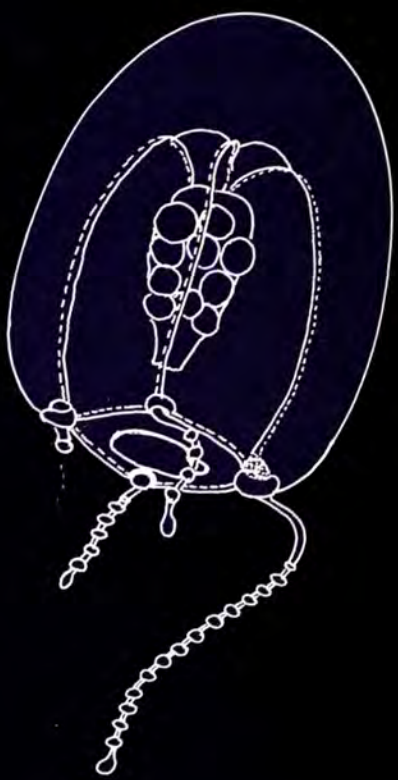
Canadian Bulletin of Fisheries and Aquatic Sciences

Hydromedusae of British Columbia and Puget Sound



M. N. Arai and
A. Brinckmann-Voss

BULLETIN 204
Ottawa 1980

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HYDROMEDUSAE OF BRITISH COLUMBIA AND PUGET SOUND

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BULLETIN 204

Hydromedusae of British Columbia and Puget Sound

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ABSTRACT

Arai, M.N., and A. Brinckmann-Voss. 1980. Hydromedusae of British Columbia and Puget Sound. Can. Bull. Fish. Aquat. Sci. 204: 192 p.

Fifty-nine species of hydromedusae are described from British Columbia and adjacent waters. A pictorial key of these species is included. In addition to two new species whose descriptions have already been published, four more new species are described, six are recorded from the area for the first time, and a number of taxonomic revisions are made. The family Pandeidae is discussed and the new family Halimedusidae separated from it. Detailed distributions in the Pacific area and brief notes on the general zoology are included.

Key words: Hydromedusae, Pacific, taxonomy, distribution.

RÉSUMÉ

Arai, M.N., and A. Brinckmann-Voss. 1980. Hydromedusae of British Columbia and Puget Sound. Can. Bull. Fish. Aquat. Sci. 204: 192 p.

Le rapport décrit 59 espèces d'hydroméduses de la Colombie-Britannique et des eaux adjacentes, avec une clé des espèces en images. Outre deux nouvelles espèces dont la description a déjà été publiée, le rapport décrit quatre autres nouvelles espèces, signale la présence de six especes pour la première fois dans la région, et présente un certain nombre de révisions taxinomiques. Les auteurs étudient la famille Pandeidae dont ils séparent la nouvelle famille Halimedusidae. Le rapport présente en détail la distribution des espèces dans la région du Pacifique ainsi que des notes brèves sur leur zoologie en général.

Mots clés: Hydroméduses, Pacifique, taxinomie, distribution.

INTRODUCTION

This bulletin deals with the hydromedusae of British Columbia and adjacent waters. The area covered extends from 54°40'N latitude to 48°25'N latitude and is bounded on the west by a straight line drawn from 54°40'N, 135°W to 48°25'N, 130°W. In addition the Puget Sound region is included.

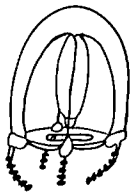
The bulletin is based primarily on collections made by the Pacific Biological Station, Nanaimo, B.C. and examined by A. Brinckmann-Voss (Brinckmann-Voss 1974) and on fresh collections made by the authors in the spring and summers of 1972 to 1977. In identifying these collections it became apparent that the complexity of the medusan fauna was not reflected in previous taxonomic papers from the area. In the bulletin, 59 species are described. Two new species arising from this work, *Sarsia viridis* and *Leuckartiara foersteri* (Brinckmann-Voss 1980, Arai and Brinckmann-Voss 1980), have already been described elsewhere. In the present bulletin, four more new species are included as "sp." and will be described when more material becomes available. Six species are recorded from the area for the first time. Examination of recent collections let us revise some of the species names listed in the technical report (Brinckmann-Voss 1974). The technical report should therefore be used only in conjunction with this bulletin.

It is our opinion that, due to the unusual complexity of speciation in the area, even this bulletin does not reflect the entire range of variation present. We prepared it as a base and starting point for further taxonomic and ecological work and to help physiologists and biochemists identify specimens more easily. For this reason seven species which previous authors have recorded from the area but which we have not collected are included for completeness. We have also included two species (*Velella velella* and *Bythotiara huntsmani*) for which only the hydroids have so far been collected in the field, and two species (*Heterotiara anonyma* and *Bythotiara depressa*) which have been collected just outside the research area.

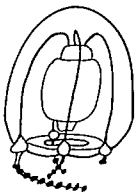
For each species an original photograph by M.N.A. or drawing by A.B.-V., synonymy, specific characters, description of medusa, and where necessary a discussion of taxonomy are given. Detailed distributions within the research area and slightly less detailed distributions for the Pacific Ocean are included. Key papers are listed for distributions in other oceans. Where the hydroid is known, papers including details of the life cycle are described. Similarly sections of brief notes on the general zoology of the species (physiology, feeding, nematocysts, seasonal occurrence, etc.) are designed both to be of interest in themselves and to offer access to the relevant literature. The comprehensive literature search was completed December 1977 although a number of more recent papers are included.

The main body of the bulletin is preceded by a pictorial key (Fig. 1). For terminology the reader should consult a textbook or the introductory section of The Medusae of the British Isles (Russell 1953).

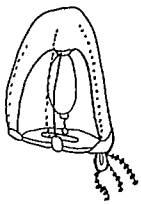
Fig. 1. Pictorial key - on following 3 pages - of species of British Columbia and Puget Sound.



