lamellae of mouthplates, indicate that all four nectophores are originals, not replacements (see Section 3.3).

Anterior nectophores both 25 mm long, conical but somewhat flattened laterally, with surfaces smooth, anterior end rounded and posterior end truncate, comprising distal portion with ostium and adjacent posterior portion with prominent median mesogloea protuberance; ostium directed upper-distally, with velum intact (Fig. 44A); mesogloea turgid; hydroecium replaced by median mesogloea protuberance in posterior region, to which stem and posterior nectophore are attached in life (Fig. 44A); this protuberance fitting into proximal end of hydrocial opening on proximal surface of posterior nectophore (Fig. 44B) in life; somatocyst filiform, 6–8 mm long, lying parallel to axis of lower section of nectosac; nectosac large, elongate, with thick opaque musculature with bend in long axis at 1/3 nectophore length; nectosac diameter smaller between ostium and bend than between bend and anterior end; disjunct pedicular canal originating at presumed junction of external pedicular canal and somatocyst on median mesogloea process (stem lost in all anterior nectophores examined) and passing along process in midline to lower side of ostial ring canal, becoming partly enclosed in groove near ostium; “ascending” surface diverticulum passing from lower end of disjunct pedicular canal along posterior surface of nectophore towards lower surface for short distance (Fig. 44A); upper radial canal of nectosac originating at junction with lateral radial canals and ostial ring canal adjacent to ostium, passing anteriorly along lower wall of nectosac (in midline) to its anterior end, around onto upper surface of nectosac, and continuing posteriorly along nectosac upper wall (in midline) to ostial ring canal (Fig. 44A); lateral radial canals originating from junction with upper canal and ostial ring canal on lower side of ostium, forming elongate loop on lateral surfaces of nectosac, with transverse commissural canal connecting anterior limb of loop with lower section of upper canal, and inserting onto ostial ring canal laterally (as shown for right canal in Fig. 44A); lateral radial canal with short diverticulum at anterior end of loop; lower radial canal and internal pedicular canal not developed; buds of reserve (replacement) nectophores not identified.

Posterior nectophores 29 and 33 mm long, elongate, laterally flattened, with smooth surface, truncate proximal end, cusps and mouthplate at distal end, and rounded lower-proximal angle in lateral view (Fig. 44B); mouthplate a deeply emarginate distal lamella with two rounded lobes, each having prominent upper pad (Fig. 44C, up); hydroecium extensive, deeper proximally than distally, and delimited laterally by extensive right and left wings (Fig. 44B); nectosac with thick opaque musculature and two incomplete annular constrictions (Fig. 44B, anc); disjunct pedicular canal 2 mm long, originating from presumed insertion point of external pedicular canal from stem, near proximal end of hydroecium, and passing distally to internal pedicular canal, curving slightly over swollen region of hydroecial wall (Fig. 44B); internal pedicular canal short, forming 5-way junction with radial canals; upper radial canal of nectosac passing proximally from 5-way junction on lower wall of nectosac, in midline, over proximal end of nectosac and onto upper nectosac surface, then distally along upper surface to ostial ring canal (Fig. 44B); lower radial canal passing in midline from 5-way junction to ostial ring canal; lateral radial canals originating from 5-way junction and looping over lateral wall of nectosac, first distally, then proximally, and inserting laterally on ostial ring canal (at distal end of nectophore); lateral radial canal with short diverticulum from distal loop (Fig. 44B).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: from Baja California to San Francisco (Alvariño 1980c, 1991); California region (Margulis and Vereshchaka 1994); California Current, off San Diego or Catalina Island (Purcell 1980); off San Diego (Purcell 1981b); off Oregon (Pearcy 1972); 39°–45°N, 160°–170°E, North Pacific (Stepanjants 1967). Other regions: many records from remainder of tropical and semi-tropical Pacific and from other oceans, also mostly from warm waters (Alvariño 1971; Suárez and Gasca 1991; Pagès et al. 2006).

Vertical. The two samples in the present collection were from 300 and 300–0 m, within the depth range of those recorded off California (Alvariño 1991).

Notes

The date of A. Costa's publication, 1862, is based on Sherborn (1910, 1937, p. 40). The description

and plates were included in the *Fauna del Regno di Napoli*, which was published in parts from 1829 to 1886. Early volumes were written by O.-G. Costa (see *Diphyes bipartita* under *Chelophyses appendiculata*) and later volumes by his son, A. Costa.

Most early authors used cusp number to separate *Sulculeolaria quadridentata* (four cusps) from *S. quadrivalvis* (two cusps) (Bigelow 1918, 1931; Browne 1926; Bigelow and Sears 1937; Stepanjants 1967). However, C. Carré (1979) showed that original anterior nectophores of *S. quadrivalvis* are quadridentate, whereas regenerated ones are bidentate. Thus, the two names are synonyms. C. Carré (1979) also showed that in regenerated nectophores the upper cusps (as *dorsal teeth*) are reduced in size or lost, the somatocyst is less sinuous, and the mouthplate is shorter, while the upper pads on the lappets of the distal (as *basal*) lamella become smaller and are finally lost. Regenerated posterior nectophores lose their annular constrictions and the lobes on their distal lamella, and the upper pads are progressively reduced.

C. Carré (1979) noted that in *Sulculeolaria quadrivalvis*, lateral cusps (as teeth) are developed in NA₁, NA₂, NP₁, and NP₂ but are absent in NA₃ and NP₃ (see Section 3.3). He also found that upper (as *dorsal*) pads are developed on the mouthplate in NA₁ and NA₂ but are absent in NA₃ (see Section 3.3). Thus, the present Canadian Pacific specimens all represent original nectophores, as noted above. Only characters of original nectophores are included in the above species diagnosis.

Several species of *Sulculeolaria* are accurately figured by Pagès and Gili (1992b), including *S. quadrivalvis*. However, they mistakenly describe the commissural canals of the anterior nectophore as linking to the lower (as "ventral") radial canal instead of the upper (as "dorsal") canal (Fig. 44A), but correctly note that in replacement nectophores these canals sometimes do not reach the upper canal. In *Sulculeolaria* species the disjunct pedicular canal of the anterior nectophore inserts onto the radial canals (and the ostial ring canal) at the level of the ostium, so a lower radial canal is not developed.

10.2.3.2. Subfamily Diphyinae Moser, 1925

Diagnosis

Diphyidae with nectophores not replaced and typically having angular borders and longitudinal ridges; anterior nectophore typically with pointed

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

anterior end, larger than posterior nectophore (latter sometimes absent or reduced in size), but without commissural canals between lateral and upper radial canals. Bracts typically ridged, of varied lengths, comprising proximal head-piece with phyllocyst and distal neck-shield but no bracteal canals; cormidium separating from stem as free-swimming eudoxid, each eudoxid producing many gonophores.

Notes

This subfamily includes many of the best known and commonest siphonophore species in the world's oceans. Their success is attributable chiefly to a streamlined body and the ability to bud many gonophores from each eudoxid. This has resulted in a reduction in stem length, which allows the stem to be completely withdrawn into the hydroecium during locomotion, unlike that of the more primitive sulculeolariine diphyid *Sulculeolaria quadrivalvis* described in Section 10.2.3.1.

Diphyines are smaller than sulculeolariines and typically comprise two nectophores that fit tightly together to form a single functional locomotory unit. The posterior nectophore typically bears a swollen process, or apophysis, at the proximal end that fits exactly into the hydroecium of the anterior nectophore. The stem extends posteriorly from its origin between the two nectophores (at the base of the somatocyst of the anterior nectophore) into the gutter-like hydroecium of the posterior nectophore, whence it extends farther posteriorly for feeding. A posterior nectophore is not developed in some diphyine species, such as *Muggiaeae* species (see *M. atlantica* below), *Diphyes chamissonis*, and *Eudoxoides spiralis*; and the stem is withdrawn directly into the hydroecium of the anterior nectophore during locomotion.

The subfamily includes six well-established genera: *Diphyes*, *Lensia*, *Muggiaeae*, *Dimophyes*, *Chelophyes*, and *Eudoxoides* (Totton 1965a; Pugh 1999b). The genus *Lensia* was introduced by Totton (1932) for 6 species that did not fit neatly into the other diphyine genera, and since his time an extraordinary total of 42 species have been referred to it. Some of these species should probably be referred to new genera, but such a revision is outside the scope of the present work. Furthermore, several *Lensia* species are likely invalid, as discussed below. The present Canadian Pacific collection contains representatives of four diphyine genera, *Lensia*, *Dimophyes*, *Muggiaeae*, and *Chelophyes*; *Diphyes* and *Eudoxoides* are absent

because most inhabit warmer waters. An extra genus, *Eudoxia*, was originally introduced for diphyid and clausophyid eudoxids of unknown parentage (see synonymies of *L. conoidea*, *L. multicristata*, *Chelophyes appendiculata*, and *Chuniphyes multidentata* below), but most are now referable to an asexual species. However, the provenance of a few, including *Eudoxia macra* Totton, 1965a, is still unknown.

Furrows are present between the longitudinal ridges in most diphyine anterior nectophores, and these are well shown in several figures by Bigelow and Sears (1937, figs 33, 42, 46, as "apical" views). Totton (1941) also notes their importance in his discussion of the diphyine species *Lensia grimaldi*, pointing out on page 166 that furrows allow the outer nectophore surface to "fold inwards like the cover between the ribs of an umbrella, and then have enough elasticity to expand the nectosac again". He adds the interesting comment "Here we have a mechanism the habitual functioning of which lends itself to evolutionary change". Totton clearly shows the furrows in *L. grimaldi* (1941, fig. 29), and in the present figures of nectophores of diphyine and clausophyid species from Canadian Pacific waters, furrows are indicated by long broken lines (see below).

The generic diagnoses given below for Canadian Pacific diphyines are based mainly on characters of the anterior nectophore, following Totton (1965a) and Pugh (1999b).

Genus *Lensia* Totton, 1932

Diagnosis

Diphyinae with anterior nectophore typically having five or more distinct longitudinal ridges (except *Lensia asymmetrica*, *L. campanella*, *L. meteori*, and *L. subtilis*), typically all complete in five- and seven-ridged forms, including upper ridge; distal lamella dividing into two lappets without pointed cusps; hydroecium typically reduced and not extending anterior of ostium (except in *L. asymmetrica*, *L. havock*, *L. hostile*, *L. lelouvetean*, and *L. quadriculata*); posterior nectophore typically present.

Type species: *Lensia subtiloides* (Lens and van Riemsdijk, 1908).

Notes

This is a catch-all genus that includes all those diphynid species not referable to other, more distinctive genera (Pugh 1999b), as mentioned above. However, previous authors (Pugh 1999b; Pugh and Pagès 1995) have noted that not all are valid. Pugh (1999b) identified only 20 *Lensia* species from the South Atlantic. He found that *Lensia asymmetrica*, shown elsewhere to be a valid species (Pugh and Pagès 1997), is absent from this area.

The present author has examined all *Lensia* specimens collected from Canadian Pacific waters and representative specimens of the other *Lensia* species held in the huge NHM collections (listed under *L. achilles* below). However, other species could not be checked and have therefore been assessed from the literature alone. It is concluded from these studies that of the 42 nominal species so far described, only 22 are likely to be valid: *L. achilles*, *L. ajax*, *L. asymmetrica*, *L. campanella*, *L. challenger*, *L. conoidea*, *L. cordata*, *L. exeter*, *L. fowleri*, *L. grimaldi*, *L. hardy*, *L. havock*, *L. hostile*, *L. hotspur*, *L. hunter*, *L. leloupi*, *L. lelouveteau*, *L. meteori*, *L. multicristata*, *L. quadriculata*, *L. subtilis*, and *L. subtiloides*. A further two species, *L. pannikari*, *L. tottoni*, may also be valid, but others are probably conspecific with valid species, some possibly representing unusual growth forms never found again. The species diagnoses given below are based on the characters of the 22 species listed above.

Separation of *Lensia* species is based on characters of the anterior nectophore alone, since posterior nectophores are so far known for only nine species. Pugh (1999b) and Margulis and Alekseev (1985) recognized four main groups of *Lensia* species, based on the number and completeness of the longitudinal ridges, and the present author concurs. The species with five longitudinal ridges are *L. achilles*, *L. challenger*, *L. conoidea*, *L. cordata*, *L. fowleri*, *L. hardy*, *L. hotspur*, *L. leloupi*, and *L. subtiloides*; the species with seven longitudinal ridges are *L. havock*, *L. hunter*, and *L. multicristata*; the multi-ridged (or multi-striate) species are *L. ajax*, *L. exeter*, *L. grimaldi*, *L. hostile*, *L. lelouveteau*, and *L. quadriculata*; and the species in which the ridges are either difficult to discern or absent are *L. asymmetrica*, *L. campanella*, *L. meteori*, and *L. subtilis*. The present collection contains two five-ridged species, two seven-ridged species, and one multi-striate species. Other *Lensia* species reported from the more southerly northeast Pacific

include five with ranges that extend north to at least off Point Conception on the California coast: *L. challenger*, *L. hotspur*, *L. ajax*, *L. grimaldi*, and *L. subtilis* (*L. cossack* is herein considered a synonym of *L. campanella*, following Margulis and Alekseev 1985) (see records in Alvariño 1985).

In addition to whether or not longitudinal ridges are prominent, and their number, courses, and degree of completeness, several other characters are of taxonomic importance for separating *Lensia* species. They include the length of the mouthplate and hydroecium, the shape of the somatocyst, and the presence or absence of a notch, or emargination, in the posterior border of the lower facet where it joins the anterior wall of the hydroecium. Two additional characters are important in separating the six multi-ridged species, the presence or absence of a velar ridge and the presence of many small cross-ridges between the longitudinal ridges; these characters are discussed further below under *L. hostile*. The species diagnoses given below are therefore derived from a character matrix drawn up by the present author, based on the expression of these characters in the 22 *Lensia* species herein recognized as valid.

In the species descriptions given below, structures are described in relation to their disposition along the long anterior-posterior axis of the anterior nectophore, as shown in Figures 3A and B, not the orientation that most conveniently fits a "portrait" view on the page. The latter orientation has been used in descriptions by most previous authors, but in the present work the extent of the hydroecium and somatocyst is related to nectophore length (from the ostium) rather than to nectophore height.

Lensia achilles Totton, 1941

(Figs 45, 46)

Diphyes truncata Bigelow, 1913: text-fig. 2, pl. 6 fig. 5 (not pl. 6 figs 3, 4, = *Lensia conoidea*) (not Sars, 1846: 41, pl. 7, = *Lensia conoidea*).

Lensia achilles Totton, 1941: 149, figs 6, 7; Totton, 1965a: 171, text-fig. 106; Totton, 1965b: fig. 4; Patriti, 1970a: 293, figs 5A and B; Alvariño, 1981: 409, fig. 174.36; Kirkpatrick and Pugh, 1984: 87, fig. 33; Margulis and Alekseev, 1985: 79, pl. 2v; Alvariño et al., 1990: 30, fig. 42; Pugh, 1999b: 489, fig. 3.87.

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Lensia sp. aff. *leloupi* Totton, 1965a: 162, text-fig. 98.

Lensia baryi Totton, 1965b: 71, figs 1, 2; Alvariño, 1981: 409; Margulis and Alekseev, 1985: 9, pl. 2a; Alvariño et al., 1990: 30, fig. 43; Mapstone and Arai, 1992: 5.

Lensia achilles bigelowi Stepanjants, 1967: 177, figs 118a–c, 119a and b; Stepanjants, 1970: 242, figs 8a and b; Margulis and Alekseev, 1985: 9, fig. 2h.

Lensia eltanin Alvariño and Wojtan, 1984: 51, fig. 2.

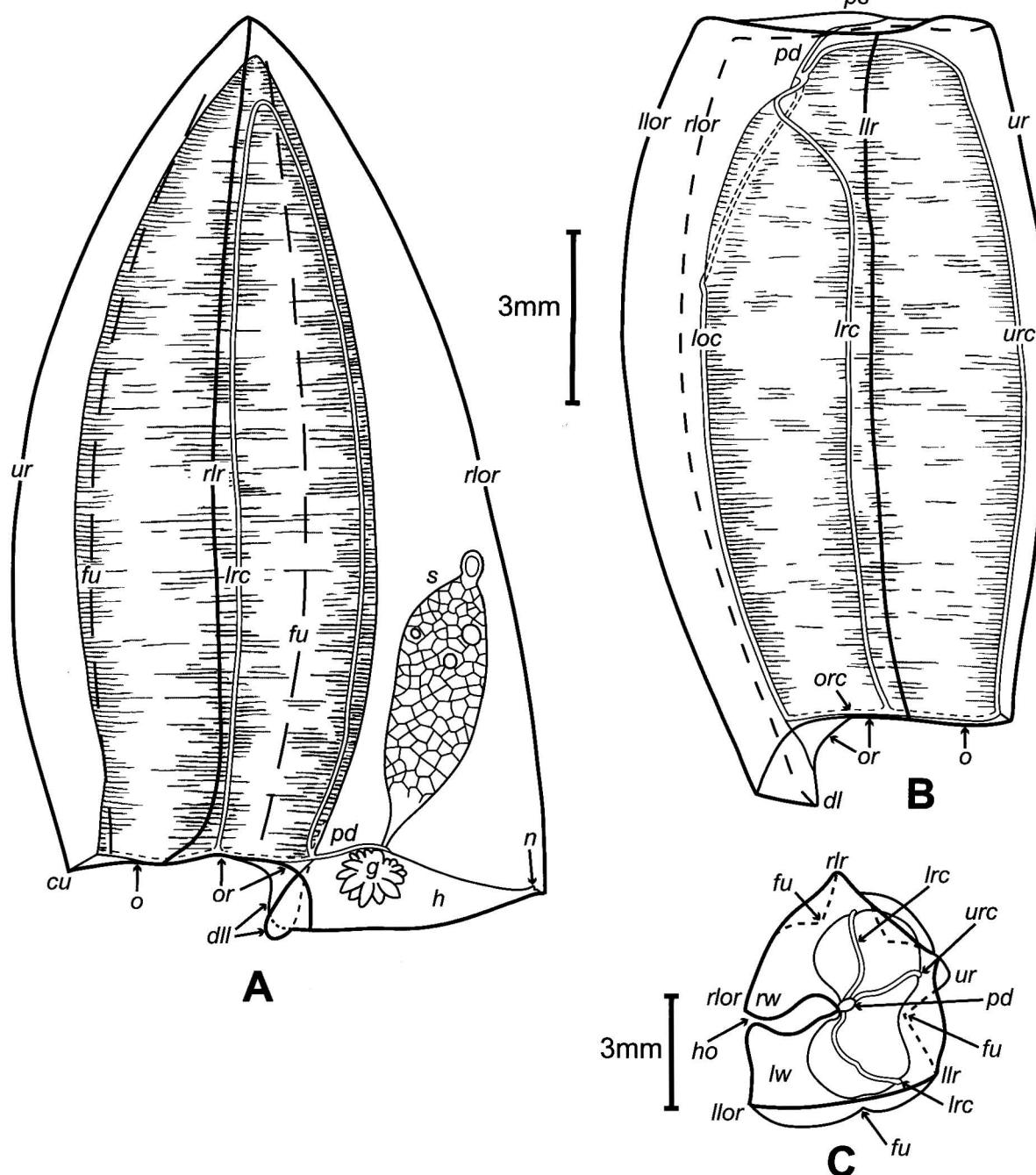


Fig. 45. *Lensia achilles*: A: anterior nectophore, right lateral view; B: posterior nectophore, left lateral view; C: posterior nectophore, proximal view (*cu*, cusp; *dll*, distal lamella (lappets); *fu*, furrow; *g*, gastrozooid(s); *h*, hydroecium; *ho*, hydroecial opening; *llr*, left lateral ridge; *llor*, left lower ridge; *loc*, lower radial canal; *lrc*, lateral radial canal; *lw*, left wing; *n*, notch; *o*, ostium; *or*, ostial ridge; *orc*, ostial ring canal; *pd*, disjunct pedicular canal; *ps*, proximal surface; *rlr*, right lower ridge; *rr*, right lateral ridge; *rw*, right wing; *s*, somatocyst; *ur*, upper ridge; *urc*, upper radial canal).

Diagnosis

Anterior nectophore with five complete longitudinal ridges, laterals bending upwards towards ostium; somatocyst cylindrical or spindle-shaped, varied in thickness and length, reaching 1/5–3/5 nectophore length; hydroecium short, with short mouthplate and anterior hydroecial wall at ostial level; posterior border of lower facet slightly emarginate; posterior nectophore developed.

Material examined

One hundred and ninety-three anterior nectophores and 105 posterior nectophores from Canadian Pacific stations LB12 (450 m) (Fig. 45B) BCPM 996-244-3, LB12 (300, 0–450, 400–0 m), LB13 (300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–500 m) (Fig. 45A) BCPM 996-244-1, LB14 (0–300, 0–500, 500, 0–700, 700 m), LB16 (300 m) (Fig. 45C) BCPM 996-244-2, LB16 (0–700 m) (Fig. 46A) BCPM 996-245-1, LB16 (0–300, 300, 0–500, 500, 700 m), LB17 (0–300, 300, 0–500, 500, 0–700, 700 m), LC9 (0–300, 0–500, 500, 500–0 m), LC10 (0–500, 500, 500–0, 0–575, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 0–500, 500, 0–700, 700, 700–0 m), A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and LD10 (300 m); 6 eudoxids, 29 bracts from stations LB13 (0–300, 0–500, 500, 0–700, 700 m), LB14 (500 m) (Fig. 46B) BCPM 996-245-3, LB14 (0–500 m), LB16 (0–500, 700 m), LB17 (0–500, 0–700 m), LC10 (0–575, 500, 500–0, 700–0, 700 m), LC11 (500, 700 m), and A4 (0–500, 0–700 m); 21 anterior nectophores and 6 posterior nectophores collected near thermal vent from tows 1 (1750–0, 1900–0 m), 2 (1700–0 m), and 3 (1910–1850, 1935–1910 m) (Fig. 11, Table 1); 3 anterior nectophores and 1 posterior nectophore from the Strait of Georgia (for details of sampling area see Mapstone and Arai 1992). Specimens of *Lensia achilles* from the NHM collections: Reg. Nos 1958.1.8.292, holotype, 1 anterior nectophore (33°07'S, 4°30'E); 1958.1.8.298–299, 8 anterior nectophores (34°05'S, 16°00'E); 1958.1.8.300, 1 anterior nectophore (33°20'–33°46'S, 15°18'–15°08'E); 1958.1.8.301–303, 5 anterior nectophores (33°20'–33°46'S, 15°18'–15°08'E); 1958.1.8.304–305, 6 anterior nectophores (1°11'S, 5°38'E); 1958.1.8.320, 1 anterior nectophore (35°14'S, 6°49'E); 1958.1.8.321, 1 anterior nectophore (34°05'S, 16°00'E); 1958.1.8.323–324, 4 anterior nectophores (33°20'–33°46'S, 15°18'–15°08'E); 1958.1.8.325, 1 anterior nectophore (27°24'S, 39°21'E); 1959.8.10.115, 1 anterior nectophore (37°50'S, 35°47'E); 1985.12.9.57, 2 anterior

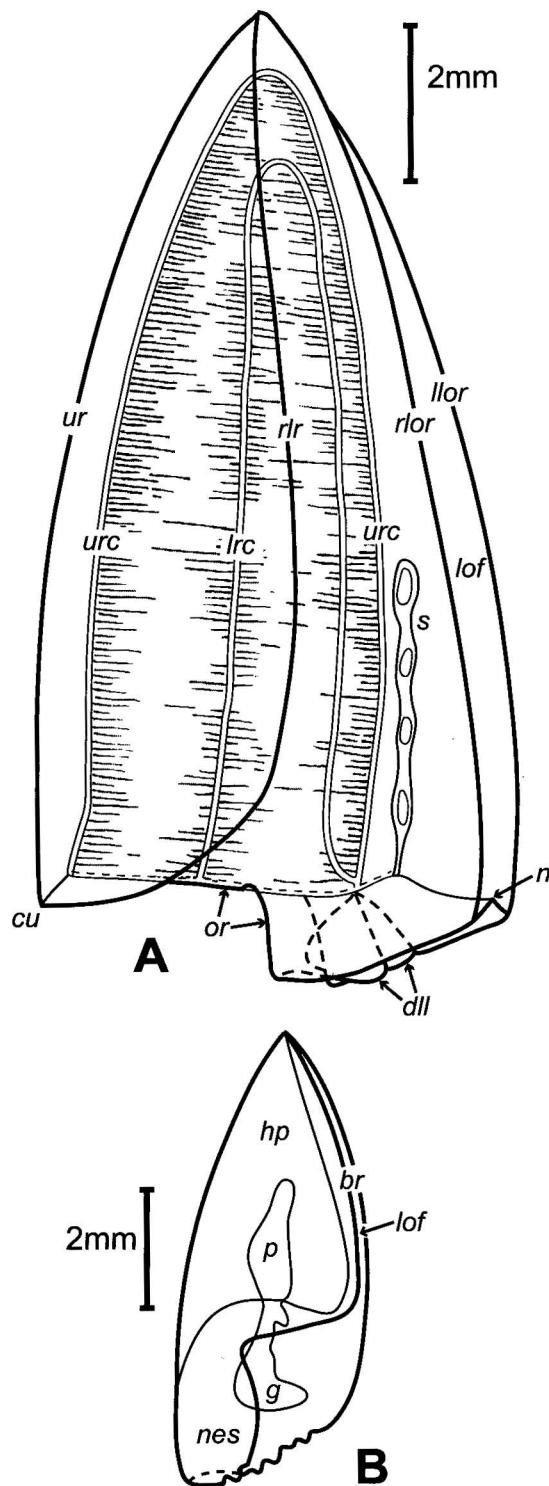


Fig. 46. *Lensia achilles*: A: anterior nectophore, right lateral view; B: bract, right lateral view (br, bracteal ridge; cu, cusp; dll, distal lamella (lappets); g, gastrozooid; hp, head-piece; llor, left lower ridge; lof, lower facet; lrc, lateral radial canal; n, notch; nes, neck-shield; or, ostial ridge; p, phylloctyst; rlor, right lower ridge; rlr, right lateral ridge; s, somatocyst; ur, upper ridge; urc, upper radial canal).

nectophores ($45^{\circ}54'N$, $09^{\circ}39'W$); also specimens labelled *L. baryl*: Reg. No. 1973.5.20.1, 3 syntypes, 2 anterior nectophores, and 1 posterior nectophore ($52^{\circ}14'N$, $127^{\circ}23'W$); specimens of *L. cordata* Reg. Nos 1958.1.8.312, holotype, 8 anterior nectophores ($06^{\circ}05'N$, $52^{\circ}00'E$); 1958.1.8.209, 32 anterior nectophores ($00^{\circ}06'S$, $49^{\circ}45.4'E$); 1958.1.8.314, 1 anterior nectophore ($06^{\circ}05'N$, $52^{\circ}00'E$); 1958.1.8.316, 28 anterior nectophores ($06^{\circ}05'N$, $52^{\circ}00'E$); specimens of other *Lensia* species: Reg. Nos 1958.1.8.333, 1 anterior nectophore of *L. ajax* ($02^{\circ}39'N$, $50^{\circ}46'E$); 1985.12.10.21, 1 anterior nectophore of *L. campanella* ($5^{\circ}20'S$, $39^{\circ}20'E$); 1985.19.9.51, 11 anterior nectophores of *L. cossack* ($40^{\circ}15'N$, $10^{\circ}15'W$); 1973.4.26.35, 18 anterior nectophores of *L. challenger* ($05^{\circ}35.5'S$, $83^{\circ}14.8'W$); 1958.3.7.134, 2 anterior nectophores of *L. exeter* ($06^{\circ}05'N$, $52^{\circ}00'E$); 1973.4.26.36, 11 anterior nectophores of *L. fowleri* ($05^{\circ}35.5'S$, $83^{\circ}14.8'W$); 1973.4.26.52, 1 anterior nectophore of *L. grimaldi* ($34^{\circ}52'N$, $21^{\circ}20'E$); 1958.3.7.292, 2 nectophores of *L. hardy* ($40^{\circ}52'S$, $30^{\circ}6'W$); 1958.3.7.443, 6 anterior nectophores of *L. hotspur* ($33^{\circ}3.75'S$, $17^{\circ}5'E$); 1959.10.23.77, 4 anterior nectophores of *L. hunter* ($36^{\circ}1'S$, $00^{\circ}4'E$); 1958.4.29.106, 32 anterior nectophores of *L. leloupi* ($00^{\circ}44'S$, $08^{\circ}38'E$); 1958.3.7.503, 1 anterior nectophore of *L. lelouvetateau* ($45^{\circ}28'S$, $179^{\circ}06'E$); 1959.3.28.7, 1 anterior nectophore of *L. meteori* ($17^{\circ}54'S$, $01^{\circ}18'W$); 1954.4.2.18–19, 16 anterior nectophores and 6 posterior nectophores of *L. subtilis* (Bay of Villefranche); 1958.4.29.188, 4 anterior nectophores of *L. subtiloides* ($12^{\circ}2'N$, $44^{\circ}23'E$). Also examined were 29 anterior nectophores of *L. achilles* from Discovery Station 10105 No. 12 ($54^{\circ}24'-36^{\circ}N$, $12^{\circ}16'-40^{\circ}W$) (kindly loaned by P.R. Pugh).

Description of material

Anterior nectophores up to 18 mm long, pentagonal, somewhat laterally flattened, with pointed anterior end and lower facet with inverted-V-shaped notch (emargination) in posterior border (Figs 45A, 46A); notch either very shallow (in turgid nectophores; Fig. 45A) or shallow (in more flaccid nectophores, Fig. 46A, *n*); upper longitudinal ridge typically with short distal cusp; lateral longitudinal ridges curving upwards towards ostium distally, with curve long and prominent in flaccid nectophores (Fig. 46A) and shorter and somewhat less prominent in turgid nectophores (Fig. 45A); left and right lower longitudinal ridges delimiting sides of elongate triangular lower facet (Fig. 46A), with posterior end of facet broad across right-left nectophore

axis; ridges smooth in turgid nectophores, and with “crests” in flaccid nectophores (see note below); ostial ridge bordering ostium on upper and lateral sides and extending down each side of distal lamella to posterolateral borders of nectophore as two struts supporting mouthplate (distal lamella); latter broad across right-left axis and short along anterior-posterior axis, dividing into two large rounded lappets similar in size and with smooth inner borders; lappets overlapping in turgid nectophores (Fig. 45A), typically reflexed into hydroecium in flaccid nectophores (Fig. 46A); four longitudinal furrows discernible in best preserved nectophores between upper and lateral ridges and between lateral ridges and lower nectosac border (two right furrows shown in Fig. 45A); furrows extending from near anterior end of nectophore to ostium; upper part of nectophore, including upper ridge, reflexed into nectosac along lines of two lateral ridges in some flaccid nectophores (not illustrated); mesogloea turgid to flaccid; hydroecium shallow, with anterior wall approximately level with ostium in lateral view (Figs 45A, 46A); somatocyst varying in length (see diagnosis above), typically opaque, and swollen with many oil droplets and constriction near tip enclosing single oil droplet (Fig. 45A), atypically more translucent and thin, without constriction, and having either several oil droplets (Fig. 46A) or none (not illustrated); nectosac with thick musculature in best preserved nectophores (Figs 45A, 46A), muscles lost during preservation in some others; disjunct pedicular canal originating at somatocyst-stem junction on anterior wall of hydroecium and passing to ostial ring canal on lower side of nectosac (Fig. 45A); upper radial canal originating from junction of ostial ring canal with disjunct pedicular canal (on lower side of nectosac), passing anteriorly along lower surface of nectosac, over anterior end of nectosac, and back along upper surface of nectosac to insert onto ostial ring canal in upper midline (Fig. 46A); lateral radial canals each originating from junction of upper radial canal with ostial ring canal on lower nectosac surface, following elongate looped course over lateral nectosac wall, and rejoining ostial ring canal closer to upper side of nectosac (Figs 45A, 46A); lower radial canal not developed; ostial ring canal not clearly discernible in any specimens but deduced position indicated by fine broken line in Figures 45A, 46A; velum lost during preservation; external pedicular canal linking stem with anterior wall of hydroecium (at base of somatocyst) very short and obscured by stem components in Figure 45A; internal pedicular canal not developed.

Posterior nectophores up to 13 mm long, with truncate proximal articular surface, broad distal ostium, and short distal lamella extending distad of ostium on lower side (Fig. 45B); two prominent asymmetric hydroecial wings arising from lower side of nectophore, enclosing hydroecium, and extending from proximal surface to distal lamella, with lower margin of right wing more pointed than that of left wing (Fig. 45C); five longitudinal ridges, all complete: upper ridge, right and left lateral ridges, and right and left lower ridges; lateral ridges each curving upwards slightly towards ostium; right lower ridge bordering elongate hydroecial opening and left lower ridge bordering left lower lateral margin of nectophore (Fig. 45C); ostial ridge circumscribing upper and lateral regions of ostium and extending as strut distally to join posterior end of lower ridge on each side of distal lamella (Fig. 45B); distal lamella short, undivided, with entire distal border straight; four longitudinal furrows, between upper and lateral ridges and between lateral ridges and lower ridges, most easily discerned in proximal view (Fig. 45C) (excluded from Fig. 45B because less obvious in lateral view); mesogloea flaccid; hydroecium shallow and elongate, extending along lower surface of nectophore from proximal to distal end, of approximately uniform depth throughout (across upper-lower axis); disjunct pedicular canal short, originating at proximal end of hydroecium (Figs 45B and C) and passing distally along hydroecial wall to point of origin of radial canals on lower surface of nectosac (Fig. 42B); internal pedicular canal not developed; nectosac with radial canals originating together from disjunct pedicular canal; upper radial canal passing first upwards over proximal end of nectosac, then distad along upper wall of nectosac to insert onto upper side of ostial ring canal (presumed position) (Fig. 45B); lower radial canal passing from same junction distally along lower surface of nectosac in midline to lower side of ostial ring canal; lateral radial canals each passing from junction with disjunct pedicular canal and upper and lower radial canals, over lateral walls of nectosac, following slightly sigmoid course (through two obtuse angles) proximally, and inserting distally onto lateral regions of ostial ring canal (Fig. 45B).

Eudoxids probably referable to this species (see notes below) comprising bract and gonophore. Bracts 3–7 mm long, with conical head-piece (see Section 10.2.3) and lower facet delimited by two bracteal ridges (Fig. 46B); neck-shield asymmetric

and elongate, with left side longer than right side, and right side with notch / right angle near junction with head-piece; bracteal hydroecium shallow and distal margin of bract typically scalloped; phyllocyst central, extending proximally to 1/2 length of bract (from proximal surface of bracteal hydroecial cavity). Gonophores 3–7 mm long (not illustrated), with proximal end narrower than distal end and having four complete longitudinal ridges (two extending distally onto short mouthplate); nectosac large and filling gonophore; hydroecium and mantle canals not discerned.

Distribution

Geographic. Canadian Pacific waters: Jervis Inlet (Mackie 1985); northern Strait of Georgia (Mackie 1985); central Strait of Georgia (Mackie 1985; Mapstone and Arai 1992); off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993); Knight Inlet (Mackie 1985); Burke Channel (Totton 1965b). Northeast Pacific: off San Diego (Alvariño 1967b, 1985); off Monterey, California (Alvariño 1985); California region (Margulis and Vereshchaka 1994). Other regions: few other Pacific records, from subtropical to high southern and northern latitudes (Alvariño et al. 1990; Margulis and Vereshchaka 1994); similarly sparse records from other oceans, though reported to be widespread in the Atlantic (Margulis 1971; Kirkpatrick and Pugh 1984).

Vertical. In the present study *Lensia achilles* was collected from 300, 500, and 700 m and between 1910 and 1935 m. At a number of locations in the Strait of Georgia and adjacent inlets it was recorded between 150 and 600 m (Mackie 1985), and records from elsewhere are from a range of at least 0–2000 m (Alvariño 1967b; Margulis 1971; Pugh 1974b; Casanova 1980).

Notes

The name *Lensia achilles* was introduced by Totton (1941) for a deep-water orange diphyid collected at three Discovery stations off southwest Africa. It had five complete ridges in the anterior nectophore, including lateral ridges bending upwards (previously *dorsad*) near the ostium, and a spindle-shaped somatocyst (Totton 1941). Later, two more small and superficially similar diphyines, *L. baryi* and *L. cordata*, from Burke Inlet, Vancouver Island, and the east coast of Africa, respectively, were added to the genus (Totton 1965b). Both also had upwardly

curving lateral ridges and an anterior hydroecial wall approximately level with the ostium, but differed in the shapes of their somatocysts. A number of specimens of these three species from the NHM collections were examined by the present author, as well as a specimen of *L. achilles* from the North Atlantic kindly loaned by P.R. Pugh (see list above), and were compared with the large number of similar *Lensia*-type nectophores collected in Canadian Pacific waters. From this comparison, it is clear that *L. cordata* represents a distinct species because the somatocyst is shorter than that of any other specimens examined, and extends to a maximum of only 1/10 nectophore length (from the ostium). However, in the remaining specimens the somatocyst varies from 1/4 to 1/2 nectophore length and forms a continuous series from the short to the more elongate condition. Somatocyst length is unrelated to mesogloal turgidity; the somatocyst can be elongate in both turgid and flaccid nectophores, as shown in Figures 45A and 46A, and also short in both types (not illustrated).

Two other characters that Totton (1965b) uses to distinguish the anterior nectophores of *Lensia baryi* from those of *L. achilles* include the absence of a notch, or emargination, in the posterior border of the triangular lower facet of *L. baryi*, and the absence of crests on the ridges. Close examination of the NHM *Lensia* nectophores reveals a very shallow notch in the posterior margin of the lower facet of all *L. baryi* nectophores and a deeper one in those of *L. achilles*. Thus, it is herein concluded that the extent of the notch is related to mesogloal turgidity, since the notch is shallow to very shallow in turgid nectophores and slightly deeper in more flaccid ones. Cresting of the ridges is also related to mesogloal turgidity, since in nectophores with turgid mesogloea there is no adhesion of the epidermis below each ridge to produce a "crest", whereas in flaccid nectophores such crests are often apparent, though they are almost certainly a preservation artefact. For these reasons, *L. baryi* in samples from Canadian Pacific waters is considered a junior synonym of *L. achilles*, as given in the synonymy list above.

Lensia achilles bigelowi (Stepanjants, 1967) differs from *L. a. achilles* only in having two hollows in the anterior wall of the hydroecium of the anterior nectophore, one on each side of the midline. Similar

hollows were observed in a few of the present *L. achilles* nectophores, and have also been shown in some anterior nectophores of *L. conoidea* (Bigelow and Sears 1937, figs 32A and B); they are not herein considered to be a character of sufficient significance to justify the designation of *L. a. bigelowi* as a separate subspecies.

The bracts here tentatively ascribed to *Lensia achilles* are of similar proportions to those illustrated by Stepanjants for *L. a. bigelowi* (1967, fig. 119B; 1970, fig. 8B), although the scalloped margin of the neck-shield was not shown by Stepanjants, probably because this margin is very translucent and the scallops are difficult to identify. Stepanjants' material is therefore referred to *L. achilles* in the synonymy given above. Phyllocysts of these tentative Canadian Pacific *L. achilles* bracts are shorter than those of *L. conoidea* bracts collected in the same area (see description below). No bracts of *L. multicristata* were found in the present collection, but published figures of bracts referable to this species have shorter phyllocysts (see below) than those of either *L. achilles* or *L. conoidea*. Pugh and Pagès (1995, p. 189) note that in bracts of *Lensia* species "The shape of the phyllocyst appears, to some extent, to reflect that of the somatocyst in the anterior nectophore", as already noted in Section 10.2.3, and this seems to be true for bracts of both *L. achilles* and *L. conoidea*. Also, the neck-shield of the Canadian Pacific *L. achilles* bracts is longer than that of the *L. conoidea* bracts collected. Although both bract types are herein referred to *L. achilles* and *L. conoidea*, it is not possible to be completely certain of their identity because bracts are still unknown for the two other species described below from deeper Canadian Pacific waters, *L. havock* and *L. hostile*.

Illustrations of both anterior and posterior nectophores of *Lensia eltanin* (Alvariño and Wojtan 1984, figs 2a and b) are similar to those given here for *L. achilles* (figs 45A and B), and indeed, the present author concurs with Pugh (1999b) in referring *L. eltanin* to *L. achilles*. Pugh also states that the posterior nectophore of *L. achilles* has not been described, whereas that previously referred to *L. baryi* by Totton (1965b, p.73, Figs 2A-C) is now referable to *L. achilles* (see above), and is also described and figured in the present work.

***Lensia conoidea* (Keferstein and Ehlers, 1860)**

(Figs 47, 48)

Diphyes sp. Stuwitz, 1836: 251, pl. 9 figs 1–14.

Diphyes truncata Sars, 1846: 41, pl. 7 figs 1–15; Bigelow, 1913: 73 (in part), pl. 6 figs 3, 4 (not text-fig. 2, = *Lensia achilles*; not pl. 6 fig. 5, indet.) (not Quoy and Gaimard, 1827: 7, pl. 1 figs 1–7, = *Diphyes dispar*); Sverdrup, 1921: 28, pl. 4 figs 18a–c; Browne, 1926: 77; Hong, 1964: 114 (in part), pl. 7 fig. 3 (not Chiu, 1954: 47, pl. 6 fig. 22, indet.).

Galeolaria truncata: Huxley, 1859: 38; Haeckel, 1888b: 363; Vanhöffen, 1906: 15, figs 10–12; Lens and van Riemsdijk, 1908: 57; Bigelow, 1911b: 346 (in part); Moser, 1917: 729 (in part), ?pl. 2 figs 1, 2; Moser, 1920: 177 (in part); Moser, 1925: 154 (in part), pl. 4 figs 3, 4 (not pl. 3 figs 7, 8, indet.) (not Kawamura, 1915e: 429, pl. 12 fig. 13, or Kawamura, 1954: 102, = ? *Sulculeolaria monoica* or *S. turgida*).

Diphyes conoidea Keferstein and Ehlers, 1860: 259; Keferstein and Ehlers, 1861: 16, pl. 1 fig. 26, pl. 3 fig. 10, and pl. 5 figs 6, 7, 26d.

Epibulium truncata: Haeckel, 1888a: 35.

Diphyes appendiculata Vanhöffen, 1906: 15 (in part), figs 10–12 (not Eschscholtz, 1829: 138 and 139, pl. 12 fig. 7, = *Chelophyes appendiculata*).

Lensia truncata: Totton, 1932: 364.

Lensia conoidea: Totton, 1936: 235; Bigelow and Sears, 1937: 48 (in part), figs 27–30a, 32–34 (not fig. 30b, = *L. subtiloides*, or figs 31, 35, = indet.); Totton, 1954: 114, fig. 56; Patriti, 1964: 217 (in part), pl. 4 figs c, d; Totton, 1965a: 162, text-fig. 99A and pl. 31 fig. 11; D. Carré, 1967: 233, pl. 1 figs 1–3; Daniel, 1974: 132 (in part), text-figs 10o and p; Alvariño, 1981: 410 (in part), fig. 174.39; Kirkpatrick and Pugh, 1984: 88, figs 34A–C; Pagès and Gili, 1992b: 87 (in part), ?fig. 29; Pugh and Pagès, 1995: figs 4a and b; Pugh, 1999b: 490, figs 3.89, 3.107; Gamulin and Kršinic, 2000: 61 (in part), figs 30a–c.

Lensia conoidea conoidea Stepanjants, 1967: 180; Margulis and Alekseev, 1985: 9.

Lensia conoidea pacifica Stepanjants, 1967: 180, fig. 121; Margulis and Alekseev, 1985: 9, pl. 2k.

Lensia conoidea (lapsus calami) Xu and Zhang, 1978: 41; Gao et al., 2002: 128 (in part), fig. 69.

Diagnosis

Anterior nectophore with five complete longitudinal ridges, laterals straight; somatocyst tubular or spindle-shaped, of variable thickness, and reaching 1/2 nectophore length; hydroecium short, with very short mouthplate and anterior hydroecial wall lying posterior of ostium; posterior border of lower facet not emarginate; posterior nectophore developed.

Material examined

Four thousand, four hundred and twenty-four anterior nectophores and 3550 posterior nectophores from Canadian Pacific stations LB8 (130 m), LB12 (0–300, 300, 400–0, 0–450, 450 m), LB13 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–300, 300, 0–500, 500, 500–0, 0–700, 700 m), LB16 (0–300, 300, 0–500, 500, 0–700, 700 m), LB17 (0–300 m) (Figs 47A and B) BCPM 996-246-1, LB17 (0–300, 300, 300–0, 0–500, 500, 0–700, 700 m), LC2 (0–60 m), LC6 (0–80 m), LC9 (0–300, 300, 300–0, 0–500, 500, 500–0 m), LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–575, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and LD10 (300 m); 31 bracts and 2 eudoxids from stations LB12 (450 m), LB13 (700 m) (Fig. 47C) BCPM 996-247-1, LB13 (0–500, 500–0, 0–700, 700, 700–0 m), LB14 (0–300, 0–500 m), LB16 (0–300, 300, 0–700 m), LB17 (0–300, 500 m), LC9 (500 m), LC10 (500, 500–0, 700–0 m), LC11 (500, 0–700, 700 m), and A4 (0–300, 0–500, 0–700 m); 26 anterior nectophores and 10 posterior nectophores collected near thermal vent from tows 1 (1750–0, 1750–1800, 1900–0 m), 2 (1700–0, 0–2200 m), and 3 (1845–2100, 1910–1850 m) (Fig. 11, Table 1). Specimens of *Lensia conoidea* from the NHM collections: 10 anterior nectophores, 33 bracts, and 8 gonophores Reg. Nos 1950.7.31.182–200 and 1950.7.31.94–121 (both from the Manihine Irish Collection, Station 5 off southwest Ireland), 1985.12.9.41 (45°54'N, 09°39'W), and 1973.5.31.77 (Bay of Villefranche).

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

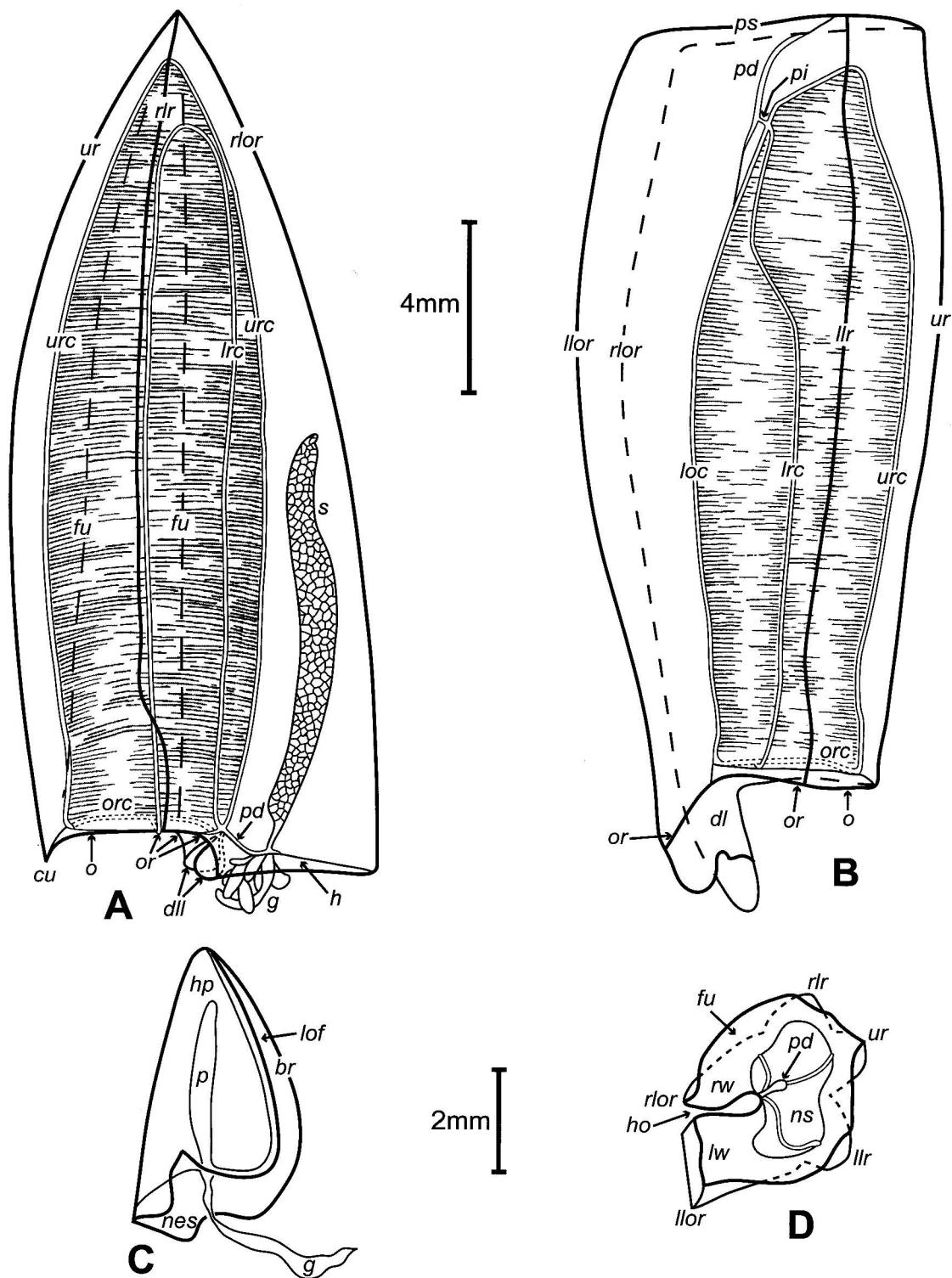


Fig. 47. *Lensia conoidea*: A: anterior nectophore, right lateral view; B: posterior nectophore, left lateral view; C: bract, right lateral view; D: posterior nectophore, proximal view (*br*, bracteal ridge; *cu*, cusp; *d(l)*, distal lamella (lappets); *fu*, furrow; *g*, gastrozooid(s); *h*, hydroecium; *ho*, hydroecial opening; *hp*, head-piece; *llr*, left lateral ridge; *llor*, left lower ridge; *loc*, lower radial canal; *lof*, lower facet; *lrc*, lateral radial canal; *lw*, left wing; *nes*, neck-shield; *ns*, nectosac; *o*, ostium; *or*, ostial ridge; *orc*, ostial ring canal; *p*, phylloctyst; *pd*, disjunct pedicular canal; *pi*, internal pedicular canal; *ps*, proximal surface; *rlr*, right lower ridge; *rlr*, right lateral ridge; *rw*, right wing; *s*, somatocyst; *ur*, upper ridge; *urc*, upper radial canal).

Description of material

Anterior nectophores up to 25 mm long, slender, pentagonal, somewhat laterally flattened, with pointed anterior end (Fig. 47A) and lower facet with straight posterior border (not illustrated); upper longitudinal ridge with short pointed distal cusp; lateral longitudinal ridges straight and bending inwards slightly towards ostium distally (effectively away from viewer in lateral view shown in Fig. 47A, giving false impression that this ridge bends downwards towards ostium); lower longitudinal ridges delimiting elongate sides of slender triangular lower facet; all ridges smooth; ostial ridge bordering ostium on upper and lateral sides and extending down each side of distal lamella to posterolateral borders of nectophore as two struts supporting mouthplate; distal lamella broad across right-left axis, very short along anterior-posterior axis, comprising two rounded lappets of similar sizes, with left lappet overlapping right lappet in upper view (not illustrated); four longitudinal furrows discernible on lateral surfaces from near anterior end of nectophore to ostium (two right furrows only shown in Fig. 47A); mesogloea turgid; hydroecium very shallow with anterior wall lying posterior of ostial aperture in lateral view, typically flat (Fig. 47A) and atypically slightly hollowed out on each side of hydroecial midline (not illustrated); somatocyst elongate, tubular, with short stalk, consistently extending to same length in almost all specimens measured, typically thickened along entire length (Fig. 47A), atypically thinner throughout (not illustrated); nectosac with thick opaque musculature in all nectophores; disjunct pedicular canal passing from somatocyst-stem junction (on anterior wall of hydroecium) to ostial ring canal on lower side of nectosac (Fig. 47A); upper radial canal originating from ostial ring canal at this junction, passing anteriorly along lower surface of nectosac, over anterior end, returning along upper surface of nectosac, and inserting onto ostial ring canal in midline on upper side of nectosac (Fig. 47A); lateral radial canals originating from same ostial ring canal junction, passing anteriorly along lateral walls of nectosac, and looping over near anterior end, returning to ostial ring canal and inserting onto it midlaterally (Fig. 47A); lower radial canal not developed; ostial ring canal lying in velum (approximate course indicated by fine broken line in Fig. 47A); velum occupying 1/2 diameter of ostial aperture, aligned at right angles to long axis of nectophore, only evident in posterior view (not illustrated); external pedicular canal very short and occluded by stem components in Figure 47A; internal pedicular canal not developed.

Posterior nectophores up to 18 mm long and slender, with truncate proximal articular surface, narrow distal ostium, and elongate distal lamella extending distad from ostium on lower side (Fig. 47B); distal lamella dividing into two asymmetric lobes distally, with right lobe slightly longer than left (Fig. 47B); two prominent asymmetric hydroecial wings on lower side of nectophore, enclosing hydroecium and extending from proximal surface to distal lamella; left wing deep across upper-lower axis, with blunt, broad lower margin, and right wing shallower, with pointed lower margin (Fig. 47D); five longitudinal ridges, all complete and approximately straight: upper ridge, right and left lateral ridges, and right and left lower ridges; right lower ridge bordering elongate hydroecial opening, left lower ridge bordering left lower lateral margin of nectophore (Fig. 47D); ostial ridge circumscribing ostium on upper and lateral sides and extending distally as strut to distal end of lower ridge on each side of distal lamella (Fig. 47B); four longitudinal furrows between upper and lateral ridges and between lateral ridges and lower ridges, unclear in lateral view, but easily discerned in proximal view (Fig. 47D); mesogloea turgid; hydroecium an elongate cavity extending along lower surface of nectophore from proximal end to distal end, deepest at proximal end (along upper-lower axis), shallower at distal end (Fig. 47B); disjunct pedicular canal originating at proximal end of hydroecium (Fig. 47D), passing distally along hydroecium as shown in Figure 47B, and extending distally for short distance beyond origin of internal pedicular canal; latter short and thick, inserting onto nectosac at approximately 9/10 nectophore length (from ostium) and giving rise to four radial canals: upper radial canal initially extending proximally over pointed proximal end of nectosac and then distally along upper wall of nectosac to upper side of ostial ring canal (Fig. 47B); lower radial canal extending distally along lower wall of nectosac in midline to lower side of ostial ring canal; lateral radial canals extending over lateral walls of nectosac and following slightly sigmoid course to ostial ring canal, as shown in Figure 47B; ostium lying in velum (approximate course indicated by fine broken line in Fig. 47B).