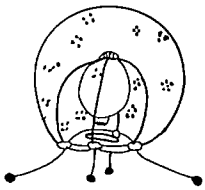
Euphysa japonica



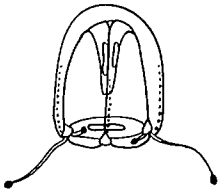
Euphysa tentaculata



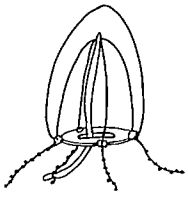
Hybocodon prolifer



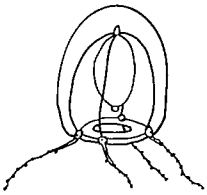
Plotocnide borealis



Velella velella



Sarsia apicula



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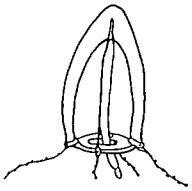

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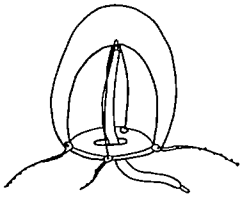

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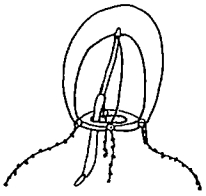

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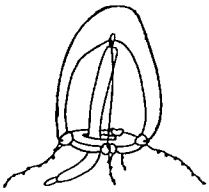

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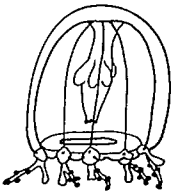

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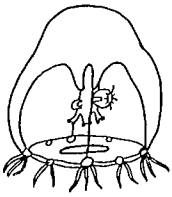

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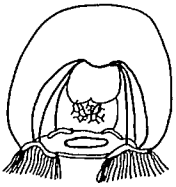
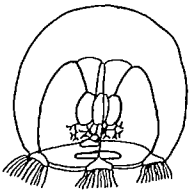
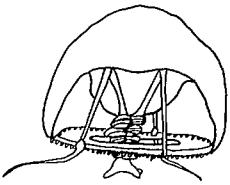


Bougainvillia multitentaculata



Bougainvillia superciliaris



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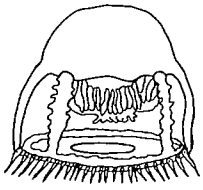
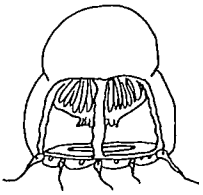
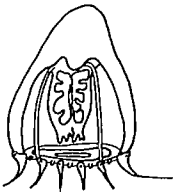


Catablema multicirrata

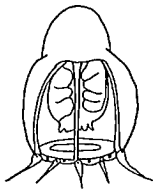


Catablema nodulosa

Halitholus pauper



Halitholus sp. I



Halitholus
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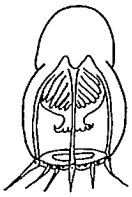

Leuckartiara
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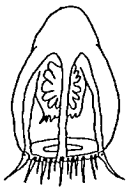

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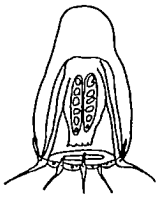

Leuckartiara
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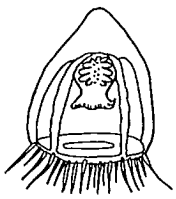

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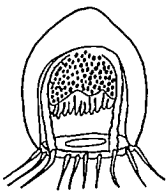

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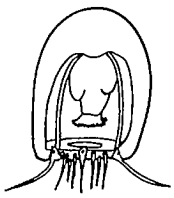

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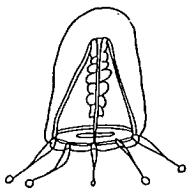
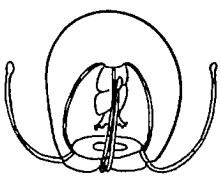


Bythotiara
depressa



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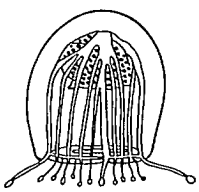

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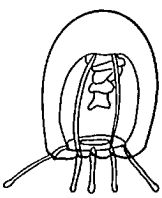

Heterotiara
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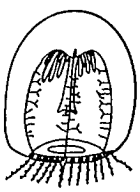

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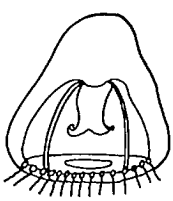

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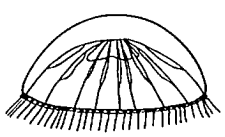

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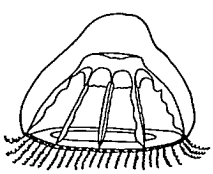

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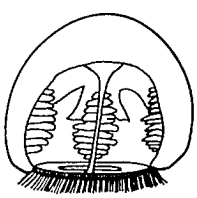

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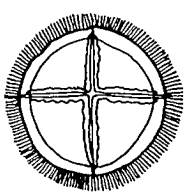

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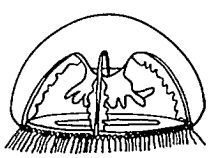

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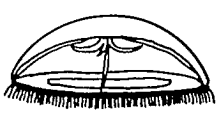

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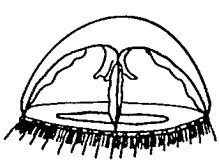

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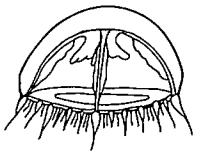

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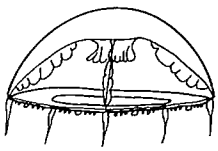

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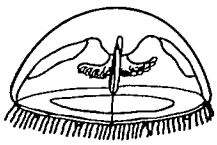

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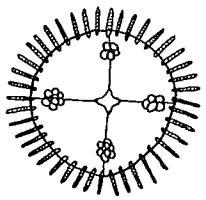

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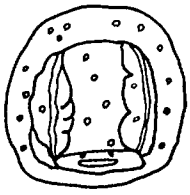
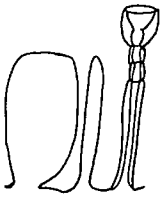
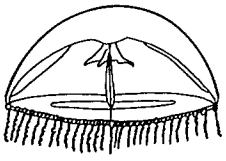