Eudoxids probably referable to this species (see notes below) comprising bract and gonophore. Bracts 4–5 mm long, with conical head-piece and lower facet delimited by two bracteal ridges (Fig. 47C); neck-shield asymmetric and short, with left side slightly longer than right, and right side

with distinctive notch or right angle at junction with head-piece; bracteal hydroecium shallow, with distal margin of bract either smooth or with small scallops (not shown); phyllocyst central, sometimes swollen medially, extending to 4/5 bract length (from proximal surface of bracteal cavity). Gonophores 3–5 mm in length (not illustrated); proximal end truncate and narrower than distal end; four complete longitudinal ridges, straight or slightly twisted; mouthplate short and entire; nectosac filling gonophore and having four straight radial canals; hydroecium and mantle canals not discerned.

Distribution

Geographic. Canadian Pacific waters: central Strait of Georgia (Mapstone and Arai 1992); off west coast of Vancouver Island (present collection, see

list of stations above; first reported in Arai et al. 1993). Northeast Pacific: off California and Baja California (Alvariño 1980c, 1985); California coastal waters (Alvariño and Kimbrell 1987); off San Diego, California (Alvariño 1967b); San Diego Bay (Mackie and Boag 1963); Monterey Bay (Silguero and Robison 2000); off Oregon (Pearcy 1972); Friday Harbor (Mackie and Mackie 1963; Mills 1981); 40°–60°N, 150°–120°W, northeast Pacific (Stepanjants 1967). Other regions: many records from elsewhere in the Pacific, with more from temperate than from tropical latitudes (for example, Alvariño et al. 1990; Gasca and Suárez 1992a; Palma et al. 1999; Gao et al. 2002); *Lensia conoidea* has a similar latitudinal distribution in the Atlantic (Alvariño 1981; Kirkpatrick and Pugh 1984) and is considered common north of latitude 40°N (Pugh 1990), though it was rated a worldwide cosmopolitan species by Margulis (1989).

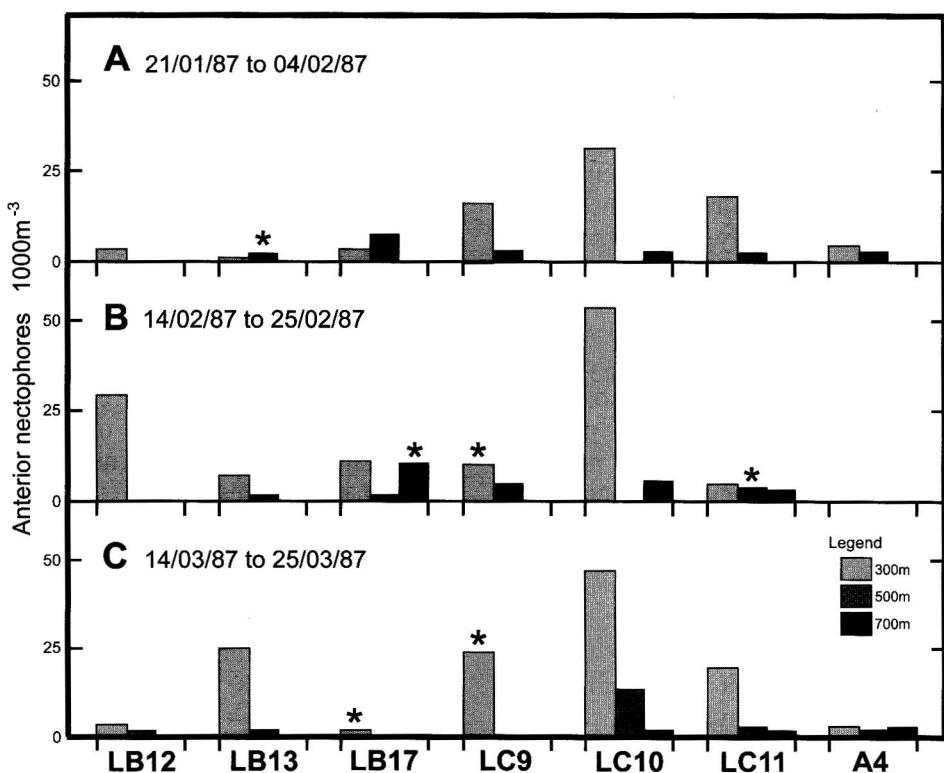


Fig. 48. Winter and spring abundance of anterior nectophores of *Lensia conoidea* at seven stations during three cruises, from 21 January to 4 February 1987 (A), 14 to 25 February 1987 (B), and 14 to 25 March 1987 (C). An asterisk denotes a sample collected at night; all other samples were collected during daylight hours.

Vertical. Margulis (1972a) classified *Lensia conoidea* as a broadly tropical species that inhabits deeper layers in tropical regions and shallower layers in temperate regions. Off Vancouver Island it was more abundant at 300 m than at 500 or 700 m during daylight hours (Fig. 48) and a similar depth range was noted for *L. conoidea* in Californian waters (Alvariño 1967b, 1985; Silguero and Robison 2000). *Lensia conoidea* was also collected between 1750–1800 and 1850–1910 m in samples from the hydrothermal-vent plume. In the North Atlantic the depths at which maximum numbers were collected varied from the top few hundred metres to 1500 m at different locations (Pugh 1990 and references therein). Diel migration (see Section 4.1) has been reported in this species at some locations (Angel et al. 1982; Pugh 1984; Andersen et al. 1992, 2001b; Sardou and Andersen 1993).

Notes

Sars (1846) was the first author to reasonably figure *Lensia conoidea*, showing the characteristically long, slender somatocyst of the anterior nectophore and the unique elongate and partially bilobed mouthplate of the posterior nectophore. However, Bigelow (1911b, 1913) and Moser (1925) later confused *L. conoidea* with *L. subtiloides* (as *Diphyes subtiloides*) and *L. multicristata* (as *Muggiae kochi*), and Moser (1925) also confused *L. conoidea* with *L. fowleri* (as *D. fowleri*) and *C. appendiculata* (as *D. sieboldii*). Hence, most entries for these authors are designated “in part” in the synonymy given above, and many of their mistakes were first noted by Totton (1965a, p. 162). Although *L. conoidea* and *L. subtiloides* are both five-ridged species, with all ridges complete and lateral ridges straight, the anterior nectophore of *L. subtiloides* differs from that of *L. conoidea* in being typically much shorter (maximum 5 mm) and having a shorter, oblique, ovoid somatocyst. In *L. conoidea* the somatocyst is cylindrical and longer, reaching 1/2 nectophore length (range 2/5–1/2) in specimens from Canadian Pacific waters, and nectophores typically extend to 23 mm (range 7–25 mm). In the NHM *L. conoidea* specimens examined, the somatocysts were slightly longer, extending to 3/5 nectophore length (from the ostium), but the nectophores themselves were shorter, reaching only 9 mm maximum length. The somatocyst of the *L. conoidea* specimen shown by Pagès and Gili (1992b, fig. 29) is shorter than in any of the material examined for the present work, and may have either been damaged or come from an atypical population.

A recent figure of an *L. conoidea* anterior nectophore by Gamulin and Kršinic (2000, fig. 30a) from the Mediterranean shows a somatocyst within the length range of those found in Canadian Pacific waters, and a clear upper cusp (absent from *L. subtiloides*) at the ostium, although the somatocyst is more spindle-shaped than in Canadian Pacific specimens; the synonymy given by these authors is designated “in part” because they list a paper by Moser. It was emphasized by Pugh (1999b, p. 491) that *L. subtiloides* is “largely an Indo-Pacific neritic species” and therefore absent from the Mediterranean. *Lensia conoidea* is a common species in the Mediterranean (Bouillon et al. 2004).

In many anterior nectophores from Canadian Pacific *Lensia conoidea*, the length attained by the somatocyst is similar to that of the longest *L. achilles* somatocysts measured; however, the two species can be distinguished not only by the different courses followed by their lateral longitudinal ridges (straight in *L. conoidea*, bending upwards near the ostium in *L. achilles*), but also by the type of thickening of the somatocyst. In *L. conoidea* the somatocyst is evenly thickened along its length whether or not it contains large oil droplets, whereas the surface of the *L. achilles* somatocyst follows the contours of large oil droplets (in preserved specimens) whether swollen and spindle-shaped (Fig. 45A) or thin throughout (Fig. 46A).

Posterior nectophores of *Lensia conoidea* are easily distinguishable from those of the other nine *Lensia* species for which such nectophores are known because they have a unique elongate and asymmetrically bilobed mouthplate (Fig. 47B). Bigelow (1913) correctly assigned a posterior nectophore illustrated in his plate 6 figures 3 and 4 to *L. conoidea* (as *Diphyes truncata*) even though the anterior nectophore he showed in his text-figure 2 under the same name is in fact that of *L. achilles* (see the synonymy for this species above). Since then, the few authors who have figured the posterior nectophore of *L. conoidea* have likewise identified it correctly, including Bigelow and Sears (1937) and Kirkpatrick and Pugh (1984).

Stepanjants (1967) and Margulis and Alekseev (1985) refer large specimens of *Lensia conoidea* from the Pacific to a new subspecies, *Lensia conoidea pacifica*, with the type specimen, No. 2/9224, held at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (Savitskaja 1977). This

subspecies is distinguished from *L. c. conoidea* by a deeper hydroecium and wrinkles around the ostium. However, these minor features are unlikely to reflect morphological differences, and are probably due to diet or changes occurring at preservation. The present author does not, therefore, recognize this subspecies.

Most bracts herein identified as referable to *Lensia conoidea* were collected in the same samples as anterior and posterior nectophores of *L. conoidea*, and in the absence of other diphyid species. Comparing them with bracts of *L. conoidea* from the NHM collections (from the Bay of Villefranche, identified by A.K. Totton) reveals that in Totton's *L. conoidea* specimens the phyllocyst is more elongate and slender and the neck-shield shorter than in the bracts ascribed to *L. achilles* in the present work (see above). The eudoxid of *L. conoidea* has been described several times since it was first reported by Sars (1846), and a more detailed illustration by Moser (1917) was repeated in her other papers and also by Totton (1965a), Kirkpatrick and Pugh (1984), and Bouillon et al. (2004). Other less detailed illustrations are given by Sverdrup (1921), Patriti (1964), D. Carré (1967), Pugh and Pagès (1995), and Pugh (1999b). The Canadian Pacific material agrees with all these figures. However, Alvariño (1981) incorrectly states that the gonophore of *L. conoidea* has five ridges, and the gonophores of all *Lensia* species, including all those referable to *Lensia* species from Canadian Pacific waters, have only four (Pugh and Pagès 1995).

Since the eudoxids of a number of *Lensia* species have not yet been described, it is only possible to be absolutely sure of the identification of any collected eudoxids when asexual stages of a single *Lensia* species are also present, or when the eudoxids of all species in the area are known. Five species of the genus *Lensia* have so far been collected from Canadian Pacific waters, of which *L. conoidea* is by far the most abundant. Eudoxids of *L. havock* and *L. hostile* have not yet been described, but anterior nectophores of these species were collected in much deeper water than the present eudoxids, so it is unlikely that the present bracts are associated with either of these species. Some of the eudoxids herein ascribed to *L. conoidea* were, however, collected in the same samples as nectophores of *L. achilles* and *L. multicristata*. As noted above, the bracts of *L. achilles* probably have a slightly shorter phyllocyst and longer neck-shield than those of *L. conoidea*, while the bracts of *L. multicristata* (see Gamulin 1966, as *Eudoxia dohrni*; Gamulin and Kršinic

2000, as *L. multicristata*) have a shorter phyllocyst than both these species, and a shorter neck-shield than *L. conoidea*.

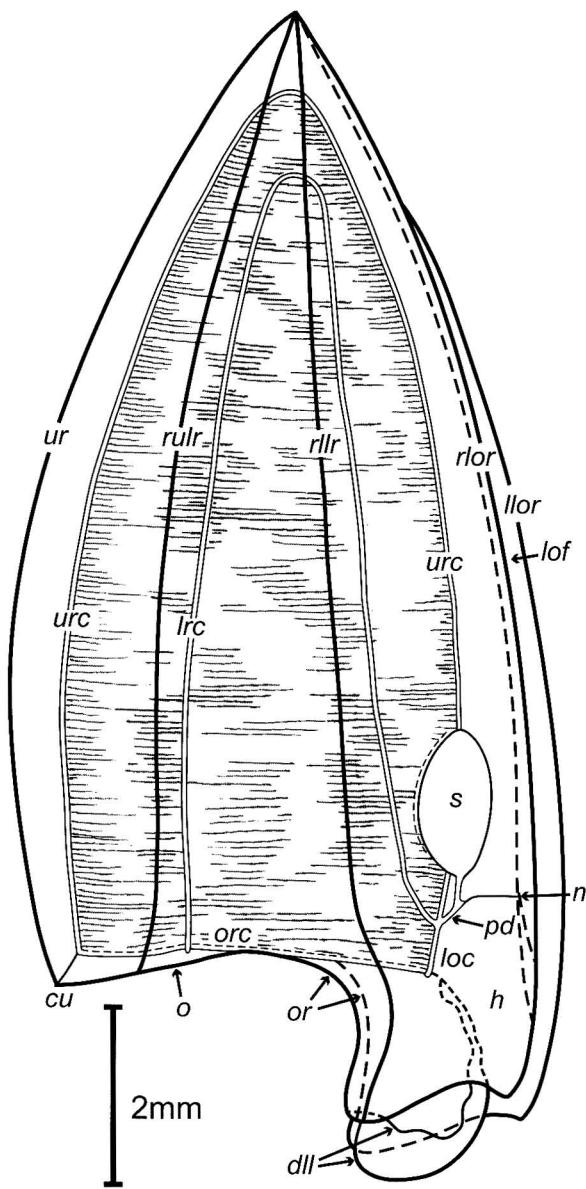


Fig. 49. *Lensia havock*, anterior nectophore, right lateral view (*cu*, cusp; *dll*, distal lamella (lappets); *h*, hydroecium; *llor*, left lower ridge; *loc*, lower radial canal; *lof*, lower facet; *lrc*, lateral radial canal; *n*, notch; *o*, ostium; *or*, ostial ridge; *orc*, ostial ring canal; *pd*, disjunct pedicular canal; *rllr*, right lower lateral ridge; *rlor*, right lower ridge; *rulr*, right upper lateral ridge; *s*, somatocyst; *ur*, upper ridge; *urc*, upper radial canal).

***Lensia havock* Totton, 1941**

(Fig. 49)

Lensia multicristata Totton, 1936: 235 (not Moser, 1925: 165, pl. 3 fig. 9, = *L. multicristata*).

Lensia havock Totton, 1941: 159, figs 17–19; Totton, 1965a: 175, text-fig. 114; Pugh, 1974b: 57; Alvariño, 1981: 412, fig. 174.45; Kirkpatrick and Pugh, 1984: 94, fig. 38; Daniel, 1985: 375, figs 100a and b; Mackie et al., 1987: 120; Pugh, 1999b: 490, fig. 3.93 (not Lin and Zhang, 1987: 105, figs 2a and b; Gao et al., 2002: 130, fig. 71, = *L. cordata*).

Muggiae havock: Stepanjants, 1967: 185, fig. 126; Stepanjants, 1975: 116; Margulis and Alekseev, 1985: 5.

Diagnosis

Anterior nectophore with seven complete longitudinal ridges, including lower laterals bending downwards slightly anterior of ostium and extending beyond ostium to distal end of mouthplate; somatocyst spindle- or club-shaped, typically reaching less than 1/5 nectophore length; hydroecium elongate, with elongate mouthplate and with anterior wall lying anterior of ostium; posterior border of lower facet deeply emarginate; posterior nectophore unknown.

Material examined

One anterior nectophore from Canadian Pacific station LB14 (700 m) (Fig. 49) BCPM 996-248-1; 19 anterior nectophores collected near thermal vent from tows 1 (1800–1750, 1900–0 m), 2 (1700–0 m), and 3 (1910–1850, 1935–1910, 1950–1935 m) (Fig. 11, Table 1). One anterior nectophore from the NHM collections, Reg. No. 1958.4.29.221 (32°00'S, 33°47'E to 32°02'S, 33°42'E).

Description of material

Anterior nectophores up to 15 mm long, conical, somewhat laterally flattened, with pointed anterior end and lower facet with deep inverted-V-shaped notch (or emargination) in posterior border (Fig. 49, n); upper longitudinal ridge with small distal cusp; upper lateral longitudinal ridges curving slightly

upwards near ostium; lower lateral longitudinal ridges continuing distad of ostium onto elongate posterolateral surfaces of nectophore, outside laterodistal struts of distal lamella and ostial ridge, and terminating at distoposterior border of nectophore (Fig. 49); lower longitudinal ridges delimiting elongate sides of narrow triangular lower facet; ostial ridge bordering ostium on upper and lateral sides and extending distally along lateral borders of distal lamella as two struts, inside lower lateral ridges, to posterior margins of nectophore; distal lamella comprising two elongate lappets, each with rounded inner margin and with left lappet typically longer than right; inner borders of lappets undulating, and reflexed into hydroecium in all specimens; nectophore surface deeply concave between all longitudinal ridges, but true courses of furrows difficult to discern, owing to flaccidity of mesogloea; hydroecium extensive, with anterior wall lying anterior of ostium and reaching almost 1/10 nectophore length (from ostium); somatocyst short and expanded laterally, reaching 3/10 nectophore length (from ostium), flat in upper–lower plane, lying close to lower wall of nectosac, and with distinct posterior stalk (Fig. 49); nectosac with thick musculature but typically poorly preserved and radial canals only clearly discernible in best specimen (shown in Fig. 49); short disjunct pedicular canal passing from origin of somatocyst on anterior wall of hydroecium to lower wall of nectosac anterior of ostium, not at ostium itself; four radial canals arising from disjunct pedicular canal and passing over nectosac: short lower radial canal extending distally to ostium; elongate upper radial canal passing anteriorly over anterior end of nectosac and returning along upper wall of nectosac to insert onto ostial ring canal (presumed position) on upper side of ostium; two lateral radial canals passing anteriorly over lateral walls of nectosac, looping near anterior end, and returning closer to upper nectosac surface, inserting onto ostial ring canal as shown in Figure 49; external pedicular canal not identified, since stems detached from all nectophores.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: California region (Margulis and Vereshchaka 1994); off San

Diego, California (Alvariño 1967b); off San Diego and Punta Eugenia, Baja California (Alvariño 1985); Santa Barbara Channel, Santa Cruz Basin, California (Alvariño 1971). Other regions: records from a few other Pacific locations (for example, Stepanjants 1967, 1970; Margulis and Vereshchaka 1994) and from other oceans, including the Atlantic (Alvariño et al. 1990; Pagès et al. 1994; Pugh 1999b), Indian Ocean (Daniel 1985), and Antarctic Ocean (Margulis 1992; Pagès and Kurbjewit 1994; Pagès and Schnack-Schiel 1996).

Vertical. *Lensia havock* has a broad depth range, from 0 to over 3400 m (Alvariño 1967b; Stepanjants 1967), but the main population may be concentrated in a narrow mesopelagic band (Pugh 1974b; Pugh et al. 1997). A single specimen taken at 700 m depth off Vancouver Island, and all others from at least 1750 m over the hydrothermal-vent plume, fit this pattern.

Notes

This species was transferred to the genus *Muggiaeae* by Stepanjants (1967) because it lacked a posterior nectophore. However, although such a nectophore has yet to be identified for *Lensia havock*, as noted by Kirkpatrick and Pugh (1984) and Totton (1965a), this species possesses several characters that are typical of (some species of) the genus *Lensia* but not of the genus *Muggiaeae*. Pugh (1974b) pointed out that *L. havock* has seven longitudinal ridges and a deeply notched posterior margin to the lower facet (well shown by Totton 1965a, fig. 114), whereas *M. atlantica* and *M. kochi* have only five ridges and a shallow indentation on the posterior margin of the lower facet (Fig. 54B). In these respects *L. havock* resembles *L. hunter* and *L. multicristata* (described below; Fig. 50A), which also have seven ridges and an elongate notch in the posterior margin of the lower facet. For these reasons the present author concurs with Pugh (1974b), who chooses to retain *L. havock* within the genus *Lensia*. His decision has been followed by subsequent authors, including Mackie et al. (1987), other than those who followed Stepanjants (1967) (noted in the synonymy) and Margulis and Vereshchaka (1994); the authors of the last paper record *L. havock* as *M. havock* from the bathypelagic region off California.

In the best specimen of *Lensia havock* from Canadian Pacific waters (14 mm in length) the extensions of the lower lateral ridges onto the posterolateral surfaces of the nectophore beyond the level of the ostium are clearly discernible, and similar extensions occur in

the four nectophores of *L. hunter* examined by the author from the NHM collections (listed under *L. achilles* above). In contrast, the lower lateral ridges of *L. multicristata* terminate at, or near to, the level of the ostium, as discussed below.

The outline of the somatocyst is often difficult to discern in *Lensia havock*, as noted by Pugh (1999b), but in the present specimens, where it is identifiable it is not as swollen across the upper-lower axis as is shown by Totton (1965a, fig. 114); this may be due either to shrinkage, because the present *L. havock* specimens are preserved in alcohol rather than formaldehyde, or to intraspecific variation. *Lensia havock* is typically found only in small numbers, and although a posterior nectophore has not yet been taken in association with the anterior nectophore, it is likely that one will be identified in the future.

Lensia multicristata (Moser, 1925)

(Fig. 50)

Muggiaeae kochi Bigelow, 1911a: 340 (in part); Bigelow, 1911b: 188 (in part), pl. 12 figs 3, 4 (not pl. 12 fig. 2, indet.) (not Will, 1844: 77, = *Muggiaeae kochi*).

Galeolaria multicristata Moser, 1925: 165 (in part), pl. 3 fig. 9.

Diphyes bigelowi Browne, 1926: 77.

Lensia multicristata: Totton, 1932: 364; Bigelow and Sears, 1937: 55 (in part), figs 40–44; Totton, 1954: 113; Totton, 1965a: 164 (in part), text-fig. 99B; Patriti, 1965b: 19, pl. 2 figs a–d; Stepanjants, 1967: 181, pls 122A and B; Daniel, 1974: 146 (in part), fig. 10s; Alvariño, 1981: 414 (not fig. 174.52, = *L. subtiloides*); Hong and Zhang, 1981: 10, pl. 3 fig. 4 (in part); Kirkpatrick and Pugh, 1984: 100, figs 43A, B, and ?C; Daniel, 1985: 248, fig. 66; Alvariño et al., 1990: 39, fig. 60; Pagès and Gili, 1992b: 91, fig. 34; Pugh, 1999b: 490, fig. 3.98; Gamulin and Kršinic 2000: 66 (in part), figs 34a–d; Gao et al., 2002: 131, fig. 72.

Lensia multicristata forme typica Leloup, 1934: 33, figs 8a–d (not Leloup, 1933, *Lensia grimaldi*, 37, pl. 1 figs 1–10, = *L. grimaldi*; not Leloup, 1934: *Lensia multicristata forme grimaldii*, 36, figs 9, 10, = *L. lelouvetae*).

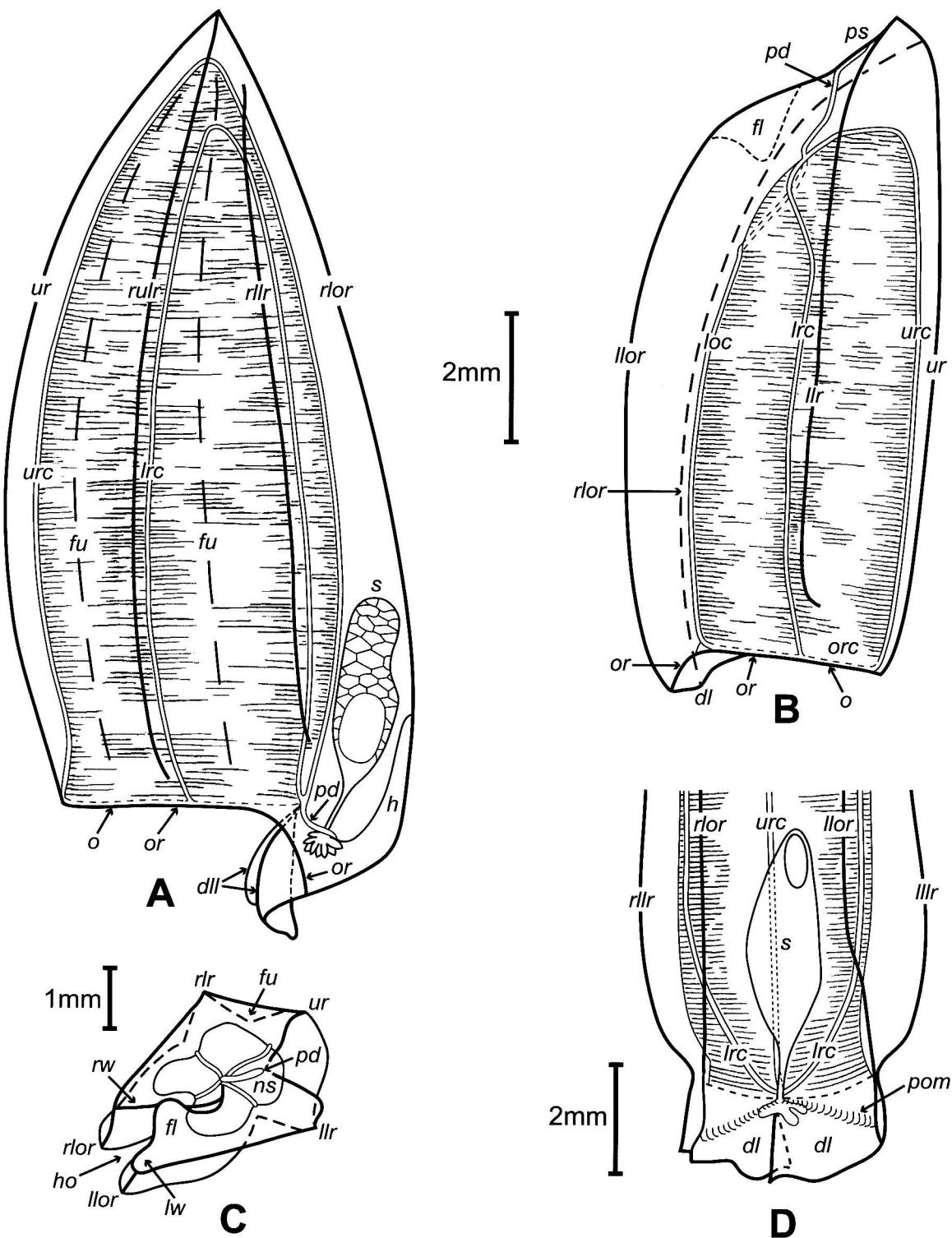


Fig. 50. *Lensia multicristata*: A: anterior nectophore, right lateral view; B: posterior nectophore, left lateral view; C: posterior nectophore, proximal view; D: part of anterior nectophore, lower view (*dl(l)*, distal lamella (lappets); *fl*, flap; *fu*, furrow; *h*, hydroecium; *ho*, hydroecial opening; *llr*, left lower lateral ridge; *llor*, left lower ridge; *llr*, left lateral ridge; *loc*, lower radial canal; *lrc*, lateral radial canal; *lw*, left wing; *ns*, nectosac; *o*, ostium; *or*, ostial ridge; *orc*, ostial ring canal; *pom*, posterior margin of lower facet; *pd*, disjunct pedicular canal; *ps*, proximal surface; *rllr*, right lower lateral ridge; *rlor*, right lower ridge; *rlr*, right lateral ridge; *rllr*, right upper lateral ridge; *rw*, right wing; *s*, somatocyst; *ur*, upper ridge; *urc*, upper radial canal).

Lensia profunda Totton, 1936: 235, *nomen nudum*.

?*Eudoxia dohrni* Gamulin, 1966: 4, fig. 6; Mackie et al., 1987: 120 (? not Patriti, 1965b: *Eudoxia tenuis* 23, pl. 4 figs a–f, = indet.).

Lensia multicristatoides Zhang and Lin, 1987, 603, fig. 1; Gao et al., 2002: 133, fig. 73.

Lensia multicristatoides Zhang and Lin, 1988: 115, figs 1, 2.

Diagnosis

Anterior nectophore with seven longitudinal ridges, including complete upper and lower ridges and incomplete upper lateral and lower lateral ridges; somatocyst cylindrical or irregularly swollen, extending from 3/10 to 1/2 nectosac length; hydroecium short, with mouthplate of moderate length; anterior hydroecial wall lying posterior of ostium on upper side of hydroecium, merging gradually into lower facet on lower side of hydroecium; posterior nectophore developed.

Material examined

Three hundred and twenty-two anterior nectophores and 183 posterior nectophores from Canadian Pacific stations LB12 (300, 0–450, 450 m), LB13 (0–300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–300 m) (Fig. 50D) BCPM 996-252-1, LB14 (0–300, 300, 0–500, 500, 0–700 m), LB16 (0–300, 300, 0–500, 0–700, 700 m), LB17 (0–500 m) (Fig. 50C) BCPM 996-253-1, LB17 (0–300, 300, 0–500, 500, 0–700 m), LC9 (500 m) (Fig. 50A) BCPM 996-251-1, LC9 (300–0, 300, 0–500, 500, 500–0 m), LC10 (575 m) (Fig. 50B) BCPM 996-250-1, LC10 (300–0, 0–500, 500, 500–0, 0–575, 575, 700, 700–0 m), LC11 (300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 700, 700–0 m); 3 anterior nectophores and 1 posterior nectophore collected near thermal vent from tow 1 (1750–0, 1900–0 m) (Fig. 11, Table 1); 18 anterior nectophores from the NHM collections, Reg. No. 1985.12.45 (40°15'N, 10°15'W).

Description of material

Anterior nectophore up to 16 mm long, conical, somewhat laterally flattened, with pointed anterior end, rounded lower lateral posterior margins (Fig.

50A), and rounded posterior margin to lower facet (Fig. 50D); ridges smooth or weakly serrated, with complete upper longitudinal and upper lateral longitudinals terminating just anterior of ostium (Fig. 50A); lower laterals terminating either anterior of ostium (Fig. 50A) or at same level as ostium (not illustrated); two complete lower ridges curving upwards posteriorly and terminating at distal end of ostial ridge (Fig. 50A); latter circumscribing ostium and extending to distoposterior border of nectophore on each side, forming two struts and delimiting distal lamella; latter comprising two lappets (Fig. 50A), each with small cusp at median angle and typically of similar sizes (Fig. 50D), atypically one lappet slightly longer than other, either right or left (not illustrated); lappets overlapping in turgid specimens (Fig. 50D), typically reflexed into hydroecium in flaccid ones (not illustrated); four furrows, between upper and upper lateral ridges and between upper lateral and lower lateral ridges (Fig. 50A); mesogloea atypically turgid (Fig. 50A), typically flaccid in present specimens, with upper half of nectophore invaginated into nectosac along line of furrows on each side of upper ridge (not illustrated); hydroecium with anterior wall lying level with or slightly posterior of ostium at point of stem attachment, extending anteriorly onto lower facet as broad concave groove representing rounded posterior border of lower facet (Figs 50A and D); somatocyst typically swollen, with one or more large yellowish oil droplets and distinct stalk, extending to between 3/10 (Fig. 50A) and 1/2 nectophore length (from ostium), atypically same thickness throughout or becoming gradually thinner towards hydroecium, often lacking small oil droplet(s) and also extending to 3/10–1/2 nectophore length (not illustrated); nectosac with musculature typically lost and presumed to have been expelled during preservation, atypically with thick muscles; disjunct pedicular canal originating at somatocyst–stem junction on anterior wall of hydroecium and passing to ostial ring canal on lower side of nectosac (Fig. 50A); upper radial canal originating from junction of ostial ring canal with disjunct pedicular canal, passing anteriorly along lower nectosac surface, over anterior end of nectosac, and back along upper nectosac surface, inserting onto ostial ring canal on upper side of nectosac in midline (Fig. 50A); lateral radial canals originating from same junction, passing anteriorly along lateral walls of nectosac, looping near anterior end, and returning to ostial ring canal, inserting in midlateral position; lower radial canal not developed; external pedicular

canal from stem to hydrocial wall very short and obscured by stem components in present material; internal pedicular canal not developed; very short “ascending” surface diverticulum extending from somatocyst–stem junction along hydroecium towards lower nectophore surface (shown in Fig. 50A but not labelled).

Posterior nectophores up to 12 mm long, with proximal articular surface consisting of pointed apophysis (on upper side) and distal surface comprising broad ostium flanked on lower side by short distal lamella (Fig. 50B); lower side of nectophore with two prominent hydrocial wings enclosing hydroecium and extending from proximal surface to distal lamella; each wing approximately symmetric in shape except for flap at proximal end of left wing, latter slightly broader than right wing across right–left axis (Fig. 50C); five longitudinal ridges: single complete upper ridge, two complete lower ridges bordering two hydrocial wings, and two incomplete lateral ridges terminating proximal of ostium and bending upwards slightly at free distal ends (Figs 50B and C); ostial ridge circumscribing upper and lateral sides of ostium and extending distally along each side of distal lamella as strut; struts terminating at distoposterior ends of lower ridges (Fig. 50B); distal lamella short, undivided, with entire distal border straight (Fig. 50B); four longitudinal furrows on lateral sides of nectophore, faint and best seen in proximal view (Fig. 50C); mesogloea flaccid; hydroecium shallow and elongate, extending along lower surface of nectophore from proximal end to distal end and of approximately uniform depth throughout (along upper–lower axis); disjunct pedicular canal originating at proximal end of hydroecium (Figs 50B and C) and passing distally along wall of hydroecium to point of origin of radial canals on lower surface of nectosac at approximately 3/4 nectophore length (Fig. 50B), atypically with short distal diverticulum beyond junction (not illustrated); internal pedicular canal not developed; nectosac with radial canals originating together from disjunct pedicular canal; upper radial canal passing over proximal end of nectosac distad along upper wall of nectosac, and inserting onto upper side of ostial ring canal (presumed position); lower radial canal passing along lower surface of nectosac in midline to lower side of ostial ring canal (Fig. 50B); lateral radial canals passing over lateral walls of nectosac, following slightly sigmoid courses (through two obtuse angles) proximally, and inserting onto lateral regions of ostial ring canal distally (Fig. 50B).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993). Northeast Pacific: from Baja California to San Francisco (Alvariño 1980c, 1985); California region (Margulis and Vereshchaka 1994); off San Diego (Alvariño 1967b); 30°–45°N, 120°–130°W, northeast Pacific (Stepanjants 1967). Other regions: many other records from Pacific (for example, Margulis 1987; Gasca and Suárez 1992b; Margulis and Vereshchaka 1994; Gao et al. 2002); present in temperate regions of other oceans (Bouillon et al. 2004).

Vertical. This species has been reported from a wide range of depths, inhabiting superficial, intermediate, and deep water layers (Margulis 1980c, 1984; Angel et al. 1982). In the present study it was found at all depths sampled, and off California it has been recorded in a depth range of at least 50–475 m (Alvariño 1985). In the North Atlantic, at 47°N, 20°W, maximum numbers of *Lensia multicristata* were found in the 250–350 m depth zone (Pugh 1990).

Notes

The anterior nectophore of *Lensia multicristata* is easily distinguished from those of the other two seven-ridged *Lensia* species (*L. havock* and *L. hunter*) by the upper lateral and lower lateral ridges, which are all incomplete distally in *L. multicristata*. In *L. havock* all ridges are complete, as described above, and the lower lateral ridges continue beyond the ostium onto the posterior surfaces of the nectophore, outside each laterodistal ostial strut. The upper laterals of *L. hunter* are similar to those of *L. multicristata*, but the lower laterals are complete and continue onto the posterolateral surfaces of the nectophore, outside the ostial struts, somewhat as they do in *L. havock*. The somatocyst of *L. hunter* is also shorter and more asymmetric (in lower view; see Totton 1941, fig. 12) than in *L. multicristata*.

The material upon which Moser founded *Lensia multicristata* included a mixture of nectophores. Most of these had 7 ridges, or “cristae”, including those illustrated in her plate 3 figure 9, but some had up to 20 ridges (Moser 1925, p. 165), which led her to coin the name *multicristata* for her new species. Leloup found more of Moser’s multi-striate nectophores in material collected by the *Meteor* (1934, p. 33), and designated two forms for the species: *L. multicristata forme typica* for those with

seven ridges and *L. multicristata* forme *grimaldi* for those with many ridges. The latter resembled, but were not identical with, a multi-striate species, *L. grimaldi*, that Leloup had introduced the previous year (Leloup 1933). In 1941 Totton recognized the second form as a new species, *L. lelouveteau*. It has numerous, mostly complete longitudinal ridges linked by a velar ridge, and is discussed further below (under *L. hostile*). *Lensia grimaldi* differs from *L. lelouveteau* in having a variable number of longitudinal ridges, with only the lower two complete, and a partial velar ridge.

A nominal species *Lensia multicristoides* was introduced by Zhang and Lin (1987, 1988 (English translation)) that differs from *L. multicristata* in having a shorter somatocyst and longer lower lateral ridges. However, in *L. multicristata* the length of the somatocyst is known to vary, as Moser mentioned in her original description of the species (1925, p. 166, as *Galeolaria multicristata*) and Bigelow and Sears (1937) show in their figure 43. The somatocyst shown by Moser (1925, pl. 3 fig. 9) reaches only 3/10 ectophore length (from the ostium), whereas that shown by Bigelow and Sears (1937, fig. 40) reaches almost 1/2 ectophore length, as do examples illustrated by Pagès and Gili (1992b, fig. 34) and Gamulin and Kršinic (2000, fig. 34a). The somatocysts of *L. multicristata* taken from Canadian Pacific waters show similar variation in length, as noted in the description above, although the longest are a little short of those illustrated by Bigelow and Sears (1937), Pagès and Gili (1992b), and Gamulin and Kršinic (2000). The somatocyst of *L. multicristoides* lies within this range. The present specimens also vary in the length of the lower lateral ridge, which in some ectophores extends as far as that shown by Zhang and Lin (1987) and in others is shorter, reaching only the point shown in Figure 50A. The present author therefore concludes that *L. multicristoides* Zhang and Lin, 1987 is a junior synonym of *L. multicristata* (Moser, 1925).

Moser's original figure of the anterior ectophore of *Lensia multicristata* (1925, pl. 3 fig. 9) shows the upper ridge to be incomplete at the posterior end, as are also the upper lateral and lower lateral ridges. However, the upper ridge is complete in all specimens from the present collection, and was also found to be complete by Browne (1926, as *Diphyes bigelowi*), Bigelow and Sears (1937), and all subsequent authors who give species diagnoses for *L. multicristata*. It

is therefore concluded by the present author that Moser was mistaken in this regard. The lower facet of the anterior ectophore is narrowly triangular, as was clearly shown by Bigelow and Sears (1937, fig. 42, marked by the tip of the somatocyst), and its posterior end is rounded, merging imperceptibly into the hydroecium and lacking a distinct posterior edge (Fig. 50D). The hydroecium is bordered on the upper side by two lappets, which form the mouthplate, and these have a small tooth (cusp) on each of their inner distal corners, as shown in Figure 50D and also by Bigelow and Sears (1937, fig. 41).

The posterior ectophore of *Lensia multicristata* differs from the anterior ectophore in having five longitudinal ridges instead of seven, and laterals that, like the upper laterals and lower laterals of the anterior ectophore, are incomplete distally. However, this ectophore was not identified by either Moser (1925) or Bigelow and Sears (1937), and indeed was considered hard to distinguish by Pugh (1999b). Leloup (1934) was the first author to positively associate it with the anterior ectophore, and he gives three good figures of the posterior ectophore in his paper (figs 8B–D). One of these (fig. 8D) clearly shows a distinctive flap on the proximal surface, and this is also present in all the *L. multicristata* posterior ectophores from Canadian Pacific waters (Fig. 50C), although a flap is absent from the posterior ectophores of the other *Lensia* species herein described. Such a flap is also shown by Kirkpatrick and Pugh (1984, fig. 43B), although not described in the text, and is described as "a small tongue-shaped projection" by Totton (1965a, p. 164). The incomplete lateral ridges curve characteristically towards the upper surface at their distal ends (Fig. 50B), and this is well shown by Leloup (1934, fig. 8B) and reproduced in figure 43B of Kirkpatrick and Pugh (1984), but was missed by Patriti (1965b, pl. 2), who appears to show, incorrectly, lateral ridges that are complete. Totton (1965a, p. 164) describes a "slight median notch" in the distal lamella (as *mouthplate*) of the posterior ectophore, which is evident in figure 8C of Leloup (1934) and is referred to as "a small median tooth" by Kirkpatrick and Pugh (1984, p. 100), although such a notch was not identified in the present material.

The eudoxid of *Lensia multicristata* is thought by Mackie et al. (1987) to be that figured by Gamulin (1966, fig. 6) as *Eudoxia dohrni*. Moreover, Kirkpatrick and Pugh (1984) and Pugh (1999b)

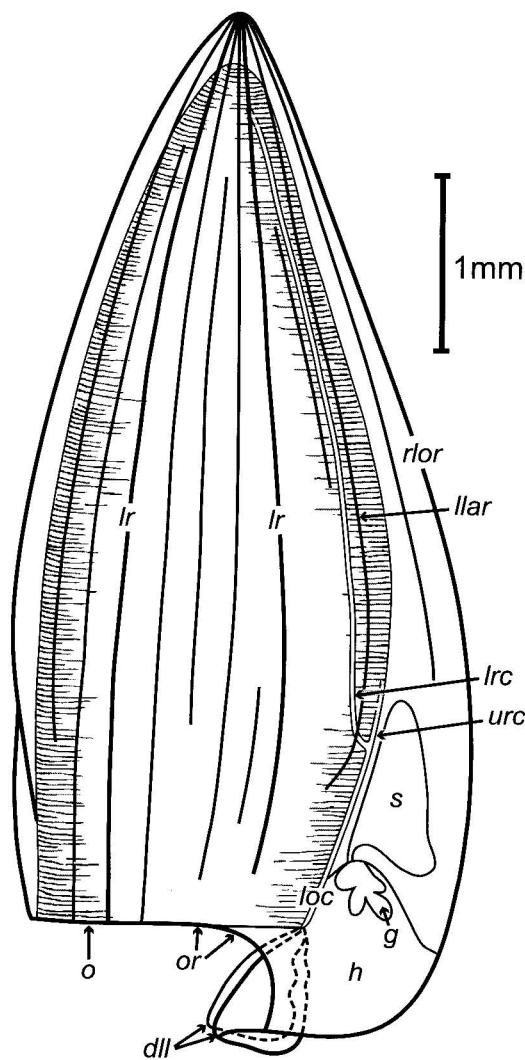


Fig. 51. *Lensia hostile*, anterior nectophore, right lateral view (dll, distal lamella (lappets); g, gastrozooid(s); h, hydroecium; llar, lower lateral ridge; loc, lower radial canal; lr, lateral ridge; lc, lateral radial canal; o, ostium; or, ostial ridge; rlor, right lower ridge; s, somatocyst; urc, upper radial canal).

tentatively refer *Eudoxia tenuis* of Patriti (1965b) to *L. multicristata*. Since Pugh and Pagès (1995, 1997) point out that the shape and proportions of the phyllocyst in bracts of *Lensia* species resemble those of the somatocyst of the anterior nectophore, it seems more likely that *E. tenuis* is a young bract of *L. conoidea*, since it has a long phyllocyst. *Eudoxia dohrni*, in contrast, has a shorter phyllocyst, and in this respect resembles the somatocyst of the anterior nectophore of *L. multicristata*. Another bract from

the Adriatic Sea, which also has a short phyllocyst, is referred by Gamulin and Kršinic to *L. multicristata* (2000, fig. 34c). Thus, the present author refers *E. dohrni* to *L. multicristata* in the synonymy given above, but this conclusion must remain tentative until a closer association can be demonstrated between this bract and anterior nectophores of *L. multicristata*.

***Lensia hostile* Totton, 1941**

(Fig. 51)

Lensia hostile Totton, 1941: 161, figs 20–22; Kirkpatrick and Pugh, 1984: 96, fig. 39; Margulis and Alekseev, 1985: 11, fig. 3d.

Lensia zenkevitchi Margulis, 1970: 148, fig. 1; Margulis and Alekseev, 1985: 13, fig. 3e.

Diagnosis

Anterior nectophore with 15 or more longitudinal ridges, many incomplete; velar ridges and multiple small cross-ridges between longitudinal ridges absent; somatocyst an inverted heart shape, extending to 1/4–1/3 nectophore length; hydroecium elongate, with mouthplate of moderate length and anterior hydroecial wall lying anterior of ostium; posterior border of lower facet deeply emarginate; posterior nectophore unknown.

Material examined

Six anterior nectophores collected from Canadian Pacific waters near thermal vent in tows 1 (1900–0 m), 2 (1935–1910 m), and 3 (1910–1850 m) (Fig. 51) BCPM 996-249-1 (Fig. 11, Table 1); specimens of *Lensia hostile* from the NHM collections: Reg. Nos 1958.3.7.335, holotype, 1 anterior nectophore (32°01'S, 93°40'E); 1958.3.7.338, 22 anterior nectophores (00°06'S, 49°45'E).

Description of material

Anterior nectophores 6–9 mm long, conical, somewhat laterally flattened, with pointed anterior end, rounded posterior margins to lower lateral surfaces (Fig. 51), and ill-defined posterior margin to lower facet, merging imperceptibly with anterior surface of hydroecium (not illustrated); upper longitudinal ridges not evident in present material

and distal cusps absent; up to eight “lateral” longitudinal ridges (more in largest specimens, only two labelled in Fig. 51), with only one or two complete; up to three incomplete lower lateral longitudinal ridges on each side (Fig. 51), separated from lateral longitudinal ridges by weak longitudinal furrow (represented, for clarity, by gap instead of broken line in Fig. 51); two lower longitudinal ridges delimiting narrow triangular lower facet and curving round posteriorly in hydroecial region, terminating at laterodistal edges of mouthplate (only right lower ridge shown in Fig. 51); ostial ridge bordering ostium on upper and lateral sides and extending posteriorly along each side of mouthplate as two struts, joining lower longitudinal ridges distally; mouthplate a distal lamella of two lappets, with undulating inner borders; latter reflexed into hydroecium in some specimens (not illustrated); mesogloea flaccid; hydroecium extending to less than 1/10 nectophore length, and with anterior wall convex in lateral view (Fig. 51); somatocyst an inverted heart shape (in lower view only), lying close to lower wall of nectosac and with short stalk in best specimen, but stalk typically indistinct; disjunct pedicular canal too small to be discerned (but presumed to extend from origin of somatocyst, where stem attached, along anterior wall of hydroecium to nectosac); nectosac fragile and with only small portion of radial canals discernible; upper radial canal extending anteriorly from presumed junction with disjunct pedicular canal, and giving rise to lateral radial canals as shown in Figure 51; lower radial canal extending from origin of upper radial canal posteriorly to ostial ring canal (presumed position); internal pedicular canal not identified.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: California region (Margulis and Vereshchaka 1994); off San Diego (Alvariño 1967b); off Punta Eugenia, Baja California, and San Diego and Monterey, California (Alvariño 1985). Other regions: few Pacific records, with most from high southern latitudes (Alvariño et al. 1990); widely distributed in North Atlantic from the equator to latitude 60°N (Kirkpatrick and Pugh 1984); also recorded from South Atlantic (Alvariño 1981; Pagès et al. 1994), Indian Ocean (Totton 1941), and Antarctic Ocean (Pugh et al. 1997).

Vertical. Some of the present six specimens collected over the hydrothermal-vent plume came

from samples taken between 1850 and 1935 m (see above), but others came from a broader overall depth range. No specimens were present in the much more extensive collections from 700 m and shallower. This agrees with the world distribution for this species, which has a largely meso- and bathypelagic range (Pugh 1974b, 1984, 1999b; Margulis and Vereshchaka 1994; Pugh et al. 1997), with few specimens recorded from epipelagic layers (Casanova 1980; Alvariño et al. 1990).

Notes

Lensia hostile is distinguishable from the multi-ridged species *L. exeter*, *L. grimaldi*, and *L. lelouveteau* by the absence of a velar ridge. This ridge crosses all or part of the lateral surfaces of the nectophore a short distance anterior of the ostium, lies orthogonal to the longitudinal ridges, and connects some or all of them together (see Pugh 1999b, figs 3.102 (*L. exeter*), 3.103 (*L. grimaldi*), and 3.105 (*L. lelouveteau*)). *Lensia hostile* can be separated from another multi-ridged species, *L. ajax*, by the length of the hydroecium and the shape of the somatocyst. In the latter species the hydroecium lies at the same level as the ostium and the somatocyst reaches less than 1/10 nectophore length (see Pugh 1999b, fig. 3.101), whereas in *L. hostile* the anterior hydroecial wall lies anterior of the ostium and the somatocyst is longer, extending to 1/4 nectophore length or more (from the ostium). *Lensia hostile* is distinguishable from a newly introduced species, *L. quadriculata* Pagès, Flood and Youngbluth, 2006, by the absence of many short cross-ridges between the longitudinal ridges (but see discussion below).

A new species, *Lensia zenkevitchi*, was introduced by Margulis (1970) and said to differ from *L. hostile* in having smaller nectophores, longer mouthplate lappets (as *dorsal lobes of the hydroecium*), and posterior borders to the hydroecium (as *ventral lobes*) of unequal sizes. However, comparison of the *L. hostile* nectophores from Canadian Pacific waters with 23 from the NHM collections (see list above) reveals considerable variation in both the number of complete and incomplete longitudinal ridges and the shape of the lower lateral nectophore border. In Canadian Pacific nectophores and smaller NHM nectophores, all <9 mm long, these borders are curved, as shown in Figure 51. In larger NHM nectophores, 12.5 mm long, they are more angular, and in the largest holotype nectophore (Reg. No. 1958.3.7.335), which is 16 mm long, these borders are not only angular but also longer

on the lower side of the hydroecium than on the upper side. This nectophore is illustrated by Totton (1941, fig. 20) and reproduced by Pugh (1999b, fig. 3.141). It forms part of a continuous series with the Canadian Pacific material and the 22 nectophores in the other NHM sample (Reg. No. 1958.3.7.338). It is concluded here, therefore, that overall size, shape of the lower lateral posterior nectophore border, and number of longitudinal ridges are all variable in *L. hostile*, and that *L. zenkevitchi* Margulis, 1970 should be regarded as conspecific with *L. hostile*.

Another new multi-striate species, *Lensia quadriculata*, has recently been introduced by Pagès et al. (2006), and this species shares several characters with *L. hostile*. Both have a somatocyst that resembles an inverted heart in shape and a hydroecium of similar proportions (compare Fig. 51 with Pagès et al. 2006, fig. 3). Additionally, the posterior border of the new species resembles that described for the large *L. hostile* holotype nectophore described above, although it differs from the more rounded posterior border of other *L. hostile* nectophores examined. However, the presence of many short cross-ridges between the longitudinal ridges clearly distinguishes *L. quadriculata* from *L. hostile*.

Genus *Dimophyes* Moser, 1913a

Diagnosis

Diphyinae with anterior nectophore lacking longitudinal ridges; distal lamella undivided and without cusps; hydroecium extending anterior of ostium to 1/5 nectophore length; reduced posterior nectophore present.

Type species: *Dimophyes arctica* (Chun, 1897a) by monotypy.

Notes

The generic name *Dimophyes* was first introduced by Moser in 1913, not in her 1925 monograph as was previously concluded by Totton (1965a) and subsequent authors.

Several other diphynine species lack distinctive longitudinal ridges, including *Muggiaeabargmannae* and the five *Lensia* species noted above. However,

these six species differ from *Dimophyes* in having a mouthplate in the anterior nectophore that is divided into two lappets. Species referable to *Chelophyses*, *Eodoxoides*, and *Muggiaeaa* (except *M. bargmannae*) can also be distinguished from *Dimophyes* by their divided mouthplate, the lappets of which all have pointed cusps, except those of the genus *Muggiaeaa*. Species of *Diphyes*, which also have an undivided mouthplate (except *D. antarctica*), can be distinguished from *Dimophyes* by the ridges on their nectophores.

Dimophyes arctica (Chun, 1897a)

(Figs 52, 53)

Diphyes arctica Chun, 1897a: 19, pl. 1 figs 1–5, 9; Vanhöffen, 1897: 274, pl. 2 fig. 3; Römer, 1901: 174; Broch, 1908: 1; Vanhöffen, 1906: 17, figs 16–18; Bigelow, 1911b: 347; Bigelow, 1913: 76; Moser, 1912c: 539, figs 24–27; Sverdrup, 1921: 28, pl. 4 figs 19a and b; Browne, 1926: 75.

Eudoxia arctica: Chun, 1897a: 21, pl. 1 figs 6–8, 10; Römer, 1901: 174.

Diphyes borealis Chun, 1897a: 99.

Muggiaeaa arctica: Schneider, 1898: 89.

Eudoxia eschscholtzi Johannsen and Levinsen, 1903: 282 (not Busch, 1851: pl. 4 figs 7–10 and pl. 5 figs 1–9, = *Muggiaeaa kochii*).

Diphyes (kunftig Dimophyes) arctica: Moser, 1912b: 408.

Dimophyes (Diphyes) arctica: Moser, 1913a: 146.

Dymophyes arctica (lapsus calami) Moser, 1915b: 659.

Dimophyes arctica: Moser, 1924b: 516, fig. 504; Moser, 1925: 389, pl. 26; Totton, 1932: 363; Totton, 1965a: 184, pl. 33 figs 1, 2, 7 and text-fig. 122; Stepanjants, 1967: 194, figs 134–136; Daniel, 1974: 151, fig. 12; Pugh, 1974b: 64; Stepanjants, 1975: 112, fig. 7; Alvariño, 1981: 417, fig. 174.57; Kirkpatrick and Pugh, 1984: 106, fig. 47; Mapstone and Arai, 1992: 3, figs 1, 2; Pagès and Gili, 1992b: 93; Stepanjants and Dianov, 1997: 154, figs 1–9.

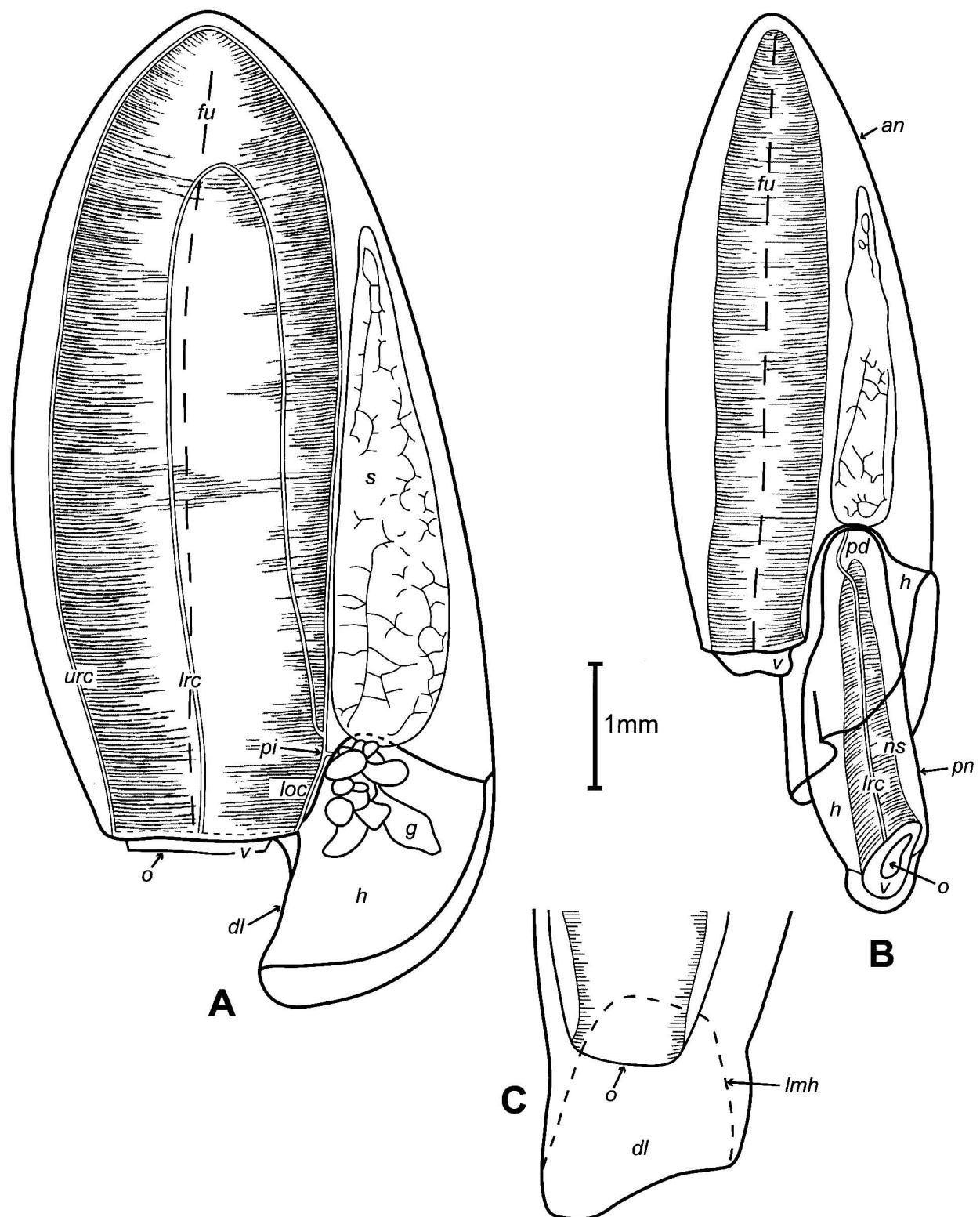


Fig. 52. *Dimophyes arctica*: A: anterior ectophore, right lateral view (derived from Mapstone and Arai 1992); B: anterior ectophore with posterior ectophore attached; C: distal lamella of anterior ectophore, upper view (an, anterior ectophore; dl, distal lamella; fu, furrow; g, gastrozooid(s); h, hydroecium; lmh, limit of hydroecium; loc, lower radial canal; lrc, lateral radial canal; ns, nectosac; o, ostium; pd, disjunct pedicular canal; pi, internal pedicular canal; pn, posterior ectophore; s, somatocyst; urc, upper radial canal; v, velum).

Lensia lelouveteau (eudoxid) Alvariño and Wojtan, 1984: 57, fig. 5; Pugh and Pagès, 1995: 181 (non Totton, 1941: 163, fig. 23, = *Lensia lelouveteau*).

Diagnosis

With the characters of the genus.

Material examined

Seven hundred and seventy-five anterior nectophores from Canadian Pacific stations LB2 (30 m), LB12 (0–300, 300, 400–0, 0–450, 450 m), LB13 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–300, 300, 0–500, 500, 500–0, 0–700 m), LB16 (0–300, 300, 0–500, 500, 500–0, 0–700, 700 m), LB17 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700 m), LC9 (0–300, 300, 300–0, 0–500, 500, 500–0 m), LC10 (700 m) BCPM 996-254-1, LC10 (700–0 m) BCPM 996-253-2, LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–575, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and LD10 (300 m); 96 eudoxid bracts (69 with attached gonophores) from stations LB12 (300, 0–450, 450 m), LB13 (0–300, 300, 0–500, 500, 700, 700–0 m), LB14 (300, 0–500, 500, 0–700 m), LB16 (0–500, 500, 0–700 m), LB17 (300, 0–500, 500, 0–700 m), LC9 (0–500, 500 m), LC10 (500 m) BCPM 996-253-3, LC10 (300, 500, 500–0, 0–575, 575, 700, 700–0 m), LC11 (300, 0–500, 500, 700, 700–0 m), A4 (300, 0–500, 500–0, 0–700, 700, 700–0 m), and LD10 (700 m); 29 anterior nectophores collected near thermal vent from tows 1 (1750–0, 1800–1750, 1900–0 m), 2 (1700–0 m), and 3 (1950–1935, 1910–1850 m); 2 eudoxid bracts (1 with attached gonophore) from tow 3 (1910–1850 m) (Fig. 11, Table 1); 30 anterior nectophores and 1 posterior nectophore from Strait of Georgia, 49°16'N, 123°40'W (illustrated specimens were collected from 111 m (Fig. 52A), 244 m (Fig. 52B), 299 m (Fig. 52C), and 195 m (Fig. 53)). *Dimophyes arctica* specimens from the NHM collections, Reg. No. 1958.9.17.16, 7 anterior nectophores (60°34'N, 62°51'W).

Description of material

Anterior nectophores up to 9 mm long, conical, laterally flattened, in lateral view width varying from expanded across upper-lower axis with rounded

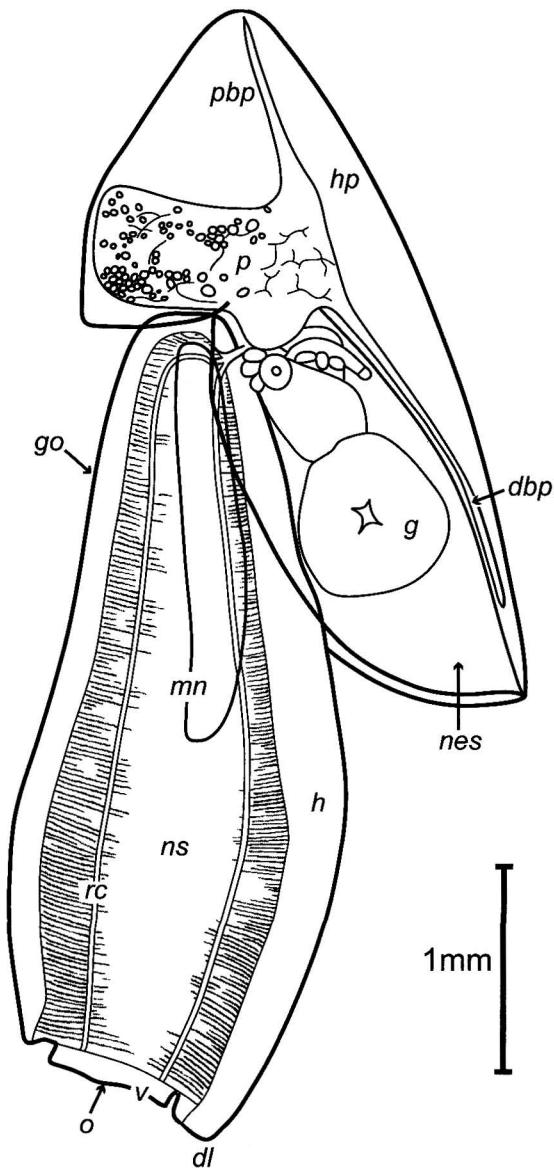


Fig. 53. *Dimophyes arctica*, eudoxid, lateral view (derived from Mapstone and Arai 1992) (dbp, distal branch of phyllocyst; dl, distal lamella; g, gastrozooid; go, gonophore; h, hydroecium; hp, head-piece; mn, manubrium (gonophore); o, ostium; nes, neck-shield; ns, nectosac; p, phyllocyst; pbp, proximal branch of phyllocyst; rc, radial canal (gonophore); v, velum).

anterior end and shallow longitudinal furrow on each lateral surface (Fig. 52A) to narrow across this axis with more acute anterior end and deep longitudinal furrows on lateral surfaces (Fig. 52B); other nectophores of intermediate width (across upper-lower axis) and with furrows of varied depths; majority of nectophores containing varied amounts of thick opaque nectosac muscles; some expanded nectophores lacking muscles, although typically with some muscle strands intact;

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

narrowest nectophores typically with up to 80% of muscles present; latter attaching to inner lateral surfaces of nectophore but detached from upper and lower surfaces; during preservation, muscles presumed either to have pulled upper and lower nectophore surfaces towards each other, creating two deep lateral furrows, or to have been lost via ostium; nectophores from samples taken in Strait of Georgia almost all expanded (Fig. 52A); mouthplate an elongate distal lamella merging imperceptibly with lateral walls of hydroecium (no ostial ridges) (Fig. 52A), and broader across left-right nectophore axis than ostium (Fig. 52C); distal margin of distal lamella asymmetric, with left side longer than right; mesogloea turgid to somewhat flaccid; anterior wall of hydroecium extending to 1/5 nectosac length (from ostium), with anteriormost point on left side of nectophore (Figs 52A and C); angle at which anterior wall of hydroecium meets lower nectophore surface variable and unrelated to width of nectophore across upper-lower axis; somatocyst elongate, reaching 3/4 nectophore length (from ostium), inverted carrot shape, typically swollen throughout and containing oil droplets, occupying most of space between lower wall of nectosac and that of nectophore (Figs 52A and B); atypically slender (not illustrated); stalk of somatocyst short, originating from anterior wall of hydroecium amongst stem components (Fig. 52A); nectosac typically with radial canals either intact (Fig. 52A) or forming impressions on inner nectophore surface, atypically not discerned (Fig. 52B); disjunct pedicular canal originating at somatocyst-stem junction on anterior wall of hydroecium and passing posteriorly for short distance before penetrating mesogloea as internal pedicular canal (obscured by anterior hydrocial wall in Fig. 52A); internal pedicular canal short (shown in Fig. 52A but not labelled), inserting onto lower wall of nectosac and giving rise to upper and lower radial canals only; upper canal passing anteriorly for short distance, giving off two lateral radial canals, then continuing to anterior end of nectosac, passing over it, and returning distally (posteriorly) along upper surface of nectosac to ostial ring canal (presumed position); lower radial canal extending posteriorly from origin at internal pedicular canal to ostial ring canal; lateral radial canals passing over lateral walls of nectosac, looping near anterior end, and returning to ostial ring canal closer to upper nectosac surface (Fig. 52A); external pedicular canal too small to be discerned.

Single posterior nectophore 2 mm long, with narrow truncate proximal end, smooth surface, and

short, rounded distal mouthplate (Fig. 52B); ostium opening upper-distally and containing velum; hydrocial wings extending length of nectophore, enclosing hydroecium; latter deep proximally, shallower distally; disjunct pedicular canal extending from proximal end of nectophore distally for 0.4 mm and inserting onto nectosac as shown in Figure 52B; nectosac slender, with upper radial canal passing over nectosac apex and then distally to ostial ring canal (presumed position), lower radial canal passing directly to ostial ring canal, and lateral radial canals following straight courses to ostial ring canal (only lateral radial canals shown in Fig. 52B).

Eudoxids, comprising bract and attached gonophore, reaching 7 mm in length (Fig. 53). Detached bracts up to 3 mm long, without ridges, each having conical head-piece and long neck-shield; phyllocyst expanded, with short thin proximal branch extending to proximal end of bract, and longer thin distal branch extending almost to distal border of neck-shield (Fig. 53); phyllocyst also having short lateral extensions (not illustrated). Gonophores 3–7 mm long; elongate, without discernible ridges, having elongate shallow hydroecium extending distally as short distal lamella; ostium with intact velum in some specimens (Fig. 53); distal margin of distal lamella rounded in upper view (not illustrated); nectosac with thick musculature and four straight radial canals, but ostial ring canal not discernible; elongate manubrium present in many gonophores from Strait of Georgia collection, enlarged in some and apparently ready to release gametes (Fig. 53); mantle canals not discerned.

Distribution

Geographic. Canadian Pacific waters: Jervis Inlet, northern Strait of Georgia (Mackie 1985), central Strait of Georgia (Mackie 1985; Mapstone and Arai 1992); Kulleet Bay (Purcell 1989, 1991); Saanich Inlet (Mills 1982; Mackie and Mills 1983; Mackie et al. 1987); off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993); inlets off Nootka Sound and Hecate Channel (Mackie 1985); Knight Inlet (Mackie 1985). Northeast Pacific: off California and Baja California (Alvariño 1980c); California region (Margulis and Vereshchaka 1994); off San Diego (Alvariño 1967b, 1991); off San Francisco (Alvariño 1991); Friday Harbor (Mills 1981); 50°00'N, 145°00'W and 55°58'N, 150°46'W, northeast Pacific (Berkeley and Berkeley 1960); 53°53'N, 144°53'W, northeast Pacific (Bigelow 1913). Other regions:

many other Pacific records from the Bering Sea through the tropics to the Antarctic Ocean (for example, Stepanjants 1970; Alvariño et al. 1990; Gao 1990; Pagès and Orejas 1999; Coyle and Hunt 2000); it has a similar distribution in other oceans and has been rated a near-cosmopolitan species, although the effects of temperature and upwelling on reproduction and biomass in the tropics are unclear (Lin 1993; Stepanjants and Dianov 1997; Gasca 1999b); not recorded from the Mediterranean (Casanova 1980).

Vertical. In temperate latitudes *Dimophyes arctica* is generally most abundant in shallower water. Off the west coast of Vancouver Island, the maximum abundance of nectophores was recorded at 300 m, although this species was also collected from at least 1800 m. *Dimophyes arctica* was also collected in the upper 300 m in other locations in the Canadian Pacific area (Mackie and Mills 1983; Mackie 1985; Mapstone and Arai 1992). Off San Diego it was found in deeper water (3040–2620 m) by day and in shallower water (460–410 m) by night (Alvariño 1967b), although in general the species is considered to be a diurnal nonmigrant in temperate and subtropical areas (Pugh 1974b, 1984; Casanova 1980).

In the present samples from Canadian Pacific waters, anterior nectophores were most abundant in samples from 300 and 0–300 m depth, whereas eudoxoids were most abundant in samples from 500–700 m. These two life stages were also differentially distributed in the Strait of Georgia (Mapstone and Arai 1992), Saanich Inlet (Mackie and Mills 1983), the northwest Pacific (Stepanjants 1970), and the northeast Atlantic (Pugh 1974b). At deeper levels eudoxoids are less likely to be subjected to the seasonal temperature fluctuations typically found in shallower water (Thomson 1981). However, no differential depth distribution of *D. arctica* populations was found in the Weddell Sea (Pagès and Schnack-Schiel 1996; Pugh et al. 1997).

Notes

Two types of anterior nectophore have been identified in *Dimophyes arctica* (Stepanjants 1967; Pugh 1974b; Stepanjants and Dianov 1997) and designated “wide” and “narrow”. Wide nectophores have a rounded apex (anterior end in the above description) and few or no discernible nectosac muscles, whereas narrow nectophores are more pointed at the anterior end and have a distinct

opaque musculature. Stepanjants and Dianov (1997) associated wide nectophores with eudoxid production, and concluded that narrow nectophores are characteristic of nonbreeding colonies. However, the large number of *D. arctica* anterior nectophores collected from Canadian Pacific waters (see above) are wide, narrow, and “intermediate”, and the type does not appear to be correlated with the presence or absence of eudoxids in any sample (either the same sample or an equivalent deeper sample). Small numbers of eudoxids were present throughout the extensive sampling period. It is concluded, therefore, that the appearance or presence/absence of nectosac musculature in *D. arctica* is a direct result of changes occurring at preservation. Some nectophores void their muscles through the ostium at death and thus appear wide, others are in the process of voiding their musculature and appear intermediate, and yet others have contracted but retained their nectosac muscles, and appear narrow because the upper and lower walls of the latter are brought closer together by muscular contraction and “frozen” in this state at death. Consequently, longitudinal furrows on the lateral surfaces of the nectophore deepen.

The nectophores of some small diphid species seem to be prone to narrowing at preservation, since the same phenomenon has been reported for *Lensia asymmetrica* by Pugh and Pagès (1997). It is also apparent when figures of preserved and twisted nectophores of *L. campanella* (see Totton 1965a, fig. 100A) are compared with those drawn from live material (C. Carré 1968b), which are broader and relatively little twisted. In life, nectophores of *Dimophyes arctica* are likely to appear distended and broad, with shallow lateral furrows.

In anterior nectophores of *Dimophyes arctica* collected from Canadian Pacific waters the radial canals of the nectosac do not all originate together from the internal pedicular canal as in most other diphid species. Instead, the latter canal gives rise to the upper and lower radial canals only, and the lateral radial canals arise (either together or slightly staggered) from the upper canal a short distance anterior of this junction (Fig. 52A). A similar arrangement is seen in *Lensia hostile* (Fig. 51), where the lateral canals arise from a more anterior point than in *D. arctica*.

Eudoxoids of *Dimophyes arctica* from the present Canadian Pacific collection reach a maximum size of only 7 mm, which is 2 mm shorter than the largest *D. arctica* eudoxoids recorded elsewhere (Stepanjants

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1967; Kirkpatrick and Pugh 1984) and 4 mm shorter than an atypically large *D. arctica* eudoxid collected by Stepanjants (1975, fig. 7) in the Caribbean Sea. Eudoxids described by Alvariño and Wojtan (1984) and referred to *Lensia lelouveteau* were reexamined by Pugh and Pagès (1995) and found to have a single distal branch (as *basal branch*) extending from the phyllocyst into the neck-shield. The latter authors therefore referred these eudoxids to *D. arctica* and noted that in this species the distal branch arises from the phyllocyst itself, not from the point at which the phyllocyst attaches to the gastrozoid. Two branches of the latter type are characteristic of bracts of *Gilia reticulata* and several clausophyid species. They are now thought to represent bracteal hydroecial canals, as discussed in Sections 10.2.3.3 and 10.2.4.

Genus *Muggiaeae* Busch, 1851

Diagnosis

Diphyinae with anterior nectophore having five longitudinal ridges (except *Muggiaeae bargmannae*), all complete, including upper ridge; distal lamella dividing into two lappets without cusps; hydroecium extending anterior of ostium to 3/10 nectophore length; posterior nectophore absent.

Type species: *Muggiaeae kochi* (Will, 1844).

Notes

Four species are presently referred to the genus *Muggiaeae*: *M. kochi* (Will, 1844), *M. atlantica* Cunningham, 1892, *M. bargmannae* Totton, 1954, and *M. delsmani* Totton, 1954 (see Totton 1965a). All except *M. bargmannae* have five complete longitudinal ridges. This character distinguishes them from *Chelophyes* species, which have a short and incomplete upper ridge (see below). The hydroecium of *Muggiaeae* species is more elongate than that of the 12 five-ridged *Lensia* species herein considered valid, and also that of the *Lensia* species with either very weak ridges or none (see above). The two species referred to the genus *Eudoxoides* also have five complete ridges, but their mouthplates have more elongate lappets and extend farther posteriorly as two long and serrated ostial cusps (Pagès and Gili 1992b, figs 42, 43). In species of the genera *Diphyes* and *Dimophyes* the mouthplate is entire instead of being composed of two lappets as in *Muggiaeae* species. However, Pugh (1999b) noted that nectophores of *M. bargmannae* may still

be easily confused with those of *D. arctica* because both species are small and unridged.

Although only one species of *Muggiaeae* has so far been collected from Canadian Pacific waters (*M. atlantica*), a second species, *M. kochi*, was recorded by Murbach and Shearer (1902, 1903) from nearby Puget Sound. However, these authors noted that their single specimen corresponded almost precisely to *Diphyes bipartita*, a species subsequently referred by Bigelow (1911b) to *Chelophyes appendiculata*. The latter species is represented in the present collection, and the synonymy list for *C. appendiculata* given below includes *D. bipartita*.

Lensia havock was referred by Stepanjants (1967) to *Muggiaeae* because it lacks a posterior nectophore, but in other respects it has more affinities with the two other seven-ridged *Lensia* species, *L. multicristata* and *L. hunter*, as discussed above. It is therefore retained within the genus *Lensia* in the present work, following Pugh (1974b, 1999b) and Mackie et al. (1987).

Another species, *Muggiaeae cantabrica* Alcazar, 1982, was described from eight nectophores only, and had a somatocyst which was shorter than that of *M. atlantica*, and an apparently unique blind canal arising from near the origin of the lateral radial canal. Other characters, however, are identical with those of *M. atlantica*. *Muggiaeae cantabrica* has never been recorded again, and it seems likely that the record is based on some atypical *M. atlantica* nectophores with stunted somatocysts and extra growths from the radial canals, or that these features represent preservation artefacts. *Muggiaeae cantabrica* is therefore assumed by the present author to be an invalid species, pending future investigation of the holotype material.

Muggiaeae atlantica Cunningham, 1892

(Fig. 54)

Muggiaeae (Diphyes) kochii Bourne, 1889: 321 (not Will, 1844: 77, pl. 2 fig. 22, = *M. kochi*).

Muggiaeae atlantica Cunningham, 1892: 212, figs 1, 2; Vanhoffen, 1906: 13 (in part), figs 8, 9; Bigelow, 1911b: 187 (in part), pl. 7 fig. 1 and pl. 9 figs 7, 8; Kawamura, 1915a: 193; pl. 7 fig. 1 (this plate is in 1915b); Moser, 1925: 106, pl. 1 fig. 5; Russell, 1938a: 441,

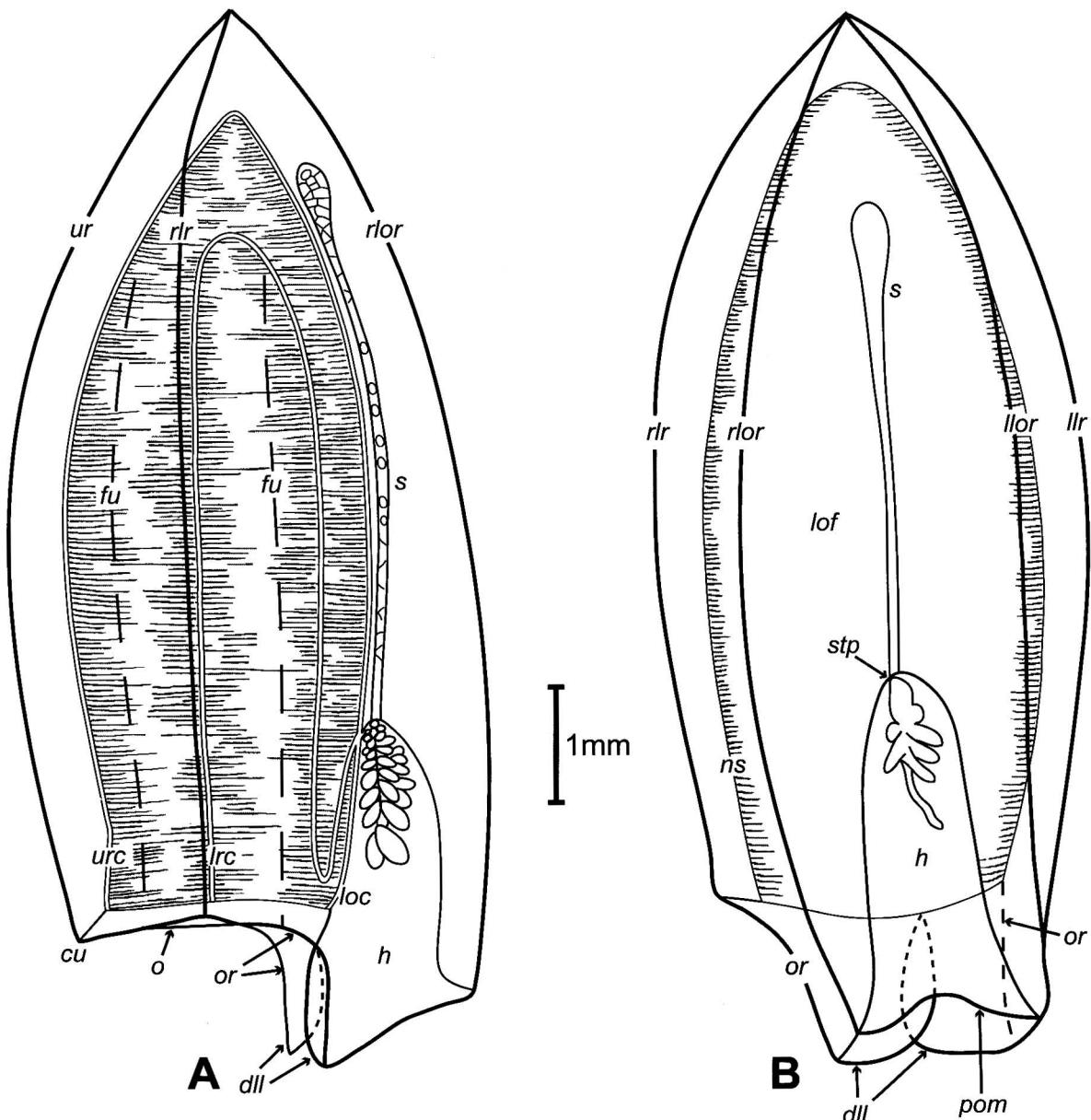


Fig. 54. *Muggiaeae atlantica*: A: anterior nectophore, right lateral view; B: anterior nectophore, lower view (radial canals omitted) (*cu*, cusp; *dll*, distal lamella (lappets); *fu*, furrow; *h*, hydroecium; *llor*, left lower ridge; *llr*, left lateral ridge; *loc*, lower radial canal; *lof*, lower facet; *lrc*, lateral radial canal; *ns*, nectosac; *pom*, posterior margin of lower facet; *o*, ostium; *or*, ostial ridge; *r lor*, right lower ridge; *r lr*, right lateral ridge; *s*, somatocyst; *stp*, stem-attachment point; *ur*, upper ridge; *urc*, upper radial canal).

figs 1–6; Russell, 1938b: 159, fig. 88; Chiu, 1954: 46, fig. 22; Cervigon, 1958: 30, fig. 10; Hong, 1964: 111, pl. 1 fig. 3; Stepanjants, 1967: 183, figs 124, 125; Palma, 1973: 48, pls 23, 24; Alvariño, 1981: 421, fig. 174.63; Santander et al., 1981: 16, pl. 3; Freeman, 1983: 604, figs 9, 10, 14–16; Daniel, 1985: 254, fig. 69; Girola, 1991: 291, figs 2, 3; Suárez and Gasca, 1991: 118, pl. 6 fig. 42; Pagès and Gili, 1992b: 93, fig. 38; Gamulin and Kršinic 2000: 100, fig. 57.

Diphyes sp. Darwin (unpublished) in Keynes, 2000: 259, pl. 15 fig. 1.

Diagnosis

Anterior nectophore with five complete longitudinal ridges; somatocyst extending to 4/5 nectophore length and hydroecium to 3/10 nectophore length.

Material examined

One thousand, two hundred and seventy-seven anterior nectophores from Canadian Pacific stations LB2 (0–28, 28, ?–0, 30, ? m), LB4 (85–88, 88–0, ?, ?–0, 95 m), LB6 (0–70, 70–85, 80, 80–0, 0–90, 90, 90–0 m), LB8 (130 m), LB13 (300, 700–0 m), LB14 (0–300, 0–500 m), LB16 (0–300, 0–500, 500, 0–700, 700 m), LC2 (0–?, 90 m) (Fig. 54) BCPM 996-255-1, LC2 (90 m) BCPM 996-256-1, LC2 (0–60, 0–?, 60 m), LC4 (?–0–? m), LC6 (70, 70–0, ?, 0–0–80, 80 m), LC10 (575–0 m), LC11 (500–0 m), A4 (300–0, 700–0 m), and LD2 (30 m) (Fig. 11, Table 1); specimens of *Muggiaeae atlantica* from the NHM collections: Reg. No. 1985.12.9.69, 3 anterior nectophores ($30^{\circ}30'N$, $10^{\circ}15'W$).

Description of material

Anterior nectophores up to 11 mm long, pentagonal, laterally flattened, with pointed anterior end and broadest across upper–lower axis at mid-nectophore level (Figs 54A and B); lower facet somewhat asymmetric, with slightly emarginate concave posterior margin (Fig. 54B); longitudinal ridges with slight serrations, strongest near distoposterior end of nectophore (serrations not discernible at magnification of Fig. 54); upper longitudinal ridge with short distal cusp (Fig. 54A); ostial ridge circumscribing ostium and extending to distoposterior border of nectophore on each side, forming two struts and delimiting distal lamella; latter with lappets having smooth inner margins and serrated distal margins; lappets similar in size or with either right or left longer; four furrows, between upper and lateral longitudinal ridges and between lateral and lower longitudinal ridges, shallow in turgid distended nectophores (Fig. 54A), deeper in more flaccid, less distended nectophores (not illustrated); mesogloea turgid to flaccid; hydroecium elongate, with convex anterior wall extending to 2.5 mm anterior of ostium (Fig. 54A); somatocyst elongate, tubular, slender, and lying close to lower wall of nectosac throughout, extending to 1 mm posterior of anterior end of nectosac in all mature specimens (Fig. 54), and also only extending to this position in immature nectophores (not illustrated); somatocyst typically containing oil droplets, with or without expanded tip, atypically thicker throughout (not illustrated); nectosac with translucent muscles; disjunct pedicular canal short, originating at somatocyst–stem junction on anterior wall of hydroecium (Fig. 54B), passing to lower wall of nectosac (shown in Fig. 54A but not labelled), and giving rise to four radial canals: upper radial canal

passing anteriorly along lower surface of nectosac and over anterior end, returning along upper surface of nectosac, and inserting onto ostial ring canal in midline on upper side; lower radial canal extending posteriorly from junction with disjunct pedicular canal, along lower surface of nectosac, and inserting onto ostial ring canal on lower side; lateral radial canals initially extending posteriorly from junction with disjunct pedicular canal, then looping anteriorly and passing along lateral surfaces of nectosac to near anterior end, looping again, and returning to insert onto ostial ring canal midlaterally; internal pedicular canal absent and external pedicular canal too short to be discerned in present material.

Distribution

Geographic. Canadian Pacific waters: Strait of Georgia (Gardner 1977); Strait of Georgia off Qualicum (Purcell 1990); Nanoose Bay (Purcell 1990); Strait of Georgia off Horsewell Bluff (Purcell 1990); Kuleet Bay (Purcell 1989, 1990, 1991); Ladysmith Harbour (Berkeley and Berkeley 1960); Long Harbour, Annette Inlet (Purcell 1990); Saanich Inlet (Mills 1982; Mackie and Mills 1983; Larson 1985, 1986, 1987); off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993); Barkley Sound (Purcell 1990); Hunt Inlet, Big Bay (Purcell 1990); Alliford Bay, Huston Inlet, Section Cove, Poole Inlet, Cumshewa Inlet, off Alder Island, all in Queen Charlotte Islands (Purcell 1990). Northeast Pacific: from Baja California to San Francisco (Alvariño 1980b and c; Alvariño and Kimbrell 1987); California region (Margulis and Vereshchaka 1994); off southern California (Bigelow 1911b; Seapy 1980); off San Diego (Alvariño 1967b); Santa Monica Bay (Brewer et al. 1984); Monterey Bay (Bigelow and Leslie 1930); $39^{\circ}13'N$, $123^{\circ}14'W$, off Sonoma County, California (Hobson and Chess 1988; Hobson et al. 1996); off Oregon (Pearcy 1972); Friday Harbor (Berkeley and Berkeley 1960; Mackie and Boag 1963; Miller 1979; Mills 1981; Purcell 1981b, 1982); East Sound and off Orcas Island (Freeman 1983). Other regions: extending along the coast of North and Central America south of latitude $30^{\circ}N$ from Mexico to Costa Rica and Panama (Bigelow 1911b; Alvariño 1969, 1972; Gasca and Suárez 1992a and b; Margulis and Vereshchaka 1994); many other Pacific records, mostly from temperate and subtropical latitudes (for example, Alvariño et al. 1990; He et al. 1992; Lin 1993; Toyokawa and Terazaki 1994; Palma and Rosales 1995, 1997; Palma et al. 1999; Kitamura et

al. 2003). *Muggiae atlantica* is one of the few neritic siphonophore species, and is found almost exclusively in nearshore waters (Mackie et al. 1987).

Vertical. Off Vancouver Island, 98% of nectophores in discrete depth samples were from the uppermost 100 m of the water column. Mills (1982) and Mackie and Mills (1983) observed the species primarily in the top 75 m in Saanich Inlet. Elsewhere in the world this species has been most frequently recorded from just below the surface down to 50–75 m (Alvariño 1980b and c; Southward and Barrett 1983; Gili et al. 1987a and b; Gao 1990; Pagès and Gili 1991b). Although it has been classified as inhabiting intermediate and surface layers (Margulis 1980b, 1984), there are infrequent records from deeper than 200 m.

Notes

Charles Darwin is the first person known to have accurately drawn a nectophore of *Muggiae atlantica*, in a notebook during the voyage of the *Beagle* in 1834. He identified it as a *Diphyes* species and although he drew it upside down, his notes include an accurate description of a live specimen. This drawing was published for the first time in a compilation of Darwin's notebooks by his grandson Richard Darwin Keynes (Keynes 2000).

Variability in the length of the somatocyst relative to that of the nectosac in *Muggiae atlantica* was first noted by Bigelow (1911b) in material from the eastern tropical Pacific. He found that in small specimens (3–4 mm long) the anterior end ("tip") of the somatocyst lay anterior of the anterior end of the nectosac, whereas in larger specimens (6–7 mm long) the somatocyst was either coincident with the end of the nectosac or terminated just posterior of it. However, his figure of a 7 mm long nectophore (Bigelow 1911b, pl. 7 fig. 1) shows a somatocyst distinctly longer than the nectosac. In the majority of published figures of *M. atlantica*, the tips of the somatocyst and nectosac are approximately coincident (for example, Cunningham 1892, fig. 1; Kawamura 1915b, pl. 7 fig. 1; Cervigon 1958, fig. 10; Totton 1965a, fig. 119b; Stepanjants 1967, fig. 124a; Pagès and Gili 1992b, fig. 38; Gamulin and Kršinic 2000, fig. 57), while in a few the somatocyst terminates anterior of the nectosac (Bigelow 1911b, pl. 7 fig. 1; Santander et al. 1981, fig. 3a; Daniel 1985, fig. 69; Suárez and Gasca 1991, pl. 6.42; Carré and Carré 1995, fig. 197a) and in one figure it terminates posterior of the nectosac (Palma 1973, pl. 23 figs 1, 2). In all

Canadian Pacific specimens the somatocyst terminates consistently 0.5–1 mm posterior of the anterior end of the nectosac (Fig. 54A), and in this respect these nectophores resemble those taken from the South Pacific, off Valparaíso (Palma 1973), and differ from those collected in the tropical eastern Pacific (Bigelow 1911b).

Genus *Chelophyes* Totton, 1932

Diagnosis

Diphyinae with anterior nectophore having five longitudinal ridges: three complete ridges, short incomplete upper ridge, and one long incomplete ridge; distal lamella dividing into two lappets, each with pointed cusp; hydroecium extending anterior of ostium to 1/10 nectophore length; posterior nectophore present.

Type species: *Chelophyes appendiculata* (Eschscholtz, 1829).

Notes

Two species are presently referred to this genus: *Chelophyes appendiculata* (Eschscholtz, 1829) and *C. contorta* (Lens and van Riemsdijk, 1908). As Totton notes, these two species "resemble each other more than either resembles other (diphyine) species" (Totton 1965a, p. 185). Their main distinguishing feature is a short upper ridge in the anterior nectophore, and both species also have one other incomplete but longer ridge, which in *C. appendiculata* is the left lateral ridge and in *C. contorta* is the right lower ridge (Pugh 1999b, as *left lateral ridge* and *right ventral ridge*). In this respect they differ from *Muggiae* species (except *M. bargmannae*), which have five complete longitudinal ridges (see above). *Chelophyes* species also differ from *M. atlantica* and the *Lensia* species collected in Canadian Pacific waters in having an angular serrated mouthplate with inner distal cusps.

Chelophyes contorta was not found in Canadian Pacific waters. It occurs in warm temperate regions, mainly the Indo-Pacific region (Pagès and Gili 1992b), and the northernmost records for the northeast Pacific are from off Baja California (Fuñes-Rodríguez 1985; Alvariño 1991; Gasca and Suárez 1992b).

Chelophyes appendiculata
(Eschscholtz, 1829)

(Fig. 55)

Diphyes appendiculata Eschscholtz, 1829: 138, pl. 12 fig. 7; Huxley, 1859: 34, pl. 1 figs 2a–c (in part); Haeckel, 1888b: 152 (in part); Schneider, 1898: 85; Bigelow, 1911b: 248, pl. 7 figs 5, 6, pl. 8 figs 7, 8, pl. 9 fig. 6, pl. 10 fig. 6, and pl. 11 fig. 1; Bigelow, 1918: 420 (not Bigelow 1911b: pl. 11 fig. 9, = *Eudoxoides mitra*); Browne, 1926: 71; Hong, 1964: 113, pl. 7 fig. 4.

Diphyes bipartita O.-G. Costa, 1841: 4, pl. 4.

Diphyes elongata Hyndman, 1841: 165, figs 1–4.

?*Eudoxia messanensis* Gegenbaur, 1853: 285, pl. 16 fig. 4.

Diphyes gracilis Gegenbaur, 1853: 309, pl. 16 figs 5–7 (not Bedot, 1896: 370, figs 4, 8, = *Eudoxoides mitra*).

Diphyes sieboldii Kölliker, 1853: 36, pl. 11 figs 1–8; Gegenbaur, 1854: 448; Keferstein and Ehlers, 1861: 15, pl. 3 figs 1–3; Müller, 1871: 262, pl. 11 fig. 1 and pl. 12 fig. 1 (not figs 2–4); Spagnolini 1870: 617; Lens and van Riemsdijk, 1908: 49; Lochmann, 1914: 271, text-figs 3–5 and pl. 7 figs 4, 5; Candeias, 1932: 9, figs 7, 7a, 8.

Eudoxia campanula: Leuckart, 1853: 43, pl. 3 figs 16–18; Müller, 1871: 262, pl. 11 figs 2–4 and pl. 13 fig. 10; Chun, 1897a: 24 (in part) (not Lens and van Riemsdijk, 1908: 48, pl. 7 fig. 62, indet.).

Diphyes acuminata Leuckart, 1853: 61, pl. 3 figs 11–14; Leuckart, 1854: 274, pl. 11 figs 11–13; Gegenbaur, 1854: 449; Gegenbaur, 1859: 375, pl. 29 fig. 22; Spagnolini, 1870: 621.

Galeolaria aurantiaca Vogt, 1854: 119 (in part), pl. 21 fig. 1 (not fig. 2, indet.; not 110, pls 18–20 figs 1–5, = *Sulculeolaria quadrivalvis*).

?*Eudoxoides sagittata* Huxley, 1859: 59, pl. 4 fig. 1.

Eudoxia campanulata Fewkes, 1880a: 145.

Diphyes siboldii (*lapsus calami*) Bedot, 1882: 122.

Diphyes bipartita: Chun, 1888a: 1158; Chun,

1897a: 24; Mayer, 1900: 74, pl. 34 figs 114, 114a; Vanhöffen, 1906: 18, text-figs 19–21 and ?fig. 22; Le Danois, 1913: 31, figs 18–21.

Diphyes elongata: Haeckel, 1888b: 152.

Cucullus campanula: Haeckel, 1888b: 111.

Cucullus elongatus: Haeckel, 1888b: 110.

Diphyopsis appendiculata: A. Agassiz and Mayer, 1902: 160, pl. 9 figs 38, 39 (not *Ersaea appendiculata* A. Agassiz and Mayer, 1902: 160, pl. 9 fig. 40, = *Diphyes dispar eudoxid*); Bigelow 1904: 265.

Muggiae kochii Murbach and Shearer, 1902: 71, 1903: 189 (not Will, 1844 77, pl. 2 fig. 22, = *M. kochii*).

Diphyes sieboldi: Moser, 1913a: 147; Moser, 1925: 231 (in part), pl. 11, pl. 12 figs 1–3, 8 and pl. 13 figs 3, 4 (not 245, text-fig. 39 and pl. 12 figs 4–7, indet.).

Diphyes siboldi (*lapsus calami*): Candeias, 1929: 276, fig. 7.

Chelophyes appendiculata: Totton, 1932: 354; Kramp, 1939: 16; Totton, 1954: 127, pl. 4 figs 1, 3; Cervigon, 1958: 26, figs 2–8; Patriti, 1964: 228, pl. 9; Totton, 1965a: 185, pl. 32 fig. 4, pl. 33 fig. 6, and text-figs 123 and 124; Stepanjants, 1967: 191 (in part), figs 131, 132a (not fig. 132b); Palma, 1973: 49 (in part), pl. 27 figs 1–5; Daniel, 1974: 154 (in part), text-figs 12k–n; Alvariño, 1981: 418, fig. 174.59; Kirkpatrick and Pugh, 1984: 108, fig. 48; Purcell, 1984: 315; Daniel, 1985: 263, figs 72a–e; Mackie et al., 1987: fig. 36; Pagès and Gili, 1992b: 95, fig. 40; Carré and Carré, 1995: 555, figs 180a–f; Gamulin and Kršinic, 2000: 103, figs 59a–c.

?*Eudoxia russelli* Totton, 1932: 355, text-figs 25, 26.

Diagnosis

Anterior nectophore with lower facet and somatocyst not noticeably twisted to right; only right lateral and right and left lower longitudinal ridges reaching anterior end of nectophore; left lateral ridge terminating just posterior of anterior end.

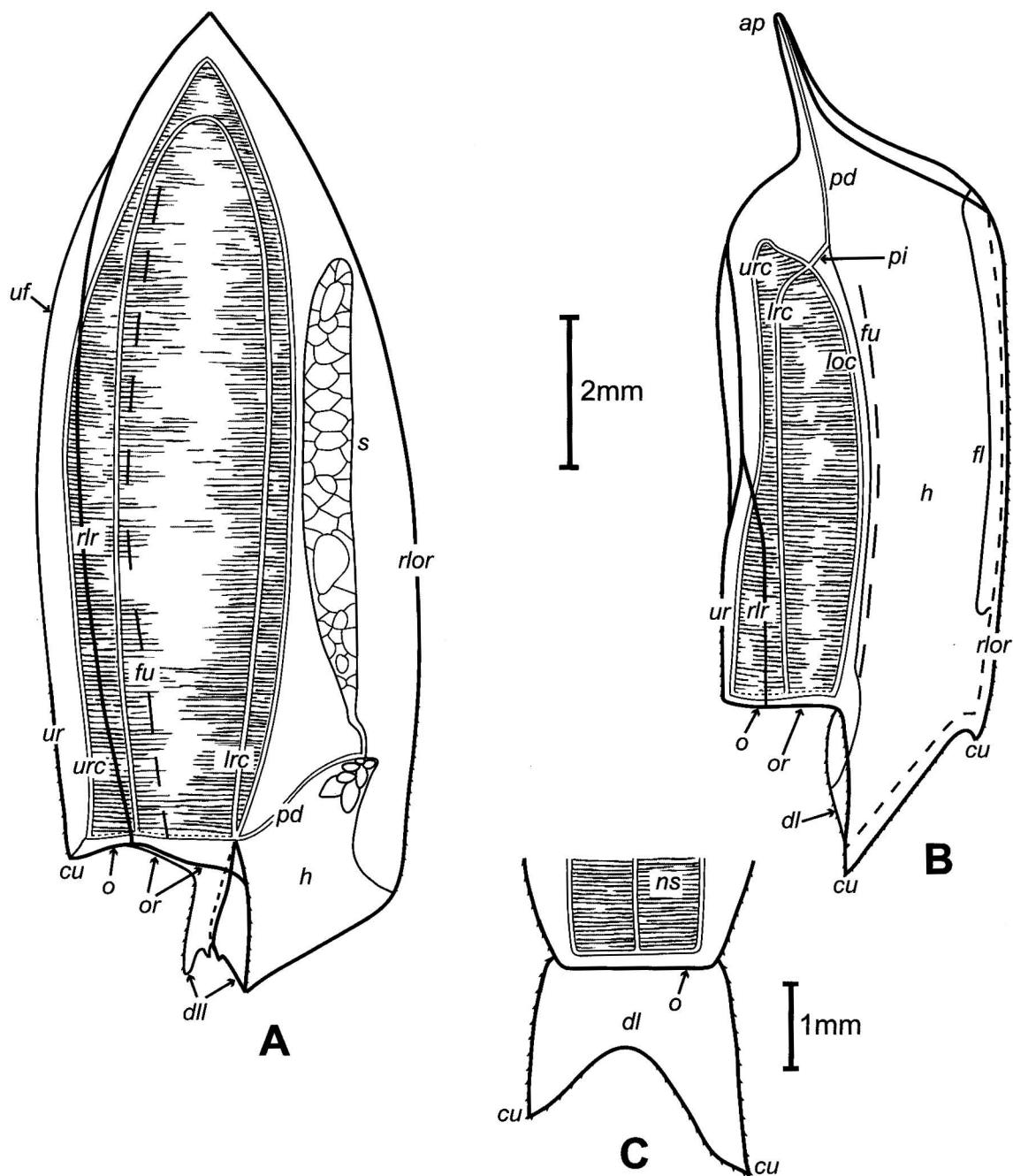


Fig. 55. *Chelophyes appendiculata*: A: anterior nectophore, right lateral view; B: posterior nectophore, right lateral view; C: distal lamella of posterior nectophore, upper view (ap, apophysis; cu, cusp; dl(l), distal lamella (lappets); fl, flap; fu, furrow; h, hydroecium; loc, lower radial canal; lrc, lateral radial canal; ns, nectosac; o, ostium; or, ostial ridge; pd, disjunct pedicular canal; pi, internal pedicular canal; rlor, right lower ridge; rlr, right lateral ridge; s, somatocyst; uf, upper facet; ur, upper ridge; urc, upper radial canal).

Material examined

Two anterior nectophores and 1 posterior nectophore from Canadian Pacific stations LB4 (88–0 m) (Fig. 55) BCPM 996-257-1 and LB14 (0–500 m) (Fig. 11, Table 1); specimens of *Chelophyes appendiculata*

from the NHM collections: Reg. Nos 1958.6.5.141, 13 anterior nectophores (31°55'S, 55°06'E to 31°55'S, 55°05'E); 1947.11.21.210-22, 25 anterior nectophores and 16 posterior nectophores (50°14'N, 12°12'W).

Description of material

Anterior nectophores both 13 mm long, pentagonal, laterally flattened, with pointed anterior end and elongate flat narrow upper facet anterior of upper ridge (Fig. 55A); lower facet broad with flat surface and emarginate concave posterior margin (not illustrated); lower and ostial ridges with some serrations posteriorly; upper ridge short, extending anteriorly only as far as 1.2 mm from ostium; right lower ridge complete; ostial ridge bordering ostium and extending to posterior border of nectophore on each side, forming two struts and delimiting distal lamella; lappets of latter having straight smooth inner margins, slightly concave serrated distal margins, and cusp at each inner angle; lappets similar in size and with slight overlap; furrow between each lateral longitudinal ridge and lower longitudinal ridge (Fig. 55A); mesogloea turgid and opaque; hydroecium with lateral profile having appearance of cat's claw; somatocyst elongate, reaching 1/2–7/10 nectosac length, swollen with oil droplets in one specimen; nectosac with moderately thick muscles; disjunct pedicular canal elongate, originating at somatocyst–stem junction on anterior wall of hydroecium and passing to ostial ring canal on lower side of nectosac (Fig. 55A); upper radial canal originating from junction of ostial ring canal with disjunct pedicular canal, passing anteriorly along lower surface of nectosac, over anterior end, and returning along upper nectosac surface to insert onto ostial ring canal (presumed position) on upper side of nectosac; lateral radial canals originating at same junction, passing anteriorly along lateral walls of nectosac, looping near to anterior end, and returning to midlateral region of ostial ring canal (Fig. 55A); lower radial canal not developed; internal pedicular canal absent and external pedicular canal too short to be discerned in present material.

Posterior nectophore 9 mm long, with proximal articular surface comprising pointed apophysis (Fig. 55B) fitting closely into hydroecium of anterior nectophore in life, and distal ostium with elongate distal lamella extending distally from lower side; lower surface of nectophore flanked by two prominent hydroecial wings enclosing hydroecium and extending from proximal end of nectophore to distal lamella; elongate flap projecting towards hydroecial midline from inner surface in left hydroecial wing; five longitudinal ridges: short incomplete upper ridge extending proximally from ostium, two incomplete elongate lateral ridges, and two incomplete elongate lower ridges extending

from ostium to level of proximal end of nectosac; all ridges serrated; broad, elongate upper facet between left and right lateral ridges and broad, elongate lateral facets between lateral and lower ridges (shown in Fig. 55B but not labelled); ostial ridge enclosing ostium and extending down lateral sides of distal lamella to join lower ridges distally; distal lamella prominent, with central emargination and two large lateral pointed cusps, right cusp longer than left (Fig. 55C); two longitudinal furrows on lateral sides of nectophore; mesogloea turgid and opaque; hydroecium deep and elongate, extending along lower surface of nectophore from proximal end to distal end and of approximately uniform depth throughout (across upper–lower axis); left wing with flap on inner surface (enclosing stem in life); disjunct pedicular canal originating at proximal end of apophysis and passing distally along hydroecial wall to level of proximal end of nectosac (Fig. 55B); short internal pedicular canal penetrating mesogloea from disjunct pedicular canal and inserting onto lower wall of nectosac near proximal end; nectosac with radial canals originating together from internal pedicular canal; upper radial canal extending over proximal end of nectosac and then passing distad to upper side of ostial ring canal (presumed position); lower radial canal passing distad along lower surface of nectosac to lower side of ostial ring canal (Fig. 55B); lateral radial canals curving slightly upwards before extending distad along lateral surfaces of nectosac to insert onto ostial ring canal laterally; external pedicular canal from stem to point of apophysis not identified.

Distribution

Geographic. Canadian Pacific waters: Active Pass (Brinckmann-Voss 1974); off Vancouver Island (Wailes 1929); off west coast of Vancouver Island (present collection, see list of stations above); off Esperanza Inlet (McMurrich 1916); Kingcome Inlet (Brinckmann-Voss 1974); Burke Channel (Fulton 1968). Northeast Pacific: off Baja California to mid-California (Alvariño 1980b and c); off San Diego (Bigelow 1911b; Alvariño 1967b); Santa Barbara Channel (Clarke 1966, cited in Alvariño 1971); off San Pedro, Santa Catalina Island, and San Diego (Ritter 1903); Californian coastal waters (Alvariño 1991); off Baja California and California (Alvariño and Kimbrell 1987); California region (Margulis and Vereshchaka 1994); off northern California coast (Bigelow 1913); off Oregon (Pearcy 1972); North Pacific north to latitude 45°N (Stepanjants

1967); Puget Sound (Murbach and Shearer 1903). Other regions: many records from remainder of Pacific (for example, Alvariño 1971; Margulis 1987; Alvariño et al. 1990; Lin 1993). *Chelophyes appendiculata* is a warm temperate species with a near-cosmopolitan distribution, and is probably the most common siphonophore worldwide (Pagès and Gili 1992b).

Vertical. Only two colonies were found in the present collection and were taken from between 500 m and the surface. Margulis (1980b, 1984) placed this species in a group inhabiting surface, intermediate, and deep waters. However, other reviewers consider *Chelophyes appendiculata* to be primarily epipelagic (Mackie et al. 1987) and this conclusion is supported by a number of records worldwide (Pugh 1974b; Michel and Foyo 1976; Musaeva 1976; Alvariño 1980b; Palma 1985; Gili et al. 1987a; Laval et al. 1989; Pagès and Gili 1991b; Andersen et al. 1992b, 2001; Margulis and Vereshchaka 1994; Sardou et al. 1996; Buecher 1999).