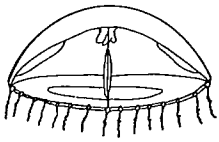
Orthopyxis compressa



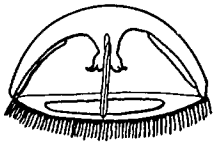
Orthopyxis compressa



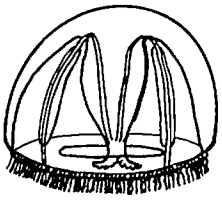
Phialidium gregarium



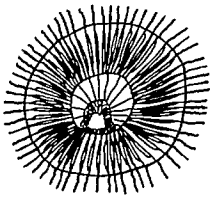
Phialidium lomae



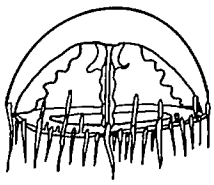
Eirene mollis



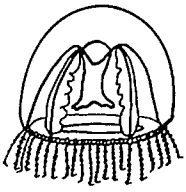
Eutonina indicans



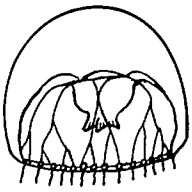
Aequorea victoria



Eperemetus typus

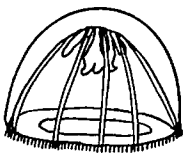


Gonionemus vertens

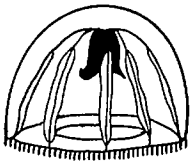


Proboscidactyla flavicirrata

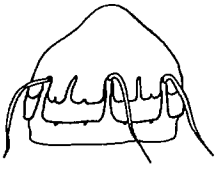
Aglantha digitale



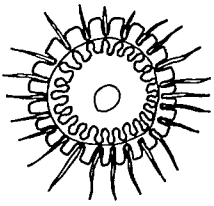
Crossota rufobrunnea



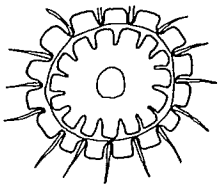
Pantachogon haeckeli



Aegina citrea



Solmissus incisa



Solmissus marshalli

ORDER ANTHOMEDUSAE

Hydromedusae with considerable variation in form, with umbrella usually deep bell-shaped; with gonads almost invariably situated on stomach, very rarely extending perradially on subumbrella; with or without ocelli; without statocysts. Hydroids with tentacles of various structure and position; if in one whorl with up to 8 tentacles only.

Family Tubulariidae

Anthomedusae with umbrella with or without apical projection; with four radial canals; with stomach not extending beyond umbrella margin; with simple circular mouth; with gonads completely surrounding stomach; with four or fewer marginal tentacles; without ocelli.

Genus *Euphysa* Forbes, 1848

Tubulariidae with one to four tentacles, often unequally developed, but all of the same structure; apex rounded, dome-like; tentacles usually moniliform. Hydroid; *Heteractis*, where known.

Type species: *E. aurata* Forbes, 1848.

Euphysa japonica (Maas, 1909)

Sarsia japonica Maas, 1909: 6; Bigelow, 1913: 4; Uchida, 1927a: 180.
Sarsia flammea Foerster, 1923: 236 (non *S. flammea* Linko, 1904: 212).
Euphysa japonica Kramp, 1928: 30; Uchida, 1933: 127.
Euphysa flammea Yashnov, 1948: 68 (in part); Mackie and Mackie, 1963: 64.
Corymorpha flammea Naumov, 1960: 211 (in part).

Specific characters: Four tentacles all alike, even in youngest stages.

Description of medusa: Medusa up to 11 mm, rarely to 15 mm high. Umbrella cylindrical, moderately thick. Manubrium broad, about as long as or shorter than bell cavity. Gonads encircling manubrium completely leaving only area near mouth free. Tentacles either moniliform throughout or with scattered groups of nematocysts in proximal parts of tentacles, forming more complete rings towards distal part of tentacle. Living specimens almost colorless or with scarlet manubrium and tentacle bulbs.

Hydroid: Not known.

Discussion of taxonomy: *Euphysa japonica* is not distinguishable from *E. flammea* in adult stages. Earlier workers (Kramp 1928; Uchida 1933) suggested that the tentacles of *E. japonica* were moniliform, whereas those of *E. flammea* had scattered groups of nematocysts. In the present work the smallest specimens were found to have moniliform tentacles, whereas larger specimens have tentacles with nematocyst patches proximally and rings distally.

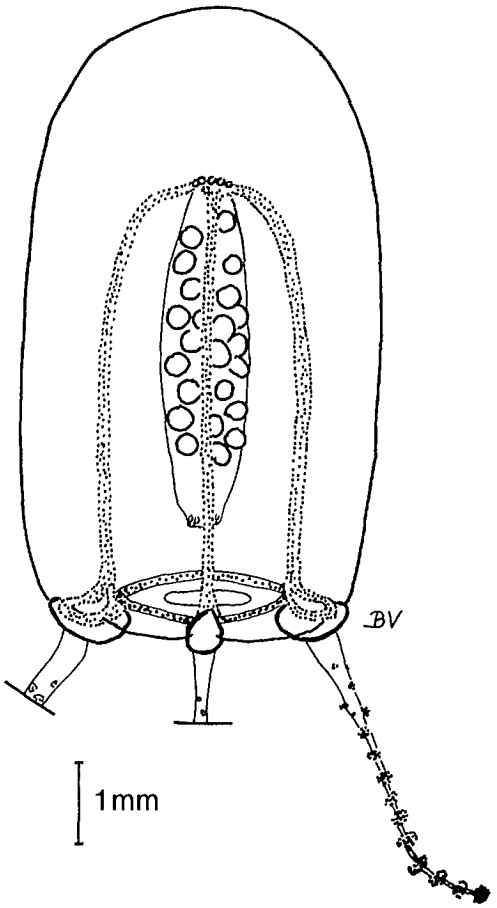


Fig. 2. *Euphysa japonica*, Sooke Harbour.

The only clear difference between the species is that in *E. flammea* the youngest stages have only one tentacle, with the other three tentacles added successively to reach the adult condition of four equal tentacles when the medusa is over 6 mm high (Kramp and Damas 1925). Uchida (1927a) showed, however, that *E. japonica* specimens as small as 1 mm already possess four tentacles. Foerster (1923) reported (as *Sarsia flammea*) specimens from British Columbia as small as 1 mm with four tentacles. Kramp (1928) reported 2.5 mm specimens of *E. japonica* from the Strait of Georgia with four well developed tentacles and we have collected 1.5 mm specimens with four tentacles from Departure Bay. As no young *E. flammea* specimens have been reported from the Pacific we may assume that all Pacific specimens belong to *E. japonica* and that *E. flammea* is present in the Arctic and northernmost Atlantic Oceans.

Distribution:

British Columbia and Puget Sound;
Jervis Inlet (present work); Strait of Georgia (Kramp 1928); Strait of Georgia, off Mitlenatch Island (Brinckmann-Voss 1974); Nanaimo Region (Fraser 1932); Strait of Georgia, off Five Finger Island (Foerster 1923; Brinckmann-Voss 1974; present work); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Northumberland Channel (Foerster 1923; Brinckmann-Voss 1974); Cowichan Bay (present work); Brentwood Bay (present work); San Juan Archipelago (Fraser 1932); Friday Harbor (Lenhoff 1964; Jha and Mackie 1967; Mackie and Passano 1968; present work); Sooke Harbour (present work); Kyoquot Sound (Brinckmann-Voss 1974); Hecate Strait, off Banks Island (Foerster 1923; Brinckmann-Voss 1974).