Notes

Definitive nectophores of *Chelophyes appendiculata* were referred to six nominal species during the 1800s, which resulted in many confused synonymies and variant spellings and combinations. By the end of that century, the polygastric (asexual) stage of *C. appendiculata* (as *Diphyes appendiculata*) had become reasonably well established, but some confusion existed over the identity of its eudoxid, which was most frequently mistaken for that of *Eudoxoides mitra* (and possibly as *E. sagittata*, see synonymy above). However, Totton (1965a) commented that because eudoxids can now be obtained from living animals, there is no longer any doubt about their identity, as his own clear figures of a bract and a eudoxid (figs 124A and B, respectively) show. He also noted earlier (Totton 1954) that Moser's figure (1925, pl. 12 fig. 8) gives a good representation of a eudoxid of *C. appendiculata*. Another reasonable figure of a eudoxid is given by Cervigon (1958), though Pugh (1999b) notes that eudoxids of *C. appendiculata* are still indistinguishable from those of *C. contorta* in plankton samples. All eudoxid synonymies listed above are linked directly to polygastric (asexual) colonies of *C. appendiculata* unless preceded by a question mark.

A single specimen of a diphyid from Puget Sound that was first identified as *Muggiaeae kochi* by

Murbach and Shearer (1902) was shortly afterwards noted to be very similar to Mayer's figure of *Diphyes bipartita* from the Tortugas, Florida (Murbach and Shearer 1903). Despite this, the latter authors referred their specimen to *Diphyes chamissonis*, as did Totton (1965a). However, Shih et al. (1971) pointed out that this was probably a misidentification, since *D. chamissonis* is a tropico-equatorial species; they therefore referred it to *Chelophyes appendiculata* and the present author concurs.

10.2.3.3. Subfamily Giliinae Pugh and Pagès, 1995

Diagnosis

Diphyidae with nectophores having ridged reticulum on surface; anterior nectophore with rounded anterior end, probably larger than posterior nectophore. Bract with reticulum of ridges on surface, comprising proximal head-piece and broad distal neck-shield; head-piece with globular phyllocyst; neck-shield with two hydroecial bracteal canals arising from stem-attachment point and extending distally; cormidium separating from stem as free-swimming eudoxid, each eudoxid producing gonophore(s).

Notes

The small diphyid species *Gilia reticulata* was first described as *Lensia reticulata* by Totton (1954) from three anterior nectophores collected in the Indian Ocean; it was referred to the genus *Lensia* because it resembled the multi-striate species *L. exeter*. Later, Pugh and Pagès (1995) reassessed the taxonomic status of the species, based on examination of a larger collection of specimens from the Southern Ocean and the northeast Atlantic, and referred it to a new subfamily. They redescribed the anterior nectophore and described the posterior nectophore, bract, and gonophore for the first time. Whilst noting that the nectophores display characters typical of the Diphyidae, these authors pointed out that the eudoxids more closely resemble those of the family Clausophyidae. In particular, the bract has two bracteal canals arising from the base of the phyllocyst and extending into the neck-shield, similar to those found in clausophyid bracts, and the gonophore has five ridges instead of the four typically found in ridged diphyid gonophores. Thus, they decided to retain the species in the family Diphyidae, whilst referring it to a new subfamily, Giliinae, a decision with which the present author concurs.

Genus *Gilia* Pugh and Pagès, 1995

Diagnosis

With the characters of the subfamily.

Type species: *Gilia reticulata* (Totton, 1954) by monotypy.

Gilia reticulata (Totton, 1954)

(Fig. 56)

Lensia reticulata Totton, 1954: 118, text-fig. 61; Totton, 1965a: 172, text-figs 108, 109; Stepanjants, 1967: 183, fig. 123; Stepanjants, 1970: 243 (in part), fig. 10a (not fig. 10b, indet.); Alvariño and Wojtan, 1984: 56 (in part), fig. 4b (not fig. 4a, = ?*Heteropyramis crystallina*); Alvariño et al., 1990: 39, figs 61A and B (not fig. 61C, = ?*Heteropyramis crystallina*); Margulis, 1992: 129.

Gilia reticulata: Pugh and Pagès, 1995: 181, figs 1–3; Pugh, 1999b: 491, figs 9.13, 10.9; Pagès et al., 2006: 367, figs 2A–D.

Diagnosis

With the characters of the subfamily.

Material examined

Two anterior nectophores from Canadian Pacific station LB16 (700 m) (Fig. 56) BCPM 996-245-2 (Fig. 11, Table 1); specimens of *Lensia reticulata* from NHM collections: Reg. Nos 1952.11.19.2, holotype, 1 anterior nectophore (00°06'S, 49°45'E); 1958.4.29.103, paratype, 1 anterior nectophore (34°47'S, 34°27'E).

Description of material

Anterior nectophores 3.0 and 3.5 mm long, conical, laterally flattened, with broad, rounded anterior end; ostium with broad distal opening (Fig. 56); lower facet narrow, reticulate, and with elongate slit-like notch in posterior border (not illustrated); ridges forming reticulate pattern over lateral and upper nectophore surfaces, with prominent lateral velar ridge projecting outwards laterally on each side and lying 0.4 mm anterior of ostium (Fig. 56); velar ridges

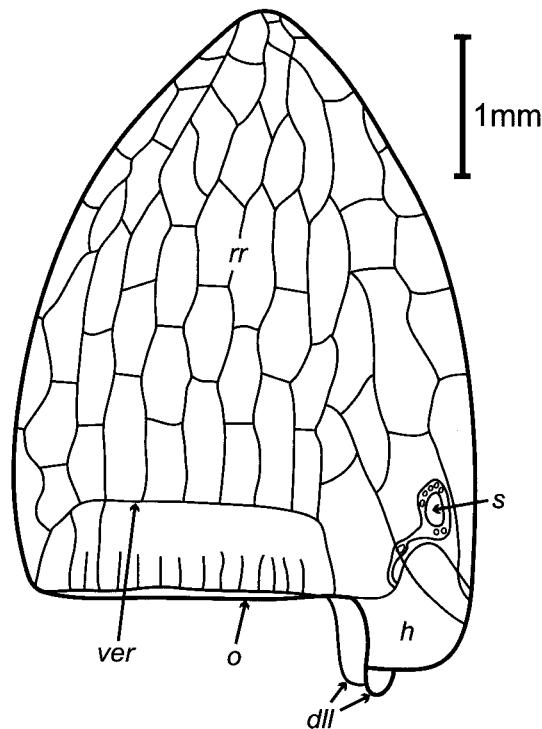


Fig. 56. *Gilia reticulata*, anterior nectophore, right lateral view (dll, distal lamella (lappets); h, hydroecium; o, ostium; rr, reticulum of ridges; s, somatocyst; ver, velar ridge).

originating at ostium near mouthplate on each side, extending anteriorly for 0.4 mm, and then turning upwards, passing along upper-lower nectophore axis for some distance before turning distally again and terminating at ostium close to upper midline (Fig. 56); many short longitudinal ridges extending from beyond velar ridge to ostial border; cusps absent; mouthplate divided into two overlapping elongate rounded lappets; mesogloea flaccid; hydroecium with anterior wall lying anterior of ostium, and with notch in border of lower facet also extending anterior of ostium (Fig. 56); somatocyst small, rounded, containing oil droplets in both specimens, and with elongate stalk extending as shown in Figure 56, with origin on upper wall of hydroecium slightly anterior of ostium; disjunct pedicular canal from somatocyst to nectosac not discernible; nectosac and radial canals not discerned.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: California region (Margulis and Vereshchaka 1994); off San Diego,

California (Alvariño 1967b, 1985). Other regions: a few other widely distributed Pacific records (Alvariño et al. 1990; Margulis 1992; Lin 1993); also some from the Atlantic (Pugh and Pagès 1995; Pagès et al. 2006) and a few from the Indian Ocean (for example, Margulis 1992).

Vertical. This small diphyid has been recorded over a wide depth range, principally between 500 and 2000 m (Alvariño 1967b; Pugh and Pagès 1995; Pagès et al. 2006); the present samples were both from 700 m, which falls within this range.

Notes

Recently published photographs of an anterior nectophore of *Gilia reticulata* by Pagès et al. (2006, fig. 2) show that in what is presumed to be freshly caught material, the nectophores are quite rounded. This contrasts with the nectophores collected from Canadian Pacific waters, as well as those examined from the NHM collections, which are all laterally flattened, as described above.

Although no nectosac was discerned in the two anterior nectophores of *Gilia reticulata* taken in Canadian Pacific waters, one is well shown in two figures of anterior nectophores by Pugh and Pagès (1995, figs 1A and B). The nectosac can be seen filling the nectophore in these figures, as is typical of nectophores of the family Diphyidae (see above). No posterior nectophore of *G. reticulata* was found in the present collection, but this nectophore was figured for the first time by Pugh and Pagès (1995, fig. 1D), who show a large nectosac filling all of the nectophore except the hydroecial cavity on the lower surface. The mouthplate of the anterior nectophore of *G. reticulata* is also well developed (Fig. 56) compared with that of the Clausophyidae, and in this respect this species resembles other diphyid calycophorans, all of which have a mouthplate that projects distoposteriorly beyond the ostium. A well-preserved mouthplate is apparent in a photograph of an anterior nectophore of *G. reticulata* by Pagès et al. (2006, fig. 2A).

The three posterior nectophores referred by Stepanjants (1970, fig. 10b) to *Lensia reticulata* were shown by Pugh and Pagès (1995) to be dissimilar to those of *Gilia reticulata*. Similarly, one of the gonophores referred to this species by Alvariño and Wojtan (1984) was found by Pugh and Pagès (1995) to be referable to *Heteropyramis crystallina*.

10.2.4. Family CLAUSOPHYIDAE

Totton, 1965a

Diagnosis

Calycophorae with dissimilar nectophores, typically two, with anterior nectophore partially apposed to and partially linearly adjoined to elongate posterior one, atypically only anterior one developed; nectophore(s) either with longitudinal ridges or smooth; mouthplate absent in anterior nectophore (except in *Clausophyes laetmata*), present or absent in posterior nectophore; somatocyst in both nectophores typically simple, swollen, and reaching anterior end of nectophore; cormidia with bracts, except in Clausophyinae (*Crystallophyses* produces a unique sexual stage termed the fuseudoxid); bract with phyllocyst variously shaped, and two bracteal canals passing into neck-shield (except *Crystallophyses*).

Notes

This family was originally introduced by Totton (1965a) for six species of diphyomorphs in the genera *Chuniphyes*, *Clausophyes*, *Crystallophyses*, *Heteropyramis* and *Thalassophyses*. Four of these genera were placed by Moser (1925) in a Tribus Intermediae of the family Diphyidae (Chuniphyinae, Clausophyinae, Crystallophyinae and Thalassophyinae) and the fifth was placed in the now invalid family Monophyidae (Heteropyramidinae). Totton (1965a) regarded Moser's classification as unsound (see Section 10.2.4.4) and concluded that *Heteropyramis* was more closely related to the former four genera than to the Diphyidae. He therefore referred all to the Clausophyidae (Totton 1965a), a family distinguished by the presence of a somatocyst in both nectophores (when developed) and two canals (as "horns", or branches, of the phyllocyst) in the bract; these characters are included in the family diagnosis given above.

In the recent molecular analysis by Dunn et al. (2005b) the three clausophyids tested form two clades that are sister to all other diphyomorphs, suggesting that of the four families composing this group (see Section 10.2), the Clausophyidae is likely to be closest to the ancestral diphyomorph stock. Additionally, as Pugh (2006a) states on page 1004, "it is to be hoped that in follow-up studies of the molecular genetics of siphonophores more clausophyid taxa will be included . . (which) will help to resolve whether or not, as the data of Dunn et

al. (2005b) appear to indicate, the family Clausophyidae is a natural grouping". Totton (1954) concludes that clausophyids show certain affinities with abylids, and mentions on page 140 that the gonophores of both have five ridges, whereas those of diphyids have only four. However, in the consensus tree of Dunn et al. (2005b) the single abylid tested is nested within other diphyid species, not among the three clausophyids analyzed, so more genetic analyses are clearly needed on species of both families before any real phylogenetic relationships can be demonstrated.

The family Clausophyidae currently comprises five genera, *Chuniphyes*, *Kephyses*, *Clausophyes*, *Heteropyramis*, and *Crystallophyes*, and species of all except *Crystallophyes* are represented in Canadian Pacific waters. Four of these genera have been established since the time of Totton (1954) and their characters are succinctly summarized by Pugh (1999b). More recently, two new taxonomic works have been published; the first shows that *Crystallophyes amygdalina*, currently monotypic for the genus *Crystallophyes*, produces a fuseudoxid (Pagès and Pugh 2002), and the second introduces a new genus, *Kephyses*, for the previously enigmatic species *Clausophyes ovata* (Pugh 2006a).

The subfamily Crystallophyinae Moser, 1925 was reintroduced by Pagès and Pugh (2002) for the genus *Crystallophyes* on the strength of the fuseudoxid produced by *C. amygdalina*, but other genera remain unassigned. New subfamilies are therefore introduced for these genera in the present work, using earlier names wherever possible. Thus, Chuniphyinae Moser, 1925 is reintroduced for *Chuniphyes*, Clausophyinae Bigelow, 1913 for *Clausophyes*, and Heteropyramidinae Moser, 1925 for *Heteropyramis*. For the genus *Kephyses* Pugh, 2006a, a new subfamily, Kephynae, is herein introduced. The diagnostic characters for these subfamilies (see below) are similar in significance and status to those used to distinguish the three currently recognized subfamilies of the family Diphyidae (see Sections 10.2.3.1, 10.2.3.2, and 10.2.3.3).

In clausophyids both nectophores contain somatocysts, and this led Totton (1965a) to suggest that the anterior nectophore might represent a retained larval nectophore. However, in abylids, where the larval nectophore is known to become the anterior nectophore, a somatocyst is not developed in the posterior nectophore, as mentioned above. Since

the abylid tested by Dunn et al. (2005b) is not closely related to the three clausophyids, it seems likely that retention of a larval nectophore as the definitive anterior nectophore might have occurred more than once amongst diphyomorphs. Possibly, however, it appeared only once, in the clade shown by Dunn et al. (2005b) to comprise *Abylopsis tetragona* and *Diphyes dispar* (see Section 10.2.3), though more molecular data are needed to substantiate this hypothesis.

The axes in clausophyid nectophores are of the diphyomorph type (see Section 10.2.3), except that in the anterior nectophore the stem is attached to the lower surface at a more anterior point than in most diphyids, and in the posterior nectophore the stem is attached to the lower surface at a point somewhat distad of the proximal end. Thus, in the complete colony, the two nectophores appear staggered along the anterior-posterior axis, as shown for *Chuniphyes multidentata* by Bigelow (1911b, pl. 8 fig. 9). Also, the mouthplate, or distal lamella, is developed differently in the Clausophyidae, being present only in the posterior nectophore (following the definition of the mouthplate given in Section 10.2.3), except in *Clausophyes laetmata*. A small cross-process has been described in anterior nectophores of some clausophyids, lying across the right-left axis on the lower side of the ostium (*Chuniphyes multidentata*; see below), but this does not extend posteriorly beyond the ostial cusps, and so is herein considered too short to be termed a distal lamella.

10.2.4.1. Subfamily Chuniphyinae Moser, 1925

Diagnosis

Clausophyidae with two nectophores, ridged and cusped; eight longitudinal ridges in anterior nectophore and six in posterior nectophore; descending surface diverticulum present in posterior nectophore only; cormidia with bracts, each released as free-living eudoxid comprising bract with two bracteal canals and gonophore with five ridges.

Notes

This subfamily was introduced by Moser (1925) for *Chuniphyes multidentata* and *C. problematica*. The former species was first described 17 years earlier by Lens and van Riemsdijk (1908) and the latter was added by Moser herself, although Leloup (1934) subsequently showed it to be the gonophore of a *Chuniphyes* eudoxid. Totton added a second species, *C. moserae*, in 1954. The subfamily is easily

distinguished from other clausophyid subfamilies by the presence of eight and six longitudinal ridges in the anterior and posterior nectophores, respectively.

The number of ridges was not, however, taken into account by Margulis (1988), who relegated *Crystallophyes* to a junior synonym of *Chuniphyes* because she considered the posterior nectophore of *Crystallophyes amygdalina* to be almost identical with that of *Chuniphyes moserae*, and the anterior nectophores of the two species to have very similar somatocysts. In contrast, Pagès and Pugh (2002) comment that ridge number is of fundamental importance in the Clausophyidae, and that in *Crystallophyes* there are only five ridges per nectophore, whereas in *Chuniphyes* there are either eight or six, as noted above. Additionally, the nectophores of *C. amygdalina* are smaller, measuring only circa 10 mm in length (Totton 1965a, fig. 134) and the nectosac is relatively large, extending to 75% of the length of the nectophore (from the ostium). In *Chuniphyes* species, mature nectophores are larger (25–39 mm in length) and have a relatively short nectosac, extending to only 60%–70% of the length of the nectophore (from the ostium). Also, a prominent distal lamella is present in posterior nectophores of the two *Chuniphyes* species, whereas none is developed in *Crystallophyes*. For these reasons both Pugh (1999b) and Pagès and Pugh (2002) recognize *Chuniphyes* and *Crystallophyes* as distinct genera, and the present author concurs.

Genus *Chuniphyes* Lens and van Riemsdijk, 1908

Diagnosis

With the characters of the subfamily.

Type species: *Chuniphyes multidentata* Lens and van Riemsdijk, 1908.

Chuniphyes multidentata Lens and van Riemsdijk, 1908

(Figs 57, 58, 59, 60)

Chuniphyes multidentata Lens and van Riemsdijk, 1908: 13, text-figs 12–23, pl. 1 figs 9–11 and pl. 2 figs 12–15; Bigelow, 1911a: 348; Bigelow, 1911b: 262, pl. 8 fig. 9, pl. 10 fig. 7, and pl. 12

fig. 6; Bigelow, 1913: 73; Bigelow, 1918: 425; Bigelow, 1931: 566, figs 208, 209; Moser, 1920: 180; Moser, 1925: 357 (in part), pl. 23 figs 2–4 and pl. 24 figs 1, 2 (not pl. 23 fig. 1, = *Chuniphyes moserae*); Leloup, 1934: 45; Totton, 1954: 131, text-fig. 66b; Totton, 1965a: 194 (in part), text-fig. 132B; Stepanjants, 1967: 167 (in part), figs 107, 108, ?109; Daniel, 1974: 167 (in part), text-figs 13I–N, ?O, and P; Zhang and Zhang, 1980: 121, figs 1, 2; Alvariño, 1981: 423, fig. 174.67; Kirkpatrick and Pugh, 1984: 118, figs 52A–D; Margulis, 1988: 1275, figs 2a, b, d, e, and zh; Pugh, 1999b: 492, figs 3.112, 2.120; Pagès and Pugh, 2002: 335.

?*Chuniphyes problematica* Moser, 1925: 360, pl. 24 fig. 3 and pl. 25 figs 1, 2; Stepanjants, 1975: 116, fig. 12.

?*Eudoxia problematica*: Leloup, 1934: 46, figs 12, 13; Patriti, 1965a: 158.

Chuniphyes multicristata (*lapsus calami*) Bigelow and Sears, 1937: 60, figs 48A–C.

Diagnosis

Anterior nectophore with longitudinal lateral ridges each bifurcating at 4/5 nectophore length (from ostium); somatocyst with thin posterior branch, discrete swollen central region expanding laterally across right–left nectophore axis, and thin elongate anterior branch. Posterior nectophore with right hydroecial flap relatively elongate and almost as long as left hydroecial flap.

Material examined

Six hundred and seventy-five anterior nectophores and 607 posterior nectophores from Canadian Pacific stations LB12 (0–450 m) (Fig. 58C) BCPM 996-258-2, LB12 (0–300, 300, 400–0, 0–450, 450 m), LB13 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–500 m) (Figs 57A, 58D) BCPM 996-250-2, LB14 (0–300, 300, 0–500, 500, 500–0, 0–700, 700 m), LB16 (0–500, 500, 0–700, 700 m), LB17 (0–300, 300, 300–0, 0–500, 500, 0–700, 700 m), LC9 (0–500 m) (Figs 57B and D, 58A and B) BCPM 996-258-1, LC9 (0–300, 300, 300–0, 0–500, 500, 500–0 m), LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–575, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m);

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

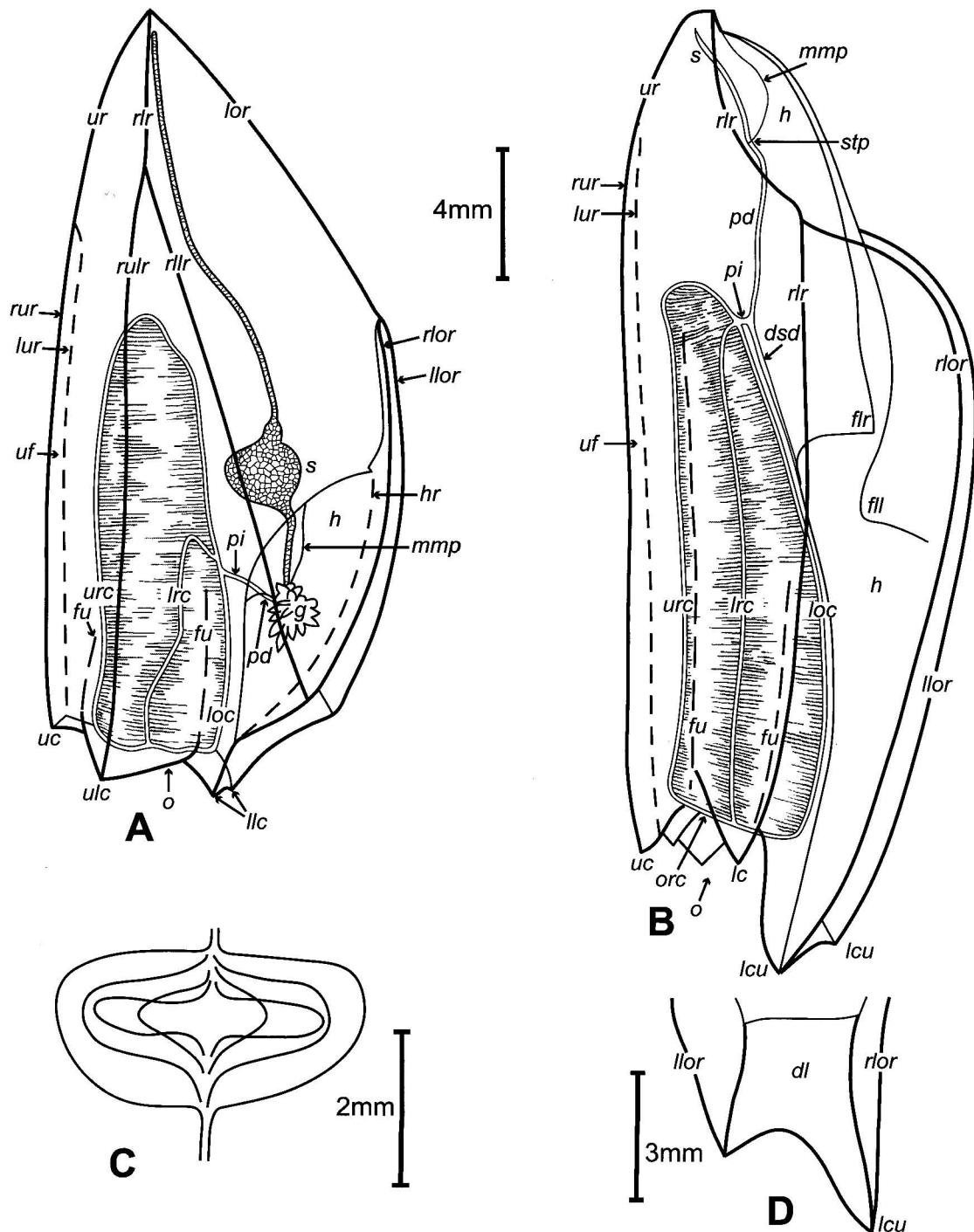


Fig. 57. *Chuniphyes multidentata*: A: anterior nectophore, right lateral view (reconstructed from several nectophores); B: posterior nectophore, right lateral view; C: various somatocyst shapes in anterior nectophores, lower view; D: distal lamella of posterior nectophore, upper view (*dl*, distal lamella; *dsd*, descending surface diverticulum; *flf*, left flap; *flr*, right flap; *fu*, furrow; *g*, gastrozooid; *h*, hydroecium; *hr*, hydroecial ridge; *lc*, lateral cusp; *lcu*, lower cusp; *llc*, lower lateral cusp; *llor*, left lower ridge; *loc*, lower radial canal; *lor*, lower ridge; *lrc*, lateral radial canal; *lur*, left upper ridge; *mmp*, median mesogloea protuberance; *o*, ostium; *orc*, ostial ring canal; *pd*, disjunct pedicular canal; *pi*, internal pedicular canal; *rllr*, right lower lateral ridge; *rlor*, right lower ridge; *rlr*, right lateral ridge; *rulr*, right upper lateral ridge; *rur*, right upper ridge; *s*, somatocyst; *stp*, stem-attachment point; *uc*, upper cusp; *uf*, upper facet; *ulc*, upper lateral cusp; *ur*, upper ridge; *urc*, upper radial canal).

8537 gonophores (some with attached bracts, some separate bracts) and 9 complete eudoxoids from stations LB8 (?–0 m), LB12 (0–300, 300, 400–0, 0–450, 450 m), LB13 (0–300, 300, 0–500, 500, 500–0, 0–700, 700, 700–0 m), LB14 (0–500 m) (Fig. 59C) BCPM 996-230-3, LB14 (0–300, 300, 0–500, 500, 500–0, 0–700, 700 m), LB16 (0–300, 300, 0–500, 500, 0–700, 700 m), LB17 (0–300, 300, 300–0, 0–500, 500, 0–700, 700 m), LC9 (0–300, 300, 300–0, 0–500, 500, 500–0 m), LC10 (0–575 m) (Figs 59A and B) BCPM 996-230-2, LC10 (0–300, 300, 300–0, 0–500, 500, 500–0, 575, 575–0, 700, 700–0 m), LC11 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), A4 (0–300, 300, 300–0, 0–500, 500, 500–0, 0–700, 700, 700–0 m), and LD10 (300 m); 5 anterior nectophores, 4 posterior nectophores, and 4 gonophores collected near thermal vent from tows 1 (1900–0 m), 2 (0–2200 m), and 3 (1845–1200 m) (Fig. 11, Table 1); specimens of *Chuniphyes multidentata* from the NHM collections: Reg. Nos 1959.1.1.25, 39 anterior nectophores (35°13'S, 17°51'E to 34°57'S, 17°48'E); 1959.1.1.33, 72 posterior nectophores (35°13'S, 17°51'E to 34°57'S, 17°48'E); 1982.11.30.330, 1 anterior nectophore and 1 posterior nectophore (34°30'N, 12°00'W to 37°56'N, 12°14'W).

Description of material

Anterior nectophores large, up to 25 mm long, conical, with pointed anterior end and distal ostium flanked by ostial cusps (Fig. 57A); longitudinal ridges prominent, pale gold: four ridges at anterior end, subdividing into eight ridges in anterior to mid-nectophore region; upper ridge subdividing into right and left upper ridges at 7/10 nectophore length and lower ridges subdividing into right and left lower ridges at 3/5 nectophore length; upper ridges and upper lateral ridges terminating as pointed cusps at ostium; upper cusps short (Figs 57A, 58C; also shown in Fig. 58A but not labelled), upper lateral cusps longer (Figs 57A, 58A), each with two short serrated ridges passing from point of each cusp to lateral nectophore surface, inserting just anterior of ostium (shown in Fig. 58C); lower lateral ridges rejoining each lower ridge at 1/10 nectophore length and each terminating as pointed lower lateral cusp distally (Figs 57A, 58A–C); cusps pale gold, right and left cusps of each pair similar in length; four furrows, two on each lateral surface, arising at two insertion points of each upper lateral cusp (Fig. 58C) and passing anteriorly; furrow closest to upper ridge shorter than furrow closest to lower lateral ridge

(Fig. 57A); small cross-process connecting two lower cusps (Fig. 58C); mesogloea thick, robust; hydroecium deep, with broad opening on lower surface extending to 3/5 nectophore length (Figs 57A, 58B), bordered by two small hydroecial ridges extending as shown in Figure 57A but not connecting with lower ridges; median mesogloea protuberance arising from wall of hydroecium closest to nectosac and projecting towards hydroecial opening on lower nectophore surface; somatocyst elongate, originating on median mesogloea protuberance at 1/5 nectophore length and extending to anterior end of nectophore (Figs 57A, 58B); thickened median section of variable width (Fig. 57C) and thin anterior section typically following approximately straight course, atypically zigzagging, with diverticulum at each angle (not illustrated); nectosac extending to 3/5 nectophore length (Figs 57A, 58A and B, radial canals mostly omitted from latter two figures); short median canal passing along median mesogloea protuberance from origin of somatocyst to origin of internal pedicular canal, comprising short ascending surface diverticulum and short disjunct pedicular canal separated by broad insertion point of external pedicular canal (Fig. 58D); internal pedicular canal passing through mesogloea to nectosac, inserting at 1/5–1/4 nectophore length and giving rise to upper and lower radial canals only (Fig. 57A); radial canals (Fig. 57A) reconstructed from several nectophores; upper radial canal passing anteriorly over anterior end of nectosac and then distally to ostial ring canal; lower radial canal passing directly to ostial ring canal; lateral radial canals (where discernible) arising, either together or staggered, from upper canal just anterior of junction of upper and lower radial canals with internal pedicular canal (Fig. 57A); each lateral canal forming anterior loop before following slightly sinuous distal course to ostial ring canal; latter lying within inner edge of infolded velum and following undulating course around ostium (Figs 57A, 58C, velum omitted for clarity); external pedicular canal short and contracted in all nectophores with intact stems (Fig. 58D), hidden within stem mass in Figure 57A; descending surface diverticulum not developed.

Posterior nectophores up to 34 mm long, elongate, with conical proximal end and distal ostium flanked by ostial cusps subtending asymmetric elongate distal lamella (Figs 57B and D); ridges and cusps pale gold, slightly serrated distally; two extensive hydroecial wings on lower side of nectophore, enclosing hydroecium and extending from proximal

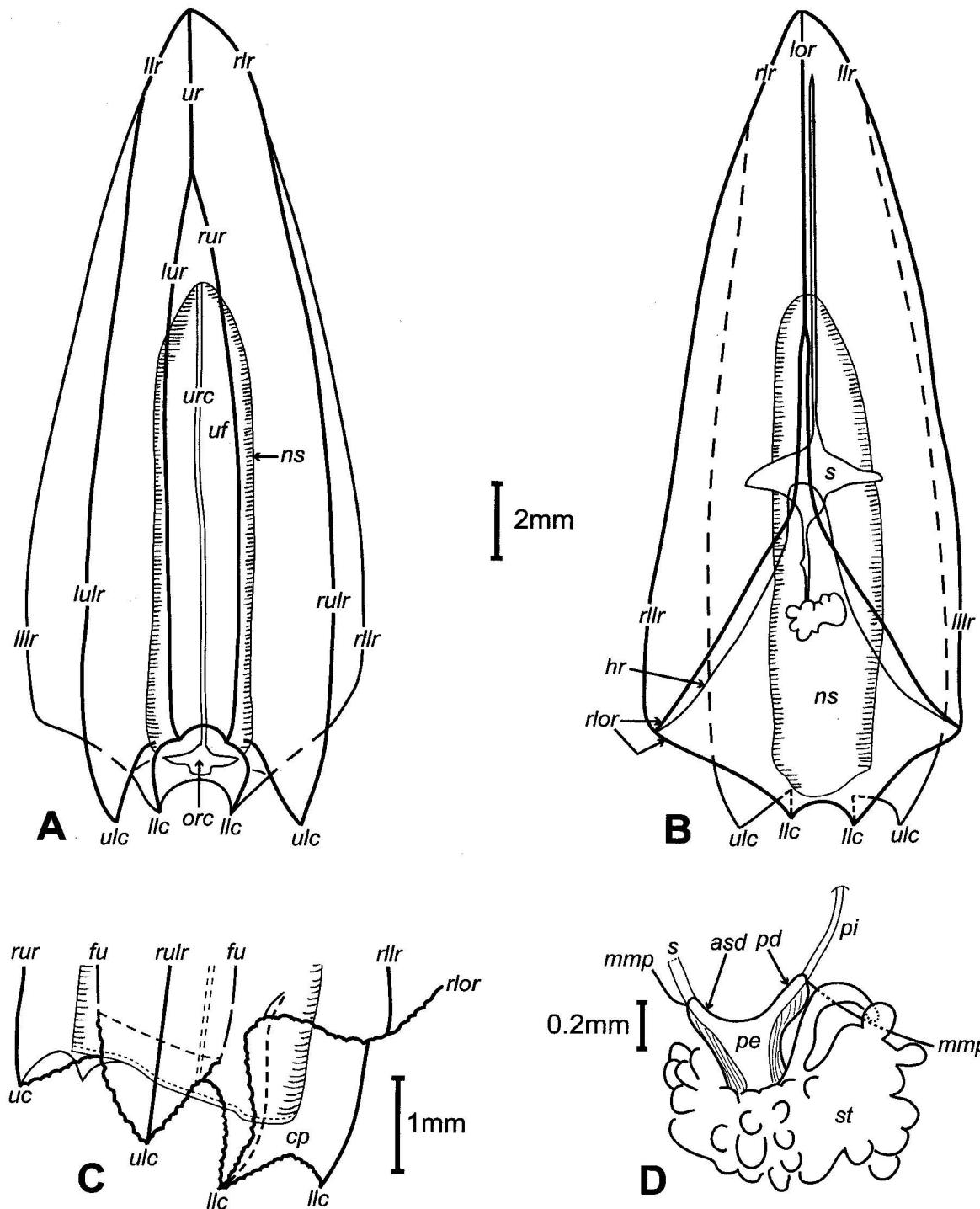


Fig. 58. *Chuniphyes multidentata*: **A:** anterior nectophore, upper view; **B:** anterior nectophore, lower view; **C:** anterior nectophore, lateral view of ostial region; **D:** anterior nectophore, detail of stem-attachment region (*asd*, ascending surface diverticulum; *cp*, small cross-process; *fu*, furrow; *hr*, hydrocial ridge; *llc*, lower lateral cusp; *llr*, left lateral ridge; *llr*, left lower lateral ridge; *lor*, lower ridge; *lulr*, left upper lateral ridge; *lur*, left upper ridge; *mmp*, median mesogloal protuberance; *ns*, nectosac; *orc*, ostial ring canal; *pd*, disjunct pedicular canal; *pe*, external pedicular canal; *pi*, internal pedicular canal; *rllr*, right lower ridge; *rllr*, right lateral ridge; *rulr*, right upper lateral ridge; *rur*, right upper ridge; *s*, somatocyst; *st*, stem; *uc*, upper cusp; *uf*, upper facet; *ulc*, upper lateral cusp; *ur*, upper ridge; *urc*, upper radial canal).

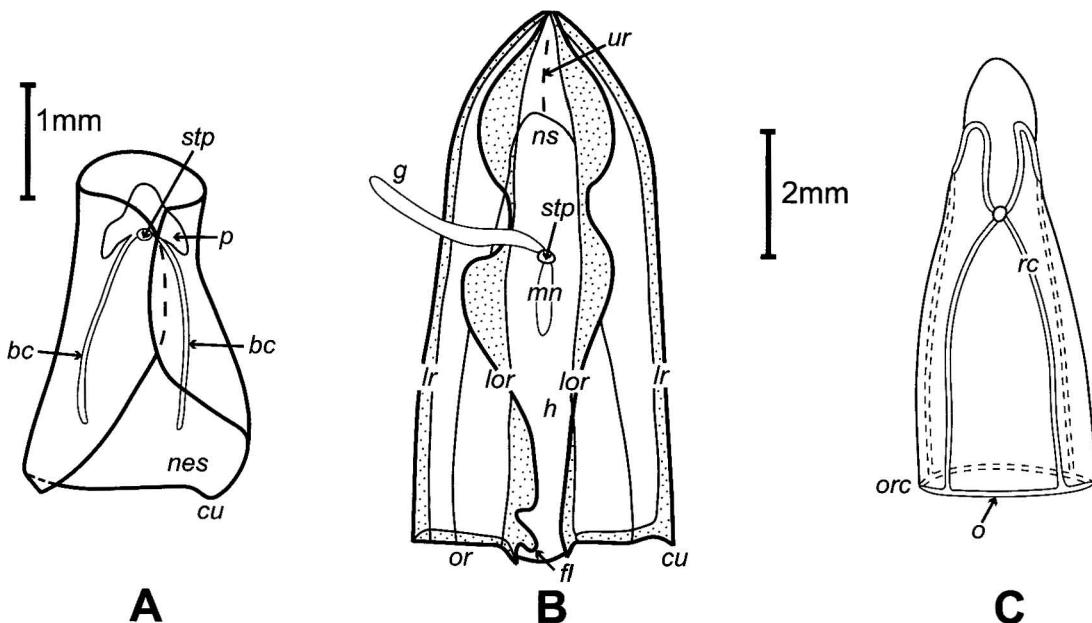


Fig. 59. *Chuniphyes multidentata*: A: bract, lower view; B: gonophore, lower view (stippling represents ridge crests); C: nectosac of gonophore, lower view (*bc*, bracteal canal; *cu*, cusp; *fl*, flap; *g*, gastrozooid; *h*, hydroecium; *lor*, lower ridge; *lr*, lateral ridge; *mn*, manubrium; *nes*, neck-shield; *ns*, nectosac; *o*, ostium; *or*, ostial ridge; *orc*, ostial ring canal; *p*, phyllocyst; *rc*, radial canal; *stp*, stem-attachment point; *ur*, upper ridge).

surface to distal lamella (Fig. 57B); longitudinal ridges comprising upper ridge extending from proximal point to 17/20 nectophore length (from ostium) and subdividing into right and left upper ridges; latter delimiting narrow elongate upper facet and each extending distally as short upper cusp (Fig. 57B); right and left lateral ridges each extending from proximal point to tip of lateral cusp and giving off lower ridge on each side at 3/4 nectophore length (from ostium); lower ridges continuing distally along lower edges of hydroecial wings and terminating as lower cusps on each side of distal lamella; right lower cusp longer than left, and distal lamella with emarginate distal border (Fig. 57D); mesogloea thick; hydroecium extensive, with flap on inner surface of each hydroecial wing thickened along region of attachment to wing; right flap extending distally to 1/2 nectophore length and left flap to 2/5 nectophore length (from ostium) (Fig. 57B); flaps enclosing stem in life; median mesogloea protuberance extending into hydroecium between flaps at proximal end of nectophore (Fig. 57B, *mmp*); somatocyst vermiform, extending from distal end of median mesogloea protuberance to proximal end of nectophore (Fig. 57B); disjunct pedicular canal elongate and extending along hydroecial wall in midline from origin of somatocyst to origin of internal pedicular canal (Fig. 57B, *pd*); latter short and inserting

onto median radial canals near proximal end of nectosac; nectosac and radial canals only preserved in some nectophores; upper radial canal extending proximally for short distance, over proximal end of nectosac, and distally to ostial ring canal; lateral radial canals arising from insertion point of internal pedicular canal, each immediately turning distad and following approximately straight course to ostial ring canal; lower radial canal following straight course to ostial ring canal; descending surface diverticulum originating at internal pedicular canal and extending distally along hydroecial wall as shown in Figure 57B.

Eudoxid bracts small, thin across upper-lower bracteal axis, and up to 3 mm along proximal-distal bracteal axis, relatively few collected, and either loose (Fig. 59A) or still attached to gonophore (not illustrated); many bracts presumed lost, owing to small size; bracteal head-piece short, with slight proximal notch in some specimens (not illustrated), neck-shield elongate and typically wrapping around aperture marking point of attachment to gastrozooid and gonophore (Fig. 59A, *stp*) and enclosing bracteal hydroecium; distal margin of neck-shield with cusp at each distolateral angle; phyllocyst typically triangular and symmetric in lower view (Fig. 59A), atypically asymmetric laterally (not illustrated);

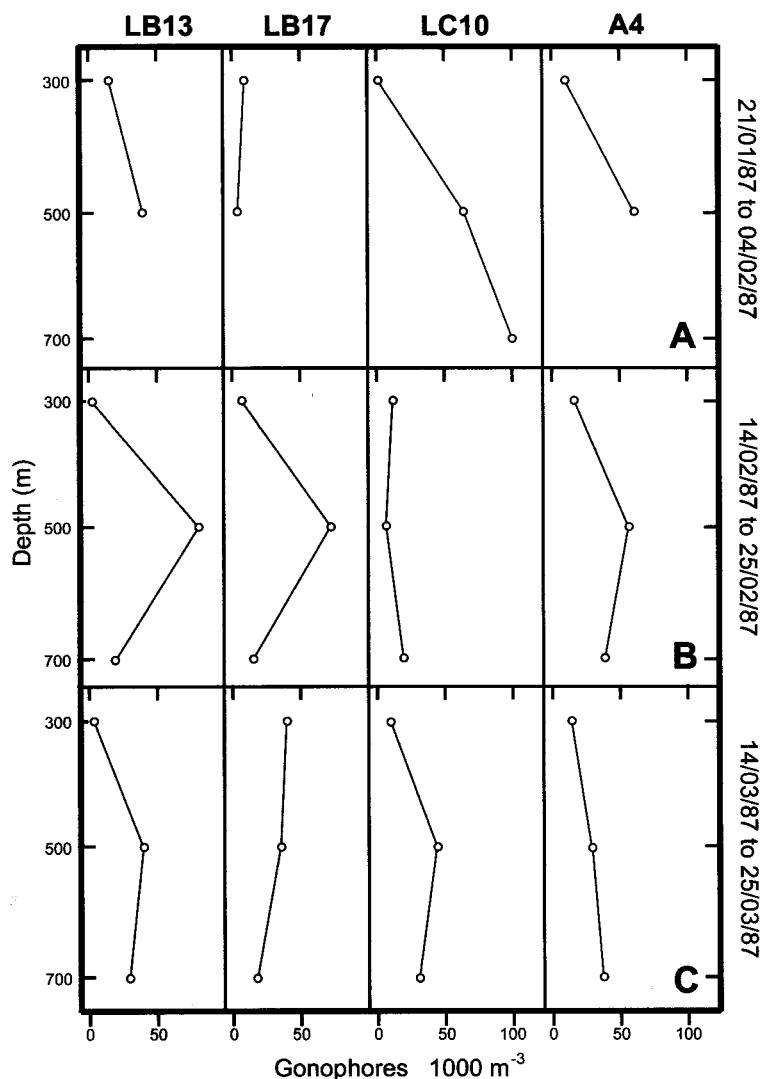


Fig. 60. Winter and spring abundance of *Chuniphyes multidentata* gonophores at four stations during three cruises, from 21 January to 4 February 1987 (A), 14 to 25 February 1987 (B), and 14 to 25 March 1987 (C).

two bracteal canals, thin, elongate, and extending from point of attachment of phyllocyst to stem (*stp*) to distal region of neck-shield; branches with tips either thin (Fig. 59A) or swollen (not illustrated), atypically with small diverticulum near tip (not illustrated).

Gonophores elongate and larger than bracts, 4–9 mm along proximal–distal axis, with short upper–lower axis and broad right–left axis, five complete longitudinal ridges and ostial ridge (Fig. 59B); ridges pale gold and translucent except for opaque flaps on lower ridges distad of stem-attachment

point; ridges typically pleated and weakly serrated distally; lower ridges expanding into two symmetric proximal flaps, two asymmetric median flaps, and single distal flap typically arising on right lower ridge only (Fig. 59B), atypically on left ridge (not illustrated); hydroecium shallow and gutter-like, extending along length of lower surface from proximal to distal end; elongate gastrozooid arising from aperture marking point of attachment to bract in many gonophores (Fig. 59B, *stp*); nectosac bell-shaped in expanded gonophores, widest at ostium (Fig. 59C); four radial canals originating at point of attachment to bract and passing to ostial ring

canal as shown in Figure 59C; manubrium in many gonophores, but gametes not discerned; mantle canals not evident.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993); 53°05'N, 138°31'W, edge of shelf (Bigelow 1913). Northeast Pacific: off Baja California to mid-California (Alvariño 1980c, 1991); 32°16'N, 124°05'N to 32°05'N, 124°02'W; 36°36'N, 122°31'W to 36°38'N, 122°34'W, California region (Margulis and Vereshchaka 1994); off San Diego (Alvariño 1967b); Santa Barbara Channel and Santa Cruz Basin (Alvariño 1971); off Point Conception (Haddock and Case 1999); Monterey Bay (Bigelow and Leslie 1930; Silguero and Robison 2000); off Oregon (Pearcy 1972). Other regions: a number of other Pacific records (for example, Alvariño 1971; Alvariño et al. 1990; Lindsay 2006); also from North Atlantic (Kirkpatrick and Pugh 1984; Pagès et al. 2006), South Atlantic (for example, Alvariño 1980a, 1981), and Indian Ocean (Daniel 1985).

Vertical. West of Vancouver Island, *Chuniphyes multidentata* was recorded during daylight hours at 300, 500, and 700 m. At other Pacific locations it has rarely been found above 200 m (Silguero and Robison 2000), but has been collected down to at least 2600 m (Alvariño 1967b, 1991). It is considered meso- and bathypelagic off California (Margulis and Vereshchaka 1994), as well as in other locations worldwide, such as the North Atlantic (Pugh 1990) and Antarctic Ocean (Alvariño et al. 1990).

In the present study eudoxid gonophores were 15 times more numerous than anterior nectophores throughout the sampling period (January–May 1987), with a maximum density of 112 gonophores·m⁻³ recorded at 500 m depth in February (Fig. 60). Eudoxids were 24% more numerous than anterior nectophores at a site in the northeast Atlantic during April 1974 (Pugh 1984), and at 450 and 600 m they dominated the siphonophore fauna.

Notes

The type specimen of this species is located in the Zoological Museum, Amsterdam (van Soest 1975), and comes from the Molucca Sea in the Philippines.

Early descriptions of *Chuniphyes multidentata* date from 1908, and some may have been based on samples that also included nectophores of *C. moserae*, since the latter species was not described until 1954 (see synonymy for *C. moserae*). The main character which separates the two species is the shape of the somatocyst of the anterior nectophore: in *C. multidentata* it is laterally expanded but in *C. moserae* it is not. Totton (1965a) concluded that a figure of a complete *C. multidentata* colony by Bigelow (1911b, pl. 8 fig. 9), which had a particularly swollen somatocyst in the anterior nectophore, should be referred to *C. moserae*. However, in some of the present anterior nectophores the somatocyst is similarly very swollen (Fig. 57C), and other features of Bigelow's colony are characteristic of *C. multidentata*. These include, in the anterior nectophore, a discrete junction between the swollen region of the somatocyst and its thin anterior branch, bifurcation of the lateral ridge at 4/5 nectophore length, and the position of the median mesogloal protuberance at 1/5 nectophore length; also, there are conspicuous pointed cusps in both nectophores. Bigelow's illustration is therefore herein referred to *C. multidentata*. In contrast, a figure labelled *C. multidentata* by Moser (1925, pl. 23 fig. 1) is considered in the present work to represent *C. moserae*, and is discussed further below. Daniel (1974) also collected a complete specimen of *C. multidentata*, and her description corresponds closely to that of the present Canadian Pacific specimens.

In posterior nectophores of *Chuniphyes multidentata* from Canadian Pacific waters, bifurcations of the upper and lateral ridges are consistent with those described by Totton (1965a, p. 196). The latter author found that the upper (as "dorsal") ridge divided at 8% of nectophore length (from the proximal end) and the lateral ridges divided at 25% of nectophore length. However, he did not give equivalent percentages for *C. moserae*; in the species description below, the distances of these ridge bifurcations are presented as fractions from the ostium.

An ostial ridge is identified in all ridged diphyid species described in Section 10.2.3 (except *Gilia reticulata*), but in *Chuniphyes* species such a ridge is not developed because the ridges that delimit the lateral cusps insert separately on the lateral surfaces of the nectophore. These are described above for *C. multidentata* as originating at the point of each cusp and inserting either onto the lateral nectophore surface itself (upper lateral cusps of the

anterior nectophore and lateral cusps of the posterior nectophore) or onto the ostial edge inside these "outer" cusps. These serrated ridges on the anterior nectophore of *C. multidentata* are shown in detail in Figure 58C. Thus, no single ostial ridge encircles the ostium in either *C. multidentata* or *C. moserae*.

The figures of the bract and gonophore of *Chuniphyes* given by Leloup (1934) show variations in the shape of the phyllocyst and five ridges in the gonophore, both features described above for the present specimens collected in Canadian Pacific waters. However, both Totton (1965a) and Pugh (1999b) conclude that eudoxids of *C. multidentata* and *C. moserae* are indistinguishable. In contrast, the present loose gonophores, bracts, and complete eudoxids collected were only associated with nectophores of *C. multidentata*, and indeed, a very large number of gonophores were collected from the main sampling area (see list above; Fig. 60). Since the single polygastric colony of *C. moserae* collected (see below) came from near the thermal vent, a location non-coincident with the main sampling area (Fig. 11, inset), the gonophores and bracts described above are referred to *C. multidentata*.

Bracts of *Chuniphyes multidentata* have a shorter head-piece and longer neck-shield than those of *Gilia reticulata*, but the bracteal canals are similar and originate at the same point on the bract: the base of the phyllocyst. This is the point where the gastrozoid and gonophore are attached (Pugh and Pagès 1995). The two distal bracteal canals also resemble the hydroecial canals of prayid bracts (Pugh and Pagès 1995, p.189).

***Chuniphyes moserae* Totton, 1954**

(Fig. 61)

Chuniphyes multidentata Moser, 1925: 357 (in part), pl. 23 fig. 1 (not Bigelow, 1911b: pl. 8 fig. 9, or Lens and van Riemsdijk, 1908: 13, pl. 1 figs 9–11 and pl. 2 figs 12–15, = *Chuniphyes multidentata*).

Chuniphyes moserae Totton, 1954: 131, fig. 66a; Totton, 1965a: 196, pl. 35 fig. 2 and text-fig. 132A; Stepanjants, 1967: 168, figs 110, 111; Daniel, 1974: 169, figs 13q, 14a; Daniel, 1985: 287, figs 174h and i; Alvariño, 1981: 422 (in part), fig. 174.66A; Alvariño et al., 1990: fig.

67A; Margulis, 1988: 1277, figs 2v and g; Pugh, 1999b: 492, fig. 3111 (not Alvariño, 1981: fig. 174.66B or Alvariño et al., 1990: fig. 67B, = *Chuniphyes multidentata*).

Diagnosis

Anterior nectophore with longitudinal lateral ridges each bifurcating at 19/20 nectophore length (from ostium); somatocyst with short thin posterior branch, swollen central region extending along anterior-posterior nectophore axis only and narrowing gradually into long thin anterior branch. Posterior nectophore with right hydroecial flap much shorter than left hydroecial flap.

Material examined

One anterior nectophore and 1 posterior nectophore collected from Canadian Pacific waters near thermal vent in tow 2 (0–2200 m) (Fig. 61) BCPM 996-259-1 (Fig. 11, Table 1); specimens of *Chuniphyes moserae* from the NHM collections: Reg. Nos 1958.11.21.174, 1 anterior nectophore and 1 posterior nectophore (34°47'S, 34°27'E); 1958.11.21.175–6, 3 anterior nectophores (06°05'N, 52°00'E); 1958.11.21.177, paratype, 1 anterior nectophore and 2 posterior nectophores (7°42'S, 44°14'E); 1958.11.21.179–181, holotype, 2 anterior nectophores and 2 posterior nectophores (58°35'S, 92°6'E); 1958.11.21.182, paratype, 1 anterior nectophore (66°16'S, 13°23'W); 1958.11.21.183, 1 anterior nectophore (35°13'S, 17°51'E to 34°57'S, 17°48'E).