Pacific Ocean;
52°55'N, 173°30'E, off Attu Island, Aleutian Islands (Bigelow 1913); 51°33'N, 156°20'E, Okhotsk Sea off Kuril Islands (Uchida 1933); Akkeshi Bay, Hokkaido (Uchida 1940); Pacific Ocean, off Todohokke, Hokkaido (Maas 1909); Ishikari Bay, off Takashima (Uchida 1927a); Ishikari Bay, off Oshoro, Hokkaido (Uchida 1927a); Japan Sea, off Rebun Island (Uchida 1927a).

Notes: Gladfelter (1973) analyzed the mechanical properties of swimming of this species, Jha and Mackie (1967) examined the nerve elements present, and Mackie and Passano (1968) described the electrical activity and behavior associated with nonnervous epithelial conduction. Mackie and Mackie (1963) noted the luminescence of the subumbrellar sheet, and also described the nematocysts; stenoteles, basitrichous haplonemes, desmonemes and microbasic euryteles.

In British Columbia isolated specimens of *Euphysa japonica* have been obtained throughout the year, but it is common in sheltered waters such as Brentwood Bay April to June.

Euphysa tentaculata Linko, 1904

Euphysa tentaculata Linko, 1904: 214; Kramp, 1926: 22, pl. 1; Künne, 1935: 63; Kramp, 1961: 38; Mackie and Mackie, 1963: 66.
Corymorpha tentaculata Hartlaub, 1907: 85; 1917: 394; Naumov, 1960: 211.
?Sarsia tubulosa var. *Sarsia mirabilis* Mayer, 1910: 53 (in part, non *Oceania tubulosa* Sars, 1835: 25).

Specific characters: Adult medusae with one long tentacle, two about half as long, one bulb lacking or with rudimentary tentacle.

Description of medusa: Umbrella of adult medusa 4 to 6 mm high, cylindrical, moderately thick. Manubrium slightly shorter than bell cavity. Gonads encircling stomach completely, leaving short part of manubrium free at both ends. Mouth opening surrounded by ectodermal ring containing nematocysts. Four tentacular bulbs of same structure but unequal size; with largest opposite smallest and with two remaining bulbs of intermediate size; largest bulb carrying long moniliform solid tentacle, intermediate bulbs of medusae over about 1 mm high carrying shorter tentacles of similar structure, fourth bulb sometimes with rudimentary tentacle. Living specimens colorless or with scarlet manubrium and tentacular bulbs.

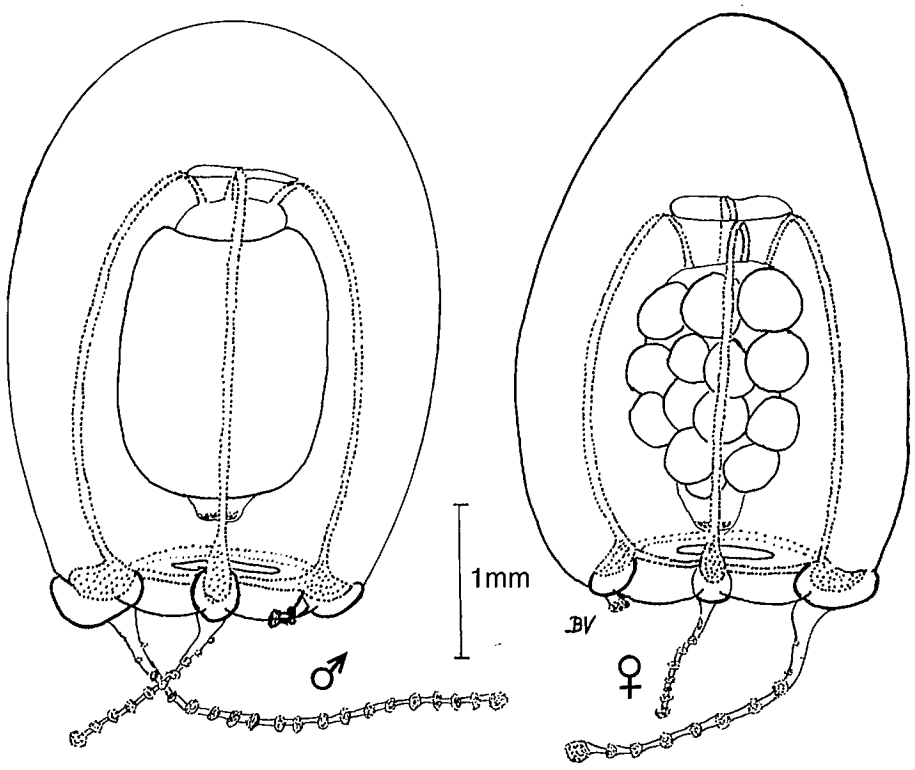


Fig. 3. *Euphysa tentaculata*, ♂ and ♀ medusae, Brentwood Bay.

Hydroid: Not known.

Distribution:

British Columbia and Puget Sound;
Departure Bay (present work); Brentwood Bay, Saanich Inlet (present work); Friday Harbor (Mackie and Mackie 1963).

Atlantic Ocean;
See Kramp (1927, 1942), Künne (1935), Kändler (1950) and Lacroix (1963) for details.

Arctic Ocean;
See Linko (1904), Kramp (1942), Pertzova (1972), and Zelickman (1972) for details.

Notes: The nematocysts of the long tentacle are stenoteles, desmonemes and basitrichous haplonemes (Mackie and Mackie 1963). To date this rare medusa has been found only in Brentwood and Departure Bays in April and in Friday Harbor in June.

Genus *Hybocodon* L. Agassiz, 1862

Tubulariidae without pointed apical process to umbrella; with or without exumbrellar nematocyst tracks; with one simple or compound marginal tentacular bulb with 1-4 tentacles; remaining three perradial bulbs rudimentary.

Type species: *H. prolifer* L. Agassiz, 1862.

Hybocodon prolifer L. Agassiz, 1862

Coryne fritillaria Steenstrup, 1842: 11 (medusa non hydroid).
?Diplonema islandica Green, 1857: 247, pl. 15.
?Steenstrupia owenii Green, 1857: 248, pl. 15.
?Steenstrupia globosa Sars, 1859: 101; Sars, 1877: 20, pl. 1.
Hybocodon prolifer L. Agassiz, 1862: 243, pl. 25; Böhm, 1878: 195, pl. 7; Haeckel, 1879: 33; Browne, 1896: 446; C. Hargitt, 1901: 222; 1902a: 20; Hartlaub, 1907: 98; Mayer, 1910: 38, pl. 2, 3 (in part); Bigelow, 1913: 6; Uchida, 1925: 78; Kramp, 1926: 33, pl. 1; C. Hargitt, 1927: 498; Sanderson, 1930: 224; Russell, 1939a: 3; 1953: 79, pl. 3; Kramp, 1959a: 86; 1961: 43.
Steenstrupia fritillaria L. Agassiz, 1862: 343.
Amphicodon fritillaria Haeckel, 1879: 36; Browne, 1895: 243.
?Amphicodon globosus Haeckel, 1897: 36.
Amphicodon amphipleurus Haeckel, 1879: 37, pl. 1.
Steenstrupia californica Fewkes, 1889a: pl. 22.
Steenstrupia occidentalis Fewkes, 1889b: 107.
Auliscus pulcher Saemundsson, 1899: 425, pl. 4.
Tubularia prolifer Bonnevie, 1899: 28, pl. 1; Vervoort, 1946: 109; Naumov, 1960: 215.
?Amphicodon gravidum Linko, 1904: 215.
Hybocodon occidentalis Hartlaub, 1905: 545.
Hybocodon christinae Hartlaub, 1905: 546; 1907: 102; Mayer, 1910: 43.
Hybocodon pulcher Hartlaub, 1905: 545; 1907: 96; Mayer, 1910: 43.
?Hybocodon gravidum Hartlaub, 1907: 104.
?Hybocodon islandicus Hartlaub, 1907: 104.
Hybocodon amphipleurus Hartlaub, 1907: 106.
Hybocodon chilensis Mayer, 1910: 42 (in part, non *H. chilensis* Hartlaub, 1905: 545).
Hybocodon prolifera Ostenfeld, 1916: 42; Fulton, 1968: 11.
Tubularia pulcher Broch, 1916: 22.
Tubularia christinae Naumov, 1960: 217.

Specific characters: The fully developed tentacle bulb with one or more moniliform tentacles, and with medusa buds at least in immature stages.

Description of medusa: Umbrella bell-shaped, higher than wide with rounded summit; with margin oblique to vertical axis; 2 to 4 mm, rarely to 5 mm, in height. Exumbrella of most speciemens with five meridional nematocyst tracks, two of which issue from the tentacular bulb. Stomach large, cylindrical, not reaching beyond umbrella margin. Mouth surrounded by narrow ring of nematocyst batteries. Gonad surrounding stomach, leaving short upper and distal portion free. Color of living specimens, bulbs, mouth and upper

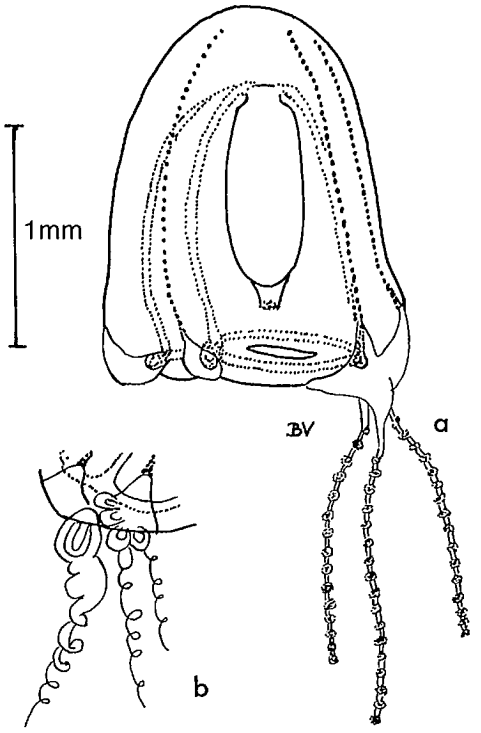


Fig. 4. *Hybocodon prolifer*. a. Medusa collected in May with ripening gonads and no medusae buds on tentacle base, Sooke Harbor. b. Tentacle base of a medusa collected in March with medusae buds, Departure Bay.

end of stomach red or reddish-brown, stomach pale yellow, exumbrellar nematocyst tracks pink or colorless.

Hydroid: first described by L. Agassiz (1862). Further details of the life cycle have been added by A. Agassiz (1862), Browne (1895, 1905b), Saemundsson (1899), Bonnevie (1899), C. Hargitt (1902b, 1905), G. Hargitt (1917), Perkins (1904), Müller (1908), Broch (1916), Kramp (1926), Uchida (1927a), Aurich (1958), Uchida and Nagao (1960a), Bodo (1969), and Bodo-Toularastel (1972). In addition to the asexual budding of medusae from the tentacle bulb, the hydroid reaches the actinula stage while still in the umbrella cavity of the medusa and may later be found free-floating in the plankton.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (Fulton 1968); Departure Bay (Fraser 1914; present work); Brentwood Bay (present work); Friday Harbor (Mackie and Mackie 1963).

Pacific Ocean;
Santa Barbara Channel, Calif. (Fewkes 1889a); Monterey Bay, off Santa Cruz,

Calif. (Fewkes 1889b); Dutch Harbor, Aleutian Islands (Bigelow 1913); 51°31'N, 156°20'E, Okhotsk Sea off Kuril Islands (Uchida 1933); Akkeshi Bay, Hokkaido (Uchida 1940, Uchida and Nagao 1960a); Mutsu Bay, off Asamushi (Uchida 1927a, 1927b, 1938b); Sea of Japan (Naumov 1956a); Ishikari Bay, off Takashima, Hokkaido (Uchida 1927a); Ishikari Bay, off Oshoro, Hokkaido (Uchida 1925).

Atlantic Ocean;
See Hartlaub (1907), Kramp (1926, 1927, 1930, 1939, 1942), M'Intosh (1926), Fish (1925), Watson (1930), Sanderson (1930), Runnström (1932), Künne (1935, 1952), Frost (1937), Fish and Johnson (1937), Russell (1938b), Kändler (1950), Franc (1951), Deevey (1952), Vannucci (1956), Aurich (1958), Werner (1959), Kühl (1962), Allwein (1968), Robins (1969), Calder (1971), Boyd et al (1973), Kühl and Mann (1973) and Fraser (1974) for details.

Arctic Ocean;
See Kramp (1942), Dunbar (1942), Grainger (1962), and Zelickman (1972) for details.

Notes: *Hybocodon prolifer* has been observed eating copepods (Lebour 1922) and young cuttlefishes (M'Intosh 1926).

In the present work the species was obtained from Departure Bay and Brentwood Bay in late March to May, although Fraser (1914) recorded a single specimen from Departure Bay in February.

Genus *Plotocnide* Wagner, 1885

Tubulariidae without pointed apical projection; nematocysts scattered or in scattered clumps on exumbrella; with four equally developed solid tentacles each with a large terminal knob of nematocysts.