Description of material

Anterior nectophore from present collection large, 30 mm long, conical, with pointed anterior end and distal ostium flanked by four short, insignificant ostial cusps (Fig. 61A); four longitudinal ridges at anterior end, subdividing into eight ridges in anterior region; upper ridge subdividing into right and left upper ridges at 4/5 nectophore length (from ostium) and lower ridge subdividing into right and left lower ridges at 7/10 nectophore length (from ostium); upper and upper lateral ridges terminating as very short rounded cusps at ostium, with two short serrated ridges connecting distal point of each upper lateral cusp with lateral nectophore wall; lower lateral ridges rejoining each lower ridge at 1/5 nectophore length and each lower ridge terminating, without forming cusp, at posterior end of hydroecium (Fig. 61A); four furrows, extending anteriorly as shown in Figure 61A (two furrows on right lateral surface)

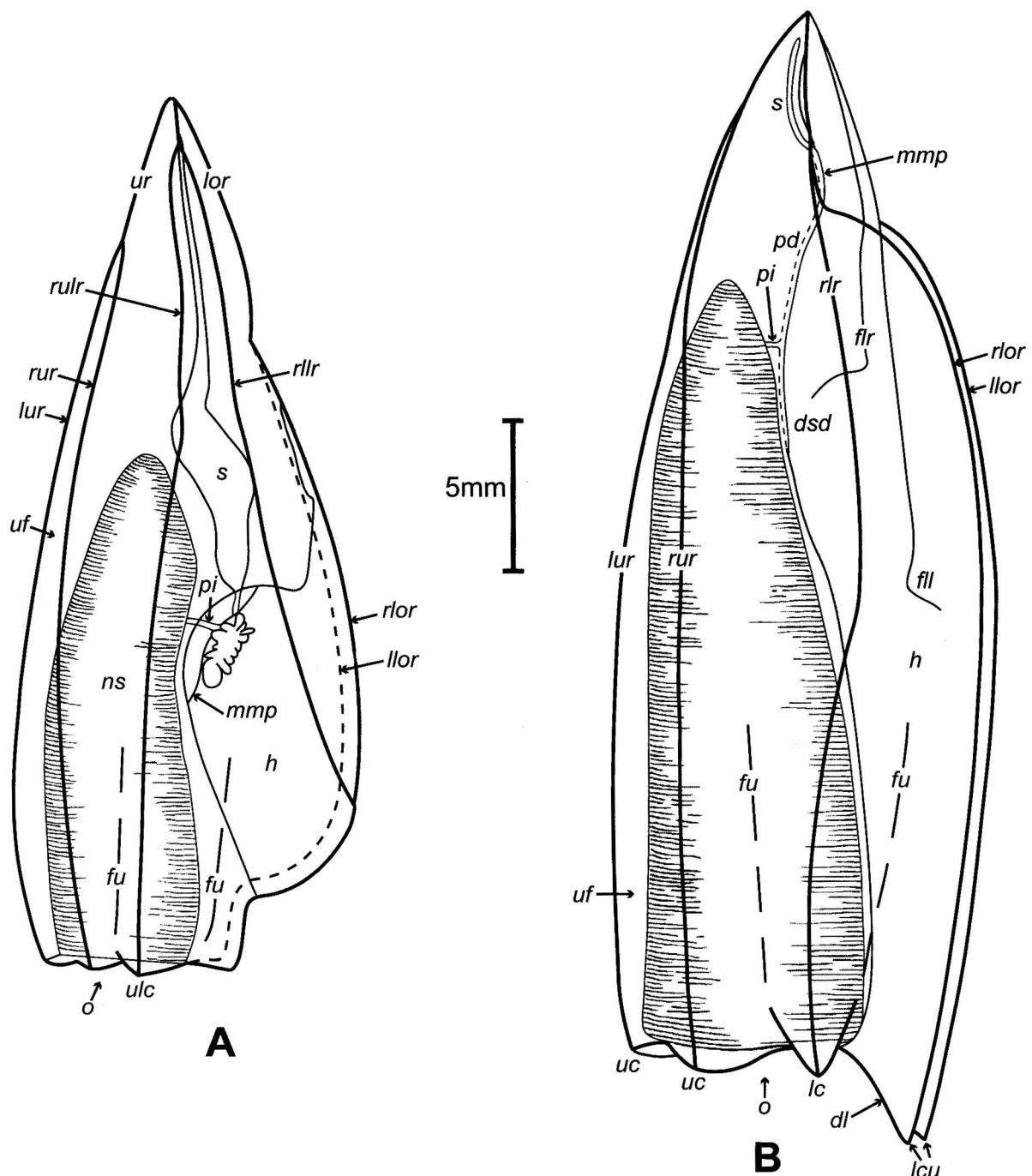


Fig. 61. *Chuniphyes moserae*: A: anterior nectophore, right lateral view; B: posterior nectophore, right lateral view (*dl*, distal lamella; *dsd*, descending surface diverticulum; *fll*, left flap; *flr*, right flap; *fu*, furrow; *h*, hydroecium; *lc*, lateral cusp; *lcu*, lower cusp; *llor*, left lower ridge; *lor*, lower ridge; *lur*, left upper ridge; *mmp*, median mesogloea protuberance; *ns*, nectosac; *o*, ostium; *pd*, disjunct pedicular canal; *pi*, internal pedicular canal; *rllr*, right lower lateral ridge; *rlor*, right lower ridge; *rlr*, right lateral ridge; *rllr*, right upper lateral ridge; *rur*, right upper ridge; *s*, somatocyst; *uc*, upper cusp; *uf*, upper facet; *ulc*, upper lateral cusp; *ur*, upper ridge).

from insertion points of each upper lateral cusp; mesogloea firm; hydroecium with elongate opening on lower surface and two weak hydroecial ridges on

inner surfaces, near lower borders (not illustrated); median mesogloea protuberance elongate and shallow, most extended along anterior-posterior

nectophore axis; somatocyst elongate, without irregular walls, originating on median mesogloea protuberance at 2/5 nectophore length and extending to anterior end of nectophore (Fig. 61A); nectosac extending to 3/5 nectophore length, with musculature only partly preserved (excluding radial canals); short median canal passing along median mesogloea protuberance from origin of somatocyst to origin of internal pedicular canal, comprising short ascending surface diverticulum and short disjunct pedicular canal, separated by insertion of external pedicular canal (obscured by stem components in Fig. 61A); internal pedicular canal originating at 2/5 nectophore length and passing to nectosac as shown in Figure 61A; descending surface diverticulum absent.

Posterior nectophore from present collection large, 38 mm long, with conical proximal end and distal ostium flanked by approximately symmetric ostial cusps, with lower cusps subtending distal lamella of moderate length (Fig. 61B, *dl*); ridges and cusps pale gold, slightly serrated distally; two extensive hydroecial wings on lower side of nectophore extending from proximal to distal end and enclosing elongate hydroecium; longitudinal ridges comprising upper ridge extending from pointed proximal end to 17/20 nectophore length (from ostium), subdividing into right and left upper ridges; latter each extending to ostium, terminating in shallow rounded upper cusp, and upper ridges together enclosing elongate upper facet; right and left lateral ridges passing distally from proximal point to ostium and each terminating as pointed lateral cusp (Fig. 61B); lower ridges each arising from lateral ridges at 9/10 nectophore length and passing distally along edges of hydroecial wings to cusp tips at distal end of distal lamella; latter with shallow emargination; mesogloea soft; hydroecium extensive, with flap on inner surface of each hydroecial wing (Fig. 61B); right flap extending distally to 7/10 nectophore length (from ostium) and left flap extending distally to 2/5 nectophore length; somatocyst filiform, extending from point of insertion of external pedicular canal on median mesogloea protuberance into mesogloea to proximal end of nectophore (Fig. 61B); disjunct pedicular canal elongate, extending distally from origin of somatocyst along upper wall of hydroecium (in midline) to origin of internal pedicular canal at 7/10 nectophore length; latter short and inserting onto nectosac as shown in Figure 61B; radial canals of nectosac not discernible in present specimen; descending surface diverticulum originating at junction of disjunct pedicular canal with internal pedicular canal and extending distally along hydroecial wall as shown in Figure 61B.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: Gulf of California (Alvariño 1969); off San Diego (Alvariño 1967b); 32°16'1N, 124°05'2N to 32°05'4N, 124°02'1W; 36°35'5N, 122°30'8W to 36°38'0N, 122°34'3W, California region (Margulis and Vereshchaka 1994); off Oregon (Pearcy 1972); North Pacific (Stepanjants 1967). Other regions: some records from throughout remainder of Pacific (for example, Alvariño 1971; Alvariño et al. 1990; Lindsay 2006), and some also from other oceans (for example, Margulis 1972b; Stepanjants 1975; Alvariño 1981; Daniel 1985; Pagès et al. 2006).

Vertical. The single specimen of *Chuniphyes moserae* collected from Canadian Pacific waters was from a 0–2200 m deep tow near the hydrothermal vent. Elsewhere, most collections have been made from deeper water. Off San Diego it was collected in a 0–460 m tow but also in deeper tows (Alvariño 1967b), in the Gulf of California it was collected from 1701 m depth (Alvariño 1969), and it was considered by Margulis and Vereshchaka (1994) to be a bathypelagic species in the Pacific off California. In more extensive collections it has been recorded with maximum abundance at 1600–1800 m depth in the eastern Weddell Sea (Pugh et al. 1997) and typically between 500 and 2005 m in the Weddell Gyre (Pagès et al. 1994), but it was also found in the top 500 m in the latter study.

Notes

Totton introduced *Chuniphyes moserae* in his 1954 Indian Ocean report, and his holotype was collected from the northern part of the Southern Ocean where it borders the Indian Ocean. This specimen currently bears Reg. No. 1958.11.21.179-181 and comprises two anterior and two posterior nectophores, although Totton (1954) gave it a different number. He also studied two other Discovery specimens, one from off Italian Somaliland and one from off Zanzibar, now registered as 1958.11.21.175-6 and 1958.11.21.177, respectively. Examination of these nectophores, together with other material also identified by A.K.Totton as *C. moserae* (see list above), shows that the characters exhibited by the specimen from Canadian Pacific waters fall within the range exhibited by the NHM specimens. Thus, in the anterior nectophore of *C. moserae* the bifurcation of the upper ridge lies closer to the pointed anterior end than in that of *C. multidentata*, the lateral

ridges divide considerably closer to this end of the nectophore (except in anterior nectophores of some immature NHM *C. moserae*), though not necessarily at exactly the same distance on each side, and the lower ridge in *C. moserae* bifurcates anterior of the anterior end of the nectosac (in *C. multidentata* it bifurcates at the same level as the anterior end of the nectosac). Other specific differences in the anterior nectophore of *C. moserae* include a more anteriorly situated median mesogloal process and internal pedicular canal (compare Fig. 61A with Fig. 57A), and more rounded and less-developed ostial cusps. In the posterior nectophore of *C. moserae* the upper ridge divides closer to the proximal end than in that of *C. multidentata*, as does the division of the lateral ridge into lateral and lower ridges. Within the hydroecium of the posterior nectophore the right flap of *C. moserae* is considerably shorter than the left flap, reaching only 7/10 nectophore length (from the ostium), whereas in *C. multidentata* this flap is longer, extending to 1/2 nectophore length, and its end is situated much closer to the distal end of the left flap. In *C. moserae* the distal lamella of the posterior nectophore is of moderate length and moderately asymmetric and the ostial cusps are not sharply pointed, whereas in *C. multidentata* the distal lamella is longer and more distinctly asymmetric (Fig. 57D) and the ostial cusps are markedly pointed distally.

The anterior nectophore of *Chuniphyes multidentata* figured by Moser (1925, pl. 23 fig. 1) was referred by Totton (1954) to *C. moserae* because both the bifurcation of the lateral ridge and the position of the median mesogloal protuberance (and associated internal pedicular canal, all shown in Moser's figure but not labelled) lie too close to the anterior end to be attributable to *C. multidentata*. In contrast, Moser's ostial cusps appear to be too pointed to belong to *C. moserae*. Totton placed greater emphasis on the ridge and stem attachment region characters than on the cusps, and the present author concurs. Figures of the nectophores of *C. moserae* given by Stepanjants (1967) and Daniel (1974) show most of the features herein considered characteristic of the species, including the shape of the somatocyst of the anterior nectophore and the relative lengths of the two internal flaps in the posterior nectophore. However, the somewhat posterior location of the bifurcation of the lower ridge in the lower view of an anterior nectophore by Stepanjants (1967, fig. 110B) is more similar to the position of this bifurcation in *C. multidentata*. Despite this, it is likely that Stepanjant's specimen was *C. moserae*. Daniel

positively identified only two anterior nectophores of *C. moserae* in her collection from the Indian Ocean, and although her figure is small (1974, fig. 13Q), it shows a swollen elongate somatocyst diagnostic of *C. moserae*.

The ostial cusps of *Chuniphyes moserae* are not illustrated in detail in the present work, since they are less developed than those of *C. multidentata*. However, weak ridges are identifiable, albeit not serrated, and insert onto the nectophore surface in a similar way to those shown for *C. multidentata* (Fig. 58C). Thus, nectophores of *C. moserae* lack the distinct ostial ridge found in those of species in the family Diphyidae, as do those of *C. multidentata*.

The bract and gonophore of *Chuniphyes moserae* have not yet been positively identified, and none were associated with the present *C. moserae* specimen. As noted above, Pugh (1999b) states that bracts and gonophores of *C. moserae* are indistinguishable from those of *C. multidentata*.

10.2.4.2. Subfamily Kephyinae subfam. nov.

Diagnosis

Clausophyidae with two nectophores, lacking ridges and cusps, and with descending surface diverticula in both nectophores; cormidia with bracts, released as free-living eudoxids, each comprising a bract with two bracteal canals and gonophore without distinctive ridges.

Notes

This subfamily is introduced here for the monotypic genus *Kephyes* recently established by Pugh (2006a), as noted in Section 10.2.4. It differs from the other clausophyid subfamilies in having a nectosac that effectively fills the nectophore, and from all except the Heteropyramidinae in having no median mesogloal protuberance in the hydroecium; in these respects it resembles the family Diphyidae, as pointed out by Pugh (2006a) (see also Section 10.2.3). Other characters of the subfamily, in contrast, are typical of the family Clausophyidae, including the partial apposition of the two nectophores of the colony, as shown by Keferstein and Ehlers (1861, pl. 5 fig. 1) and Pugh (2006a, fig. 5A), a hydroecium in the anterior nectophore that opens along much of the lower surface, and a bract with two bracteal canals extending into the neck-shield.

Genus *Kephyes* Pugh, 2006a

Diagnosis

With the characters of the subfamily.

Type species: *Kephyes ovata* (Keferstein and Ehlers, 1860).

Kephyes ovata (Keferstein and Ehlers, 1860)

(Fig. 62)

Diphyes ovata Keferstein and Ehlers, 1860: 260; Keferstein and Ehlers, 1861: 17, pl. 3 fig. 4 and pl. 5 figs 1–5, 26b; Bigelow, 1913: 70 (not Bigelow, 1913: 71, pl. 6 figs 1, 2, = *Clausophyes galeata*).

Galeolaria (Diphyes) ovata: Chun, 1897b: 73, fig. 14.

Galeolaria ovata: Chun, 1897a: 14, text-fig. 1.

Clausophyes ovata Moser, 1925: 362 (in part) (not pl. 24 fig. 4 and pl. 25 figs 3, 4, = *Clausophyes moserae*); Totton, 1954: 133 (in part), fig. 67; Totton, 1965a: 193 (in part), pl. 35 figs 6–10 and text-fig. 131 (not pl. 35 figs 1, 4, 5, = *Clausophyes moserae*); Alvariño, 1981: 424 (in part), fig. 174.6B (not fig. 174.6A, = *Clausophyes moserae*); Daniel, 1985: 383 (in part), figs 115c–f (not figs 115a and b, = *Clausophyes moserae*); Margulis, 1988: 1270, figs 1i–n; Pugh and Pagès, 1993: 596; Pugh and Pagès, 1995: 189, figs 4d and e; Mills et al., 1996: 156; Gamulin and Kršinic, 2000: 140 (in part), figs 90a–d; Pagès and Pugh, 2002: 334; Bouillon et al., 2004: 218 (in part), fig. 130I (not figs 130G and H, = *Clausophyes moserae*) (not Totton and Fraser, 1955c: 2, fig. 2, = *Clausophyes moserae*).

Clausophyes massiliana Patriti, 1969: 255, figs 1–3; Kirkpatrick and Pugh, 1984: 116, figs 51A–D.

Kephyes ovata Pugh, 2006a: 999, figs 2, 3, 5A.

Diagnosis

With the characters of the subfamily.

Material examined

Five anterior nectophores, 3 posterior nectophores, 36 bracts, and 34 gonophores from Canadian Pacific stations LB13 (500 m) (Figs 62C and D) BCPM 996-239-2, LB14 (0–500 m) (Fig. 62B) BCPM 996-247-2, LB17 (500 m) (Fig. 62A) BCPM 996-250-3, LB17 (0–500 m), LC9 (500 m), LC10 (575–0, 700–0 m), and A4 (0–700 m) (Fig. 11, Table 1).

Description of material

Anterior nectophores small, up to 10 mm long, with rounded anterior end, short right–left nectophore axis, and elongate anterior–posterior nectophore axis, but without small distal extensions from hydroecial wings in present specimens (Fig. 62A); longitudinal furrow on each lateral surface; mesogloea flaccid; hydroecium extending along lower nectophore surface to 7/10 nectophore length, enclosed by lateral hydroecial wings, and with upper wall (adjacent to nectosac) flat, not forming median mesogloal protuberance; somatocyst tubular and short, originating near anterior end of hydroecium at 7/10 nectophore length, slightly swollen in all specimens, and extending anteriorly into anterior end of nectophore (Fig. 62A); nectosac large, almost filling nectophore, and with musculature only partially preserved; radial canals also only partially preserved, reconstructed from all nectophores collected, and with canal walls composed of cubical epithelium (at $\times 50$ magnification, with staining); stem-attachment point (insertion of external pedicular canal) coincident with very short internal pedicular canal (too short for inclusion in Fig. 62A); ascending surface diverticulum extending anteriorly from stem-attachment point to origin of somatocyst; disjunct pedicular canal absent; upper radial canal passing anteriorly from internal pedicular canal, over anterior end of nectosac, and then distoposteriorly along upper nectosac surface to ostial ring canal; lateral radial canals originating from internal pedicular canal, passing over lateral walls of nectosac, following slightly sinuous courses (Fig. 62A), and inserting onto ostial ring canal laterally (portion not preserved); lower radial canal passing directly to ostial ring canal; descending surface diverticulum not preserved in present specimens, but extent deduced and indicated by broken lines in Figure 62B; external pedicular canal not preserved.

Posterior nectophores small, up to 11 mm long, with bluntly conical proximal end, truncate distal end, short right–left nectophore axis, and elongate

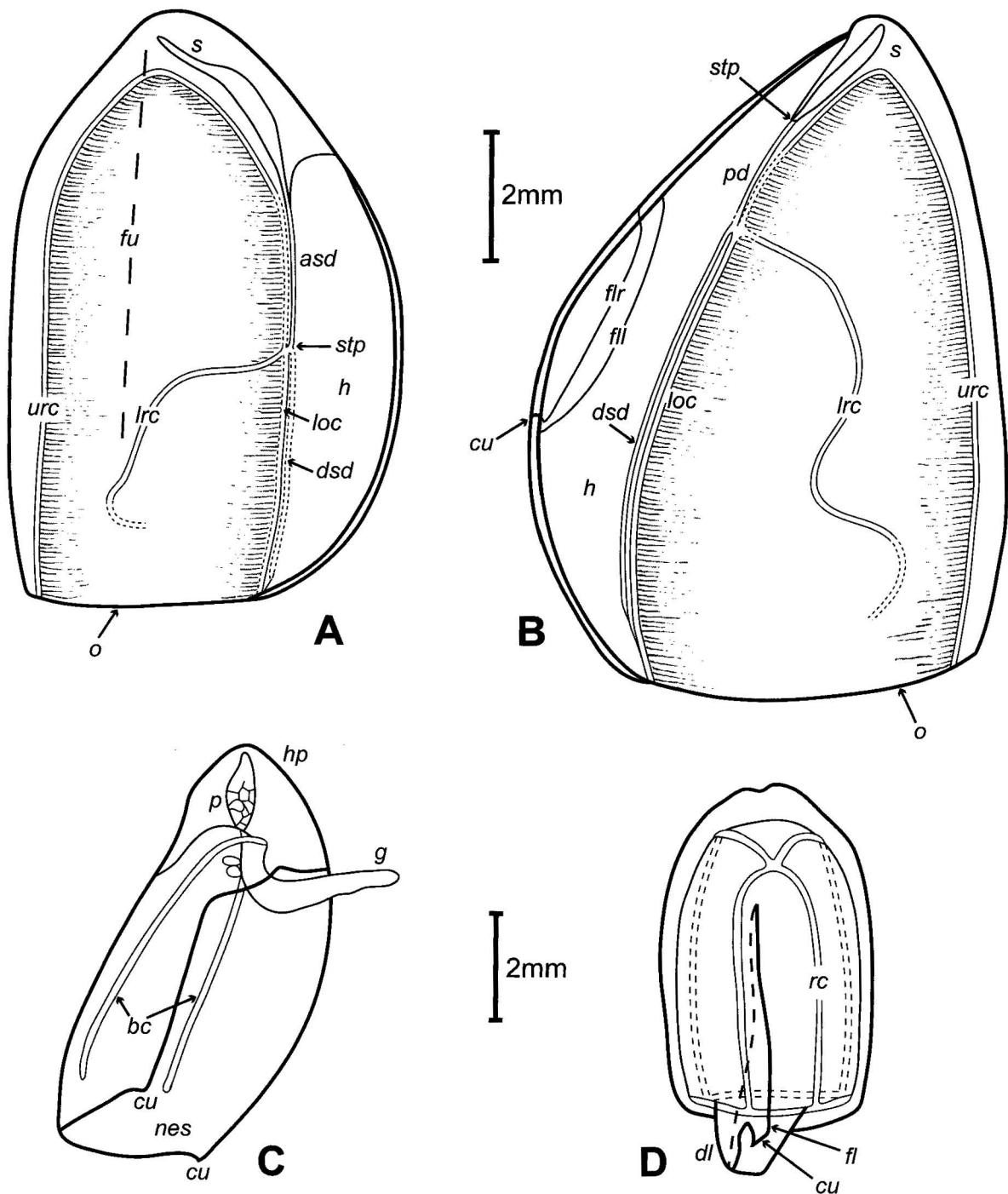


Fig. 62. *Kephyses ovata*: **A:** anterior nectophore, right lateral view; **B:** posterior nectophore, left lateral view; **C:** bract, lower lateral view; **D:** gonophore, lower view (*asd*, ascending surface diverticulum; *bc*, bracteal canal; *cu*, cusp; *dl*, distal lamella; *dsd*, descending surface diverticulum; *fl*, flap; *fl*, left flap; *flr*, right flap; *fu*, furrow; *g*, gastrozooid(s); *h*, hydroecium; *hp*, head-piece; *loc*, lower radial canal; *lrc*, lateral radial canal; *nes*, neck-shield; *o*, ostium; *p*, phyllocyst; *pd*, disjunct pedicular canal; *rc*, radial canal; *s*, somatocyst; *stp*, stem-attachment point; *urc*, upper radial canal.

longitudinal furrow on lateral surfaces (not shown in Fig. 62B); no small distal extensions of hydroecial wings identified in present specimens; mesogloea flaccid; hydroecium elongate, extending along lower nectophore surface from proximal end to distal end, and with two extensive hydroecial wings enclosing hydroecial cavity (Fig. 62B); each wing with in-turned lateral flap; right flap with small distal cusp, left flap without cusp in present material; somatocyst short, thickened proximally, and containing granular material, originating at stem-attachment point and passing through mesogloea to proximal end of nectophore; disjunct pedicular canal of moderate length, extending from stem-attachment point distally to origin of radial canals at 3/5–7/10 nectophore length (Fig. 62B); internal pedicular canal not identified in present specimens; nectosac extensive, filling nectophore, and with only portions of musculature and radial canals preserved; upper radial canal identified at anterior end of nectosac and passing along upper surface of nectosac to ostial ring canal, remainder deduced (broken lines); courses of lateral radial canals following sinuous curves, but distal regions not preserved, so course of left lateral radial canal indicated by broken lines in Figure 62B; lower radial canal extending distally from junction with disjunct pedicular canal to ostial ring canal; descending surface diverticulum elongate and extending from junction of radial canals with disjunct pedicular canal distally along upper wall of hydroecium to near distal end of nectophore (Fig. 62B); external pedicular canal and stem not preserved.

Eudoxid bracts up to 7 mm long, smooth, with short head-piece having rounded proximal end and asymmetric elongate distal neck-shield; latter typically having two small cusps on distal border (Fig. 62C); phyllocyst typically swollen and reaching proximal end of bract, atypically thin (not illustrated); two short longitudinal bracteal canals arising from junction of phyllocyst with gastrozooid and tentacle (too short to be shown in Fig. 62C), each giving rise to elongate hydroecial bracteal canal; latter extending into neck-shield, with ends either not swollen (Fig. 62C) or swollen (not illustrated).

Gonophores up to 8 mm long, conical, with rounded proximal end and large nectosac (Fig. 62D); surface smooth except for flap on one side of lower surface; latter typically arising on right side of gonophore and terminating as small distal cusp, atypically arising on left side (not illustrated); short distal lamella arising from lower surface of ostium and extending distally;

nectosac filling gonophore and opening as broad ostium, with four radial canals originating together from lower surface; canals passing over nectosac as shown in Figure 62D and all inserting onto ostial ring canal distally; mantle canals not discerned in present specimens.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: 32°16'N, 124°05'W to 32°05'N, 124°02'W; 36°36'N, 122°31'W to 36°38'N, 122°34'W, California region (Margulis and Vereshchaka 1994). Other regions: only seven other Pacific records (Margulis and Vereshchaka 1994), but widely distributed in North Atlantic (Kirkpatrick and Pugh 1984; Pagès et al. 2006; Pugh 2006a); also recorded twice from Mediterranean (Keferstein and Ehlers 1861; Patriti 1969).

Notes

Kephys ovata was the first clausophyid species to be introduced, albeit as a diphyid, and was named *Diphyes ovata* by Keferstein and Ehlers (1860) for its oval, rather than conical, nectophores. These authors found a complete colony off Messina in the Mediterranean, which they illustrated in plate 5 figure 1 of their 1861 paper. Their figure shows a somatocyst in both nectophores, and other figures in the same paper show attached cormidia with bracts that have two bracteal hydroecial canals passing into the neck-shield. Chun (1897a and b), while not collecting any material himself, recognized that *D. ovata* represented an intermediate condition between prayids and diphyids, and thus moved it to a new subfamily, Galeolariinae, which he erected for species of *Galeolaria* (now *Sulculeolaria*; see Section 10.2.3.1) because he thought that the posterior nectophore of this genus also had a somatocyst.

A second species, *Clausophyes galeata*, was introduced in 1908 by Lens and van Riemsdijk for a single nectophore collected near the equator, off Indonesia, that differed from all other diphyomorph nectophores known at that time. Shortly afterwards, three whole specimens of *C. galeata* were collected by Bigelow (1913) from the northwest Pacific, and their similarity to the Mediterranean species *Diphyes ovata* noted; both species have a somatocyst in the posterior nectophore as well as in the anterior nectophore. Bigelow (1913) went on to refute the

referral of *D. ovata* to the Galeolariinae because he concluded that the somatocyst identified by Chun in the posterior nectophore of *Sulculeolaria* was in reality a scar left by the muscular lamella when the nectophore broke away from the stem; indeed, such a scar is herein identified as a disjunct pedicular canal in *S. quadrivalvis* (see Section 10.2.3.1). Bigelow therefore referred both *C. galeata* and *D. ovata* to a new subfamily, Clausophyinae, whilst recognizing that each represented a distinct species, since only in the posterior nectophore of *C. galeata* is a mouthplate developed.

Unfortunately, the species of Keferstein and Ehlers (1861) was then mistaken for another *Clausophyes* species by Moser (1925), who described what she incorrectly assumed were further specimens of *Diphyes ovata* from the tropical North Atlantic and referred them to the genus *Clausophyes*. Her mistake did not come to light until 1988, when Margulis pointed out that the specimens figured by Moser (1925) have a mouthplate in the posterior nectophore, whereas those of Keferstein and Ehlers (1861) do not. Margulis (1988) therefore introduced a new name, *moserae*, for Moser's species, but at the same time relegated it to a subspecies of the older species *C. galeata*.

The subspecific status of *Clausophyes galeata moserae* was subsequently reevaluated by Pugh and Pagès (1993), who concluded that *C. moserae* was indeed a valid species (mentioned on their page 599), and the present author concurs. The status of *C. ovata* has also now been reassessed by Pugh (2006a), who transfers it to a new genus, *Kephyses*, because the cormidia contain bracts that are released as free-swimming eudoxids when mature, whereas in *C. moserae* no bracts are developed (see description below). The nectophores of *K. ovata* also more closely resemble those of diphyids, as noted above, than do those of *C. moserae*. Pugh (2006a) constructed his name *Kephyses* from the initial letter of the surnames of Keferstein and Ehlers and fully reviewed the nomenclatural history of *K. ovata*. He has produced a useful time line for the main nomenclatural changes that have occurred for *K. ovata*, *C. galeata*, and *C. moserae* over the years (Pugh 2006a, fig. 1), and this figure can be used by the reader in conjunction with the full synonymy for *K. ovata* given above and that for *C. moserae* given below.

Few specimens of *Kephyses ovata* have so far been described, and there are no specimens in the

NHM collections. The species is redescribed by Pugh (2006a) from new material collected by submersible, and the present specimens (Figs 62A and B), which were net-caught, show slightly less extensive hydroecial wings than are apparent in Pugh's nectophores (2006a, figs 2A and B), and slightly broader nectosacs (across the upper–lower nectophore axis). The small extensions of the hydroecial wings below the ostium are also not apparent in the Canadian Pacific nectophores, which are delicate and may not have preserved well. However, in Pugh's material these two extensions are only connected by a small cross-process, which is similar to that described below for the anterior nectophore of *Clausophyes moserae* and of insufficient size to constitute a distal lamella as defined above (see Section 10.2.4).

The posterior nectophores of *Kephyses ovata*, therefore, differ from those of *Clausophyes* and *Chuniphyses* species in having no distal lamella. In this respect they resemble the two nectophores of *Crystallophyes amygdalina* and the single nectophore of *Heteropyramis* species (see below). However, *K. ovata* differs from both *Crystallophyes* and *Heteropyramis* species in having no ridges, and from *Heteropyramis* species in having two nectophores in the mature colony.

The presence of two bracteal canals in the bract of *Kephyses ovata* is characteristic of the family, as noted above, and the shape of the bract differs somewhat from that of species in the genus *Chuniphyses*. It has a solid head-piece similar to that found in *Heteropyramis* bracts, but no ridges; bracts of the latter genus have four ridges and a shorter neck-shield than those of *K. ovata* (see below). *Chuniphyses* bracts also have a relatively elongate neck-shield with two bracteal canals, but the head-piece is thin and leaf-like and contains little mesogloea (Fig. 59A). *Kephyses ovata* bracts also resemble those of *Gilia reticulata* in having a swollen head-piece and a neck-shield with two bracteal canals, but the latter bracts differ in having a network of ridges covering the outer surface (see Section 10.2.3.3). There are also similarities between *K. ovata* bracts and those of diphyine diphyids, since the latter all have a swollen head-piece (Figs 46B, 47C, 53), although the neck-shield is generally shorter (except in *Dimophyes arctica*) and never has any bracteal canals. *Kephyses ovata* bracts also differ from the sexual stage in the life cycle of *Crystallophyes amygdalina*, which has a unique fuseudoxid, as discussed above.

Gonophores of *Kephyses ovata* have only one small incomplete ridge, as described above, whereas the discrete gonophores of other clausophyids have five ridges (*Chuniphyes multidentata* (Fig. 59B), *Heteropyramis* species). Thus, they differ from those of *Gilia reticulata*, which also have five ridges as mentioned above, and from those of many diphyine diphycids, which have only four ridges (*Chelophyes appendiculata*, *Diphyes* species, *Eudoxoides spiralis*, *Muggiae atlantica*, and some *Lensia* species).

10.2.4.3. Subfamily Clausophyinae

Bigelow, 1913

Diagnosis

Clausophyidae with two nectophores (except *C. laetmata*) but without ridges, cusps, or descending surface diverticula; cormidia without bracts.

Notes

This subfamily was originally introduced by Bigelow (1913) for the genus *Clausophyes*, based on *C. galeata* Lens and van Riemsdijk, 1908. In the present work *C. moserae* (Margulis, 1988), *C. laetmata* Pugh and Pagès, 1993, and *C. tropica* Pugh, 1995 are also referred to the Clausophyinae, based on the new subfamily diagnosis given above. Only one of these species, *C. moserae*, has so far been identified from Canadian Pacific waters.

The most distinctive character of the subfamily is the absence of bracts in the cormidia, as recently noted by Pagès and Pugh (2002) and Pugh (2006a) and mentioned above. This character has previously been identified in only two prayomorph calycophoran groups: all species in the family Hippopodiidae (see Section 10.2.2) and the prayid species *Gymnopraria lapislazula* (Haddock et al. 2005). Thus, it seems likely that within the Calycophorae an absence of bracts has evolved more than once, which raises an interesting question: is it a plesiomorphic or an apomorphic character? The latter seems possible, since, as Dunn et al. (2005) have pointed out, in the Calycophorae there has been a general trend towards zooid loss. However, one might expect the production of a eudoxid with a buoyant bract to aid species dispersal, although this is not borne out by the relatively large number of specimens of *Clausophyes moserae* and *Vogtia serrata* collected in Canadian Pacific waters.

Genus *Clausophyes* Lens and van Riemsdijk, 1908

Diagnosis

With the characters of the subfamily.

Type species: *Clausophyes galeata* Lens and var. Riemsdijk, 1908.

Clausophyes moserae (Margulis, 1988)

(Fig. 63)

?*Clausophyes galeata* Moser, 1913b: 233; Stepanjants, 1967: 170, figs 112A and B.

Clausophyes ovata Moser, 1925: 362 (in part), pl. 24 fig. 4, pl. 25 fig. 3, and pl. 25 fig. 4 (in part); Totton, 1954: 133 (in part) (not fig. 67, = *Kephyses ovata*); Totton, 1965a: 193 (in part), pl. 35 figs 1, 4, 5 (not text-fig. 131 and pl. 35 figs 6–10, = *Kephyses ovata*); Alvariño, 1981: 424 (in part), ?fig. 174.68A (not fig. 174.68B, = *Kephyses ovata*); Kirkpatrick and Pugh, 1984: 114 (in part), figs 50A and B (in part) (not fig. 50C, = *Kephyses ovata*); Daniel, 1985: 383 (in part), figs 115a and b (not figs 115c–f, = *Kephyses ovata*); Bouillon et al., 2004: 218 (in part), figs 130G and H (not fig. 130I, = *Kephyses ovata*).

Clausophyes galeata moserae Margulis, 1988: 1273, pl. 1 fig. Zh and ?pl. 1 figs D, E.

Clausophyes moserae: Pugh and Pagès, 1993: 599, figs 3A–D, 5A–C; Pugh, 1995, 458; Mills et al., 1996: 156; Pugh, 1999b: 492, fig. 3.115; Pugh, 2006a: 999, fig. 5B.

Diagnosis

Anterior nectophore with somatocyst having smooth surface, nectosac reaching 3/5–7/10 nectophore length (from most posterior point of ostium) and without inner flaps on hydroecial wings or a mouthplate (distal lamella). Posterior nectophore with distal lamella undivided, somatocyst with smooth surface and regular shape, hydroecium with two small flaps at distal end of left hydroecial wing,

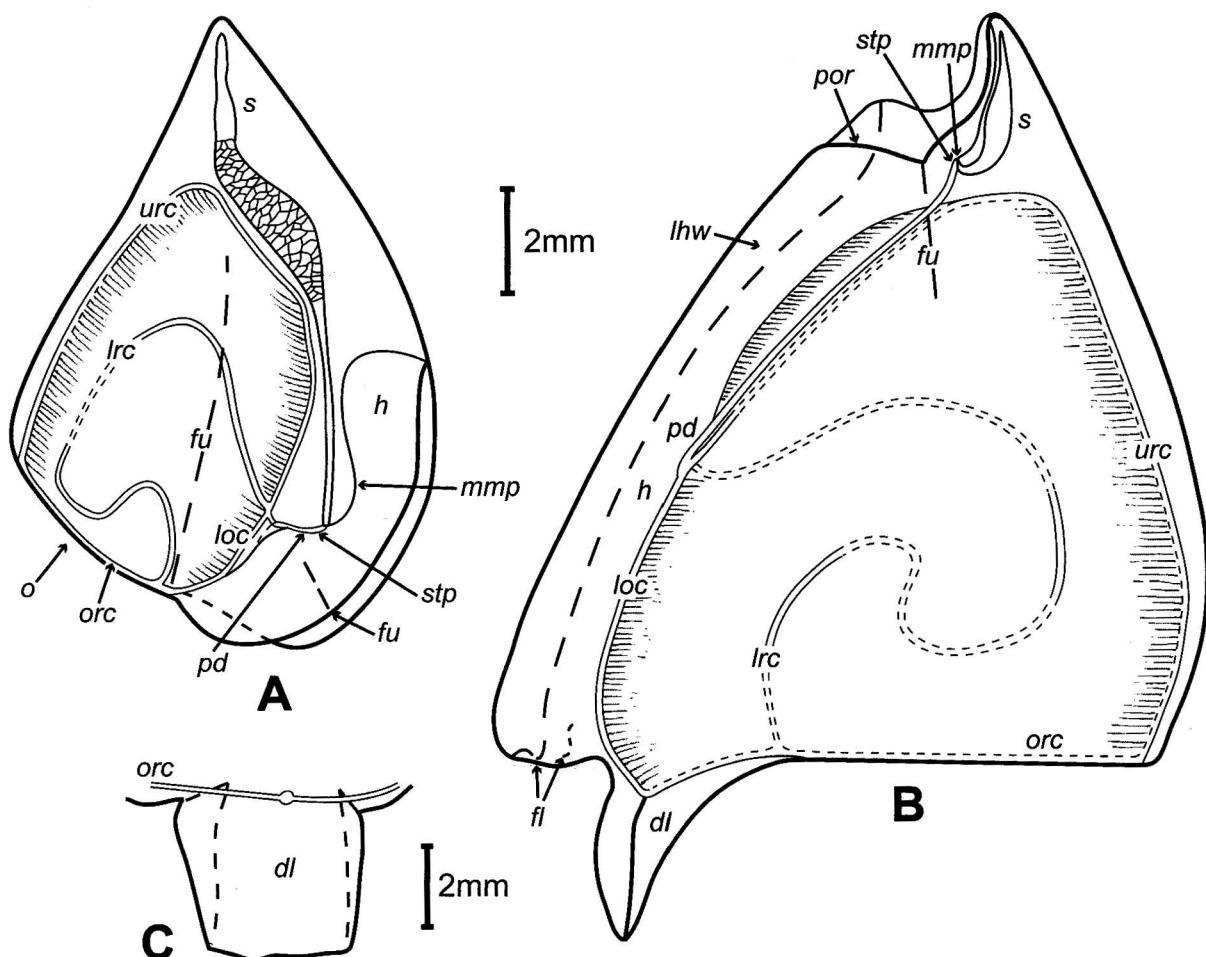


Fig. 63. *Clausophyes moserae*: A: anterior nectophore, right lateral view; B: posterior nectophore, left lateral view; C: distal lamella of posterior nectophore, upper view (*dl*, distal lamella; *fl*, flap; *fu*, furrow; *h*, hydroecium; *lhw*, left hydrocial wing; *loc*, lower radial canal; *lrc*, lateral radial canal; *mmp*, median mesogloea protuberance; *o*, ostium; *orc*, ostial ring canal; *pd*, disjunct pedicular canal; *por*, proximal ridge; *s*, somatocyst; *stp*, stem-attachment point; *urc*, upper radial canal).

lacking deep proximal hollow and finger-shaped processes on inner lateral hydrocial surfaces; stem-attachment point immediately proximal of somatocyst origin.

Material examined

One hundred and forty-seven anterior nectophores and 119 posterior nectophores from Canadian Pacific stations LB13 (0–500, 500, 500–0, 0–700, 700 m), LB14 (0–500, 0–700 m), LB16 (0–500, 500, 0–700, 700 m), LB17 (0–500, 500, 0–700, 700 m), LC10 (500, 500–0, 0–575, 575, 575–0, 0–700, 700, 700–0 m), LC11 (700, 700–0 m), A4 (700–0 m) (Fig. 63) BCPM 996-223-2, and A4 (0–500, 500–0, 0–700, 700, 700–0 m); 5 anterior

nectophores and 5 posterior nectophores collected near thermal vent from tows 1 (1800–1750, 1900–0 m), 2 (1800–1700 m), and 3 (1845–2100, 1950–1935 m) (Fig. 11, Table 1); 1 anterior nectophore from Station B-7 (48°43'N, 126°39'W), oblique vertical tow to 1200 m, collected 27 February 1982 from just outside main study area. Specimens of *Clausophyes moserae* (as *Clausophyes ovata*) from the NHM collections: Reg. Nos 1985.12.9.84, 7 anterior nectophores and 10 posterior nectophores (41°5'N, 14°38'W); 1985.12.8.85, 7 anterior nectophores and 15 posterior nectophores (45°54'N, 09°39'W). Also *Clausophyes galeata* Reg. No. 1957.1.1.220, 1 posterior nectophore (58°35'S, 92°06'E); *Clausophyes laetmata*, holotype, Reg. No. 1993.5.26.1–2, 2 anterior nectophores (63°23'S,

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

58°25'W); and *Clausophyes tropica*, holotype, Reg. No. 1995.17, 1 anterior nectophore and 1 posterior nectophore (0°22'S, 22°04'W).

Description of material

Anterior nectophores 9–11 mm long, pear-shaped in lateral view, with pointed anterior end, short right-left axis, and elongate anterior-posterior axis, lacking distal ostial cusps (Fig. 63A); gold in colour; longitudinal furrow on each lateral surface extending anteriorly from posterior side of ostium, and short diagonal furrow typically also present, arising from lower border of hydroecium; furrows typically U-shaped in section, either shallow or deep; mesogloea flaccid; hydroecium on lower nectophore surface bordered by rounded wings; latter extending anteriorly to anterior end of hydrocial cavity at 2/5 nectophore length (from ostium), and posteriorly to beyond ostium; hydrocial opening slit-like, and always shorter than nectosac in present material (Fig. 63A); median mesogloal protuberance prominent, filling much of hydrocial cavity, and with stem portions attached in some nectophores (not illustrated); somatocyst tubular and elongate, extending from posterior surface of median mesogloal protuberance at 3/20 nectophore length to anterior point of nectophore, with slightly swollen anterior portion, swollen midsection, and long thin posterior portion, atypically thicker or thinner than shown in Figure 63A; nectosac extending to 4/5 nectophore length, with oblique ostial opening; velum typically present (not illustrated); short median canal 1 mm long passing from somatocyst, along groove in median mesogloal protuberance, to internal pedicular canal and comprising: broad insertion point of external pedicular canal adjacent to origin of somatocyst (labelled as stem-attachment point (*stp*) in Fig. 63A), and short disjunct pedicular canal from external pedicular canal to internal pedicular canal; internal pedicular canal 0.2 mm long, passing through mesogloea to nectosac (shown in Fig. 63A but not labelled); radial canals originating together from internal pedicular canal, with courses shown in Figure 63A reconstructed from several specimens (fine broken lines indicate deduced courses); upper radial canal passing over anterior end of nectosac in midline and returning along upper nectosac surface to ostial ring canal; lateral radial canals each following extensive looped course over lateral surface of nectosac and inserting onto ostial ring canal posterolaterally; lower radial canal passing in midline directly to lower region of ostial ring canal.

Posterior nectophores 14–21 mm long, triangular in lateral view, with short right-left axis and prominent distal lamella (Fig. 63B); gold in colour, with short longitudinal furrow passing distally from proximal ridge of nectophore on each lateral surface; distal lamella with distal edge having varied profile, typically with small protruding point just left of centre in upper view (Fig. 63C), and typically serrated (serrations are too small to show in Fig. 63C); other lamellae with approximately straight distal borders, or with slightly hollowed-out lower surface (not illustrated); mesogloea flaccid; hydroecium elongate and shallow, extending length of lower surface, and bordered laterally by two hydrocial wings (only left wing shown in Fig. 63B); each wing folded inwards along most of length and fused to inner wall (extent of left wing infolding indicated by coarse broken line in Fig. 63B); left wing with two small flaps at distal end in all nectophores, flap nearer nectosac slightly proximal to that nearer wing border; right wing also folded inwards for most of length and fused to inner wall, but without obvious distal flap (not illustrated); both wings turning outwards near proximal end of nectophore, fusing to adjacent nectophore surface, and forming two proximal ridges; latter extending to pointed proximal end of nectophore (only left ridge shown in Fig. 63B); somatocyst originating on small median mesogloal protuberance in midline of hydroecium, near proximal end, typically discernible in lateral view, atypically obscured by swollen walls on each side (not illustrated); disjunct pedicular canal elongate, extending distally from origin of somatocyst (at approximately 7/10 nectophore length from ostium) along upper wall of hydroecium to origin of four radial canals at 2/5 to 1/2 nectophore length (internal pedicular canal not developed); nectosac extending to 3/4 nectophore length, with broad ostium opening distally (Fig. 63B); course of upper radial canal not discerned, but presumed to pass over proximal end of nectosac and distally along upper wall of nectophore to ostial ring canal; lateral radial canals only partially preserved, so remainder of courses looping over lateral walls of nectosac deduced; lower radial canal extending directly from origin of four radial canals to ostial ring canal.

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above; first reported in Arai et al. 1993); vicinity of Vancouver Island (Stepanjants 1967). Northeast Pacific: off Baja California to California

(Alvariño 1991); off San Diego (Alvariño 1967b). Other regions: many other Pacific records, almost all from high southern latitudes (Alvariño et al. 1990); widespread in Atlantic (Kirkpatrick and Pugh 1984), some records from Indian Ocean (for example Daniel 1985).

Vertical. This species was collected off Vancouver Island primarily in samples taken at 500 and 700 m depth, but also in samples from shallower water and down to at least 1935 m over the thermal vent. Similarly, off California it was collected (as *Clausophyes ovata*) in a number of 350–475 and 475–600 m deep tows (Alvariño 1991). Worldwide this species has been classified as inhabiting deep and intermediate layers (Margulis 1980b, 1984), and its distribution in the Atlantic is bathypelagic (Kirkpatrick and Pugh 1984, as *C. ovata*, definitive nectophores only).

Notes

Clausophyes moserae was originally described by Moser (1925) as *C. ovata* because she mistook her species for *Diphyes ovata* of Keferstein and Ehlers (1860), as noted above. This was brought to light by the work of Margulis (1988), and indeed, only resolved satisfactorily when Pugh and Pagès (1993) finally described sufficient differences from *C. galeata* to justify recognition of *C. moserae* as a separate species. More recently, Pugh (2006a) has shown that species in the genus *Clausophyes* lack bracts, as also noted above, and thus the bract previously referred by Totton (1954, 1965a) to “*Clausophyes ovata*” of Moser (1925) is herein referred to *Kephyses ovata*, as in the synonymy for the latter species given above.

Differences between *Clausophyes moserae* and *C. galeata* enumerated by Pugh and Pagès (1993) can be summarized as follows: nectophores of *C. moserae* are typically only half the length of those of *C. galeata*, with the somatocyst of the former having a smooth, regular outline, whereas that of the latter is irregular. In the posterior nectophore of *C. moserae* there is an undivided distal lamella (as mouthplate), whereas in *C. galeata* this structure is emarginate (notched) and bears two lateral pointed cusps of varied lengths, and sometimes also has a conical protuberance on its upper surface. The left hydroecial wing of the posterior nectophore of *C. moserae* bears two small flaps at its distal end, on the

inner surface, but that of *C. galeata* has only a single flap. Also in the posterior nectophore of *C. moserae* the looped course of the lateral radial canal is only moderately complex, whereas in *C. galeata* both the inner loop and the outer loop of this canal are more extensive (see Pugh and Pagès 1993, fig. 6). Finally, two finger-like processes protrude from the inner walls of the hydroecium in the proximal region of the posterior nectophore of *C. galeata*, and there is also a deep hollow in the upper hydroecial wall just distal of the small median mesogloal protuberance. In the posterior nectophore of *C. moserae* there are no such processes or hollow, and the stem-attachment point lies immediately proximal of the origin of the somatocyst in the posterior nectophore, whereas in *C. galeata* it lies a short distance distal of it, in the aforementioned deep hollow.

Two new species have been added to the genus *Clausophyes* in recent years: *C. laetmata* Pugh and Pagès, 1993 and *C. tropica* Pugh, 1995. *Clausophyes tropica* seems to be intermediate between *C. moserae* and *C. galeata*, since its anterior nectophore resembles that of *C. moserae* in shape, whereas its somatocyst is irregular, like that of *C. galeata*. Despite these similarities, its nectosac extends to only 2/5 nectophore length (from the ostium), much less than that of either *C. moserae* or *C. galeata*; the latter nectosacs typically reach 7/10 nectophore length (see *C. moserae* diagnosis above). *Clausophyes laetmata* is unique in possessing only an anterior nectophore, which has a mouthplate (distal lamella) similar to that found in the posterior nectophores of other *Clausophyes* species. Pugh (1995, 2006a) has suggested that whereas in other *Clausophyes* species the larval nectophore is probably retained and becomes the anterior nectophore (see Totton 1965a, p. 192), in *C. laetmata* it could be shed early on, leaving only a single nectophore in the mature colony.

In all anterior nectophores of *Clausophyes moserae* collected from Canadian Pacific waters, the nectosac is consistently longer than the hydroecium, whereas in a few of those collected by Pugh and Pagès (1993) from the North Atlantic, Indian, and Southern oceans, the nectosac and hydroecium are similar in length. In all the present posterior nectophores of *C. moserae* collected, a second small flap was identified on the inner surface of the left hydroecial wing, although in a few of those examined by Pugh and Pagès (1993) no flap was found.

10.2.4.4 Subfamily Heteropyramidinae
Moser, 1925

Diagnosis

Clausophyidae with single nectophore having five longitudinal ridges but no cusps or descending surface diverticulum; cormidia with bracts, each released as free-living eudoxid comprising bract with two bracteal canals and gonophore with five ridges.

Notes

Moser (1925) originally introduced this subfamily for a new species, *Heteropyramis maculata*, which she described from several specimens taken in the Atlantic. However, she also found another similar species, *Thalassophyes crystallina*, in the South Atlantic and Southern Ocean, though she placed it in a different subfamily. Subsequently, Totton (1965a) combined the two subfamilies (together with three others) into a new family, Clausophyidae, as noted above. As also noted above, Pagès and Pugh (2002) recently reintroduced the subfamily Crystallophyinae, so the subfamily Heteropyramidinae is herein reinstated for the two species currently referred to the genus *Heteropyramis* (see below).

Genus *Heteropyramis* Moser, 1925

Diagnosis

With the characters of the subfamily.

Type species: *Heteropyramis maculata* (Moser, 1925).

Notes

Two very similar genera, *Heteropyramis* and *Thalassophyes*, were introduced by Moser (1925) for the small species *H. maculata* and *T. crystallina*. However, Moser concluded that in *H. maculata* only one nectophore is developed, whereas in *T. crystallina* the shape of the hydroecium suggested that a posterior nectophore should also be present, although none was found. Moser (1925) therefore placed *H. maculata* in a subfamily of the Monophyidae (erected for several other calycophorans with only a single nectophore, but later abandoned) and *T. crystallina* in a subfamily of the Diphyidae. Totton (1954, 1965a), in contrast, placed these two species in the same group, and also commented on their similarity, suspecting that they differed only in the

absence of opaque spots, although he did not make them congeneric. *Thalassophyes* was not referred to *Heteropyramis* until the review of Margulis (1988), and this referral has been accepted by all subsequent researchers, including the present author. However, Margulis (1988) also concluded that *H. crystallina* is a junior synonym of *H. maculata*, whereas Pugh (1999b) disagreed and accepted both species, as does the present author.

Heteropyramis species differ from other clausophyids in developing only a single nectophore in the asexual (polygastric) colony, and in this respect resemble species of the diphyine genus *Muggiaeae*, two species in other diphyine genera (see Section 10.2.3.2), and certain abyliids. However, most other characters are typical of the family Clausophyidae, including a nectophore with a short nectosac and hydroecium with an elongate opening on the lower surface, and a eudoxid bract with two bracteal canals in the neck-shield. *Heteropyramis* species also lack a median mesogloal protuberance in the hydroecium for stem attachment, a character that they share with the clausophyid subfamily Kephyinae (see Section 10.2.4.2) and the family Diphyidae (see Section 10.2.3).

***Heteropyramis crystallina* (Moser, 1925)**

(Fig. 64)

Thalassophyes crystallina Moser, 1925: 367, pl. 23 figs 5, 6; Totton, 1954: 141, text-figs 72A–C; Totton, 1965a: 201, text-figs 136A–C; Alvariño, 1981: 425, fig. 174.72; Kirkpatrick and Pugh, 1984: 124, fig. 55; Pagès and Gili, 1989: 56, fig. 3; Alvariño et al., 1990: 48, fig. 74.

Heteropyramis maculata Moser, 1925: ?pl. 2 fig. 9; Totton, 1954: text-fig. 71A; Totton, 1965a: text-fig. 135A; Alvariño 1981: fig. 174.71B; Margulis, 1988: 1279 (in part), fig. 3B,?figs 3A, D, and G; Alvariño et al., 1990: 73B; Margulis, 1992: 129 (in part) (not Moser, 1925: 117, pl. 2 figs 1–8, 10, 11, Totton, 1954: 137, text-figs 71B–D, Totton, 1965a: 199, text-figs 135B–D, Alvariño 1981: 425, fig. 174.71A, Margulis 1988: fig. 3V, or Alvariño et al., 1990: 47, figs 73A and B, = *Heteropyramis maculata*).

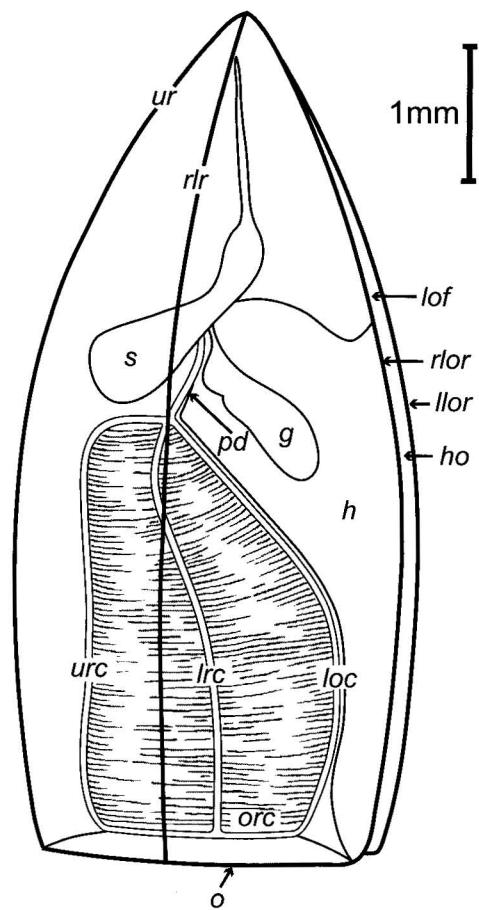


Fig. 64. *Heteropyramis crystallina*, anterior nectophore, right lateral view (*g*, gastrozooid(s); *h*, hydroaecium; *ho*, hydroaecial opening; *llor*, left lower ridge; *loc*, lower radial canal; *lof*, lower facet; *lrc*, lateral radial canal; *o*, ostium; *orc*, ostial ring canal; *pd*, disjunct pedicular canal; *rlor*, right lower ridge; *rlr*, right lateral ridge; *s*, somatocyst; *ur*, upper ridge; *urc*, upper radial canal).

Lensia reticulata Alvariño and Wojtan, 1984: gonophores in sample USNM 61069 (not Totton, 1954: 118, text-fig. 61 or Totton 1965a: 172, text-fig. 110, = *Gilia reticulata*).

Heteropyramis crystallina: Pagès et al., 1994: 886; Pugh and Pagès, 1995: 182; Pugh, 1999b: 493, figs 3.118, 3.121; Pugh and Pagès, 2002: 335, figs 2A and B (not *Heteropyramis alcala* Alvariño and Frankwick, 1983: 686 or Alvariño et al., 1990: 46, figs 72A–D, = *Heteropyramis maculata*; not *Thalassophyes ferrarii* Alvariño and Frankwick, 1983: 689, figs 4, 5 or Alvariño et al., 1990: 50, figs 75A, B, A', and B', = *Crystallophyes amygdalina*).