Type species: *P. borealis* Wagner, 1885.

Plotocnide borealis Wagner, 1885

Plotocnide borealis Wagner, 1885: 74, pl. 4; Hartlaub, 1907: 68; 1914: 251; Yashnov, 1939: 108; Kramp, 1942: 22; Beyer, 1955: 94; Naumov, 1960: 221; Uchida, 1969: 286.
Syndictyon boreale Birulya, 1896: 336.
Protiara borealis Mayer, 1910: 106 (in part).
Sarsia inabai Uchida, 1933: 126.
Eucodonium arctica Hand and Kan, 1961: 9.

Specific characters: This is the only species of the genus.

Description of medusa: Medusa hemispherical to bell shaped; 1.5 - 3.5 mm high; with gelatinous umbrella which may have a thickness of up to one third the height of the medusa. Manubrium flask-shaped, upper part with vacuolated endodermal cells which may protude up into the umbrella. Mouth simple with a ring of nematocysts. Gonads encircling stomach completely leaving only lips and uppermost portion of manubrium free. Tentacle bulbs smaller than in *Euphysa*. Tentacles threadlike with terminal swelling studded with nematocysts. Ocelli absent but with small endodermal pigment masses in

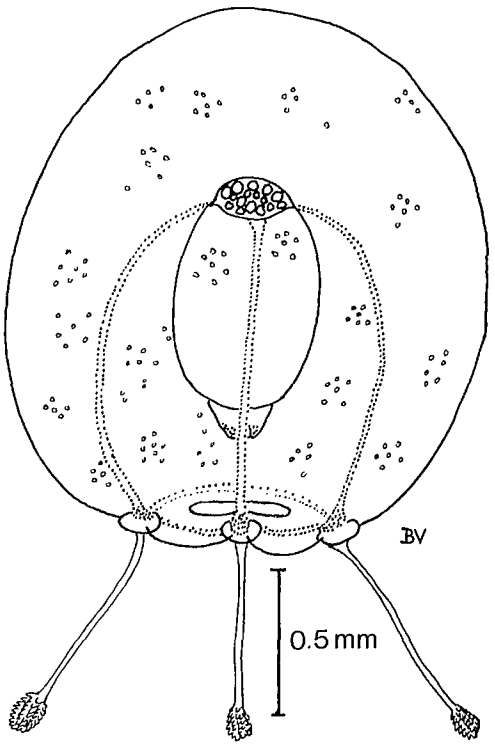


Fig. 5. *Plotocnide borealis*, young ♂, Departure Bay.

tentacle bulbs of some specimens. Color of terminal tentacle knobs and tip of manubrium red in living specimens.

Hydroid: Not known.

Distribution:

British Columbia and Puget Sound;
Deep Bay (present work); Departure Bay (present work); Parks Bay, San Juan Channel (C. Mills personal communication).

Pacific Ocean;
51°33'N, 156°20'E, Okhotsk Sea off Kuril Islands (Uchida 1933).

Atlantic Ocean;
See Kramp (1942), Beyer (1955), and Edwards (1958) for details.

Arctic Ocean;
See Kramp (1942), Naumov (1960), Hand and Kan (1961), Uchida (1969), Zelickman (1972), Zelickman and Golovkin (1972) and Kolosova (1978) for details.

Notes: The nematocysts of the terminal knob of the tentacles are desmonemes, those of the tentacle bases desmonemes and stenoteles, and those of the exumbrella stenoteles (Hand and Kan 1961). To date this medusa has been obtained on the inner side of Vancouver Island regularly in March and April.

Family Velellidae

Anthomedusae with perradial exumbrellar nematocyst rows; with four radial canals; with simple circular mouth; with gonads not completely surrounding manubrium; without ocelli. Floating hydroid colonies more conspicuous than the medusae.

Genus *Velella* Lamarck, 1801

Velellidae with two large perradial marginal bulbs, each with one or two tentacles with a terminal cnidocyst cluster (in mature medusae one long tentacle and a short second tentacle adradial to the long tentacle); with two perradial marginal bulbs without tentacles. Gonads in the male divided; female with one egg. Floating hydroid colonies with an upright sail; with a central gastrozoid, numerous feeding gonozooids and dactylozooids.

Type species: *V. velella* (Linné, 1758).

Velella velella (Linné, 1758)

Medusa velella Linné, 1758: 660; Browne, 1789: pl. 48.
Holothuria spirans Forskal, 1775: 104; 1776: pl. 26.
Phyllidoce P. Browne, 1789: 387.
Velella mutica Lamarck, 1801: 355; de Blainville, 1834: 304; Lesson, 1843: 571; Agassiz, 1865: 216; 1883: 2, pl. 1-6; Mayer, 1900: 71.
Velella tentaculata Lamarck, 1801: 355.
Velella scaphidia Péron, 1807: 43, pl. 30; Cranch, 1818: 419; de Blainville, 1834: 304; Lesson, 1843: 573; Haeckel, 1888b: 83.
Medusa pocillum Montagu, 1815: 201, pl. 14.
Aglaura crista Oken, 1815: 125.
Velella limbosa Lamarck, 1816: 482; Fleming, 1828: 500; Grant, 1833: 14; de Blainville, 1834: 304; Lesson, 1843: 568; Hollard, 1845: 248, pl. 4; Spagnolini, 1876: 304.
Velella pyramidalis Cranch, 1818: 419.
Velella sinistra Chamisso and Eysenhardt, 1821: 363, pl. 32; de Blainville, 1834: 304.
Velella oblonga Chamisso and Eysenhardt, 1821: 364, pl. 32; Eschscholtz, 1829: 171; de Blainville, 1834: 304; Brandt, 1835: 40; Lesson, 1843: 574; Haeckel, 1888b: 83.
Velella lata Chamisso and Eysenhardt, 1821: 364, pl. 32; Eschscholtz, 1829: 172; de Blainville, 1834: 304; Lesson, 1843: 575; Bigelow, 1911: 343.
Velella emarginata Quoy and Gaimard, 1824: 586, pl. 86; Lesson, 1843: 573.
Velella cyanea Lesson, 1826: pl. 6; 1830: 54; de Blainville, 1834: 304; Lesson, 1843: 577.
Velella australis de Haan, 1827: 489.
Velella pacifica de Haan, 1827: 490; Eschscholtz, 1829: 174; de Blainville, 1834: 304; Agassiz and Mayer, 1902: 159.
Velella radackiana de Haan, 1827: 490.
Velella sandwichiana de Haan, 1827: 491.
Velella pocillum Fleming, 1828: 500.

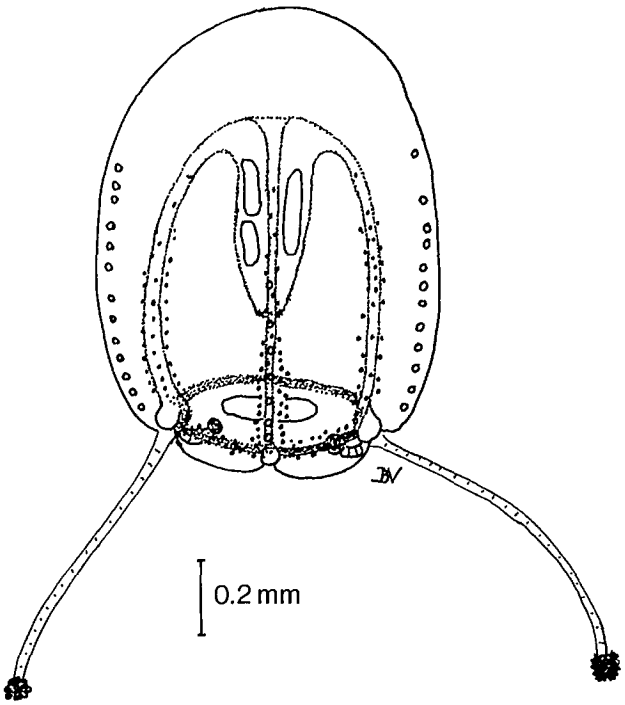


Fig. 6. *Velella velella*, ♂ laboratory-raised, Naples (after Brinckmann-Voss 1970 modified).

Rataria cordata Eschscholtz, 1829: 167, pl. 16.
Rataria pocillum Eschscholtz, 1829: 168.
Rataria mitrata Eschscholtz, 1829: 168.
Velella aurora Eschscholtz, 1829: 171; de Blainville, 1834: 304.
Velella septentrionalis Eschscholtz, 1829: 171; de Blainville, 1834: 304; Agassiz, 1865: 217.
Velella spirans Eschscholtz, 1829: 172; Vogt, 1854: 5, pl. 12; Haeckel, 1888a: 31; 1888b: 83; Chun, 1897: 93; Moser, 1925: 458; Leloup, 1929: 397, pls. 10-12; 1934: 3; 1955: 15; Blasco et al, 1975: 181, pl. 1.
Velella caurina Eschscholtz, 1829: 173; de Blainville, 1834: 304; Lesson, 1843: 578; Haeckel, 1888b: 83.
Velella tropica Eschscholtz, 1829: 174; de Blainville, 1834: 304.
Velella indica Eschscholtz, 1829: 175; de Blainville, 1834: 304.
Velella antarctica Eschscholtz, 1829: 175; Lesson, 1843: 577.
Velella patellaris Brandt, 1835: 38.
Velella oxyothone Brandt, 1835: 39.
Armenistarium velella Costa, 1841: 187, pl. 13.
Chrysomitra striata Gegenbaur, 1856: 232 (in part).
Rataria cristata Haeckel, 1888a: 31; 1888b: 79, pl. 44.
Velaria mutica Haeckel, 1888a: 31.
Velaria oblonga Haeckel, 1888a: 31.
Velaria indica Haeckel, 1888a: 31.

Fig. 7. *Velella velella*, hydroid, 17.3 mm long, Pacific Ocean west of Cape Beale. Photo. M. N. Arai.

Velella patella Haeckel, 1888b: 83.
Armenista sigmoides Haeckel, 1888b: 94, pl. 43.
Armenista mutica Haeckel, 1888b: 84.
Armenista antarctica Haeckel, 1888b: 84.
Armenista indica Haeckel, 1888b: 84.
Armenista lata Haeckel, 1888b: 84.
?Armenista lobata Haeckel, 1888b: 84.
Velella meridionalis Fewkes, 1889b: 112, pl. 1,2.
Velella velella Schneider, 1898: 194; Bigelow, 1911: 353; Boone, 1933: 38; Bigelow and Sears, 1937: 66, 125; Russell, 1939b: 358; Totton, 1954: 34; Picard, 1957: 7; Prevot, 1959: 109, pl. 6; Daniel and Daniel, 1963: 187; Brinckmann, 1964: 327; Edwards, 1966b: 283; Brinckmann-Voss, 1970: 34; Fields and Mackie, 1971: 1595.
Velella spiralis Martin, 1904: 27.
Velella subemarginata Stephens, 1905: 65.

Specific characters: This is the only species of the genus.

Description of medusa: Umbrella up to 1.5 mm high, 1.25 mm wide, bell-shaped. Manubrium short, conical, mouth opening a few days after liberation. Male gonads variable in number and position on manubrium; three or four perradial, aboral from them two or three interradial. Tentacles with one row of endodermal cells and a very thin layer of ectoderm, terminating in a large cnidocyst bulb; in newly liberated medusae tentacles only rudimentary.

Hydroid: the hydroid has been very thoroughly described during work to determine its taxonomic position. Most of the synonymy is related to the hydroid. Development has been traced from the conaria larva through the

ratarula and rataria stages to the conspicuous sailed colony. Detailed descriptions may be found in Vogt (1854), Leuckart (1854), Agassiz (1883), Bedot (1884, 1895), Haeckel (1888b), Woltereck (1904), Leloup (1929, 1954), Garstang (1946) and Brinckmann-Voss (1970).

Distribution:
Atlantic Ocean;
See Metschnikoff (1886) for details.

Notes: *Velella velella* has been included, although the medusae have not yet been collected in the Pacific, because the hydroid is a well known and conspicuous element in the fauna. Although the "chrysomitra" medusae are liberated in immense numbers from the hydroids in the laboratory, mature medusae have only once been collected in the field (Metschnikoff 1886). They have also been raised in the laboratory by Brinckmann-Voss (1964, 1970) and Rees (1975).

The sailed hydroid colonies have been found in much of the warmer portion of the Pacific, north to about 55°N (Bigelow 1911, Savilov 1956a, 1956b, 1958, 1961, Mednikov 1957, Bieri and Krinsley 1958, Bieri 1959, Beklemishev 1961, Mackie 1962, Alvariño 1971, Pearcy 1972, Sagaydachny 1974, Cheng 1975, Bieri 1977). They are frequently found off the west coasts of the Queen Charlotte Islands (Nichols 1926, Doe 1955, Savilov 1961) and Vancouver Island (Wailes 1929, Williamson 1930, Carl 1948, Gibson 1958, Mackie 1960, Beklemishev 1961, Savilov 1956b, 1961, Brinckmann-Voss 1974). The distribution apparently depends on the extent of the offshore currents. They occasionally penetrate the Strait of Juan de Fuca as far as Cadboro Bay and Port Townsend (Agassiz 1865, Bigelow 1911, Carl 1948, Fields and Mackie 1971).