Diagnosis

Nectophore lacking opaque spots; eudoxid lacking opaque spots and with bract having relatively elongate neck-shield.

Material examined

Twenty anterior nectophores collected from Canadian Pacific waters near thermal vent in tows 1 (1900–0, 1800–750 m), 3 (1950–1935 m) (Fig. 64) BCPM 996-260-1, and 3 (1935–1910, 1910–1850 m); (Fig. 11, Table 1); specimens from the NHM collections: *Heteropyramis crystallina* (as *Thalassophyes crystallina*) Reg. Nos 1959.1.1.127, 4 anterior nectophores (58°35'S, 92°06'E); 1959.1.1.128, 2 anterior nectophores and 1 bract (2°53'S, 4°21'W); *Heteropyramis maculata* Reg. No. 1958.1.1.27–28, 2 anterior nectophores, 2 bracts, and 2 gonophores (43°21'N, 19°23'W); *Crystallophyes amygdalina* Reg. Nos 1959.1.1.214, 1 anterior nectophore and 1 posterior nectophore (02°39'N, 50°46'E); 1959.1.1.215–216, 2 anterior nectophores and 1 posterior nectophore (63°28'S, 137°50'E); 1958.1.1.6, 1 posterior nectophore (53°28'S, 37°08'W).

Description of material

Anterior nectophore up to 9.5 mm long, pyramidal (Fig. 64); ridges gold-coloured, not serrated; right and left lower ridges uniting close to anterior point of nectophore, and delimiting narrow and short lower facet lying anterior of anterior end of hydroaecium (Fig. 64, *lof*); furrows, mouthplate, and cusps not evident; mesogloea flaccid; hydroaecium extending from distoposterior end of nectophore to 3/5 nectophore length (from ostium); somatocyst only discernible in best specimens and originating from short stalk at 3/5 nectophore length, expanding immediately into swollen region (stalk obscured in Fig. 64); latter region extending both anterior and posterior of stalk, and lying at 45° to long anterior-posterior axis of nectophore; somatocyst narrowing anteriorly to thin tube at 3/4 nectophore length and extending almost to anterior end of nectophore (Fig. 64); nectosac extending to 1/2 nectophore length, with broad distal ostial opening; disjunct pedicular canal short, extending from origin of somatocyst posteriorly to origin of four radial canals near anterior end of nectosac; radial canals all following approximately straight courses to ostial ring canal; internal pedicular canal not discerned; external pedicular canal inserting onto nectophore at origin of somatocyst (obscured by somatocyst in Fig. 64).

Distribution

Geographic. Canadian Pacific waters: off west coast of Vancouver Island (present collection, see list of stations above). Northeast Pacific: none. Other regions: other Pacific records are all from high southern latitudes (Alvariño et al. 1990); widespread but uncommon in other oceans (Kirkpatrick and Pugh 1984).

Vertical. *Heteropyramis crystallina* is a little known meso- and bathypelagic species (Margulies 1980b, 1984). The nectophores collected came from a depth range of at least 1800–1935 m in the plume over the central hydrothermal-vent field off Vancouver Island. This range fits within that recorded from the Weddell Sea, where the core of a large population lay within the 500–700 m depth range, but occasional specimens were collected down to at least 2600 m (Pagès and Kurbjewitz 1994; Pagès et al. 1994; Pugh et al. 1997).

Notes

The history of *Heteropyramis crystallina* is closely linked to that of *H. maculata*, although Moser (1925) originally referred the two species to different genera and even different families, as noted above. When they were later placed in the same group by Totton (1954, 1965a), he distinguished *H. crystallina* (as *Thalassophyes crystallina*) from *H. maculata* by the absence of opaque spots on the nectophores and eudoxids. More bracts without spots were referred by Pagès and Gili (1989) to *T. crystallina*, and shortly afterwards the new combination *H. crystallina* was introduced by Pagès et al. (1994) in a list of Siphonophora from the Weddell Gyre in the Southern Ocean. Pugh (1999b) then described both species from the South Atlantic and noted that the bract of *H. crystallina* had a longer neck-shield than that of *H. maculata* (compare his fig. 3.121 with fig. 3.122). Two figures of a complete *H. crystallina* eudoxid in which the bract can also be seen to have a relatively elongate neck-shield are given by Pagès and Pugh (2002, figs 2A and B). A similar eudoxid had previously been figured by Totton (1965a, fig. 135A) but erroneously referred to *H. maculata*. All these eudoxids display a five-ridged gonophore of the type typically found in the family Clausophyidae (see Section 10.2.4).

A number of gonophores referred by Alvariño and Wojtan (1984) to *Lensia reticulata* were reexamined by Pugh and Pagès (1995), and those in one sample (registered as USNM 61069; not figured by Alvariño and Wojtan) were found to be referable to *Heteropyramis crystallina*.

Variation exists in the number and distribution of opaque spots of the heteropyramidine *Heteropyramis maculata*, as clearly illustrated by Totton (1954, text-fig. 70). He believed that spot number was of intraspecific importance only. Despite this, Alvariño and Frankwick (1983) introduced a nominal species, *H. alcala*, for nectophores with 12–16 opaque spots and bracts with 7 spots. Pugh (1999b) later relegated *H. alcala* to a junior synonym of *H. maculata*, and the present author concurs. Alvariño and Frankwick (1983) also introduced a nominal species, *Thalassophyes ferrarii*, for nectophores with a longer nectosac than *H. crystallina* (as *T. crystallina*), which they describe on page 689 as extending to “near the top of the nectophore”. Since such a nectosac closely resembles that of *Crystallophyes* species (see Pugh 1999b, fig. 3.117), Pugh referred *T. ferrarii* to *C. amygdalina*, and the present author concurs.

10.2.5. Family SPHAERONECTIDAE

Huxley, 1859

Diagnosis

Calycophorae with colony comprising single small, delicate, smooth, rounded nectophore (representing retained larval nectophore); nectophore without mouthplate; somatocyst present, simple and swollen; cormidia with bracts; latter with simple phyllocyst and no bracteal canals.

Monotypic for *Sphaeronectes* Huxley, 1859.

Notes

This small family was introduced by Huxley (1859) for a single species, *Sphaeronectes köllikeri*, and later referred by Chun (1885) and Haeckel (1888a and b) to the family Monophyidae because the colonies consist of only a single nectophore. Other monophyids were subsequently added, but because they have closer affinities with other diphyomorph or prayomorph species than with each other, Totton (1932) concluded that the group was artificial and reintroduced the family Sphaeronectidae.

The single nectophore that characterizes the family Sphaeronectidae has been shown by means of rearing experiments to represent a retained larval nectophore (Totton 1954; D. Carré 1969a). Indeed, all calycophorans produce a larval nectophore early in development, which is typically shed once a definitive nectophore forms (see Section 3.1), although it can be retained as the first nectophore of the definitive pair in some groups. Definitive nectophores are

more complex than larval nectophores, and the simplicity of the sphaeronectid nectophore led earlier workers to conclude that *Sphaeronectes* was the most primitive of all calycophoran genera (for example, Bigelow 1911b; Totton 1954). However, Totton (1965a) later placed the Sphaeronectidae among the other diphyomorph families, a move supported by the recent molecular findings of Dunn et al. (2005b), summarized in Dunn and Wagner (2006, fig. 7), which indicate a closer relationship between *S. köllikeri* (as *S. gracilis*) and the other diphyomorphs tested than with the prayomorphs.

Sphaeronectids are therefore an example of paedomorphy, or retention of larval characters into the adult (polygastric) phase; they have become capable of producing sexual eudoxids without developing any definitive nectophores. *Sphaeronectes* species are smaller than most other calycophorans and as a result are frequently missed during collection with nets. *Sphaeronectes köllikeri* is included here because it was found within Canadian Pacific waters by Mackie (1985, as *S. gracilis*), as noted in Section 1, and the description given below is based on a specimen kindly loaned by P.R. Pugh.

Sphaeronectids display several characters typical of diphyomorph calycophorans, including a discrete swollen somatocyst in the nectophore and liberation of a free-living sexual (eudoxid) stage from the posterior end of the stem. The latter process is well shown in *Sphaeronectes köllikeri* (as *S. gracilis*) by C. Carré (1968e, pl. 1 fig. 1). The eudoxid is typical of the family Diphyidae (see Section 10.2.3), comprising a proximal conical head-piece containing a discrete phyllocyst, and a distal neck-shield without any bracteal canals.

Nectophores of sphaeronectids have a small hydroecial opening that extends over a relatively small surface area because a second nectophore is not attached. However, the extent of this opening is species-specific, as discussed below. A main anterior-posterior axis between the rounded anterior end of the nectophore and the centre of the ostium, and also an orthogonal upper-lower axis, are herein identified (Fig. 3G). A relatively elongate proximal-distal nectophore axis is also identifiable in all species, but is omitted from Figure 3G because it lies parallel to the anterior-posterior axis of the colony. In other species the stem-attachment point is offset from the nectophore midline, and as a result the proximal-distal nectophore axis lies at an acute angle to the anterior-posterior colony axis. The axes

of sphaeronectid bracts and gonophores are similar to those described for diphyomorph eudoxids in Sections 2.3.1 and 10.2.3.

Genus *Sphaeronectes* Huxley, 1859

Diagnosis

With the characters of the family.

Type species: *Sphaeronectes köllikeri*.

Notes

The type species of this genus was introduced by Huxley (1859) in the same paper as he introduced the family Sphaeronectidae, as noted above. Huxley described and illustrated the retained larval nectophore of *Sphaeronectes köllikeri* (1859, pl. 3 fig. 4), but did not find any associated eudoxids. Some years earlier two sphaeronectid eudoxids were described and figured by Will (1844, pl. 2 figs 28, 29) under the name *Ersaea truncata*, but their polygastric stage was not identified. Although Will's eudoxid bracts are similar to those of *S. köllikeri* figured by C. Carré (1968a, pl. 2 figs 3-4, as *S. gracilis*), their phyllocysts are shorter, and for this reason it is concluded by the present author that Will's name *truncata* does not apply to the species introduced by Huxley (1859).

Claus (1874) later found more eudoxids, which he named *Diplophysa*, and attributed them to two new sphaeronectid species that he had introduced the previous year (Claus 1873, as *Monophyses gracilis* and *M. irregularis*). He gave good figures of the polygastric stages (Claus 1874, pl. 4, figs 8, 16, 17), but placed them in a different genus to Huxley because, firstly, he concluded that his species only ever developed one nectophore, whereas Huxley thought that another might be formed later, and secondly, those of Claus came from the Mediterranean, a location far removed from the areas where Huxley had taken his specimens (the Indian Ocean, Torres Strait and off northeast Australia). Although Totton (1932) referred both genera to the family Sphaeronectidae, he later made *Monophyses* a junior synonym of the older generic name *Sphaeronectes* (Totton 1965a).

Two species, *Sphaeronectes köllikeri* (as *S. gracilis*) and *S. irregularis*, were clearly distinguished by Totton (1965a) based on differences in the position

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

of the somatocyst and courses of the lateral radial canals, but the eudoxids could not be separated. This was later achieved by C. Carré (1968e), who raised eudoxids of both species in the laboratory in the same manner as he had earlier cultured eudoxids of a third species, *S. gamulini* (C. Carré 1966). The genus *Sphaeronectes* was reviewed by C. Carré (1968e) and five species were accepted. These include three that he introduced earlier, *S. gamulini* Carré, 1966, *S. fragilis* Carré 1968c, and *S. bougisi* Carré, 1968d, and the two species known for over 140 years *S. köllikeri* and *S. irregularis* (see above for synonyms) that were introduced by Huxley (1859) and Claus (1873) respectively.

Another sphaeronectid, *Monophyes japonica*, was described by Stepanjants (1967) from off Japan, and shortly after referred by Daniel (1974) to the genus *Sphaeronectes*; the latter author noted that in many respects it resembled *S. irregularis* (Daniel 1974, 1985). The present author concurs, therefore this species is not included in the synonymy for *S. köllikeri* given below.

Sphaeronectes köllikeri is the only *Sphaeronectes* species so far found in Canadian Pacific waters, and *S. irregularis* has been reported farther south, from the California region (Margulis and Vereshchaka 1994). The nominal species *S. gigantea* was described by Fewkes (1889) from specimens collected in Monterey Bay off Santa Cruz. This species is a questionable synonym of *S. köllikeri*, since the hydroecium was described as being only a "groove or depression" and not an elongate tube as would be expected if *S. köllikeri* was being described; it is therefore omitted from the synonymy given below.

***Sphaeronectes köllikeri* Huxley, 1859**

(Fig. 65)

Sphaeronectes köllikeri Huxley: 1859: 50, pl. 3 fig. 4; Haeckel, 1888b: 130; Chun, 1892: 86, text-figs 2–5; A. Agassiz and Mayer, 1899: 177, pl. 16 figs 51, 52; Moser, 1915b: 652; Moser, 1925: 97 (in part), text-fig. 4d; Leloup, 1935: 7; Trégouboff and Rose, 1957: 345; pl. 76 fig. 9.

Monophyes gracilis Claus, 1873: 258; Claus, 1874: 30, pl. 4 figs 8–15; Chun, 1885: 514, pl. 2 figs 1, 2 (not figs 3, 4, = *Lensia subtilis*, or figs 5–7,

indet.); Haeckel, 1888a: 34; Moser, 1915b: 652; Patriti, 1964: 195 (in part); Patriti, 1970b: 298 (in part).

Diplophysa sp. Claus, 1874: 27, pl. 4 figs 1–4 and ?? (not figs 5, 6, = *?S. irregularis*).

Sphaeronectes (Monophyes) inermis Fewkes, 1880a: 146, pl. 3 fig. 6.

Diplophysa inermis Fewkes, 1880a: 142; Fewkes, 1881: 166, pl. 6 fig. 12 (not Gegenbaur, 1853); *Diplophysa inermis* 291, pl. 16 fig. 3, indet.).

Sphaeronectes gracilis: Bedot, 1882: 122; Chun, 1888a: 1154; Haeckel, 1888b: 130; Chun, 1892: 84, text-figs 2, 4, 5; Schneider, 1896: 603, text-fig. AA and pl. 43 figs 6, 9, 10; Chun, 1897b: 60, text-fig. 4; Mayer, 1900: 73, pl. 27 fig. 89; Totton, 1965a: 202, pl. 36 fig. 1 and text-figs 138, ?137; C. Carré, 1968e: 86, pl. 1 fig. 1 and pl. 2 figs 1–4; D. Carré, 1969a: 32, pl. 1 figs 1–8; Palma, 1973: 52 (in part), pl. 29 figs 1, 2; D. Carré, 1974b: pl. 1 figs 1, 2; Daniel, 1974: 173 (in part), text-figs 14c and d; Kirkpatrick and Pugh, 1984: 126, figs 56A and B; Purcell, 1984: 315; Pagès and Gili, 1992b: 100, fig. 44; Pugh, 1999b: 493, figs 3.43, 3.54; Gamulin and Kršinic, 2000: 122, figs 75a and b; Bouillon et al., 2004: 230, figs 142E and F.

Diplophysa köllikeri Haeckel, 1888a: 32; 1888b: 108; A. Agassiz and Mayer, 1899: 177, pl. 17 fig. 53.

Monophyes köllikeri Haeckel, 1888a: 34.

Sphaeronectes truncata Schneider, 1898: 75 (in part); Schneider, 1899: 13 (in part), ?figs 12, 13; Bigelow, 1911b: 184 (in part); Bigelow, 1914: 22 (in part); Browne, 1926: 59 (in part) (not Will, 1844: *Ersaea truncata* 82, pl. 2 fig. 28, indet.).

Diagnosis

Nectophore with tubular hydroecium lying anterior of nectosac, elongate, and occupying 7/10 nectophore width (across upper–lower axis); nectosac extending anteriorly to only 1/2 nectophore length, and with radial canals arising together from anterior end, laterals approximately straight; somatocyst spindle-shaped, without stalk, and extending towards upper side of nectophore. Bract with distinct hydroecium and neck-shield, phyllocyst spindle-shaped and extending to more than 1/2 bract length.

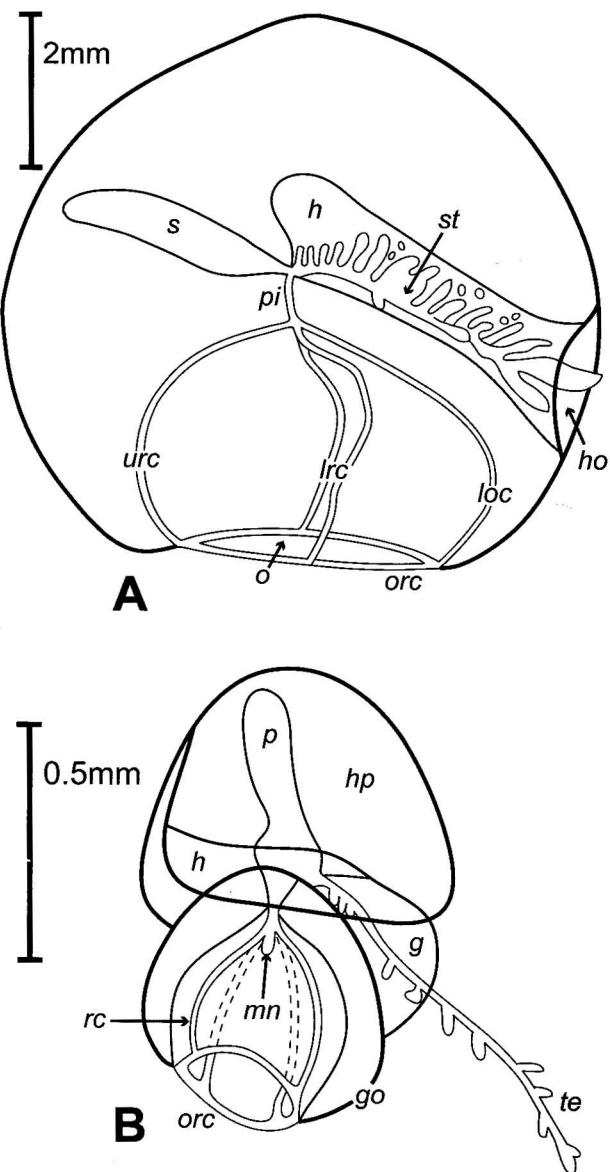


Fig. 65. *Sphaeronectes köllikeri*: A: ectophore, right lateral view; B: eudoxid, lateral view (g, gastrozooid; go, gonophore; h, hydroecium; ho, hydroecial opening; hp, head-piece; loc, lower radial canal; lrc, lateral radial canal; mn, manubrium (gonophore); o, ostium; orc, ostial ring canal; p, phyllocyst; pi, internal pedicular canal; rc, radial canal (gonophore); s, somatocyst; st, stem; te, tentacle; urc, upper radial canal).

Material examined

This species is included because it was previously recorded from Canadian Pacific waters (Mackie 1985, as *S. gracilis*; see Section 6.1), although no specimens were found in the present samples from off Vancouver Island or in others taken from the Strait of Georgia (Mapstone and Arai 1992). The

description given below and material illustrated in Figure 65 are based on a specimen collected by SCUBA in the tropical North Atlantic near the Mid-Atlantic Ridge at 6°20.1'N, 31°46.3'W (Blue Water Plankton Sample No. 1056) and kindly loaned to the present author by P.R. Pugh.

Description of material

Nectophore 5 mm long (along anterior-posterior axis) and 5 mm broad (across upper-lower axis); surface appearing crumpled but probably smooth in life; hydroecium with relatively small circular opening on lower ectophore surface containing contracted stem and attached gastrozooids (Fig. 65A); somatocyst elongate and somewhat swollen along most of length, arising from stem-attachment point in hydroecium and extending along upper-lower ectophore axis; nectosac with four radial canals originating together at anterior end, and with lateral radial canals following slightly curved courses; internal pedicular canal short and extending from stem-attachment point to origin of radial canals at anterior end of nectosac; disjunct pedicular canal not developed.

Eudoxid comprising bract and attached gonophore, measuring 1 mm from proximal end of bract to distal end of gonophore; bract with hemispherical head-piece (Fig. 65B), and shallow hydroecium with opening extending proximally for short distance as slit on lower surface; neck-shield present and extending laterally as two shallow wings enclosing hydroecium (see below); phyllocyst elongate and extending close to proximal end of bract; large attached gastrozooid with elongate tentacle extending posteriorly (gastrozooid partially obscured by gonophore in Fig. 65B); gonophore somewhat hemispherical, without ridges, and having nectosac with four straight radial canals, ostial ring canal, and small manubrium; mouthplate absent; hydroecium and mantle canals not evident.

Distribution

Geographic. Canadian Pacific waters: Jervis Inlet (Mackie 1985). Northeast Pacific: off Baja California and California (Alvariño 1991); off San Diego (Ritter 1903; Alvariño and Kimbrell 1987); California Current (Purcell 1980); off Santa Barbara (Purcell and Kremer 1983); off Santa Catalina Island, California (Purcell 1981b; Purcell and Kremer 1983); Monterey Bay (Bigelow and Leslie 1930). Other regions: some other temperate-zone and tropical Pacific records (for example, Bigelow

1911b; Margulis 1987; Pagès et al. 1990, 2001; Lin 1993; Palma and Rosales 1997; Palma et al. 1999; Kitamura et al. 2003), widely distributed in other oceans (for example, Daniel 1974; Moreno and Fdez-Alcazar 1984; Pagès 1992; Gamulin and Kršinic 1993a and b; Pagès et al. 2006).

Vertical. This species was observed from a submersible between approximately 70 and 140 m in Jervis Inlet, Vancouver Island (Mackie 1985). Off California it was collected from at least 75 m up to 11 m (Alvariño 1991). Elsewhere it has been recorded primarily in near-surface waters (Patriiti 1966; Ianora and di Carlo 1981; Pagès and Gili 1991a and b; Lakkis and Zeidane 1997).

Notes

The eudoxid of the species described above has a bract identical with that described by C. Carré (1968e) for *Sphaeronectes gracilis* (see above). However, the phyllocyst of this bract is longer than that shown by Will (1844) for the closely related *Ersaea truncata*, as discussed above. Since Huxley (1859) gave the first accurate description and figure of the polygastric stage, his species name *köllikeri* takes precedence over *gracilis* and the latter is relegated to a junior synonym.

The nectophores of *Sphaeronectes köllikeri* differ from those of the other four species in the genus in several respects. The hydroecium, which contains the contracted stem shown in Figure 65A, lies anterior of the nectosac and is linked to it by a short internal pedicular canal. In the other four species of the genus (see above) the hydroecium lies on the lower side of the nectosac and the stem apparently attaches to the nectosac directly, without an intervening internal pedicular canal. The lateral radial canals all arise together on the nectosacs of *S. köllikeri*, *S. irregularis*, *S. gamulini*, and *S. fragilis*, but in *S. bougisi* they arise from the upper radial canal only, at the anterior end of the nectosac. Furthermore, these canals are looped in *S. irregularis*, *S. gamulini*, and *S. fragilis* but they are taken as being straight in *S. köllikeri* and *S. bougisi*.

In all species of the genus the somatocyst originates from the same point on the hydroecial wall as the stem, but in *S. köllikeri* the somatocyst is short and unstalked and extends towards the upper side of the nectophore, whereas in the other four species it arises from the lower side of the nectosac (at different levels) and extends either approximately anteriorly, as in *S. irregularis*, *S. fragilis*, and *S. bougisi*, or laterally around the left side of the nectosac, as in *S. gamulini*.

The number of cormidia observed in mature colonies of *Sphaeronectes köllikeri* ranges from 30 to 60 (C. Carré 1968e, Purcell and Kremer 1983, as *S. gracilis*). C. Carré showed each cormidium to comprise a pair of buds for a bract and a gonophore, and an elongate pedicel bearing a gastrozooid with a tentacle (1968e, pl. 2 fig. 2). This cormidium is somewhat similar to that found in species of the physonect family Forskaliidae (see Section 10.1), where the gastrozooid is borne on a similarly elongate pedicel, but in the latter the pedicel is covered with bracts, and gonophores arise from a different point on the stem, because forskaliid cormidia are diffuse. In *S. köllikeri* the cormidia are discrete and each cormidium is separated from the next by an internode devoid of zooids (see Section 10.2).

The bract of *Sphaeronectes köllikeri* has a reasonably well developed hydroecium, as mentioned above, and the phyllocyst is fusiform, extending to more than half the length of the bract (along the proximal-distal axis), as is well shown in several figures by C. Carré (1968e, pl. 2 figs 3, 4). In *S. irregularis* the bracteal hydroecium is shallower and the phyllocyst shorter and more pyriform, as is also well shown by C. Carré (1968e, pl. 2 figs 5, 6). The phyllocyst of the *S. gamulini* bract is also short, but can be distinguished from those of *S. köllikeri* and *S. irregularis* by its unique mushroom shape and by the apparent absence of a bracteal hydroecium (see C. Carré 1968e, pl. 2 fig. 7). The shapes of the phyllocysts of these *Sphaeronectes* bracts, like those of other diphyids (see Section 10.2.3), mirror those of the somatocysts of their retained asexual larval nectophores.

References

- Abreu, P.C.O.V. de, and Noguiera, C.R. 1989. Spatial distribution of Siphonophora species at Rio de Janeiro Coast, Brazil. Ciênc. Cult. **41**(9): 897–902.
- Agassiz, A. 1865. Illustrated catalogue of the Museum of Comparative Zoölogy, at Harvard College. No. II. North American Acalephae. University Press, and Welsh, Bigelow, and Co., Cambridge, Mass. pp. 234.
- Agassiz, A., and Mayer, A.G. 1899. Acalephs from the Fiji Islands. Bull. Mus. Comp. Zool. Harv. Coll. **32**(9): 157–189.
- Agassiz, A., and Mayer, A.G. 1902. Reports on the scientific results of the expedition to the Tropical Pacific in charge of Alexander Agassiz by the U.S. Fish Commission steamer "Albatross", from August, 1899, to March, 1900, Commander Jefferson F. Moser, U.S.N., commanding. III. Medusae. Mem. Mus. Comp. Zool. Harv. Coll. **26**(3): 139–176.
- Agassiz, L. 1862. Siphonophorae. In Contributions to the natural history of the United States of America. Second Monograph. Vol. IV. Hydroidæ (8). Little, Brown, and Co., Boston, and Trübner and Co., London, UK. pp. 333–372.
- Alcazar, J.L. 1982. *Muggiaeae cantabrica* n. sp. (Siphonophora, Calycophorae). Bol. Ciênc. Naturaleza R.I.D.E.A. No. 29. pp. 51–57.
- Alvariño, A. 1963. Ecology of the Gulf of Thailand and the South China Sea. A report of the NAGA Expedition, 1959–1961. Southeast Asia Research Program. Report of the Scripps Institute of Oceanography, La Jolla, California, SIO Reference No. 63-6. pp. 104–108.
- Alvariño, A. 1964. Report on the Chaetognatha, Siphonophorae and Medusae of the MONSOON Expedition in the Indian Ocean: preliminary results of SIO Investigations in the Indian Ocean during Expeditions MONSOON and LUSIAD (1960–1963). Report of the Scripps Institute of Oceanography, La Jolla, California, SIO Reference No. 64-19. pp. 103–108, 209–212.
- Alvariño, A. 1967a. A new Siphonophora, *Vogtia kuruae* n. sp. Pac. Sci. **21**(2): 236–240.
- Alvariño, A. 1967b. Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae and Ctenophora off San Diego, California. Pac. Sci. **21**(4): 474–485.
- Alvariño, A. 1968a. Los quetognatos, sifonóforos y medusas en la región del Atlántico ecuatorial bajo la influencia del Amazonas. An. Inst. Biol. Univ. Nac. Auton. Méx. Sér. Ciênc. Mar Limnol. **39**(1): 41–76.
- Alvariño, A. 1968b. Two new Calycophorae, Siphonophorae. Pac. Sci. **22**(3): 340–346.
- Alvariño, A. 1969. Zoogeografía del mar de Cortés : quetognatos, sifonóforos y medusas. An. Inst. Biol. Univ. Nac. Auton. Méx. Sér. Ciênc. Mar Limnol. **40**(1): 11–54.
- Alvariño, A. 1971. Siphonophores of the Pacific with a review of the world distribution. Bull. Scripps Inst. Oceanogr. Univ. Calif. Tech. Ser. No. 16.
- Alvariño, A. 1972. Zooplancton del Caribe, Golfo de México y regiones adyacentes del Pacífico. Memorias IV Congreso Nacional de Oceanografía (México). pp. 223–247.
- Alvariño, A. 1974. Distribution of siphonophores in the regions adjacent to the Suez and Panama canals. U.S. Natl. Mar. Fish. Serv. Fish. Bull. **72**: 527–546.
- Alvariño, A. 1976. El zooplancton del Pacífico Colombiano y las pesquerías. Memorias Seminario sobre el Océano Pacífico Sudamericano, 1–5 September, Cali, Colombia. Vol. 1. Universidad del Valle, Cali, Colombia. pp. 206–271.
- Alvariño, A. 1980a. El plancton del Atlántico Suroeste. Dinámica y ecología. Bol. Inst. Oceanogr. **29**(2): 15–26.
- Alvariño, A. 1980b. Reproduction seasons and day/night bathymetric distribution of three species of Diphyinae (Siphonophorae), off California and Baja California. In Developmental and cellular biology of coelenterates. Edited by P. Tardent and R. Tardent. Elsevier/North Holland Biomedical Press, Amsterdam and New York. pp. 33–38.
- Alvariño, A. 1980c. The relation between the distribution of zooplankton predators and anchovy larvae. Calif. Coop. Oceanic Fish. Investig. Rep. **21**: 150–160.
- Alvariño, A. 1981. Siphonophorae. In Atlas del zooplancton del Atlántico Sudoccidental y métodos de trabajo con zooplancton marino. Edited by D. Boltovskoy. Publicación especial del Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina. pp. 383–441.

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- Alvariño, A. 1983. *Nectocarmen antonioi*, a new Prayinae, Calycophorae, Siphonophora from California. Proc. Biol. Soc. Wash. **96**(3): 339–348.
- Alvariño, A. 1985. Distribución batimétrica de especies del género *Lensia* en aguas de California y Baja California (Diphyidae, Siphonophorae, Coelenterata). Invest. Mar. Cent. Interdiscip. Cienc. Mar. **2**(1): 59–80.
- Alvariño, A. 1991. Abundancia y distribución batimétrica diurna y nocturna de los sifonóforos durante las cuatro estaciones del año 1969, en aguas de California y Baja California. Invest. Mar. Cent. Interdiscip. Cienc. Mar. **6**(2): 1–37.
- Alvariño, A., and Ambros, M.J.L. 1986. El zooplancton del Pacífico ecuatoriano. Invest. Mar. Cent. Interdiscip. Cienc. Mar. **3**(1): 69–110.
- Alvariño, A., and Frankwick, K.R. 1983. *Heteropyramis alcalai* and *Thalassophyes ferrarii*, new species of Clausophyidae (Calycophorae: Siphonophorae) from the South Pacific. Proc. Biol. Soc. Wash. **96**(4): 686–692.
- Alvariño, A., and Kimbrell, C.A. 1987. Abundance of zooplankton species in California coastal waters during April 1981, February 1982, March 1984 and March 1985. NOAA Tech. Mem. NMFS No. 74.
- Alvariño, A., and Wojtan, J.M. 1984. Three new species of *Lensia*, and description of the eudoxia stages of *Lensia reticulata* and *Lensia lelouveteau* (Calycophorae: Siphonophorae). Proc. Biol. Soc. Wash. **97**(1): 49–59.
- Alvariño, A., Wojtan, J.M., and Martinez, M.R. 1990. Antarctic siphonophores from plankton samples of the United States Antarctic Research Program. In Biology of the Antarctic Sea. XX. Edited by L.S. Kornicker. Antarct. Res. Ser. **49**: 1–436.
- Andersen, O.G.E. 1981. Redescription of *Marrus orthocanna* (Kramp, 1942) (Cnidaria, Siphonophora). Steenstrupia, **7**(13): 293–307.
- Andersen, V., Sardou, J., and Nival, P. 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the northwestern Mediterranean Sea. 2. Siphonophores, hydromedusae and pyrosomids. J. Plankton Res. **14**(8): 1155–1169.
- Andersen, V., Gubanova, A., Nival, P., and Ruellet, T. 2001a. Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 1. Abundance and specific composition. J. Plankton Res. **23**(3): 227–242.
- Andersen, V., Gubanova, A., Nival, P., and Ruellet, T. 2001b. Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events: 2. Vertical distributions and migrations. J. Plankton Res. **23**(3): 243–261.
- Angel, M.V., Hargreaves, P., Kirkpatrick, P., and Domanski, P. 1982. Low variability in planktonic and micronektonic populations at 1,000 m depth in vicinity of 42°N 17°W: evidence against diel migratory behaviour in the majority of species. Biol. Oceanogr. **1**(3): 287–319.
- Arai, M.N. 1988. Interactions of fish and pelagic coelenterates. Can. J. Zool. **66**(9): 1913–1927.
- Arai, M.N. 1997. Coelenterates in pelagic food webs. In Proceedings of the 6th International Conference on Coelenterate Biology, Noordwijkerhout, The Netherlands. pp. 1–9.
- Arai, M.N. 2001. Pelagic coelenterates and eutrophication: a review. Hydrobiologia, **451**: 69–87.
- Arai, M.N. 2005. Predation on pelagic coelenterates: a review. J. Mar. Biol. Assoc. U.K. **85**(3): 523–536.
- Arai, M.N., McFarlane, G.A., Saunders, M.W., and Mapstone, G.M. 1993. Spring abundance of medusae, ctenophores and siphonophores off southwest Vancouver Island: possible competition or predation on sablefish larvae. Can. Tech. Rep. Fish. Aquat. Sci. No. 1939.
- Arai, M.N., Welch, D.W., Dunsmuir, A.L., Jacobs, M.C., and Ladouceur, A.R. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. Can. J. Fish. Aquat. Sci. **60**(7): 825–829.
- Båmstedt, U., Fosså, J. H., Martinussen, M. B., and Fosshagen, A. 1998. Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. Sarsia, **83**(1): 79–85.
- Beamish, R.J., Leask, K.D., Ivanov, O.A., Balanov, A.A., Orlov, A.M., and Sinclair, B. 1999. The ecology, distribution, and abundance of midwater fishes of the subarctic Pacific gyres. Prog. Oceanogr. **43**: 399–442.
- Beaudouin, J. 1971. Données écologiques sur quelques groupes planctoniques indicateurs dans le Golfe de Gascogne. Rev. Trav. Inst. Pêches Marit. **35**(4): 375–414.
- Bedot, M. 1882. Sur la faune des Siphonophores du Golfe de Naples. Mitt. Zool. Stn. Neapel, **3**(1–2): 121–123.

- Bedot, M. 1888. Sur l'*Agalma clausi* n. sp. Rec. zool. suisse, **5**(1): 73–92.
- Bedot, M. 1896. Les siphonophores de la Baie d'Amboine : étude suivie d'une révision de la famille des Agalmidae. Rev. suisse zool. **3**(3): 367–414.
- Beklemishev, W.N. 1969. Principles of comparative anatomy of invertebrates. I. Protomorphology. Edited by Z. Kabata. Oliver and Boyd, Edinburgh. [Translated by J.M. MacLennan.]
- Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J.V., and Dutton, P.H. 2007. Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. Fish. Bull. **105**(3): 337–347.
- Berkeley, E., and Berkeley, C. 1960. Some further records of pelagic Polychaeta from the northeast Pacific north of latitude 40°N and east of longitude 175°W, together with records of Siphonophora, Mollusca and Tunicata from the same region. Can. J. Zool. **38**(4): 787–799.
- Bernstein, T. 1932. Zooplankton of Franz-Joseph Land Region. Tr. Arktich. Inst. Leningr. **2**: 3–35. [In Russian with English summary.]
- Bernstein, T. 1934. Zooplankton of the northern Kara Sea. Tr. Arktich. Inst. Leningr. **9**: 3–58. [In Russian and German.]
- Berrill, N.J. 1930. On the occurrence and habits of the siphonophore, *Stephanomia bijuga* (delle Chiaje). J. Mar. Biol. Assoc. U.K. **16**(3): 753–755.
- Bidigare, R.R., and Biggs, D.C. 1980. The role of sulfate exclusion in buoyancy maintenance by siphonophores and other oceanic gelatinous zooplankton. Comp. Biochem. Physiol. A, **66**: 467–471.
- Bigelow, H.B. 1904. Medusae from the Maldives Islands. Bull. Mus. Comp. Zool. Harv. Coll. **39**(9): 245–269.
- Bigelow, H.B. 1911a. Biscayan plankton collected during a cruise of H.M.S. "Research", 1900. Part XII. The Siphonophora. Trans. Linn. Soc. Lond. Ser. 2 Zool. **10**(10): 337–358.
- Bigelow, H.B. 1911b. Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross", from October, 1904, to March, 1905, Lieut.-Commander L.M. Garrett, U.S.N., commanding. XXIII. The Siphonophorae. Mem. Mus. Comp. Zool. Harvard Coll. **38**(2): 173–401, 32 pls
- Bigelow, H.B. 1913. Medusae and Siphonophorae collected by the U.S. Fisheries steamer "Albatross" in the northwestern Pacific, 1906. Proc. U.S. Natl. Mus. **44**(1946): 1–119.
- Bigelow, H.B. 1914. Fauna of New England: list of the Medusae, Craspedotae, Siphonophorae, Scyphomedusae, Ctenophorae. Occas. Pap. Boston Soc. Nat. Hist. **7**(12): 1–37.
- Bigelow, H.B. 1918. Some Medusae and Siphonophorae from the western Atlantic. Bull. Mus. Comp. Zool. Harv. Coll. **62**(8): 365–442.
- Bigelow, H.B. 1919. Contributions to the biology of the Philippine Archipelago and adjacent regions: hydromedusae, siphonophores and ctenophores of the "Albatross" Philippine Expedition. Bull. U.S. Natl. Mus. (Wash.) **100**(i)(5): 279–362.
- Bigelow, H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. Bull. Bur. Fish. Wash. **40** (2): 1–509. [The title page is dated 1924.]
- Bigelow, H.B. 1931. Siphonophorae from the Arcturus Oceanographic Expedition. Zoologica (N.Y.), **8**(11): 525–592.
- Bigelow, H.B., and Leslie, M. 1930. Reconnaissance of the waters and plankton of Monterey Bay, July, 1928. Bull. Mus. Comp. Zool. Harv. Coll. **70**(5): 429–581.
- Bigelow, H.B., and Sears, M. 1937. Siphonophorae. Report on the Danish Oceanographical Expeditions 1908–10 to the Mediterranean and adjacent seas. Vol. 11 (Biology). A.F. Host and Son, Copenhagen. pp. 1–144.
- Bigelow, H.B., and Sears, M. 1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. Volumetric study of the zooplankton. Mem. Mus. Comp. Zool. Harv. Coll. **54**(4): 183–378.
- Biggs, D.C. 1977a. Respiration and ammonium excretion by open ocean gelatinous zooplankton. Limnol. Oceanogr. **22**(1): 108–117.
- Biggs, D.C. 1977b. Field studies of fishing, feeding and digestion in siphonophores. Mar. Behav. Physiol. **4**(4): 261–274.
- Biggs, D.C. 1978. *Athorybia lucida*, a new species of siphonophore (Physonectae, Athorybiidae) from the North Atlantic Ocean. Bull. Mar. Sci. **28**(3): 537–542.
- Biggs, D.C., Pugh P.R., and Carré, C. 1978. *Rosacea flaccida* n. sp., a new species of siphonophore (Calycophorae Prayinae) from the North Atlantic Ocean. Beaufortia, **27**: 207–218.
- Bone, Q. 1985. Locomotor adaptations of some gelatinous zooplankton. In Physiological adaptations of marine animals. Edited by M.S. Laverack. Symp. Soc. Exp. Biol. **39**: 487–520.
- Bone, Q. 2005. Gelatinous animals and physiology. J. Mar. Biol. Assoc. U.K. **85**(3): 641–653.

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- Bone, Q., and Trueman, E.R. 1982. Jet propulsion of the calycophoran siphonophores *Chelophyses* and *Abylopsis*. J. Mar. Biol. Assoc. U.K. **62**(2): 263–276.
- Bone, Q., Carré, C., Tsutsui, I., and Inoue, I. 1999. Calycophoran siphonophore muscle fibres without any sarcoplasmic reticulum but with tubular invaginations morphologically analagous to a T-system. J. Mar. Biol. Assoc. U.K. **79**(6): 1111–1116.
- Bonnemains, J., and Carré, C. 1991. Siphonophores et velelles (1). Observés par F. Péron et C.-A. Lesueur au début du 19^e siècle. Bull. Trimest. Soc. Géol. Normandie Amis Mus. Havre, **78**(2): 33–82.
- Boone, L. 1933. Scientific results of cruises of the yachts "Eagle" and "Ara", 1921–1928, William K. Vanderbilt, commanding: Coelenterata, Echinodermata and Mollusca. Bull. Vanderbilt Mar. Mus. **4**: 1–217.
- Bouillon, J., Medel, M.D., Pagès, F., Gili, J.-M., Boero, F., and Gravili, C. 2004. Fauna of the Mediterranean Hydrozoa. Sci. Mar. **68**(Suppl. 2): 5–438.
- Bourne, G.C. 1889. Report on a trawling cruise in H.M.S. "Research" off the south-west coast of Ireland. J. Mar. Biol. Assoc. U.K. **1**(3): 306–323.
- Brandt, J.F. 1835. Prodromus descriptionis animalium ab H. Mertensio observatorum. Fascic. I. Polypos, Acalephas Discophoras et Siphonophoras, nec non Echinodermata continens. Recueil des Actes de la Séance Publique de L'Académie Impériale des Sciences de St.-Pétersbourg : 201–275. [An incorrect date of 1834 is given by some authors]
- Bray, R.A., and Gibson, D.I. 1990. The Lepocreediidae (Digenea) of fishes of the north-east Atlantic: review of the genera *Opechona* Looss, 1907 and *Prodistomum* Linton, 1910. Syst. Parasitol. **15**(3): 159–202.
- Brewer, G.D., Kleppel, G.S., and Dempsey, M. 1984. Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters of southern California. Mar. Biol. (Berl.), **80**(1): 17–28.
- Brinckmann-Voss, A. 1974. British Columbia Marine Faunistic Survey report on the Hydrozoa: Part I. Medusae. Fish. Res. Board Can. Tech. Rep. No. 492.
- Broch, H. 1908. Die Verbreitung von *Diphyes arctica*, Chun. Ark. Zool. **4**(20): 1–6.
- Brodeur, R.D., Lorz, H.V., and Pearcy, W.G. 1987. Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. NOAA Tech. Rep. NMFS No. 57.
- Browne, E.T. 1926. Siphonophorae from the Indian Ocean. III. The Percy Sladen Trust Expedition to the Indian Ocean in 1905. Trans. Linn. Soc. Lond. Ser. 2 Zool. **19**(1): 55–86.
- Buecher, E. 1999. Appearance of *Chelophyses appendiculata* and *Abylopsis tetragona* (Cnidaria, Siphonophora) in the Bay of Villefranche, northwestern Mediterranean. J. Sea Res. **41**: 295–307.
- Bullard, S.G., and Hay, M.E. 2002. Palatability of marine macro-holoplankton: nematocysts, nutritional quality, and chemistry as defenses against consumers. Limnol. Oceanogr. **47**: 1456–1467.
- Burd, B.J., and Thompson R.E. 2000. Distribution and relative importance of jellyfish in a region of hydrothermal venting. Deep-Sea Res. I. Oceanogr. Res. Pap. **47**(9): 1703–1721.
- Busch, W. 1851. Beobachtungen über Anatomie und Entwicklung einiger wirbellosen Seethiere. Verlag August Hirschwald, Berlin.
- Båmstedt, U., Fosså, J.H., Martinussen, M.B., and Fosshagen, A. 1998. Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. Sarsia, **83**(1): 79–85.
- Cairns, S.D., Calder, D.R., Brinckmann-Voss, A., Castro, C.B., Fautin, D.G., Pugh, P.R., Mills, C.E., Jaap, W.C., Arai, M.N., Haddock, S.H.D., and Opresko, D.M. 2002. Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. American Fisheries Society, Bethesda, Maryland.
- Candeias, A. 1929. Note sur quelques siphonophores Calycophorae de Madère. Bull. Soc. Port. Sci. Nat. **10**(23): 269–284.
- Candeias, A. 1932. Contribuição para o conhecimento dos Coelenterados plânctónicos das costas portuguesas. Mem. Estud. Mus. Zool. Univ. Coimbra Ser. 1, **57**: 5–11.
- Carré, C. 1966. *Sphaeronectes gamulinii* sp. n., une nouvelle espèce de Siphonophore calycophore méditerranéen. Vie Milieu, **17**: 1069–1076.
- Carré, C. 1967. Le développement larvaire d'*Abylopsis tetragona* Otto, 1823 (Siphonophore, Calycophore, Abylidæ). Cah. Biol. Mar. **8**: 185–193.
- Carré, C. 1968a. Description d'un siphonophore Agalmidae, *Cordagalma cordiformis* Totton, 1932. Beaufortia, **16**(212): 79–86.
- Carré, C. 1968b. L'eudoxie de *Lensia campanella* Moser 1925, avec des précisions sur le stade polygastrique (Siphonophore, Calycophore, Diphyidae). Bull. Mus. Natl. Hist. Nat. **40**(2): 438–445.

- Carré, C. 1968c. *Sphaeronectes fragilis* n. sp., une nouvelle espèce de Siphonophore calycophore méditerranéen. Bull. Inst. Océanogr. (Monaco), **67**(No. 1385): 1–9.
- Carré, C. 1968d. *Sphaeronectes bougisi* sp. n., nouveau Siphonophore calycophore Sphaeronectidae du plancton méditerranéen. Bull. Mus. Natl. Hist. Nat. **40**(2): 446–449.
- Carré, C. 1968e. Contribution à l'étude du genre *Sphaeronectes* Huxley, 1859. Vie Milieu, **19**: 85–94.
- Carré, C. 1969. Sur le genre *Lilyopsis* Chun 1885, avec une redescription de l'espèce *Lilyopsis rosea* Chun 1885 (Siphonophore, Prayinae) et une description de sa phase calyconula. Cah. Biol. Mar. **10**: 71–81.
- Carré, C. 1979. Sur le genre *Sulculeolaria* Blainville, 1834 (Siphonophora, Calycophorae, Diphyidae). Ann. Inst. Océanogr. **55**(1): 27–48.
- Carré, C., and Carré, D. 1969. Le développement larvaire de *Lilyopsis rosea* (Chun 1885) siphonophore, calycophore, Prayidae. Cah. Biol. Mar. **10**: 359–364.
- Carré, C., and Carré, D. 1973. Étude du cnidome et de la cnidogenèse chez *Apolemia uvaria* (Lesueur, 1811) (Siphonophore physonecte). Exp. Cell Res. **81**: 237–249.
- Carré, C., and Carré, D. 1991. A complete life cycle of the calycophoran siphonophore *Muggiae kochii* (Will) in the laboratory, under different temperature conditions: ecological implications. Philos. Trans. R. Soc. Lond. B Biol. Sci. **334**: 27–32.
- Carré, C., and Carré, D. 1995. Ordre des Siphonophores. In Traité de zoologie. Tome III. Anatomie, systématique, biologie. Fascicule II. Cnidaires. Cténaires. Edited by D. Doumenc. Masson, Paris. pp. 523–596. [The title page is dated 1993.]
- Carré, D. 1967. Étude du développement larvaire de deux siphonophores: *Lensia conoidea* (calycophore) et *Forskalia edwardsi* (physonecte). Cah. Biol. Mar. **8**: 233–251.
- Carré, D. 1968. Sur le développement post-larvaire d'*Hippopodius hippopus* (Forskal). Cah. Biol. Mar. **9**: 417–420.
- Carré, D. 1969a. Étude du développement larvaire de *Sphaeronectes gracilis* (Claus, 1873) et de *Sphaeronectes irregularis* (Claus, 1873), siphonophores calycophores. Cah. Biol. Mar. **10**: 31–34.
- Carré, D. 1969b. Étude histologique du développement de *Nanomia bijuga* (Chiaje, 1841), siphonophore physonecte, Agalmidae. Cah. Biol. Mar. **10**: 325–341.
- Carré, D. 1971. Étude du développement d'*Halostemma rubrum* (Vogt, 1852) siphonophore physonecte Agalmidae. Cah. Biol. Mar. **12**: 77–93.
- Carré, D. 1973. Étude du développement de *Cordagalma cordiformis* Totton, 1932, siphonophore physonecte, Agalmidae. Bijdr. Dierkd. **43**(1): 113–118.
- Carré, D. 1974a. Formation, migration et maturation des nématoblastes et des nématocytes chez les siphonophores. I. Mise en évidence et formation des clones de nématocystes. Ann. Embryol. Morphol. **7**(2): 205–218.
- Carré, D. 1974b. Formation, migration et maturation des nématoblastes et des nématocytes chez les siphonophores. II. Migration. Ann. Embryol. Morphol. **7**(3): 221–232.
- Carré, D., and Carré, C. 1980. On triggering and control of cnidocyst discharge. Mar. Behav. Physiol. **7**: 109–117.
- Carré, D., and Carré, C. 1986. Étude in vivo de la fécondation chez les siphonophores (Cnidaria, Hydrozoa). Nova Thalassia, **8**(2): 21–29.
- Carré, D., and Sardet, C. 1981. Sperm chemotaxis in siphonophores. Biol. Cell (Paris), **40**: 119–128.
- Casanova, J.-P. 1980. Campagnes du "Meteor" dans l'Atlantique N-E. Siphonophores, Méduses et Thécosomes: distribution verticale et comparaisons faunistiques avec la Méditerranée. Meteor Forschungsergeb. Reihe D Biol. **32**: 15–32.
- Cervigon, F. 1958. Contribución al estudio de los sifonóforos de las costas de Castellón (Mediterráneo Occidental). Invest. Pesq. **22**: 21–47.
- Cervigon, F. 1961. Descripción y consideraciones sobre los Sifonóforos de las costas occidentales de África, recogidos en las campañas del "Costa Canaria". Invest. Pesq. **18**: 9–31.
- Chamisso, A. de, and Eysenhardt, C.G. 1821. De animalibus quibusdam e classe vermium Linneana, in circumnavigatione terrae, asupicente Comite N. Romanzoff, duce Ottone de Lotzebue, annis 1815–1818. Nova Acta Physico-med. **10**(2): 342–374.
- Chan, F., Barth, J.A., Lubchenko, J., Kirincich, A., Weeks, H., Peterson, W.T. and Menge, B.A. 2008. Emergence of anoxia in the California Current large marine ecosystem. Science (Wash., D.C.), **319**(No. 5865): 920.
- Chen, Q. 1983. Siphonophores from the north and middle parts of the South China Sea. Proceedings on Marine Biological Research in the South China Sea. Ocean Press, Beijing, China. pp. 7–14. [In Chinese.]
- Chiu, S.Y. 1954. Studies on the zooplankton of Amoy. I. Hydromedusae. Acta Zool. Sin. **6**(1): 41–48. [In Chinese.]
- Chun, C. 1885. Über die cyklische Entwicklung der Siphonophoren. Sitzungsber. Preuss. Akad. Wiss. 1885: 511–529, 1 pl.

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- Chun, C. 1888a. Berichte über eine nach den Canarischen Inseln im Winter 1887/88 ausgeführte Reise. Sitzungsber. Preuss. Akad. Wiss. 1888: 1141–1173. [English translation, Ann. Mag. Nat. Hist. Ser. 6, 3(23): 214–246, 1889.]
- Chun, C. 1888b. Die pelagische Thierwelt in grösseren Meerestiefen und ihre Beziehungen zu der Oberflächenfauna. II. Coelenterata. Bibl. Zool. 1 Heft 1. pp. 12–17.
- Chun, C. 1891. Die canarischen Siphonophoren in monographischen Darstellungen. I. *Stephanophyes superba* und die Familie der Stephanophyiden. Abh. Senckenb. Naturforsch. Ges. 16: 553–627.
- Chun, C. 1892. Die canarischen Siphonophoren in monographischen Darstellungen. II. Die Monophyiden. Abh. Senckenb. Naturforsch. Ges. 18: 57–144.
- Chun, C. 1897a. Die Siphonophoren der Plankton-Expedition. Band II. Ergebnisse der Plankton-Expedition der Humboldt-Stiftung. Lipsius and Tischer, Kiel and Leipzig, Germany.
- Chun, C. 1897b. Über den Bau und die morphologische Auffassung der Siphonophoren. Verh. Dtsch. Zool. Ges. 7: 48–111.
- Clarke, W. D. 1966. Bathyphotometric studies of the light regime of organisms of the deep scattering layers. General Motors Corp., Santa Barbara, Calif., Sea Op. Dept. Tech. Rep. 66-02: 1–47.
- Claus, C. 1860. Ueber *Physophora hydrostatica* nebst Bemerkungen über andere Siphonophoren. Z. Wiss. Zool. 10(3): 295–332.
- Claus, C. 1863. Neue Beobachtungen über die Structur und Entwicklung der Siphonophoren. Z. Wiss. Zool. 12: 536–563.
- Claus, C. 1873. Ueber die Abstammung der Diplophysen und über eine neue Gruppe von Diphyiden. Nachr. Ges. Wiss. Göttingen, 9: 257–261.
- Claus, C. 1874. Die Gattung *Monophyes* Cls. und ihr Abkömmling *Diplophysa* Gbr. Schriften zoologische Inhalts. Heft 1. G.J. Manz'schen Buchhandlung, Vienna, Austria.
- Claus, C. 1877. Mittheilungen über die Siphonophoren und Medusen Fauna Triests. Verh. Zool.-bot. Ges. Wien, 26: 7–11.
- Claus, C. 1878. Ueber *Halistemma tergestinum* n. sp. nebst Bemerkungen über den feinern Bau der Physophoriden. Arb. Zool. Inst. Univ. Wien Zool. Stn. Trieste, 1: 1–56.
- Collins, A.G., 2000. Towards understanding the phylogenetic history of Hydrozoa: Hypothesis testing with 18S gene sequence data. Sci. Mar. 64(Supl.1): 5–22.
- Collins, A.G., Schuchert, P., Marques, A.C., Jankowski, T. Medina, M., and Schierwater, B. 2006. Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. Syst. Biol. 55(1): 97–115.
- Cooney, R.T. 1981. Bering Sea zooplankton and micronekton communities with emphasis on annual production. In The eastern Bering Sea shelf: oceanography and resources. Vol. 2. Edited by D.W. Hood and J.A. Calder. National Oceanic and Atmospheric Administration, Seattle, Washington. pp. 627–1339.
- Cosson, J., Carré, D., and Cosson, M.P. 1986. Sperm chemotaxis in siphonophores: identification and biochemical properties of the attractant. Cell Motil. Cytoskeleton, 6: 225–228.
- Costa, A. 1862. Osservazioni sulla *Diphyia quadrivalvis* e sui crostacei che si sviluppano entro i bottoni delle appendici urticanti. Ann. Mus. Zool. Univ. Napoli, 1: 90–94.
- Costa, O.-G. 1835–1841. Medusari. In Fauna del Regno di Napoli ossia enumerazione di tutti gli animali che abitano le diverse regioni di questo regno e le acque che le bagnano. Minerva, Naples, Italy. pp. 1–20, 1–18, 1–14, 1–10, 1–12. [The section cited here (under *Diphyia*) is included in pages 1–12 and was published in 1841 (see Sherborn 1937).]
- Coyle, K.O., and Hunt, G.L. 2000. Seasonal differences in the distribution, density and scale of zooplankton patches in the upper mixed layer near the western Aleutian Islands. Plankton Biol. Ecol. 47(1): 31–42.
- Cunningham, J.T. 1892. On a species of siphonophore observed at Plymouth. J. Mar. Biol. Assoc. U.K. 2(3): 212–215.
- Daly, M., Brugler, M.R., Cartwright, P., Collins, A.G., Dawson, M.N., Fautin, D.G., France, S.C., McFadden, C.S., Opresko, D.M., Rodriguez, E., Romano, S.L. and Stake, J.L. 2007. The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus. Zootaxa, 1668: 127–182.
- Daniel, A., Nagabhushanam, A.K., and Daniel, R. 1969. Preliminary studies of the zoological constituents of the sonic scattering layer at seven stations established in the eastern part of the Indian Ocean by the R.V. ‘Vityaz’ in 1962. Bull. Natl. Inst. Sci. India, 38(2): 585–593.
- Daniel, R. 1966. On a new Physonectae, *Frillagalma vityazi* gen. nov., sp. nov. (Siphonophora: Coelenterata) from the Indian Ocean. Ann. Mag. Nat. Hist. Ser. 13, 9(106–108): 689–692.

- Daniel, R. 1970. Some new species of Siphonophora (Coelenterata) from the Indian Ocean. *J. Zool. Soc. India*, **22**(1 and 2): 147–156.
- Daniel, R. 1973. Siphonophora collected by the R.V. ‘Gascoyne’ and R.V. ‘Diamantina’ along 110°E off the Australian coast during 1962–1963. *J. Mar. Biol. Assoc. India*, **15**(2): 865–868.
- Daniel, R. 1974. Siphonophora from the Indian Ocean. *Mem. Zool. Surv. India*, **15**(4): 1–242.
- Daniel, R. 1985. The fauna of India and the adjacent countries. Coelenterata: Hydrozoa, Siphonophora. Zoological Survey of India, Calcutta, India.
- Daniel, R., and Daniel, A. 1963. On the siphonophores of the Bay of Bengal. I. Madras coast. *J. Mar. Biol. Assoc. India*, **5**(2): 185–220.
- Daniel, A., Nagabhushanam, A. K. and Daniel, R. 1969. Preliminary studies of the zoological constituents of the sonic scattering layer at seven stations established in the eastern part of the Indian Ocean by the R.V. ‘Vityaz’ in 1962. *Bull. Nat. Inst. Sci. India* **38**(2): 585–593.
- Davenport, J. 1988. Do diving leatherbacks pursue glowing jelly? *Br. Herpetol. Soc. Bull.* **24**: 20–21.
- Dawyoff, C. 1937. Observations sur la faune pélagique des eaux Indochinoises de la mer de Chine méridionale. *Bull. Soc. zool. fr.* **61**: 461–484.
- de Blainville, H.M.D. 1830. Zoophytes. In *Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connaissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts*. Vol. 60. Edited by F.G. Levrault. Le Normat, Paris, and F.G. Levrault, Strasbourg, France. pp. 548.
- de Blainville, H.M.D. 1834. Manuel d'actinologie ou de zoophytologie. F.G. Levrault, Paris and Strasbourg, France. pp. 694, atlas, pls 100.
- delle Chiaje, S. 1822–1829. Memorie sulla storia e notomia degli animali senza vertebre del Regno di Napoli. Fratelli Fernandes, Naples, Italy. Text in four volumes (variously dated), atlas. [For the various publication dates of different sections of this work see Sherborn 1922, p. xxxvii.]
- delle Chiaje, S. 1841–1844. Animali senza vertebre del regno di Napoli. Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi negli anni 1822–30. C. Batelli, Naples, Italy. Text in one volume, atlas. [For the various publication dates of different sections of this work see Sherborn 1922, p. xxxvii.]
- Dunn, C.W. 2005. Complex colony-level organization of the deep-sea siphonophore *Bargmannia elongata* (Cnidaria, Hydrozoa) is directionally asymmetric and arises by the subdivision of pro-buds. *Dev. Dyn.* **234**: 835–845.
- Dunn, C.W., and Wagner, G.P. 2006. The evolution of colony-level development in the Siphonophora (Cnidaria: Hydrozoa). *Dev. Genes Evol.* **216**(12): 743–754.
- Dunn, C.W., Pugh, P.R., and Haddock, S.H.D. 2005a. *Marrus claudanielis*, a new species of deep-sea physonect siphonophore (Siphonophora, Physonectae). *Bull. Mar. Sci.* **76**(3): 699–714.
- Dunn, C.W., Pugh, P.R., and Haddock, S.H.D. 2005b. Molecular phylogenetics of the Siphonophora (Cnidaria), with implications for the evolution of functional specialisation. *Syst. Biol.* **54**(6): 916–935.
- Edwards, M., John, A.W.G., Hunt, H.G., and Lindley, J.A. 1999. Exceptional influx of oceanic species into the North Sea late 1997. *J. Mar. Biol. Assoc. U.K.* **79**(4): 737–739.
- Eschscholtz, F. 1825. Bericht über die zoologische Ausbeute während der Reise von Kronstadt bis St. Peter und Paul. *Oken's Isis* **16**: 733–747.
- Eschscholtz, F. 1829. System der Acalephen. Eine ausführliche Beschreibung aller Medusenartigen Strahlthiere. Ferdinand Dümmler, Berlin.
- Ferguson, J.C. 1988. Autoradiographic demonstration of the use of free amino acid by Sargasso Sea zooplankton. *J. Plankton Res.* **10**: 1225–1238.
- Fewkes, J.W. 1880a. The development of the tentacular knob of *Physophora hydrostatica*. *Bull. Mus. Comp. Zool. Harv. Coll.* **6**(7): 127–146.
- Fewkes, J.W. 1880b. The siphonophores. I. The anatomy and development of *Agalma*. *Am. Nat.* **14**(9): 617–630.
- Fewkes, J.W. 1880c. The tubes in the larger nectocalyces of *Abyla pentagona*. *Proc. Boston Nat. Hist. Soc.* **20**(3): 318–324.
- Fewkes, J.W. 1881. Studies on the jelly-fishes of Narragansett Bay. *Bull. Mus. Comp. Zool. Harv. Coll.* **8**(8): 141–182.
- Fewkes, J.W. 1882. Explorations of the surface fauna of the Gulf Stream, under the auspices of the U.S. Coast Survey. I. Notes on acalephs from the Tortugas, with a description of new genera and species. *Bull. Harv. Coll.* **9**(7): 251–289.
- Fewkes, J.W. 1883. The siphonophores. V. The Diphyae. *Am. Nat.* **17**(8): 833–845.
- Fewkes, J.W. 1885. Studies from the Newport Zoological Laboratory. XV. On the development of *Agalma*. *Bull. Mus. Comp. Zool. Harv. Coll.* **11**(11): 239–275.

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

- Fewkes, J.W. 1886. Report on the medusae collected by the U.S. Fish Commission Steamer "Albatross", in the region of the Gulf Stream, in 1883–84. U.S. Bureau of Fisheries Report for 1884. Part 12. Appendix Paper No. 36. Washington, D.C. pp. 927–980.
- Fewkes, J.W. 1888. Studies from the Newport Marine Zoölogical Laboratory. XIX. On certain medusae from New England. Bull. Mus. Comp. Zoöl. Harv. Coll. **13**(7): 209–240.
- Fewkes, J.W. 1889. New Invertebrata from the coast of California. Bull. Essex Inst. **21**(7–9): 99–146.
- Forskål, P. 1776. Icones rerum naturalium quas in itinere orientali depingi curavit Petrus Forskål. Post mortem auctoris ad regis mandatum aeri incisas edidit Carsten Niebuhr. Molleri, Hauniæ. pp. 15, pls 43.
- Fosså, J.H., Flood, P.R., Olsen, A.B., and Jensen, F. 2003. Små og usynlige, men plagsomme maneter av arten *Muggiae atlantica*. In Havets miljø 2003 Fisket og havet, særnr 2-2003. Edited by L. Asplin and E. Dahl. Kapittel 7. pp. 99–103.
- Fraser, J.H. 1950. List of rare exotic species found in the plankton by the Scottish Research Vessels in 1949. Ann. Biol. (Copenhagen), **6**: 95–99.
- Fraser, J.H. 1955. The plankton of the waters approaching the British Isles in 1953. Marine Research, No. 1. Scottish Home Department, Edinburgh. pp. 3–12.
- Fraser, J.H. 1961. The oceanic and bathypelagic plankton of the north-east Atlantic and its possible significance to fisheries. Marine Research, No. 4. Department of Agriculture and Fisheries for Scotland. pp. 1–48.
- Fraser, J.H. 1967. Siphonophora in the plankton to the north and west of the British Isles. Proc. R. Soc. Edinb. Sect. B (Biol.), **70**(1): 1–30.
- Freeman, G. 1983. Experimental studies on embryogenesis in hydrozoans (Trachylina and Siphonophora) with direct development. Biol. Bull. (Woods Hole), **165**(3): 591–618.
- Freeman, G. 1987. Localization of bioluminescence in the siphonophore *Nanomia cara*. Mar. Biol. (Berl.), **93**(4): 535–541.
- Fulton, J. 1968. A laboratory manual for the identification of British Columbia marine zooplankton. Fish. Res. Board Can. Tech. Rep. No. 55.
- Funes-Rodríguez, R. 1985. Abundancia de sifonofors y larvas de *Sardinops sagax caerulea* en el invierno (1981–1982), en Bahía Magdalena B.C.S Mexico. Invest. Mar. Cent. Interdiscip. Cienc. Mar. **2**(2): 70–76.
- Furnestin, M.-L. 1964. Les indicateurs planctoniques dans la baie ibéro-marocaine. Rev. Trav. Inst. Pêches Marit. **28**(3): 257–264.
- Gamulin, T. 1966. Contribution to the knowledge of *Lensia fowleri* (Bigelow) (Siphonophora, Calycophorae). Pubbl. Stn. Zool. Napoli, **35**(1): 1–6.
- Gamulin, T., and Kršinic, F. 1993a. Distribution and abundance of calycophores (Siphonophora, Calycophorae) in the Mediterranean and Adriatic Sea. Mar. Ecol. **14**(2): 97–111.
- Gamulin, T., and Kršinic, F. 1993b. On the occurrence of Calycophorae (Siphonophora) in the southern Adriatic and Tyrrhenian Sea: a comparison of the annual cycles off Dubrovnik and Naples. J. Plankton Res. **15**(7): 885–865.
- Gamulin, T., and Kršinic, F. 2000. Kalikofore (Siphonophora, Calycophorae) jadranskog I sredozemnog mora. [Calycophores (Siphonophora, Calycophorae) of the Adriatic and Mediterranean Seas.] Fauna Natura Croatica, **9**(2): 1–198.
- Gao, S. 1982. The medusae of the East China Sea. Stud. Mar. Sin. **19**: 34–42. [In Chinese with English abstract.]
- Gao, S. 1990. The vertical distribution of the Medusae, Pteropoda, Heteropoda and Thaliacea in the East China Sea. Stud. Mar. Sin. **31**: 83–91. [In Chinese.]
- Gao, S., Hong, H., and Zhang, S. 2002. Phylum Cnidaria, Class Hydrozoa, Subclass Siphonophora. In Fauna Sinica. Invertebrata 27. Science Press, Beijing, People's Republic of China. pp. 1–177.
- Gardner, G.A. 1977. Analysis of zooplankton population fluctuations in the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. **34**(8): 1196–1206.
- Garstang, W. 1946. The morphology and relations of the Siphonophora. Q. J. Microsc. Sci. **87**(2): 103–193.
- Gasca, R. 1993. Especies y abundancia de sifonóforos (Cnidaria: Hydrozoa) en la región sur del Golfo de México. Caribb. J. Sci. **29**(3–4): 220–225.
- Gasca, R. 1997a. Nuevos registros y ampliación de ámbito de especies de Siphonophora (Cnidaria) en aguas del Atlántico Mexicano. Rev. Biol. Trop. **45**(2): 933–934.
- Gasca, R. 1997b. Sifonóforos (Cnidaria: Hydrozoa) del Mar Caribe mexicano (agosto, 1986). Hidrobiológica (Buchar.), **7**: 51–57.
- Gasca, R. 1998. Siphonophore communities in the southern Gulf of Mexico during April–May, 1986. In Proceedings of the 2nd International Congress on Pelagic Biogeography. Edited by A.C. Pierrot-Bults and S. van del Spoel. IOC/UNESCO Workshop Rep. No. 142. pp. 120–126.

- Gasca, R. 1999a. Sifonóforos (Cnidaria) de aguas superficiales del mar Caribe mexicano (1991). Rev. Biol. Trop. **47**(Supl. 1): 113–120.
- Gasca, R. 1999b. Siphonophores (Cnidaria) and summer mesoscale features in the Gulf of Mexico. Bull. Mar. Sci. **65**(1): 75–89.
- Gasca, R., and Suárez, E. 1989a. Nota acerca de los sifonóforos (Cnidaria: Siphonophorae) del Canal de Yucatán (mayo–junio 1984). Caribb. J. Sci. **25**(1–2): 66–70.
- Gasca, R., and Suárez, E. 1989b. Sifonoforos (Cnidaria) de las costas de Quintana Roo y Yucatan (Mexico) durante el verano de 1984. Bol. Inst. Oceanogr. Venez. Univ. Oriente, **28**(1 & 2): 9–13.
- Gasca, R., and Suárez, E. 1991a. Nota sobre los sifonoforos (Cnidaria: Siphonophora) del Golfo California (Agosto–Septiembre, 1977). Cienc. Pesq. **8**: 119–125.
- Gasca, R., and Suárez, E. 1991b. Siphonophores of upwelling areas of the Campeche Bank and the Mexican Caribbean Sea. Hydrobiologia, **216/217**: 497–502.
- Gasca, R., and Suárez, E. 1992a. Sifonóforos (Cnidaria: Siphonophora) del Domo de Costa Rica. Rev. Biol. Trop. **40**(1): 125–130.
- Gasca, R., and Suárez, E. 1992b. Sifonóforos (Cnidaria: Hydrozoa) de la zona sudoccidental de la Península de Baja California, en invierno y verano durante “El Niño” 1983. Rev. Invest. Cient. **3**(1): 37–46.
- Gegenbaur, C. 1853. Beiträge zur näheren Kenntniss der Schwimmpolypen (Siphonophoren). Z. Wiss. Zool. **5**(2–3): 285–344.
- Gegenbaur, C. 1854. Ueber *Diphyes turgida* n. sp., nebst Bemerkungen über Schwimmpolypen. Z. Wiss. Zool. **5**(4): 442–454.
- Gegenbaur, K. 1859. Neue Beiträge zur näheren Kenntniss der Siphonophoren. Nova Acta Acad. Caesar. Leop. Carol. **27**: 331–424.
- Gibbons, M.J., and Thibault-Botha, D. 2002. The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. J. Mar. Biol. Assoc. U.K. **82**(5): 801–810.
- Gili, J.-M., Pagès, F., and Riera, T. 1987a. Distribución de las especies más frecuentes de sifonóforos calicóforos en la zona norte del Mediterráneo occidental. Invest. Pesq. **51**(3): 323–338.
- Gili, J.-M., Pagès, F., and Vives, V. 1987b. Distribution and ecology of a population of planktonic cnidarians in the western Mediterranean. In Modern trends in the systematics, ecology and evolution of hydroids and hydromedusae. Edited by J. Bouillon, F. Boero, F. Cicogna, and P.F.S. Cornelius. Clarendon Press, Oxford, UK. pp. 157–170.
- Gili, J.-M., Pagès, F., Sabatés, A., and Ros, J.D. 1988. Small-scale distribution of a cnidarian population in the western Mediterranean. J. Plankton Res. **10**(3): 385–401.
- Gili, J.-M., Pagès, F., and Fusté, X. 1991. Mesoscale coupling between spatial distribution of planktonic cnidarians and hydrographic features along the Galician coast (northwestern Iberian Peninsula). Sci. Mar. **55**(2): 419–426.
- Girola, C.V. 1991. *Muggiae atlantica* Cunningham, 1892 (Siphonophora, Calycophorae, Diphyidae) en aguas del Atlántico suroeste. Invest. Mar. Cent. Interdiscip. Cienc. Mar. **6**(2): 291–294.
- Graeffe, E. 1860. Beobachtungen über Radiaten und Würmer in Nizza. Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. **17**: 1–59.
- Grainger, E.H., and Grohe, K. 1975. Zooplankton data from the Beaufort Sea, 1951 to 1975. Fisheries and Marine Service Research and Development Technical Report 591, Arctic Biological Station, Department of the Environment, Ste. Anne de Bellevue, Quebec.
- Gravier, Ch. 1899. Sur un Siphonophore nouveau de la tribu des Prayidae Kölliker. Bull. Mus. Hist. Nat. Paris, **2**: 87–93.
- Greve, W. 1994. The 1989 German Bight invasion of *Muggiae atlantica*. ICES J. Mar. Sci. **51**(4): 355–358.
- Greve, W., Reiners, F., and Nast, J. 1996. Biocoenotic changes of the zooplankton in the German Bight: the possible effects of eutrophication and climate. ICES J. Mar. Sci. **53**(6): 951–956.
- Grice, G.D., and Hart, A.D. 1962. The abundance, seasonal occurrence and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. **32**(4): 287–309.
- Grimmelikhuijen, C.J.P., Spencer, A.N., and Carré, D. 1986. Organization of the nervous system of physonectid siphonophores. Cell Tissue Res. **246**(3): 463–479.
- Günther, R.T. 1903. Report on the Coelenterata from the intermediate waters of the N Atlantic, obtained by Mr George Murray during the cruise of the ‘Oceana’ in 1898. Ann. Mag. Nat. Hist. Ser. 7, **11**(59): 420–430.
- Haddock, S.H.D., and Case, J.F. 1999. Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. Mar. Biol. (Berl.), **133**(3): 571–582.
- Haddock, S.H.D., Dunn, C.D., and Pugh, P.R. 2005a. A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. J. Mar. Biol. Assoc. U.K. **85**(3): 695–707.

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- Haddock, S.H.D., Dunn, C.W., Pugh, P.R. and Schnitzler, C.E. 2005b. Bioluminescent and red-fluorescent lures in a deep-sea siphonophore. *Science (Wash. D.C.)*, **309**(5732): 263.
- Haeckel, E. 1869a. Ueber Arbeitstheilung in Natur und Menschenleben. Luderissche Berlagsbuchhandlung, Berlin.
- Haeckel, E. 1869b. Zur Entwicklungsgeschichte der Siphonophoren. *Natuurk. Verh. Prov. Utrecht Genoot. Wet.* **1**(6): 1–120.
- Haeckel, E. 1888a. System der Siphonophoren auf phylogenetischer Grundlage entworfen. *Jena Z. Naturwiss.* **22**: 1–46.
- Haeckel, E. 1888b. Report on the Siphonophorae collected by H.M.S. *Challenger* during the years 1873–1876. In *Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76*. Zoology, 28. pp. 380.
- Hardy, A.C., and Günther, E.R. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Discovery Rep.* **11**: 1–456.
- Hartog, J.C. den. 1980. Notes on the food of sea turtles: *Eretmochelys imbricata* (Linnaeus) and *Dermochelys coriacea* (Linnaeus). *Neth. J. Zool.* **30**(4): 595–610.
- Hartog, J.C. den, and van Neirop, M.M. 1984. A study of the gut contents of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zool. Verh. (Leiden)*, **209**(4): 1–36.
- Hays, G.C., Houghton, J.D.R., Isaacs, C., King, R.S., Lloyd, C., and Lovell, P. 2004. First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Anim. Behav.* **67**: 733–743.
- He, D., Wang, C., Liu, H., and Yang, G. 1992. A study on zooplankton distribution patterns and indicator species in Kuroshio upstream area and adjacent East China Sea. *Acta Oceanol. Sin.* **11**(2): 237–254.
- Heffernan, J.J., and Hopkins, T.L. 1981. Vertical distribution and feeding of the shrimp genera *Gennadas* and *Bentheogenema* (Decapoda: Penaeidea) in the eastern Gulf of Mexico. *J. Crustacean Biol.* **1**(4): 461–473.
- Herring, P. 2002. The biology of the deep ocean. Oxford University Press, Oxford, UK.
- Hissmann, K. 2005. *In situ* observations on benthic siphonophores (Physonectae: Rhodaliidae) and descriptions of three new species from Indonesia and South Africa. *Syst. Biodivers.* **2**(3): 223–249.
- Hissmann, K., Schauer, J., and Pugh, P.R. 1995. *Archangelopsis jagoa*, a new species of benthic siphonophore (Physonectae, Rhodaliidae) collected by submersible in the Red Sea. *Oceanol. Acta*, **18**(6): 671–680.
- Hobson, E.S., and Chess, J.R. 1988. Trophic relations of the blue rockfish, *Sebastes mystinus*, in a coastal upwelling system off northern California. *Fish. Bull.* **86**(4): 715–743.
- Hobson, E.S., Chess, J.R., and Howard, D.F. 1996. Zooplankters consumed by blue rockfish during brief access to a current off California's Sonoma coast. *Calif. Fish Game*, **82**(2): 87–92.
- Hong, H. 1964. Studies on the medusae of the East China Sea. 1. Siphonophora. *Contrib. Fish. Coll. Shanghai*, **1**: 111–130. [In Chinese.]
- Hong, H., and Zhang, S. 1981. Systematic studies on the siphonophores of the Xisha Islands, Guangdong Province, China. *J. Xiamen Fish. Coll.* **1**: 1–26. [In Chinese.]
- Honma, Y., and Kitami, T. 1978. Fauna and flora in the waters adjacent to the Sado Marine Biological Station, Niigata University. *Rep. Sado Mar. Biol. Stn.* **8**: 7–81.
- Hopkins, T.L. 1985. The zooplankton community of Croker Passage, Antarctic Peninsula. *Polar Biol.* **4**: 161–170.
- Hosia, A., and Bämstedt, U. 2007. Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway. *Mar. Ecol. Prog. Ser.* **351**: 113–127.
- Hosia, A., Stemmann, L., and Youngbluth, M. 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep-Sea Res. Part II: Top. Stud. Oceanogr.* **55**(1–2): 106–118.
- Huntley, M., Strong, K.W., and Dengler, A.T. 1983. Dynamics and community structure of zooplankton in the Davis Strait and northern Labrador Sea. *Arctic*, **36**(2): 143–161.
- Huxley, T.H. 1859. The oceanic Hydrozoa; a description of the Calycophoridae and Physophoridae observed during the voyage of H.M.S. "Rattlesnake" in the years 1846–1850. The Ray Society, London, UK.
- Hyndman, G.C. 1841. Note on the occurrence of the genus *Diphyia* on the coast of Ireland. *Ann. Mag. Nat. Hist. Ser.* **1**, **7**(20): 164–166.
- Ianora, A., and di Carlo, B.S. 1981. The distribution and annual cycles of Siphonophora Calicophora in the Gulf of Naples and adjacent waters. *Arch. Oceanogr. Limnol.* **20**: 51–65.

- Inoue, I., Tsutsui, I., and Bone, Q. 2005. Long-lasting potassium channel inactivation in myoepithelial fibres is related to characteristics of swimming in diphid siphonophores. *J. Exp. Biol.* **208**(24): 4577–4584.
- International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. 4th ed. International Trust for Zoological Nomenclature, London, UK.
- International Commission on Zoological Nomenclature. 2006. Opinion 2157. *Bull. Zool. Nomencl.* **63**(3): 207–208.
- Iwanzoff, N. 1896. Ueber den Bau, die Wirkungsweise und die Entwicklung der Nesselsäckchen der Coelenteraten. *Bull. Soc. nat. Moscou*, **10**: 323–354.
- Jacobs, W. 1937. Beobachtungen über das Schweben der Siphonophoren. *Z. Vgl. Physiol.* **24**: 583–601.
- Johansen, A., and Levinse, C. 1903. De Danske Farvandes plankton i Aarene 1898–1901. Part 2. K. Dan. Vidensk. Selsk. Biol. Skr. Raekke 6, **12**: 265–326.
- Johnsen, S., and Widder, E.A. 1998. Transparency and visibility of gelatinous zooplankton from the northwestern Atlantic and Gulf of Mexico. *Biol. Bull. (Woods Hole)*, **195**(3): 337–348.
- Kass-Simon, G., and Scappaticci, A.A. 2002. The behavioural and developmental physiology of nematocysts. *Can. J. Zool.* **80**(10): 1772–1794.
- Kawamura, T. 1911. “Shidarezakura Kurage” and “Nagayoraku Kurage” (*Cupulita picta*, Metschnikoff, and *Agalmopsis elegans*, Sars). *Zool. Mag. (Tokyo)* [Dobuts. Zhasshi], **23**(7): 359–363. [In Japanese.]
- Kawamura, T. 1915a. Caliconectid Siphonophorae. II. *Zool. Mag. (Tokyo)* [Dobuts. Zhasshi], **27**(4): 191–198. [In Japanese.]
- Kawamura, T. 1915b. Caliconectid Siphonophorae. III. *Zool. Mag. (Tokyo)* [Dobuts. Zhasshi], **27**(5): 317–324. [In Japanese.]
- Kawamura, T. 1915c. Caliconectid Siphonophorae. IV. *Zool. Mag. (Tokyo)* [Dobuts. Zhasshi], **27**(8): 428–440. [In Japanese.]
- Kawamura, T. 1954. A report on Japanese siphonophores with special reference to new and rare species. *J. Shiga Prefect. Jnr. Coll. Ser. A*, **2**(4): 99–129.
- Keferstein, W., and Ehlers, E. 1860. Auszug aus den Beobachtungen über die Siphonophoren von Neapel und Messina angestellt im Winter 1859–60. *Nachr. Ges. Wiss. Göttingen*, **23**: 254–262.
- Keferstein, W., and Ehlers, E. 1861. Beobachtungen über die Siphonophoren von Neapel und Messina. *Zoologische Beiträge gesammelt im Winter 1859/60 in Neapel und Messina*. Wilhelm Engelmann, Leipzig.
- Keister, J.E., and Peterson, W.T. 2003. Zonal and seasonal variations in zooplankton community structure off the central Oregon coast, 1998–2000. *Prog. Oceanogr.* **57**: 341–361.
- Keynes, R.D. (Editor). 2000. Charles Darwin's zoology notes and specimen lists from HMS *Beagle*. Cambridge University Press, Cambridge, UK.
- Kinzer, J. 1965. Untersuchungen über das Makroplankton bei Ischia und Capri und im Golf von Neapel im Mai 1962. *Pubbl. Stn. Zool. Napoli*, **34**(2): 247–255.
- Kinzer, J. 1977. On the vertical distribution of siphonophores in the upwelling area off NW Africa (Auftriebs-Expedition R.V. “Meteor”, cruise 26, 1972). *Meteor Forschergeb. Reihe D Biol.* **26**: 21–27.
- Kirkpatrick, P.A., and Pugh, P.R. 1984. Siphonophores and velellids. In *Synopses of the British Fauna (New Series)*. No. 29. Edited by D.M. Kermack and R.S.K. Barnes. E.J. Brill, Leiden, The Netherlands.
- Kitamura, M., 1998. Taxonomic study and seasonal occurrence of jellyfish in Sagami Bay. M.Sc. thesis, Tokyo University of Fisheries, Tokyo, Japan.
- Kitamura, M., Tanaka, Y., and Ishimaru, T. 2003. Coarse scale distributions and community structure of hydromedusae related to water mass structures in two locations of Japanese waters in early summer. *Plankton Biol. Ecol.* **50**(2): 43–54.
- Kölliker, A. 1853. Die Schwimmtpolypen oder Siphonophoren von Messina. Wilhelm Engelmann, Leipzig.
- Korotneff, A. 1884. Zur Histologie der Siphonophoren. *Mitt. Zool. Stn. Neapel*, **5**(2): 229–288.
- Kramp, P.L. 1939. Medusae, Siphonophora and Ctenophora. In *The Zoology of Iceland*. Vol. 2. Part 5b. Edited by A. Frioriksson and S.L. Tuxen. Levin and Munksgaard, Copenhagen and Reykjavík. pp. 1–37.
- Kramp, P.L. 1942. Siphonophora. The Godthaab Expedition 1928. *Medd. Grønl.* **80**(8): 3–24.
- Kramp, P.L. 1963. Summary of the zoological results of the ‘Godthaab’ Expedition 1928. *Medd. Grønl.* **81**(7): 1–115.
- Kršinic, F., and Njire, J. 2001. An invasion by *Muggiaea atlantica* Cunningham 1892 in the northern Adriatic Sea in the summer of 1997 and the fate of small copepods. *Acta Adriat.* **42**(1): 49–59.
- Kubota, S. 1998. A list of hydrozoans (8 orders) in Japan. *Nanki Seibutu*, **40**(1): 13–21.
- Lakkis, S., and Zeidane, R. 1997. Distribution of Siphonophora in Lebanese waters (eastern Mediterranean). In *Proceedings of the 6th International Conference on Coelenterate Biology*, Noordwijkerhout, The Netherlands. pp. 301–306.

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- Lalli, C.M., and Gilmer, R.W. 1989. Pelagic snails: the biology of holoplanktonic gastropod molluscs. Stanford University Press, Palo Alto, California.
- Larson, R.J. 1985. Trophic ecology of gelatinous predators (Cnidaria & Ctenophora) in Saanich Inlet, Vancouver Island, B.C., Canada. Ph.D. thesis, University of Victoria, Victoria, British Columbia.
- Larson, R.J. 1986. Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British Columbia. Mar. Ecol. Prog. Ser. **33**(1): 89–98.
- Larson, R.J. 1987. Daily ration and predation by medusae and ctenophores in Saanich Inlet, BC, Canada. Neth. J. Sea Res. **21**(1): 35–44.
- Larson, R.J., Harbison, G.R., Pugh, P.R., Janssen, J.A., Gibbs, R.H., Craddock, J.E., Mills, C.E., Miller, R.L., and Gilmer, R.W. 1988. Midwater community studies off New England using the Johnson Sea-Link submersibles. In Global venting, midwater, and benthic ecological processes. Edited by M.P. de Luca and I. Babb. Research Rep. 88(4), National Undersea Research Program, National Oceanic and Atmospheric Administration, US Department of Commerce, Washington, D.C. pp. 265–281.
- Lauchner, G. 1980. Diseases of Cnidaria. In Diseases of Marine Animals. Vol. 1. General Aspects, Protozoa to Gastropoda. Edited by O. Kinne. John Wiley and Sons, New York. pp. 167–237.
- Laval, P. 1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. Oceanogr. Mar. Biol. Annu. Rev. **18**: 11–56.
- Laval, P., Bracconot, J.-C., Carré, C., Goy, J., Morand, P., and Mills, C.E. 1989. Small-scale distribution of macroplankton and micronekton in the Ligurian Sea (Mediterranean Sea) as observed from the manned submersible “Cyana”. J. Plankton Res. **11**(4): 665–685.
- Le Danois, E. 1913. Coelenterés du plankton recueillis pendant la croisière océanographique du yacht “Pourquoi-Pas?” dans l’Atlantique Nord et l’Océan Glacial (sous le commandement du Dr. Charcot) — été 1912. Bull. Soc. Zool. Fr. **38**: 13–34.
- Leloup, E. 1932a. L’eudoxie d’un siphonophage calycophoride rare, le *Nectopyramis thetis* Bigelow. Bull. Mus. R. Hist. Nat. Belg. **8**(3): 1–8.
- Leloup, E. 1932b. Contribution à la répartition des siphonophores calycophorides. Bull. Mus. R. Hist. Nat. Belg. **8**(11): 1–30.
- Leloup, E. 1933. Siphonophores calycophorides provenant des Campagnes du Prince Albert 1^{er} de Monaco. Résultats des campagnes scientifiques accomplies sur son yacht par Albert 1^{er}, Prince Souverain de Monaco. Fascicule 87. Gouvernement à Monaco, Monaco. pp. 1–35.
- Leloup, E. 1934. Siphonophores calycophorides de l’océan Atlantique tropical et austral. Bull. Mus. R. Hist. Nat. Belg. **10**(6): 1–87.
- Leloup, E. 1935. Les siphonophores de la rade de Villefranche-sur-mer (Alpes Maritimes, France). Bull. Mus. R. Hist. Nat. Belg. **11**(31): 1–12.
- Leloup, E. 1936. Siphonophores calycophorides (suite) et physophorides provenant des campagnes du Prince Albert 1^{er} de Monaco. Res. Camp. Sci. Monaco, **93**: 3–36.
- Leloup, E. 1954. À propos des Siphonophores. Volume Jubilaire Victor van Straelen No. 2. Institut Royal des Sciences Naturelles de Belgique, Brussels. pp. 643–699.
- Leloup, E. 1955. Siphonophores. Report on the scientific results of the “Michael Sars” North Atlantic Deep Sea Expedition, 1910. Vol. 5. Part 2. Trustees of the University of Bergen, Bergen, Norway. pp. 1–24.
- Leloup, E. 1956. Siphonophores calycophorides de la Baie de Nhatrang-Cauda. Bull. Mus. R. Hist. Nat. Belg. **28**(5): 474–475.
- Leloup, E., and Hentschel, E. 1935. Die Verbreitung der calycophoran Siphonophoren in Südatlantischen Ozean. Wiss. Ergebn. Dtsch. Atl. Exped. “Meteor”, **12**(2): 1–31.
- Lens, A.D., and van Riemsdijk, T. 1908. The Siphonophora of the “Siboga”-Expedition. E.J. Brill, Leiden, The Netherlands. pp. 130.
- Lesson, R.-P. 1843. Histoire Naturelle des Zoophytes. Acalèphes. Nouvelle suites à Buffon. Librairie Encyclopédique de Roret, Paris.
- Lesueur, C.A. 1815. Voyage de découvertes aux terres australes. Histoire naturelle. Histoire générale et particulière de tous les animaux qui composent la famille des méduses, et de quelques autres radiates molasses. Paris. pp. 7. [British Museum Catalogue 445 e 21 – the only copy in London; date based on Goy 1980]
- Lesueur, C. A., and Petit, N. 1807. Voyage de découvertes aux terres Australes exécuté par ordre de S. M. l’Empereur et Roi. Atlas, Part 1. Imprimé par Langlois, Paris. pls 40.
- Leuckart, R. 1853. Die Siphonophoren. Zoologische Untersuchungen 1. J. Ricker’sche Buchhandlung, Giessen.
- Leuckart, R. 1854. Zur näheren Kenntniss der Siphonophoren von Nizza. Arch. Naturgesch. **20**(1): 249–377.
- Leung, Y.-M., 1970. Practical guide to the Central Arctic Siphonophora. In Taxonomic Guides to Arctic Zooplankton (II). Edited by H.A. Kobayashi. Technical Rep. No. 3, prepared under contract with the Office of Naval Research (N000014-67-A-0269-0013) by the University of Southern California, Los Angeles, California. pp. 19–29.

- Lin, M. 1993. Distribution and ecological aspects of the Siphonophora in the middle of South China Sea. *Acta Oceanol. Sin.* **12**(2): 317–322.
- Lin, M., and Chang, J. 1991. New records of siphonophores from the China Sea. *Acta Zool. Sin.* **16**(4): 496.
- Lin, M., and Zhang, J. 1987. Description of two species of deep-water *Lensia* in the central South China Sea. *Mar. Sci. Bull.* **6**(2): 105–106. [In Chinese.]
- Lin, M., and Zhang, J. 1990. Ecological studies on the hydromedusae, siphonophores and ctenophores in the Xiamen Harbour and adjacent waters. *Acta Oceanol. Sin.* **9**(3): 429–438.
- Lin, M., and Zhang, J. 1991. Ecological studies of the hydromedusae and ctenophores in the western Taiwan Strait. *Acta Oceanol. Sin.* **10**(2): 303–310.
- Lincoln, R.L., Boxshall, G.A., and Clark, P.F. 1998. A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge, UK.
- Lindsay, D.J. 2006. A checklist of midwater cnidarians and ctenophores from Sagami Bay — species sampled during submersible surveys from 1993–2004. *Bull. Plankton Soc. Jpn.* **53**(2): 104–110.
- Lindsay, D.J., and Hunt, J.C. 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific. *J. Mar. Biol. Assoc. U.K.* **85**(3): 503–517.
- Liu, H., He, D., Wang, C., and Zhu, X. 1990. The characteristics of the macroplankton community in the Kuroshio area south and east off Japan, autumn 1986: essays on the investigation of Kuroshio. Vol. 2. pp. 281–288. [In Chinese with English abstract.]
- Lo, W., and Biggs, D. C. 1996. Temporal variability in the night-time distribution of epipelagic siphonophores in the North Atlantic Ocean at Bermuda. *J. Plankton Res.* **18**(6): 923–939.
- Lochmann, L. 1914. Zur Entwicklungsgeschichte der Siphonophoren. *Z. Wiss. Zool.* **108**(2): 258–289.
- Longhurst, A.R. 1998. Ecological geography of the sea. Academic Press, San Diego, California.
- Longhurst, A.R. 2007. Ecological geography of the sea. 2nd ed. Academic Press, San Diego, California.
- Mackas, D.L. 1992. Seasonal cycle of zooplankton off southwestern British Columbia: 1979–89. *Can. J. Fish. Aquat. Sci.* **49**(5): 903–921.
- Mackas, D.L., and Galbraith, M. 1992. Zooplankton on the west coast of Vancouver Island: distribution and availability to marine birds. *Can. Wildl. Serv. Occas. Pap.* No. 75. pp. 15–21.
- Mackas, D.L., and Galbraith, M. 2002. Zooplankton community composition along the inner portion of Line P during the 1997–1998 El Niño event. *Prog. Oceanogr.* **54**: 423–437.
- Mackas, D.L., Thomson, R.E., and Galbraith, M. 2001. Changes in the zooplankton community of the British Columbia continental margin, 1985–1999, and their covariation with oceanographic conditions. *Can. J. Fish. Aquat. Sci.* **58**(4): 685–702.
- Mackas, D.L., Tsurumi, M., Galbraith, M.D., and Yelland, D.R. 2005. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: II. Mechanisms of eddy colonization by and retention of offshore species. *Deep-Sea Res. Part II. Top. Stud. Oceanogr.* **52**(7–8): 1011–1035.
- Mackie, G.O. 1962. Pigment effectors in a cnidarian. *Science (Wash. D.C.)*, **137**(No. 3531): 689–690.
- Mackie, G.O. 1963. Siphonophores, bud colonies and superorganisms. In *The Lower Metazoa. Edited by E.C. Dougherty*. University of California Press, Berkeley, California. pp. 329–337.
- Mackie, G.O. 1964. Analysis of locomotion in a siphonophore colony. *Proc. R. Soc. Lond. B Biol. Sci.* **159**: 366–391.
- Mackie, G.O. 1965. Conduction in the nerve-free epithelium of siphonophores. *Am. Zool.* **5**: 439–453.
- Mackie, G.O. 1973. Coordinated behaviour in hydrozoan colonies. In *Animal colonies: development and function through time. Edited by R.S. Boardman, A.H. Cheetham, and W.A. Oliver*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania. pp. 95–106.
- Mackie, G.O. 1978. Coordination in physonect siphonophores. *Mar. Behav. Physiol.* **5**: 325–346.
- Mackie, G.O. 1984. Fast pathways and escape behaviour in Cnidaria. In *Neural mechanisms of startle behaviour. Edited by R.D. Eaton*. Plenum Press, New York. pp. 15–42.
- Mackie, G.O. 1985. Midwater macroplankton of British Columbia studied by submersible PISCES IV. *J. Plankton Res.* **7**(6): 753–777.
- Mackie, G.O. 1986. From aggregates to integrates: physiological aspects of modularity in colonial animals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **313**: 175–196.
- Mackie, G.O. 1995. Defensive strategies in planktonic coelenterates. *Mar. Freshw. Behav. Physiol.* **26**(2–4): 119–129.
- Mackie, G.O. 1999. Coelenterate organs. *Mar. Freshw. Behav. Physiol.* **32**: 113–127.
- Mackie, G.O., and Boag, D.A. 1963. Fishing, feeding and digestion in siphonophores. *Pubbl. Stn. Zool. Napoli*, **33**(3): 178–196.
- Mackie, G.O., and Mackie, G.V. 1963. Systematic and biological notes on living hydromedusae from Puget Sound. Contributions to zoology. *Natl. Mus. Can. Bull.* No. 199. pp. 63–84.

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- Mackie, G.O., and Mackie, G.V. 1967. Mesogloal ultrastructure and reversible opacity in a transparent siphonophore. *Vie Milieu*, **18**: 47–71.
- Mackie, G.O., and Marx, R.M. 1988. Phosphatic spicules in the nematocyst batteries of *Nanomia cara* (Hydrozoa, Siphonophora). *Zoomorphology* (Berl.), **108**(2): 85–91.
- Mackie, G.O., and Mills, C.E. 1983. Use of the *Pisces IV* submersible for zooplankton studies in coastal waters of British Columbia. *Can. J. Fish. Aquat. Sci.* **40**(6): 763–776.
- Mackie, G.O., Pugh, P.R., and Purcell, J.E. 1987. Siphonophore Biology. *Adv. Mar. Biol.* **24**: 97–262.
- Mapstone, G.M. 1998. *Bargmannia lata*, an undescribed species of physonect siphonophore (Cnidaria, Hydrozoa) from Canadian Pacific waters. In Commemorative volume for the 80th birthday of Willem Vervoort in 1997. *Zool. Verh. (Leiden)*, **323**: 141–147.
- Mapstone, G.M. 2003. Redescriptions of two physonect siphonophores, *Apolemia uvaria* (Lesueur, 1815) and *Tottonia contorta* Margulis, 1976, with comments on a third species *Ramosia vitiasi* Stepanjants, 1967 (Cnidaria: Hydrozoa: Apolemiidae). *Syst. Biodivers.* **1**(2): 181–212.
- Mapstone, G.M. 2004. First full description of the large physonect siphonophore *Halistemma amphytidis* (Lesueur & Petit, 1807). *Hydrobiologia*, **530/531**: 231–240.
- Mapstone, G.M. 2005. Re-description of *Rosacea cymbiformis*, a prayine siphonophore (from the Mediterranean Sea), with comments on nectophore designation and bract orientation. *J. Mar. Biol. Assoc. U.K.* **85**(3): 709–721.
- Mapstone, G.M., and Arai, M.N. 1992. Abundance and vertical distribution of siphonophores (Cnidaria) from the Central Strait of Georgia, British Columbia, during spring and summer. Contributions to Natural Science No. 15, Royal British Columbia Museum, Victoria, B.C. pp. 1–8.
- Mapstone, G.M., and Pugh, P.R. 2004. Case 3309. *Rosacea* Quoy & Gaimard, 1827: proposed conservation of usage (Cnidaria, Siphonophora); *Desmophyes annectens* Haeckel, 1888 and *Rosacea plicata* Bigelow, 1911: proposed conservation. *Bull. Zool. Nomencl.* **61**(3): 149–153.
- Marcogliese, D.J. 1995. The role of zooplankton in the transmission of helminth parasites to fish. *Rev. Fish Biol. Fish.* **5**: 336–371.
- Margulis, R.Ya. 1969. Distribution of some siphonophore species of the suborder Physophorae in the Atlantic Ocean. *Vestn. Mosk. Univ. Ser. VI Biol.* **24**: 17–38. [In Russian.]
- Margulis, R.Ya. 1970. A new species of siphonophore *Lensia zenkevitchi* sp. n. (Siphonanthae, Calycophorae) from the Atlantic Ocean. *Zool. Zh.* **49**(1): 148–149.
- Margulis, R.Ya. 1971. Distribution of siphonophores of the genus *Lensia* (suborder Calycophorae) in the Atlantic. *Okeanologiya*, **11**: 80–84.
- Margulis, R.Ya. 1972a. Factors determining the large-scale distribution of siphonophores of the suborders Physophorae and Calycophorae in the Atlantic Ocean. *Okeanologiya*, **12**(3): 499–506. [English translation in *Oceanology*, **12**: 420–425.]
- Margulis, R.Ya. 1972b. Siphonophores of the family Diphyidae: data on distribution in the Atlantic Ocean. *Kompleksn. Issled. Prir. Okeana*, **3**: 212–228. [In Russian.]
- Margulis, R.Ya. 1974. On the distribution in the Atlantic Ocean of siphonophore families Hippopodiidae, Prayidae and Abylidiae. In Proceedings of the All-Union Hydrobiological Society. Vol. 10. Russian Academy of Sciences, Moscow, USSR. pp. 144–170.
- Margulis, R.Ya. 1976. New genera of the suborder Physophorae from the Indian Ocean. *Zool. Zh.* **55**(8): 1244–1246. [In Russian.]
- Margulis, R.Ya. 1978. The distribution of siphonophores in the western North Atlantic in the summer of 1974. *Vestn. Mosk. Univ. Ser. XVI Biol.* **3**: 1–11. [In Russian with English summary.]
- Margulis, R.Ya. 1979. Siphonophores from the Great Australian Bight. *Kompleksn. Issled. Prir. Okeana*, **6**: 219–230. [In Russian.]
- Margulis, R.Ya. 1980a. On the vertical distribution of siphonophores in the World's Oceans. In The theoretical and practical importance of coelenterates. Edited by D.V. Naumov and S.D. Stepanjants. Zoological Institute, Russian Academy of Sciences, Leningrad, USSR. pp. 60–65. [In Russian.]
- Margulis, R.Ya. 1980b. Redescription of *Tottonia contorta* and composition of the family Apolemidae (Siphonophora, Physophorae). *Zool. Zh.* **59**(3): 342–348. [In Russian.]
- Margulis, R.Ya. 1982. Two new siphonophores from Antarctic (Hydrozoa, Siphonophora). *Zool. Zh.* **61**(5): 777–780. [In Russian.]
- Margulis, R.Ya. 1984. The dependence of vertical distribution of the Siphonophora of the World Ocean on the boundaries of water layers. *Zh. Obschch. Biol.* **45**(4): 472–479. [In Russian.]
- Margulis, R.Ya. 1987. Siphonophora of the southern Pacific (Coelenterata, Hydrozoa, Siphonophora). *Vestn. Mosk. Univ. Ser. XVI Biol.* **2**: 24–28. [In Russian with English summary.]

- Margulis, R.Ya. 1988. Revision of the subfamily Clausophyinae. Zool. Zh. **67**(9): 1269–1281. [In Russian with English summary.]
- Margulis, R.Ya. 1989. Distribution of tropical Siphonophora in their expatriation areas in the northern and southern Atlantic and Pacific. Vestn. Mosk. Univ. Ser. XVI Biol. **2**: 52–59. [In Russian with English summary.]
- Margulis, R.Ya. 1992. Siphonophora from the Indian Sector of the Antarctic. Antarktika, **30**: 125–134. [In Russian with English abstract.]
- Margulis, R.Ya. 1993. *Cordagalma tottoni* sp. n. — a new siphonophore of the suborder Physonectae (Cnidaria, Hydrozoa, Siphonophora). Zool. Zh. **72**(9): 14–19. [In Russian.]
- Margulis, R.Ya. 1994. Revision of the genus *Rosacea* (Cnidaria, Siphonophora, Calycophorae, Prayidae, Prayinae). Zool. Zh. **73**(11): 15–28. [English translation, Hydrobiol. J. **31**(7): 33–50, 1995.]
- Margulis, R.Ya., and Alekseev, D.O. 1985. On the genus *Lensia* Totton, 1932 (Siphonophora, Calycophorae). Zool. Zh. **64**(1): 5–15. [In Russian with very short English summary.]
- Margulis, R.Ya., and Vereshchaka, A.L. 1994. Siphonophores from the northern Pacific. Tr. Inst. Okeanol. Akad. Nauk SSSR, **131**: 76–89. [In Russian with very short English summary.]
- Mariscal, R.N. 1974. Nematocysts. In Coelenterate biology: reviews and perspectives. Edited by L. Muscatine and H.M. Lenhoff. Academic Press, New York, pp. 129–178.
- Marques, A.C. 2001. Simplifying hydrozoan classification: inappropriateness of the group Hydroidomedusae in a phylogenetic context. Contrib. Zool. **70**(3): 175–179.
- Martin, V.J. 2002. Photoreceptors of cnidarians. Can. J. Zool. **80**(10): 1703–1722.
- Mayer, A.G. 1900. Some medusae from the Tortugas, Florida. Bull. Mus. Comp. Zoöl. Harv. Coll. **37**(2): 13–82.
- Mayer, A.G. 1904. Medusae of the Bahamas. Mem. Nat. Sci. Mus. Brooklyn Inst. **1**(1): 1–33.
- McFarlane, M.W., and Beamish, R.J. 1992. Climatic influence linking copepod production with strong year-classes in sablefish, *Anoploma fimbria*. Can. J. Fish. Aquat. Sci. **49**(4): 743–753.
- McMurrich, J.P. 1916. Notes on the plankton of the British Columbia coast. Trans. R. Soc. Can. Ser. 3, **10**(4): 75–89.
- Metschnikoff, E. 1870. Contributions to the knowledge of siphonophores and medusae. Mém. Soc. Amis Sci. Nat. Anthropol. Ethnogr. **8**(1): 295–370. [In Russian.]
- Metschnikoff, E. 1874. Studien über die Entwicklung der Medusen und Siphonophoren. Z. Wiss. Zool. **24**(1): 15–83.
- Michel, H.B., and Foyo, M. 1976. Caribbean plankton. Part I. Siphonophora, Heteropoda, Copepoda, Euphausiace, Chaetognatha and Salpidae. Office of Naval Research, Department of the Navy, Washington, D.C. pp. 1–549.
- Miller, R.L. 1979. Sperm chemotaxis in the Hydromedusae. 1. Species-specificity and sperm behaviour. Mar. Biol. (Berl.), **53**(2): 99–114.
- Mills, C.E. 1981. Seasonal occurrence of planktonic medusae and ctenophores in the San Juan Archipelago (NE Pacific). Wasmann J. Biol. **39**(1–2): 6–29.
- Mills, C.E. 1982. Patterns and mechanisms of vertical distribution of medusae and ctenophores. Ph.D. thesis, University of Victoria, Victoria, British Columbia.
- Mills, C.E., and Strathmann, M.F. 1987. Phylum Cnidaria, Class Hydrozoa. In Reproduction and development of marine invertebrates of the northern Pacific coast. Edited by M.F. Strathmann. University of Washington Press, Seattle, Washington. pp. 44–71.
- Mills, C.E., Pugh, P.R., Harbison, G.R., and Haddock, S.H.D. 1996. Medusae, siphonophores and ctenophores of the Alborán Sea, south western Mediterranean. In Advances in Hydrozoan Biology. Edited by S. Piraino, F. Boero, J. Bouillon, P.F.S. Cornelius, and J.-M. Gili. Sci. Mar. **60**(1): 145–163.
- Mohammed, A.A., and Grainger, E.H. 1974. Zooplankton data from the Canadian Arctic Archipelago. Fish. Res. Board Can. Tech. Rep. No. 460.
- Moncaleano, A., and Niño, L. 1979. Celenterados planctónicos de la Bahía de Cartagena, descripciones y notas ecológicas. Bol. Mus. Mar Bogota, **9**: 37–96.
- Moore, H.B. 1937. Marine fauna of the Isle of Man. Proc. Liverpool Biol. Soc. **50**: 5–57.
- Moore, H.B., and Corwin, E.G. 1956. The effects of temperature, illumination and pressure on the vertical distribution of zooplankton. Bull. Mar. Sci. **6**(4): 273–287.
- Moreno, I., and Fdez-Alcazar, J. 1984. Estudio del zooplancton epiplanctónico de la zona costera de Gijón. VI. Sifonoforos. Cuad. Invest. Biol. **5**: 21–28.
- Moser, F. 1912a. Die Hauptglocken, Spezialschwimmglocken und Geschlechtsglocken der Siphonophoren, ihre Entwicklung und Bedeutung. Verh. Dtsch. Zool. Ges. **22**: 320–333.

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

- Moser, F. 1912b. Über die verschiedenen Glocken der Siphonophoren und ihre Bedeutung. *Zool. Anz.* **39**: 408–410.
- Moser, F. 1912c. Über eine festsitzende Ctenophore und eine rückgebildete Siphonophore. *Sitzungsber. Ges. Naturforsch. Freunde Berl.* **10**: 522–544.
- Moser, F. 1913a. Zur geographischen Verbreitung der Siphonophoren nebst andern Bemerkungen. *Zool. Anz.* **41**(4): 145–149.
- Moser, F. 1913b. Der Glockenwechsel der Siphonophoren, Pneumatophore, Urknospen, geographische Verbreitung und andere Fragen. *Zool. Anz.* **43**(1): 223–234.
- Moser, F. 1915a. Die geographische Verbreitung und das Entwicklungszentrum der Röhrenquallen. *Sitzungsber. Ges. Naturforsch. Freunde Berl.* **6**: 203–219.
- Moser, F. 1915b. Neue Beobachtungen über Siphonophoren. *Sitzungsber. Preuss. Akad. Wiss.* 1915: 652–660.
- Moser, F. 1917. Die Siphonophoren der Adria und ihre Beziehungen zu denen des Weltmeeres. *Sitzungsber. Akad. Wiss. Wien*, **126**(9): 703–763.
- Moser, F. 1920. Nordische Siphonophoren. *Sitzungsber. Ges. Naturforsch. Freunde Berl.* **4–7**: 167–191.
- Moser, F. 1924a. Die larvalen Verhältnisse der Siphonophoren in neuer Beleuchtung. *Zoologica* (Stüttg.), **28**(73): 1–52.
- Moser, F. 1924b. Siphonophoren. In *Handbuch der Zoologie*. Vol. 1. Part 3. Edited by W. Kükenthal and T. Krumbach. Walter de Gruyter, Berlin. pp. 485–521.
- Moser, F. 1925. Die Siphonophoren der Deutschen Südpolar-Expedition 1901–1903. *Zoologie. Dtsch. Südpol.-Exped.* **17**(9): 1–541.
- Motoda, S., and Minoda, T. 1974. Plankton of the Bering Sea. In *Oceanography of the Bering Sea*. Edited by D.W. Hood and E.J. Kelley. Institute of Marine Science, University of Alaska, Fairbanks, Alaska. pp. 207–241.
- Müller, P.E. 1871. Iagtagelser over nogle Siphonophorer. *Naturhist. Tidsskr.* 7: 261–332.
- Murbach, L., and Shearer, C. 1902. Preliminary report on a collection of medusae from the coast of British Columbia and Alaska. *Ann. Mag. Nat. Hist. Ser.* 7, **9**(16): 71–73.
- Murbach, L., and Shearer, C. 1903. On medusae from the coast of British Columbia and Alaska. *Proc. Zool. Soc. Lond.* **2**: 164–192.
- Musaeva, E.I. 1976. Distribution of siphonophores in the eastern part of the Indian Ocean. *Tr. Inst. Okeanol. Akad. Nauk SSSR*, **105**: 171–197. [Translation No. 61, Institute of Oceanographic Sciences, Wormley, Godalming, Surrey, UK.]
- Naumov, D.V. 1955. Tip kishechnopolostnye – Coelenterata. In *Atlas lespozvonochnykh Daf' netvostochnykh Morey SSSR* (Phylum Coelenterata). [Atlas of the invertebrates of the Far Eastern Seas of the USSR.] Edited by A.A. Strelkov. Akademii Nauk SSSR, Moscow–Leningrad, USSR. pp. 51–68. [In Russian and English.]
- Neppi, V. 1921. I sifonofori del golfo di Napoli. *Pubbl. Stn. Zool. Napoli*, **3**: 223–228.
- Niermann, U., Bingel, F., Ergün, G., and Greve, W. 1998. Fluctuation of dominant mesozooplankton species in the Black Sea, North Sea and the Baltic Sea: Is a general trend recognisable? *Turk. J. Zool.* **22**(1): 63–81.
- Nishida, S., Pearcy, W.G., and Nemoto, T. 1988. Feeding habits of mesopelagic shrimp collected off Oregon. *Bull. Ocean Res. Inst. Univ. Tokyo*, **26**(1): 99–108.
- Östman, C. 2000. A guideline to nematocyst nomenclature and classification, and some notes on the systematic value of nematocysts. *Sci. Mar.* **64**(Suppl. 1): 31–46.
- Owen, R. 1843. Polypi. Lecture VII. In *Lectures on the comparative anatomy and physiology of the invertebrate animals* by R. Owen. Longman, Brown, Green & Longmans, London, UK. pp. 81–93.
- Pagès, F. 1992. Mesoscale coupling between planktonic cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. In *Benguela trophic functioning*. Edited by A.I.L. Payne, K.L. Brink, K.H. Mann, and R.S. Hilborn. Afr. J. Mar. Sci. **12**: 41–52.
- Pagès, F., and Gili, J.-M. 1989. Siphonophores (Cnidaria, Hydrozoa) collected during the “Magga Dan” Expedition (1966–67) from Africa to Antarctica. *Sci. Mar.* **53**(1): 53–57.
- Pagès, F., and Gili, J.-M. 1991a. Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 hours. *Hydrobiologia*, **216/217**: 355–362.
- Pagès, F., and Gili, J.-M. 1991b. Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Prog. Ser.* **75**(2–3): 205–215.
- Pagès, F., and Gili, J.-M. 1992a. Influence of Agulhas waters on the population structure of planktonic cnidarians in the southern Benguela region. In *Aspects of Hydrozoan Biology*. Edited by J. Bouillon, F. Boero, F. Cicogna, J.-M. Gili, and R.G. Hughes. *Sci. Mar.* **56**(2–3): 109–123.
- Pagès, F., and Gili, J.-M. 1992b. Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic). *Sci. Mar.* **56**(Suppl. 1): 65–112.

- Pagès, F., and Kurbjewit, F. 1994. Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica. *Polar Biol.* **14**: 243–251.
- Pagès, F., and Orejas, C. 1999. Medusae, siphonophores and ctenophores of the Magellan region. *Sci. Mar.* **63**(Suppl. 1): 51–57.
- Pagès, F., and Pugh, P.R. 2002. Fuseudoxid: the elusive sexual stage of the calycophoran siphonophore *Crystallophyes amygdalina* (Clausophyidae: Crystallophyinae). *Acta Zool. (Stockh.)*, **83**: 329–336.
- Pagès, F., and Schnack-Schiel, S.B. 1996. Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope Front (eastern Weddell Sea). *J. Mar. Syst.* **9**: 231–248.
- Pagès, F., Gili, J.-M., and Bouillon, J. 1990. The siphonophores (Cnidaria, Hydrozoa) of Hansa Bay, Papua New Guinea. *Indo-Malay. Zool.* **6**: 133–140. [The title page is dated 1989.]
- Pagès, F., Pugh, P.R., and Gili, J.-M. 1994. Macro- and megaplanktonic cnidarians collected in the eastern part of the Weddell Gyre during summer 1979. *J. Mar. Biol. Assoc. U.K.* **74**(4): 873–894.
- Pagès, F., González, H.E., and González, S.R. 1996a. Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae). *Mar. Ecol. Prog. Ser.* **139**(1–3): 69–77.
- Pagès, F., White, M.G., and Rodhouse, P.G. 1996b. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Front Zone in summer 1994. *Mar. Ecol. Prog. Ser.* **141**(1–3): 139–147.
- Pagès, F., González, H.E., Ramón, M., Sobrero, M., and Gili, J.-M. 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophora). *Mar. Ecol. Prog. Ser.* **210**: 13–24.
- Pagès, F., Flood, P., and Youngbluth, M. 2006. Gelatinous zooplankton net-collected in the Gulf of Maine and adjacent submarine canyons: new species, new family (Jeanbouilloniidae), taxonomic remarks and some parasites. *Sci. Mar.* **70**(3): 363–379.
- Pakhomov E.A. 1993. Daily vertical migrations of Antarctic microplankton: Salpidae, Ctenophora, Siphonophora, Chaetognatha, Polychaeta, Pteropoda. *Okeanologiya*, **33**(4): 587–588. [In Russian.]
- Palma, G.S. 1973. Contribución al estudio de los sifonóforos encontrados frente a la costa de Valparaíso. I. Taxonomía. *Invest. Mar. Univ. Catól. Valparaíso*, **4**(2): 17–88.
- Palma, G.S. 1977. Contribución al estudio de los sifonóforos encontrados frente a la costa de Valparaíso : aspectos ecológicas. *Mem. II Simp. Latinoam. Oceanogr. Biol. Cumaná Venezuela*, **2**: 119–133.
- Palma, G.S. 1985. Plancton marino de las aguas circundantes al archipiélago de Juan Fernández. In *Investigaciones marinas en el Archipiélago de Juan Fernández*. Edited by P. Arana. Universidad Católica de Valparaíso, Valparaíso, Chile. pp. 59–69.
- Palma, G.S. 1986. Sifonóforos fisonectes colectados frente a Punta Curaumilla, Valparaíso. *Invest. Mar. Univ. Catól. Valparaíso*, **14**: 69–78.
- Palma, G.S. 1994. Distribución del macroplancton gelatinoso en un área de desove de peces frente a la costa central de Chile (32°–33°S). *Rev. Biol. Mar. 29*(1): 23–45.
- Palma, G.S. 1999. Sifonóforos (Cnidaria, Hydrozoa) de aguas superficiales de Islas de Pascua. *Invest. Mar. Univ. Catól. Valparaíso*, **27**: 19–23.
- Palma, G.S., and Apablaza, P. 2004. Abundancia estacional y distribución vertical del zooplancton gelatinoso carnívoro en una área de surgencia en el norte del Sistema de la Corriente de Humboldt. *Invest. Mar. Univ. Catól. Valparaíso*, **32**: 49–70.
- Palma, G.S., and Aravena, G. 2001. Distribution of chaetognaths, euphausiids and siphonophores in the Magellan region. *Cienc. Tecnol. Mar.* **24**: 47–59.
- Palma, G.S., and Rosales, G.S. 1995. Composición, distribución y abundancia estacional del macroplancton de la bahía de Valparaíso. *Invest. Mar. Univ. Catól. Valparaíso*, **23**: 49–66.
- Palma, G.S., and Rosales, G.S. 1997. Sifonóforos epipelágicos de los Canales Australes Chilenos (41°30'–46°40'S). *Cienc. Tecnol. Mar.* **20**: 125–145.
- Palma, G.S., and Silva, N. 2006. Epipelagic siphonophore assemblages associated with water masses along a transect between Chile and Easter Island (eastern South Pacific Ocean). *J. Plankton Res.* **28**(12): 1143–1152.
- Palma, G.S., Ulloa, R., and Linacre, L. 1999. Sifonóforos, quetognatos u euáfusidos de los Canales Australes entre el Golfo de Penas y el Estrecho de Magallanes. *Cienc. Tecnol. Mar.* **22**: 111–142.
- Patriti, G. 1964. Les siphonophores calycophores du Golfe de Marseille. *Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars.* **35**(51): 185–258.

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

- Patriti, G. 1965a. Contribution à l'étude de siphonophores calycophores recueillis dans le Golfe de Gascogne. Note préliminaire 1. Campagne du "Job ha Zélian" (Juillet–Août 1964). Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars. **37**(53): 151–160.
- Patriti, G. 1965b. Contribution à l'étude de siphonophores calycophores recueillis dans le Golfe de Gascogne. Note préliminaire 2. Campagne du "Job ha Zélian" (Oct.–Novembre 1964). Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars. **38**(54): 15–31.
- Patriti, G. 1966. Contribution à l'étude de siphonophores calycophores recueillis dans le Golfe de Gascogne (3^e note). Campagne du "Job ha Zélian" (Oct.–Novembre 1964). Données hydrologiques. Conclusions. Rec. Trav. Stn. Mar. Endoume Fac. Sci. Mars. **41**(57): 109–115.
- Patriti, G. 1969. *Clausophyes massiliana* sp. n. nouvelle espèce de siphonophage calycophage bathypélagique des eaux Méditerranéennes. *Tethys*, **1**(2): 255–260.
- Patriti, G. 1970a. Note sur deux nouvelles espèces du genre *Lensia*, recueillies dans les eaux du large de Tuléar (S. W. de l'Océan Indien, Madagascar). Rec. Trav. Stn. Mar. Endoume Fasc. Hors Sér. Suppl. 10. pp. 103–106.
- Patriti, G. 1970b. Aperçu systématique de la faune de siphonophores des zones superficielles et subsuperficielles des eaux du large de Tuléar (S.W. de l'Océan Indien, Madagascar). Rec. Trav. Stn. Mar. Endoume Fasc. Hors Sér. Suppl. 10. pp. 285–303.
- Pearcy, W.G. 1972. Distribution and ecology of oceanic animals off Oregon. In *The Columbia River estuary and adjacent ocean waters: bioenvironmental studies*. Edited by A.T. Pruter and D.L. Alverson. University of Washington Press, Seattle, Washington. pp. 351–377.
- Péron, F. 1807. Voyage de découvertes aux terres Australes, exécuté par ordre de sa Majesté l'Empereur et Roi, sur les corvettes le *Géographe*, la *Naturaliste*, et la goélette le *Casuarina*, pendant les années 1800, 1801, 1802, 1803 et 1804. Tome Premier. Historique. Imprimerie Impériale, Paris. pp. 1–498.
- Phillips, P.J. 1972. The pelagic Cnidaria of the Gulf of Mexico: zoogeography, ecology and systematics. Ph.D. thesis, Texas A&M. University, College Station, Texas. pp. 1–212.
- Pickwell, G.V. 1970. The physiology of carbon monoxide production by deep-sea coelenterates: causes and consequences. Ann. N.Y. Acad. Sci. **174**: 102–115.
- Pickwell, G.V., Barham, E.G., and Wilton, J.W. 1964. Carbon monoxide production by a bathypelagic siphonophore. *Science (Wash., D.C.)*, **144**(No. 3620): 860–862.
- Pugh, P.R. 1974a. Letter to the Editors. *Deep-Sea Res.* **21**(9): 785–789.
- Pugh, P.R. 1974b. The vertical distribution of the siphonophores collected during the SONDE cruise, 1965. *J. Mar. Biol. Assoc. U.K.* **54**(1): 25–90.
- Pugh, P.R. 1975. The distribution of siphonophores in a transect across the North Atlantic Ocean at 32°N. *J. Exp. Mar. Biol. Ecol.* **20**: 77–97.
- Pugh, P.R. 1977. Some observations on the vertical migration and geographical distribution of siphonophores in the warm waters of the North Atlantic Ocean. In *Proceedings of the Symposium on Warm Water Zooplankton*. Special publication, UNESCO and National Institute of Oceanography, Goa, India. pp. 362–378.
- Pugh, P.R. 1983. Benthic siphonophores: a review of the family Rhodaliidae (Siphonophora, Physonectae). *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **301**: 165–300.
- Pugh, P.R. 1984. The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 7. Siphonophores. *Prog. Oceanogr.* **13**: 461–489.
- Pugh, P.R. 1989. Gelatinous zooplankton — the forgotten fauna. *Prog. Underwater Sci.* **14**: 67–78.
- Pugh, P.R. 1990. Biological collections made during Discovery CR 175 to BIOTRANS Site (c. 47°N, 20°W). Rep. 277, Institute of Oceanographic Sciences (Deacon Laboratory), Wormley, Godalming, UK.
- Pugh, P.R. 1991. Co-occurrence of hippopodiid siphonophores and their potential prey. *Hydrobiologia*, **216/217**: 327–334.
- Pugh, P.R. 1992a. A revision of the sub-family Nectopyramidinae (Siphonophora, Prayidae). *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **335**: 281–322.
- Pugh, P.R. 1992b. *Desmophyes haematogaster*, a new species of prayine siphonophore (Calycophorae, Prayidae). *Bull. Mar. Sci.* **50**(1): 89–96.
- Pugh, P.R. 1992c. The status of the genus *Prayoides* (Siphonophora: Prayidae). *J. Mar. Biol. Assoc. U.K.* **72**(4): 895–909.
- Pugh, P.R. 1995. *Clausophyes tropica* (Siphonophorae, Calycophora), a new siphonophore species from the tropical Atlantic. *Bull. Mar. Sci.* **57**(2): 453–459.
- Pugh, P.R. 1998. A re-description of *Frillagalma vityazi* Daniel 1966 (Siphonophorae, Agalmatidae). *Sci. Mar.* **62**(3): 233–245.

- Pugh, P.R. 1999a. A review of the genus *Bargmannia* Totton, 1954 (Siphonophorae, Physonecta, Pyrostephidae). Bull. Nat. Hist. Mus. Zool. Ser. **65**(1): 51–72.
- Pugh, P.R. 1999b. Siphonophorae. In South Atlantic Zooplankton I. Edited by D. Boltovskoy. Backhuys Publishers, Leiden, The Netherlands. pp. 467–511.
- Pugh, P.R. 2001. A review of the genus *Erenna* Bedot, 1904 (Siphonophora, Physonectae). Bull. Nat. Hist. Mus. Zool. Ser. **67**(2): 169–182.
- Pugh, P.R. 2002. A new species of *Rosacea* (Siphonophora: Calycophorae: Prayidae) from the Gulf of Oman. J. Mar. Biol. Assoc. U.K. **82**(1): 171–172.
- Pugh, P.R. 2003. A revision of the family Forskaliidae (Siphonophora, Physonectae). J. Nat. Hist. **37**: 1281–1327.
- Pugh, P.R. 2005. A new species of *Physophora* (Siphonophora: Physonectae: Physophoridae) from the North Atlantic, with comments on related species. Syst. Biodivers. **2**(3): 251–270.
- Pugh, P.R. 2006a. Reclassification of the clausophyid siphonophore *Clausophyes ovata* into the genus *Kephyses* gen. nov. J. Mar. Biol. Assoc. U.K. **86**(5): 997–1004.
- Pugh, P.R. 2006b. The taxonomic status of the genus *Moseria* (Siphonophora, Physonectae). Zootaxa, **1343**: 1–42.
- Pugh, P.R., and Boxshall, G.A. 1984. The small-scale distribution of plankton at a shelf station off the northwest African coast. Cont. Shelf Res. **3**(4): 399–423.
- Pugh, P.R., and Harbison, G.R. 1986. New observations on a rare physonect siphonophore, *Lychnagalma utricularia* (Claus, 1879). J. Mar. Biol. Assoc. U.K. **66**(3): 695–710.
- Pugh, P.R., and Harbison, G.R. 1987. Three new species of prayine siphonophore (Calycophorae, Prayidae) collected by a submersible, with notes on related species. Bull. Mar. Sci. **41**(1): 68–91.
- Pugh, P.R., and Pagès, F. 1993. A new species of *Clausophyes* (Siphonophorae, Clausophyidae), with a redescription of *C. galeata* and *C. moserae*. J. Mar. Biol. Assoc. U.K. **73**(3): 595–608.
- Pugh, P.R., and Pagès, F. 1995. Is *Lensia reticulata* a diphyine species (Siphonophorae, Calycophora, Diphyidae)? A re-description. Sci. Mar. **59**(2): 181–192.
- Pugh, P.R., and Pagès, F. 1997. A re-description of *Lensia asymmetrica* Stepanjants, 1970 (Siphonophorae, Diphyidae). Sci. Mar. **61**(2): 153–161.
- Pugh, P.R., and Youngbluth, M.J. 1988a. A new species of *Halistemma* (Siphonophora: Physonectae: Agalmidae) collected by submersible. J. Mar. Biol. Assoc. U.K. **68**(1): 1–14.
- Pugh, P.R., and Youngbluth, M.J. 1988b. Two new species of prayine siphonophore (Calycophorae, Prayidae) collected by the submersibles *Johnson-Sea-Link I* and *II*. J. Plankton Res. **10**(4): 637–657.
- Pugh, P.R., Pagès, F., and Boorman, B. 1997. Vertical distribution and abundance of pelagic cnidarians in the eastern Weddell Sea, Antarctica. J. Mar. Biol. Assoc. U.K. **77**(2): 341–360.
- Purcell, J.E. 1980. Influence of siphonophore behaviour upon their natural diets: evidence for aggressive mimicry. Science (Wash., D.C.), **209**(No. 4460): 1045–1047.
- Purcell, J.E. 1981a. Selective predation and caloric consumption by the siphonophore *Rosacea cymbiformis* in nature. Mar. Biol. (Berl.), **63**(3): 283–294.
- Purcell, J.E. 1981b. Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar. Biol. (Berl.), **65**(1): 83–90.
- Purcell, J.E. 1982. Feeding and growth of the siphonophore *Muggiae atlantica* (Cunningham 1893). J. Exp. Mar. Biol. Ecol. **62**: 39–54.
- Purcell, J.E. 1983. Digestion rates and assimilation efficiencies of siphonophores fed zooplankton prey. Mar. Biol. (Berl.), **73**(3): 257–261.
- Purcell, J.E. 1984. The functions of nematocysts in prey capture by epipelagic siphonophores (Coelenterata, Hydrozoa). Biol. Bull. (Woods Hole), **166**(2): 310–327.
- Purcell, J.E. 1989. Predation on fish larvae and eggs by the hydromedusa *Aequorea victoria* at a herring spawning ground in British Columbia. Can. J. Fish. Aquat. Sci. **46**(8): 1415–1427.
- Purcell, J.E. 1990. Soft-bodied zooplankton predators and competitors of larval herring (*Clupea harengus pallasi*) at herring spawning grounds in British Columbia. Can. J. Fish. Aquat. Sci. **47**(3): 505–515.
- Purcell, J.E. 1991. Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. Mar. Ecol. Prog. Ser. **72**(3): 255–260.
- Purcell, J.E. 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. Ann. Inst. Océanogr. **73**(2): 125–137.
- Purcell, J.E., and Arai, M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia, **451**: 27–44.

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- Purcell, J.E., and Kremer, P. 1983. Feeding and metabolism of the siphonophore *Sphaeronectes gracilis*. *J. Plankton Res.* **5**(1): 95–106.
- Purcell, J.E., and Mills, C.E. 1988. The correlation between nematocyst types and diets in pelagic Hydrozoa. In *The Biology of Nematocysts*. Edited by D.A. Hessinger and H.M. Lenhoff. Academic Press, San Diego, California. pp. 463–485.
- Quoy, J.R.C., and Gaimard, J.P. 1827. Observations zoologiques faites à bord de l'*Astrolabe*, en mai 1826, dans le Détriot de Gibraltar. *Ann. Sci. Nat. (Ser. 1)*, **10**: 1–21, 172–193, atlas 10, pls 1, 2, 4–9.
- Quoy, J.R.C., and Gaimard, J.P. 1833. Zoologie. IV. In *Voyage de découvertes de l'Astrolabe exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont D'Urville*. J. Tastu, Paris, France. pp. 1–390, atlas, pls 26.
- Radziejewska, T., Chojnaki, J., and Maslowski, J. 1973. New indicator species in the Baltic zooplankton. *Mar. Biol. (Berl.)*, **23**: 111–113.
- Raskoff, K.A., Purcell, J.E., and Hopcroft, R.R. 2005. Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. *Polar Biol.* **28**: 207–217.
- Razouls, S., and Thiriot, A. 1968. La macroplancton de la région de Banyuls-sur-mer (Golfe du Lion). *Vie Milieu*, **19**(1-B): 133–184.
- Rees, W.J., and White, E. 1966. New records of *Muggiaeae delsmani* and other Hydrozoa from the Indo-west Pacific. In *Some contemporary studies in marine science*. Edited by H. Barnes. George Allen and Unwin Ltd., London, UK. pp. 607–611.
- Reid, P.C., Borges, M.F., and Svendsen, E. 2001. A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish. Res.* **50**(1–2): 163–171.
- Reimer, L.W., Berger, H., Hewer, B., Lainka, H., Rosenthal, I., and Schärnweber, I. 1971. The distribution of larvae of helminths in planktonic animals of the North Sea. *Parazitologia*, **5**: 542–550. [Fish. Res. Board Can. Transl. Ser. No. 2690.]
- Rengarajan, K. 1973. Siphonophores obtained during the cruises of R.V. *Varuna* from the west coast of India and the Laccadive Sea. *J. Mar. Biol. Assoc. India*, **15**(1): 125–159.
- Rengarajan, K. 1975. Distribution of siphonophores along the west coast of India and the Laccadive Sea. *J. Mar. Biol. Assoc. India*, **17**(1): 56–72.
- Rengarajan, K. 1983. Quantitative and seasonal abundance of siphonophores along the southwest coast of India and the Laccadive Sea. *J. Mar. Biol. Assoc. India*, **25**(1 and 2): 17–40.
- Ritter, W.E. 1903. Preliminary report on the marine biological survey work carried out by the zoological department of the University of California at San Diego. *Science (Wash., D.C.)*, **18**(No. 455): 360–366.
- Robison, B., and Connor, J. 1999. *The Deep Sea*. Monterey Bay Aquarium Press, Monterey, California. pp. 80.
- Robison, B.H., Reisenbichler, K.R., Sherlock, R.E., Silguero, J.M.B., and Chavez, F.P. 1998. Seasonal abundance of the siphonophore *Nanomia bijuga*, in Monterey Bay. *Deep-Sea Res. II Top. Stud. Oceanogr.* **45**(8–9): 1741–1751.
- Roe, H.S.J. 1974. Observations on the diurnal vertical migrations of an oceanic animal community. *Mar. Biol. (Berl.)*, **28**(2): 99–113.
- Römer, F. 1901. Die Siphonophoren. In *Fauna Arctica. Band II*. Edited by F. Römer and F. Schaudinn. Gustav Fischer, Jena, Germany. pp. 171–184.
- Rosenthal, R.L., Moran-O'Connell, V., and Murphy, M.C. 1988. Feeding ecology of ten species of rockfishes (Scorpaenidae) from the Gulf of Alaska. *Calif. Fish Game*, **74**: 16–37.
- Russell, F.S. 1933. The seasonal distribution of macroplankton as shown by catches in the 2-metre Stramin ring-trawl in offshore waters off Plymouth. *J. Mar. Biol. Assoc. U.K.* **19**(1): 73–81.
- Russell, F.S. 1938a. On the development of *Muggiaeae atlantica* Cunningham. *J. Mar. Biol. Assoc. U.K.* **22**(2): 441–446.
- Russell, F.S. 1938b. On the nematocysts of hydromedusae. *J. Mar. Biol. Assoc. U.K.* **23**(1): 145–165.
- Russell, F.S. 1939. On the nematocysts of hydromedusae II. *J. Mar. Biol. Assoc. U.K.* **23**(2): 347–359.
- Rutherford, L.D., and Thuesen, E.V. 2005. Metabolic performance and survival of medusae in estuarine hypoxia. *Mar. Ecol. Prog. Ser.* **294**: 189–200.
- Sai Sastry, A.G.R., and Chandramohan, P. 1989. Planktonic coelenterates of Vasishta Godavari estuary, east coast of India. *Indian J. Mar. Sci.* **18**: 160–164.
- Sameoto, D.D. 1984. Vertical distribution of zooplankton biomass and species in northeastern Baffin Bay related to temperature and salinity. *Polar Biol.* **2**: 213–224.
- Santander, H., Luyo, R.G., Carrasco, S., Véliz, M., and de Castillo, O.S. 1981. Catálogo de zooplankton en el Mar Perúano. I. Área Pisco-San Juan. *Bol. Inst. Mar Perú (Callao)*, **6**: 1–75.

- Sardou, J., and Andersen, V. 1993. Micronecton et macroplancton en mer Ligure (Méditerranée): migrations nyctémérales et distributions verticales. *Oceanol. Acta*, **16**: 381–392.
- Sardou, J., Etienne, M., and Andersen, V. 1996. Seasonal abundance and vertical distributions of macroplankton and micronekton in the northwest Mediterranean Sea. *Oceanol. Acta*, **19**(6): 645–656.
- Sars, M. 1846. Fauna littoralis Norvegiae oder Beschreibung und Abbildungen neuer oder wenig bekannten Seethiere, nebst Beobachtungen über die Organisation, Lebensweise und Entwicklung derselben. Heft I. J. Dahl, Christiania, Denmark.
- Sars, M. 1857. Bidrag til Kundskaben om Middelhavets littoral-fauna, reisebemaerkninger fra Italien. Nytt Mag. Naturvidensk. **10**(1): 4–14.
- Savilov, A.I. 1961. The distribution of different ecological forms of *Velella lata* Ch. and Eys. and *Physalia utriculus* (La Martiniere) Esch. in the North Pacific. Tr. Inst. Okeanol. Akad. Nauk SSSR, **45**: 223–239. [In Russian with English summary.]
- Savitskaja, K.V. 1977. A list of type-species of the Hydromedusae and Siphonophora. Issled. Fauny Morei, **19**: 135–137.
- Schaeppi, T. 1906. Über die Selbstverstümmelung der Siphonophoren. Mitt. Naturwiss. Ges. Winterthur, **6**: 145–170.
- Schneider, K.C. 1896. Mittheilungen über Siphonophoren. II. Grundriss der Organisation der Siphonophoren. Zool. Jahrb. Abt. Anat. **9**: 571–664.
- Schneider, K.C. 1898. Mittheilungen über Siphonophoren. III. Systematische und andere Bemerkungen. Zool. Anz. **21**: 51–57, 73–97, 114–133, 153–173, 185–200.
- Schneider, K.C. 1899. Mittheilungen über Siphonophoren. IV. Nesselkopfe. Arb. Zool. Inst. Univ. Wien Zool. Stn. Trieste, **11**(2): 65–116.
- Seapy, R.R. 1980. Predation by the epipelagic heteropod mollusc *Carinaria cristata* forma *japonica*. Mar. Biol. (Berl.), **60**(2/3): 137–146.
- Sears, M. 1950. Notes on siphonophores. I. Siphonophores from the Marshall Islands. J. Mar. Res. **9**(1): 1–16.
- Sears, M. 1952. Notes on siphonophores. 3. *Nectopyramis spinosa* n. sp. Breviora, **3**: 1–4.
- Seguin, G. 1965. Contribution à la connaissance du plancton des eaux cotières du Brésil (Copépodes et Amphipodes exceptés) et comparaison avec celui du Sénégal. Bull. Inst. Océanogr. (Alger), **2**(3): 7–44.
- Seguin, G. 1966a. Contribution à l'étude de la biologie du plancton de surface de la baie de Dakar (Sénégal). Étude quantitative, qualitative et observations écologiques au cours d'un cycle annuel. Bull. Inst. Fondam. Afr. Noire, **28**(1): 1–90.
- Seguin, G. 1966b. Sur le zooplankton recueilli par le 'Coriolis' au large des côtes d'Afrique occidentale. Bull. Inst. Fondam. Afr. Noire, **28**(4): 1332–1355.
- Sentz-Bracconot, E., and Carré, C. 1966. Sur la biologie du nudibranche pélagique *Cephalopyge trematooides*. Parasitisme sur le siphonophore *Nanomia bijuga*, nutrition, développement. Cah. Biol. Mar. **7**: 31–38.
- Sherborn, C.D. 1910. On the dates of publication of Costa's 'Fauna del Regno di Napoli', 1829–1886. Ann. Mag. Nat. Hist. Ser. 8, **5**(miscellaneous): 132.
- Sherborn, C.D. 1922. Index Animalium. Bibliography (p. xxxvii). British Museum (Natural History), London, UK.
- Sherborn, C.D. 1937. On the dates of publication of Costa (O.G.) and (A.) Fauna del Regno di Napoli. J. Soc. Bibliogr. Nat. Hist. **1**(2): 35–47.
- Sherlock, R.E., and Robison, B.H. 2000. Effects of temperature on the development and survival of *Nanomia bijuga* (Hydrozoa, Siphonophora). Invertebr. Biol. **119**(4): 379–385.
- Shih, C.T., Figueira, A.J.G., and Grainger, E.H. 1971. A synopsis of Canadian marine zooplankton. Bull. Fish. Res. Board Can. No. 176.
- Silguero, J.M.B., and Robison, B.H. 2000. Seasonal abundance and vertical distribution of mesopelagic calycophoran siphonophores in Monterey Bay, CA. J. Plankton Res. **22**(6): 1139–1153.
- Skaer, R.J. 1973. The secretion and development of nematocysts in a siphonophore. J. Cell Sci. **13**(2): 371–393.
- Skaer, R.J. 1988. The formation of cnidocyte patterns in siphonophores. In The Biology of Nematocysts. Edited by D.A. Hessinger and H.M. Lenhoff. Academic Press, San Diego, California. pp. 165–178.
- Skaer, R.J. 1991. Remodelling during the development of nematocysts in a siphonophore. Hydrobiologia, **216/217**: 685–689.
- Southward, A.J., and Barrett, R.L. 1983. Observations on the vertical distribution of zooplankton, including post-larval teleosts, off Plymouth in the presence of a thermocline and a chlorophyll-dense layer. J. Plankton Res. **5**(4): 599–618.
- Spagnolini, A. 1870. Catalogo degli Acalefi del golfo di Napoli. Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano, **12**(3): 607–648.
- Spencer, A.N., and Schwab, W.E. 1982. Hydrozoa. In Electrical conduction and behaviour in 'simple' invertebrates. Edited by G.A.B. Shelton. Clarendon Press, Oxford, UK. pp. 73–148.
- Stechow, E. 1921. Neue Genera und Species von Hydrozoen und anderen Evertebraten. Arch. Naturgesch. Abt. A, **87**(3): 248–265.

Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific waters

- Stechow, E. 1922. Zur Systematic der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren. Arch. Naturgesch. Abt. A, **88**(3): 141–155.
- Stepanjants, S.D. 1963. A finding of Siphonophora, *Nectopyramis diomedea* Bigelow, 1911 in the Arctic Basin. Zool. Zh. **42**(12): 1866–1870.
- Stepanjants, S.D. 1967. Siphonophores of the seas of the USSR and the northern part of the Pacific Ocean. Opred. Faune Akad. Nauk SSSR, **96**. [In Russian.]
- Stepanjants, S.D. 1970. Siphonophora of the southern part of the Kurile–Kamchatka Trench and adjacent marine areas. Tr. Inst. Okeanol. Akad. Nauk SSSR, **86**: 234–249. [Translated from Russian by Israel Program for Scientific Translations, 1972.]
- Stepanjants, S.D. 1973. Revision of the subfamily Galettinae (Diphyidae, Siphonophora). Zool. Zh. **52**(5): 649–658. [In Russian with English summary.]
- Stepanjants, S.D. 1975. Species composition and distributional pattern of Siphonophora of the Caribbean, Gulf of Mexico and adjacent waters of the Atlantic. Tr. Inst. Okeanol. Akad. Nauk SSSR, **100**: 96–126. [In Russian with English summary.]
- Stepanjants, S.D. 1977a. Some peculiarities of the distribution of the surface plankton in the central part of the Pacific Ocean. Issled. Fauny Morei, **19**: 74–99. [In Russian with English summary.]
- Stepanjants, S.D. 1977b. Siphonophora of the central part of the Pacific Ocean. Issled. Fauny Morei, **20**: 54–81. [In Russian with English summary.]
- Stepanjants, S.D. 1989. Hydrozoa of the Eurasian Arctic Seas. In The Arctic seas: climatology, oceanography, geology and biology. Edited by Y. Herman. Van Nostrand Reinhold, New York. pp. 397–430.
- Stepanjants, S.D., and Dianov, M.B. 1997. The computer approach to the study of the morphological and biological peculiarities of Siphonophora *Dimophyes arctica* (Chun, 1897). Tr. Zool. Inst. Akad. Nauk SSSR, **269**: 154–161.
- Stuwitz, P. 1836. Bemerkninger over tvende nye Södrys. Mag. Naturv. Christ. **12**: 250–258.
- Suárez, E., and Gasca, R. 1991. Sifonóforos de México. Biología y Ecología. Centro de Investigaciones de Quintana Roo, Chetumal, México.
- Suárez, E., Gasca, R., Segura, L., and Biggs, D.C. 2002. Planktonic cnidarians in a cold-core ring in the Gulf of Mexico. Ann. Inst. Biol. Univ. Auton. Mex. Ser. Zool. **73**(1): 19–36.
- Sverdrup, A. 1921. Planktonundersøkelser fra Kristianiafjorden. Hydromeduser. Skr. Vidensk. Christ. I. Math–Nat. Klasse, **1**: 1–50.
- Thibault-Botha, D., and Gibbons, M.J. 2005. Epipelagic siphonophores off the east coast of South Africa. Afr. J. Mar. Sci. **27**(1): 129–139.
- Thibault-Botha, D., Lutjeharms, J.R.E., and Gibbons, M.J. 2004. Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. J. Plankton Res. **26**(9): 1115–1128.
- Thomson, R.E. 1981. Oceanography of the British Columbian coast. Can. Spec. Publ. Fish. Aquat. Sci. No. 56.
- Totton, A.K. 1932. Siphonophora. Sci. Rep. Gt. Barrier Reef Exped. **4**(10): 317–374.
- Totton, A.K. 1936. Plankton of the Bermuda oceanographic expeditions. VII. Siphonophora taken during the year 1931. Zoologica (N.Y.), **21**(4): 231–240.
- Totton, A.K. 1941. New species of the siphonophoran genus *Lensia* Totton, 1932. Ann. Mag. Nat. Hist. Ser. 11, **8**(45): 145–168.
- Totton, A.K. 1954. Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. Discovery Rep. **27**: 1–162.
- Totton, A.K. 1955. Development and metamorphosis of the larva of *Agalma elegans* (Sars) (Siphonophora Physonectae). In Papers in Marine Biology and Oceanography. Edited by M. Graham. Deep-Sea Res. **3**(Suppl.): 239–241.
- Totton, A.K. 1965a. A synopsis of the Siphonophora. British Museum (Natural History), London, UK.
- Totton, A.K. 1965b. A new species of *Lensia* (Siphonophora: Diphyidae) from the coastal waters of Vancouver, B.C., and its comparison with *Lensia achilles* Totton and another new species *Lensia cordata*. Ann. Mag. Nat. Hist. Ser. 13, **8**(85–86): 71–76.
- Totton, A.K. 1974. A method for discharging nematocysts. Deep-Sea Res. **21**(9): 786–789.
- Totton, A.K., and Fraser, J.H. 1955a. Siphonophora. Sub-order Calycophorae. Family Diphyidae. Genera *Dimophyes*, *Muggiaeae*, *Sulculeolaria*, *Chelophyses*, *Eudoxoides*. Cons. Int. Explor. Mer Zooplankton Sheet No. 55.
- Totton, A.K., and Fraser, J.H. 1955b. Siphonophora. Sub-order Calycophorae. Family Diphyidae. Genus *Lensia*. Cons. Int. Explor. Mer Zooplankton Sheet No. 56.

- Totton, A.K., and Fraser, J.H. 1955c. Siphonophora. Sub-order Calycophorae. Family Chuniphyidae. Cons. Int. Explor. Mer Zooplankton Sheet No. 57.
- Totton, A.K., and Fraser, J.H. 1955d. Siphonophora. Sub-order Calycophorae. Family Hippopodiidae. Cons. Int. Explor. Mer Zooplankton Sheet No. 59.
- Totton, A.K., and Fraser, J.H. 1955e. Siphonophora. Sub-order Physonectae. Family Agalmidae. Cons. Int. Explor. Mer Zooplankton Sheet No. 61.
- Toyokawa, M., and Terazaki, M. 1994. Seasonal variation of medusae and ctenophores in the innermost part of Tokyo Bay. Bull. Plankton Soc. Jpn. **41**(1): 71–75.
- Trégouboff, G., and Rose, M. 1957. Manuel de planktonologie méditerranéene (2 volumes). Centre National de la Recherche Scientifique, Paris, France.
- Tveite, S. 1969. Zooplankton and the discontinuity layer in relation to echo traces in the Oslofjord. Fiskeridir. Skr. Ser. Havunders. **15**: 25–35.
- Vanhöffen, E. 1897. Die Fauna und Flora Grönlands. Vol. 2. In Grönland-Expedition der Gesellschaft für Erdkunde zu Berlin, 1891–1893. Edited by E. Drygalski. W.H. Kühl, Berlin.
- Vanhöffen, E. 1906. Siphonophoren. Nord. Plankton, **11**(5): 9–39.
- van Soest, R.W.M. 1973. Planktonic coelenterates collected in the North Atlantic Ocean. Bijdr. Dierkd. **43**(1): 119–125.
- van Soest, R.W.M. 1975. A catalogue of the coelenterate type specimens of the Zoological Museum of Amsterdam. I. General Introduction: Pelagic Coelenterates. Beaufortia, **24**(310): 27–35.
- Verrill, A.E. 1865. Classification of polyps. [Extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.] Part I. Communication IX. Proc. Essex Inst. **4**(5): 145–152.
- Vogt, C. 1852. Ueber die Siphonophoren. Z. Wiss. Zool. **3**(4): 522–525.
- Vogt, C. 1854. Recherches sur les animaux inférieurs de la Méditerranée. 1. Sur les Siphonophores de la mer de Nice. Mém. Inst. Nat. Genève. **1**: 1–164.
- Wailes, G.H. 1929. The marine zooplankton of British Columbia. Mus. Art Notes Vancouver, **4**(4): 159–169.
- Wang, W., and Xu, Z. 1990. Nematocysts of some species of siphonophores and scyphomedusae in Xiamen Harbour. J. Xiamen Univ. Nat. Sci. **29**(1): 85–88.
- Weill, R. 1934. Contribution à l'étude des cnidaires et de leurs nématoctyes. I and II. Trav. Stn. Zool Wimereux, **10/11**: 347 and 353.
- Weismann, A. 1883. Die Entstehung der Sexualzellen bei den Hydromedusen : zugleich ein Beitrag zur Kenntnis des Baues und der Lebenserscheinungen dieser Gruppe. Gustav Fischer, Jena, Germany.
- Widder, E.A., Latz, M.I., and Case, J.F. 1983. Marine bioluminescence spectra measured with an optical multichannel detection system. Biol. Bull. (Woods Hole), **165**(3): 791–810.
- Widder, E.A., Bernstein, S.A., Bracher, D.F., Case, J.F., Reisenbichler, K.R., Torres, J.J., and Robison, B.H. 1989. Bioluminescence in the Monterey Submarine Canyon: image analysis of video recordings from a midwater submersible. Mar. Biol. (Berl.), **100**(4): 541–551.
- Will, J.G.F. 1844. Horae tergestinae oder Beschreibung und Anatomie der im Herbste 1843 bei Triest beobachteten Akalephen. Leopold Voss, Leipzig.
- Woltereck, R. 1905a. Bemerkungen zur Entwicklung der Narcomedusen und Siphonophoren, mit Demonstrationen. Verh. Dtsch. Zool. Ges. **15**(4): 106–122.
- Woltereck, R. 1905b. Beiträge zur Ontogenie und Ableitung des Siphonophorenstocks, mit einem Anhang zur Entwicklungsphysiologie der Agalmiden. Z. Wiss. Zool. **82**(1): 611–637.
- Wrobel, D., and Mills, C. 1998. Pacific coast pelagic invertebrates: a guide to the common gelatinous animals. Monterey Bay Aquarium, Monterey, California.
- Xu, Z., and Zhang, J. 1978. On the hydromedusae, siphonophores and scyphomedusae from the coast of the east Guangdong Province and south Fujian Province, China. J. Xiamen Univ. Nat. Sci. **17**(4): 19–36. [In Chinese with English summary.]
- Yashnov, V.A. 1952. Coelenterates from the Pacific Ocean around Kamchatka. Issled. Dal'nev. Morei, **3**: 95–98.
- Yin, J., Chen Q.C., Zhang, G., Huang, L. and Li, K., 2006. Spatial and temporal variations of zooplankton composition and quantity distribution in the upper waters around Nansha Islands. Chin. Sci. Bull. **51**(Suppl. II): 154–164.
- Zelickman, E.A. 1972. Distribution and ecology of the pelagic hydromedusae, siphonophores and ctenophores of the Barents Sea, based on perennial plankton collections. Mar. Biol. (Berl.), **17**: 256–264.

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- Zhang, J. 1977. Studies on the hydromedusae, siphonophores and ctenophores from the coast of the Kainsu and Chekian Province, China. Oceanol. Technol. Sin. 7: 95–107.
- Zhang, J. 1984. The Calycophorae (Siphonophora) from tropical waters of the western Pacific Ocean. In Proceedings on Plankton from the Tropical Region of the Western Pacific Ocean. China Ocean Press, Beijing, People's Republic of China. pp. 52–85. [In Chinese with English abstract.]
- Zhang, J., and Lin, M. 1987. On a new species of deep-water Siphonophora *Lensia multicristatoides* sp. nov. Acta Oceanol. Sin. 9(5): 603–606. [In Chinese.]
- Zhang, J., and Lin, M. 1988. On a new species of deep-water Siphonophora *Lensia multicristatoides* sp. nov. from middle South China Sea. Acta Oceanol. Sin. 7(1): 115–118. [Approximate English translation of Zhang and Lin (1987).]
- Zhang, J., and Lin, M. 1990. On a new Siphonophora from the East China Sea and South China Sea. Acta Oceanol. Sin. 12(3): 352–354. [In Chinese; English translation, Acta Oceanol. Sin. 10(4): 609–611, 1991.]
- Zhang, J., and Lin, M. 1997. Study on the ecogeography of Siphonophora in the South China Sea. Acta Oceanol. Sin. 19(4): 121–131.
- Zhang, J., and Liu, H. 1989. The Hydromedusae and Siphonophora from the water area northwest of the Antarctic Peninsula. In A collection of papers from Antarctic Science Expedition, 6. Shanghai Science and Technology Press, Shanghai, China. pp. 151–156. [In Chinese with English summary.]
- Zhang, J. and Xu, Z. 1980. On the geographical distribution of the siphonophores in the China Sea. Acta Sci. Nat. Univ. Amoiensis, 19(3): 100–108. [In Chinese with English abstract.]
- Zhang, J., and Zhang, X. 1980. Description of two deep water Siphonophora of the northern East China Sea. Acta Sci. Nat. Univ. Amoiensis, 19(3): 121–125. [In Chinese with English abstract.]
- Zhang, J., Hwang, J., Lian, G., and Tang, S. 2005. Species diversity and abundance distribution of pelagic siphonophores from Nanwan Bay of Taiwan Island in late autumn and early winter. J. Trop. Oceanogr. 24(1): 41–49.
- Zuo, T., Wang, R., Chen, Y.Q., Gao, S.W., and Wang, K. 2005. Net macro-zooplankton community classification on the shelf area of the East China Sea and the Yellow Sea in spring and autumn. Acta Ecol. Sin. 25(7): 1531–1540.

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Index of Scientific Names

A name in boldface type is the accepted binomen or part binomen of a described species, and figure numbers refer to the main account for that species. Remaining names are synonyms or the name of another genus, species, order, suborder, family, or subfamily.

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Revised catalogue numbers for specimens deposited in the Royal British Columbia Museum, Victoria, B.C.

Catalogue numbers originally allocated to specimens for deposition in the British Columbia Provincial Museum (BCPM) during the early stages of this work, are now catalogued under amended numbers. These incorporate a recent name change to the Royal British Columbia Museum (RBCM) and a slightly revised numbering system. Most specimens are allocated recognizable amended numbers, whilst 14 are allocated new numbers. All are listed below.

- BCPM 996-199-1 *Agalma elegans*, catalogue number:
RBCM 996-00199-001
- BCPM 996-200-1 *Agalma elegans*, catalogue number:
RBCM 996-00200-001
- BCPM 996-201-1 *Agalma elegans*, catalogue number:
RBCM 996-00201-001
- BCPM 996-202-1 *Bargmannia elongata*, catalogue number: RBCM 996-00202-001
- BCPM 996-203-1 *Bargmannia lata*, holotype, catalogue number: RBCM 996-00203-001
- BCPM 996-204-1 *Bargmannia lata*, paratype 1, catalogue number: RBCM 996-00204-001
- BCPM 996-205-1 *Bargmannia lata*, paratype 2, catalogue number: RBCM 996-00205-001
- BCPM 996-206-1 *Bargmannia lata*, paratype 3, catalogue number: RBCM 996-00206-001
- BCPM 996-207-1 *Bargmannia lata*, paratype 4, catalogue number: RBCM 996-00207-001
- BCPM 996-209-1 *Frillagalma vityazi*, catalogue number: RBCM 996-00209-001
- BCPM 996-210-1 *Frillagalma vityazi*, catalogue number: RBCM 996-00219-001
- BCPM 996-211-1 *Frillagalma vityazi*, catalogue number: RBCM 996-00211-001
- BCPM 996-212-1 *Marrus orthocanna*, catalogue number: RBCM 996-00212-001
- BCPM 996-213-1 *Marrus orthocanna*, catalogue number: RBCM 996-00213-001
- BCPM 996-214-1 *Nanomia bijuga*, catalogue number: RBCM 996-00214-001
- BCPM 996-215-1 *Nanomia bijuga*, catalogue number: RBCM 996-00215-001
- BCPM 996-216-1 *Apolemia* sp., catalogue number: RBCM 996-00216-001
- BCPM 996-217-1 *Apolemia contorta*, catalogue number: RBCM 996-00217-001
- BCPM 996-218-1 *Amphicaryon acaule*, catalogue number: RBCM 996-00218-001
- BCPM 996-219-1 *Amphicaryon acaule*, catalogue number: RBCM 996-00219-001
- BCPM 996-220-1 *Maresearsia praeclara*, catalogue number: RBCM 996-00220-001
- BCPM 996-221-1 *Praya dubia*, catalogue number: RBCM 996-00221-001
- BCPM 996-222-1 *Praya reticulata*, catalogue number: RBCM 996-00222-001
- BCPM 996-223-1 *Praya reticulata*, catalogue number: RBCM 996-00223-001
- BCPM 996-223-2 *Clausophyes moserae*, new number: RBCM 009-00083-001
- BCPM 996-224-1 *Rosacea cymbiformis*, catalogue number: RBCM 996-00224-001
- BCPM 996-225-1 *Rosacea plicata*, catalogue number: RBCM 996-00225-001
- BCPM 996-226-1 *Rosacea plicata*, catalogue number: RBCM 996-00226-001
- BCPM 996-227-1 *Rosacea plicata*, catalogue number: RBCM 996-00227-001
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- BCPM 996-228-2 *Nectopyramis thetis*, new number: RBCM 009-00084-001
- BCPM 996-229-1 *Nectopyramis thetis*, catalogue number: RBCM 996-00229-001
- BCPM 996-230-1 *Nectadamas diomedae*, catalogue number: RBCM 996-00230-001
- BCPM 996-230-2 *Chuniphyes multidentata*, catalogue number: RBCM 996-00230-002
- BCPM 996-230-3 *Chuniphyes multidentata*, new number: RBCM 009-00085-001
- BCPM 996-231-1 *Nectadamas diomedae*, catalogue number: RBCM 996-00231-001
- BCPM 996-232-1 *Nectadamas diomedae*, new number: RBCM 009-00086-001
- BCPM 996-233-1 *Nectadamas richardi*, catalogue number: RBCM 996-00233-001
- BCPM 996-234-1 *Nectadamas richardi*, catalogue number: RBCM 996-00234-001
- BCPM 996-235-1 *Vogtia pentacantha*, catalogue number: RBCM 996-00235-001

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- BCPM 996-236-1 *Vogtia pentacantha*, catalogue number:
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- BCPM 996-237-1 *Vogtia serrata*, catalogue number:
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- BCPM 996-238-1 *Vogtia serrata*, catalogue number:
RBCM 996-00238-001
- BCPM 996-239-1 *Vogtia serrata*, catalogue number:
RBCM 996-00239-001
- BCPM 996-239-2 *Kephyses ovata*, catalogue number:
RBCM 996-00239-002
- BCPM 996-240-1 *Vogtia serrata*, catalogue number:
RBCM 996-00240-001
- BCPM 996-241-1 *Vogtia spinosa*, catalogue number:
RBCM 996-00241-001
- BCPM 996-242-1 *Vogtia spinosa*, catalogue number:
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- BCPM 996-243-1 *Sulculeolaria quadrivalvis*, catalogue
number: RBCM 996-00243-001
- BCPM 996-244-1 *Lensia achilles*, catalogue number:
RBCM 996-00244-001
- BCPM 996-244-2 *Lensia achilles*, new number:
RBCM 009-00087-001
- BCPM 996-244-3 *Lensia achilles*, new number:
RBCM 009-00088-001
- BCPM 996-245-1 *Lensia achilles*, catalogue number:
RBCM 996-00245-001
- BCPM 996-245-2 *Gilia reticulata*, catalogue number:
RBCM 996-00245-002
- BCPM 996-245-3 *Lensia achilles*, new number:
RBCM 009-00089-001
- BCPM 996-246-1 *Lensia conoidea*, catalogue number:
RBCM 996-00246-001
- BCPM 996-246-2 *Lensia conoidea*, new number:
RBCM 009-00090-001
- BCPM 996-247-1 *Lensia conoidea*, catalogue number:
RBCM 996-00247-001
- BCPM 996-247-2 *Kephyses ovata*, new number:
RBCM 009-00091-001
- BCPM 996-247-7 *Clausophyes moserae*, new number:
RBCM 009-00092-001
- BCPM 996-248-1 *Lensia havock*, catalogue number:
RBCM 996-00248-001
- BCPM 996-249-1 *Lensia hostile*, catalogue number:
RBCM 996-00249-001
- BCPM 996-249-2 *Lensia hostile*, catalogue number:
RBCM 996-00249-002
- BCPM 996-250-1 *Lensia multicristata*, catalogue
number: RBCM 996-00250-001
- BCPM 996-250-2 *Chuniphyes multidentata*, new
number: RBCM 009-00093-001
- BCPM 996-250-3 *Kephyses ovata*, new number:
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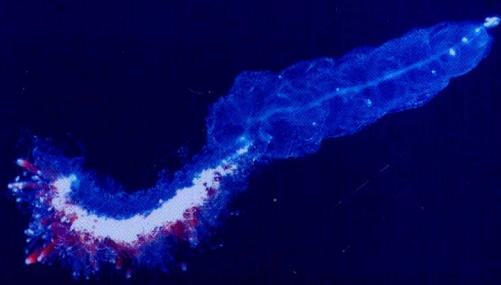


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This important work updates siphonophore taxonomy for the first time in 40 years, gives full synonymies for many common species and applies and extends the new holistic terminology recently introduced by other authors. It is divided into ten sections, including keys, general sections on systematics, life cycles, ecology (authored by Mary Arai), an extensive systematic section with detailed descriptions and diagnoses for 37 species collected from Canadian Pacific waters, plus relevant genus and family diagnoses, and a section on the worldwide distribution of these species. Fully illustrated with 65 figures (including many camera lucida line drawings). It should prove valuable to taxonomists identifying siphonophores from plankton collections, as well as researchers exploring the deep oceans using submersibles. Siphonophores lack a fossil record, yet are highly specialized hydrozoan predators; as such they provoke sustained interest from ecologists and evolutionary geneticists working on cnidarian phylogenetic relationships, and the monograph will also be of interest to these groups.



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