The medusae contain large numbers of zooxanthellae particularly in the region of the radial canals and the ring canal. The cnidocysts are macrobasic euryteles and stenoteles (Picard 1955b, Brinckmann 1964, Bouillon 1978). Atrichs were also found by Bouillon (1978).

Family Corynidae

Anthomedusae without exumbrellar nematocysts in adult specimens; with four radial canals; with simple circular mouth; with gonads completely surrounding manubrium; with ocelli on abaxial side of tentacle bulbs.

Genus *Sarsia* Lesson, 1843

Corynidae with divided or undivided gonads; with four similar perradial tentacles.

Type species: *S. tubulosa* (M. Sars, 1835).

Discussion of genus: The only genus of Corynidae present in the research area is *Sarsia* Lesson, 1843. Due to the wide range of variation within the genus on the British Columbia coast, there is considerable confusion about the different species. Rechecking specimens identified by Foerster in the Pacific Biological Station Collections, on which he based his 1923 paper, and

examining large recent living collections, we reached the conclusion that there are six *Sarsia* species present in British Columbia: *Sarsia apicula* (Murbach and Shearer, 1902), *S. japonica* (Nagao, 1962), *S. princeps* (Haeckel, 1879), *S. tubulosa* (M. Sars, 1835) blue variety, *S. viridis* n. sp. and *Sarsia* sp. Ideally identification of *Sarsia* species should always be made from numerous living specimens from the same location. However, the variation in the genus is so great that even from one collecting station it will be possible to identify only a varying percentage of specimens with all their specific characters clearly defined.

The genus is considered to include (among others which do not appear in our research area) those species previously included in the genus *Stauridiosarsia* which was distinguished by small filiform tentacles in the hydroid stage. The unsatisfactory nature of this hydroid character has been discussed by Picard (1960), Hirai (1960), Brinckmann-Voss (1970) and Rees (1975). Very often these filiform tentacles do not occur in material collected in the field and appear only in the regenerating hydranths in the laboratory. *Stauridiosarsia producta* (Wright, 1858), the type species of *Stauridiosarsia*, was therefore placed in *Sarsia* by Brinckmann-Voss (1970) and *S. japonica* is herewith also placed in *Sarsia*.

Coryne rosaria was described by A. Agassiz (in L. Agassiz 1862, 1865) from the Strait of Georgia and Rosario Strait. Although the specimens were clearly *Sarsia*, insufficient detail was given to allow identification with a particular species. Fewkes (1889a) described *Sarsia* specimens from California as (*Sarsia*) *Syncoryne rosaria* and later (1889b) redescribed them (with the same drawings) as *Syncoryne* (*Sarsia*) *occidentalis*, sp. nov. His specimens did differ from those examined by Agassiz in bell shape and maximum manubrium length so they probably were a different species. However, again insufficient detail was given to allow clear specific identification. Some immature specimens have been linked with other species. Murbach and Shearer (1902, 1903) described *Sarsia dolichogaster* (as *Dipurena dolichogaster*; later listed by Foerster (1923) as *Slabberia catenata*) and *Sarsia angulata* (as *Syndictyon angulatum*) from Victoria Harbor. These records should be declared invalid however, because immature specimens of the Corynidae - except in rare cases like *Sarsia ophiogaster* - cannot be identified.

Sarsia apicula (Murbach and Shearer, 1902)

Codonium apiculum Murbach and Shearer, 1902: 72; 1903: 165, pls. 17, 22.
Sarsia apicula Hartlaub, 1907: 17; 1917: 383.
Sarsia rosaria Mayer, 1910: 59 (in part, non *Coryne rosaria* A. Agassiz (in L. Agassiz), 1862: 340); Kramp, 1961: 31 (in part).
Sarsia mirabilis Foerster, 1923: 236 (in part, non *Sarsia mirabilis* Agassiz, 1849).
Sarsia tubulosa Mackie and Mackie, 1963: 64 (in part, non *Oceania tubulosa* M. Sars, 1835).

Specific characters: Umbrella triangular, up to 15 mm high. Apical chamber short. Manubrium and tentacles pinkish (manubrium with green or purple shading in some specimens but not blue). Gonads occupy almost entire length of manubrium. Nematocyst pads of marginal bulbs of same thickness viewed from side or front. Marginal bulbs pinkish to brownish with dark red to black ocelli.

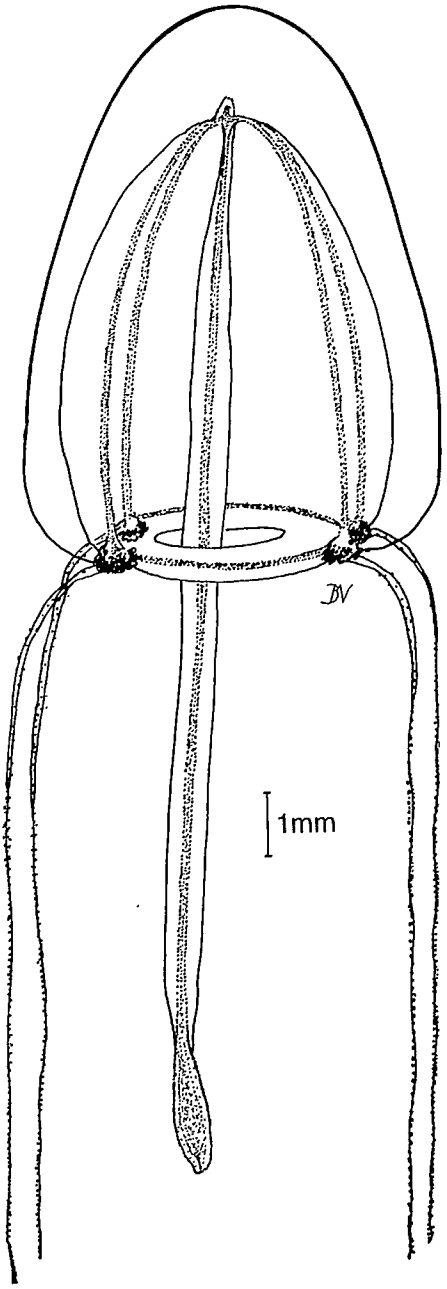


Fig. 8. *Sarsia apicula*, Sooke Harbour.

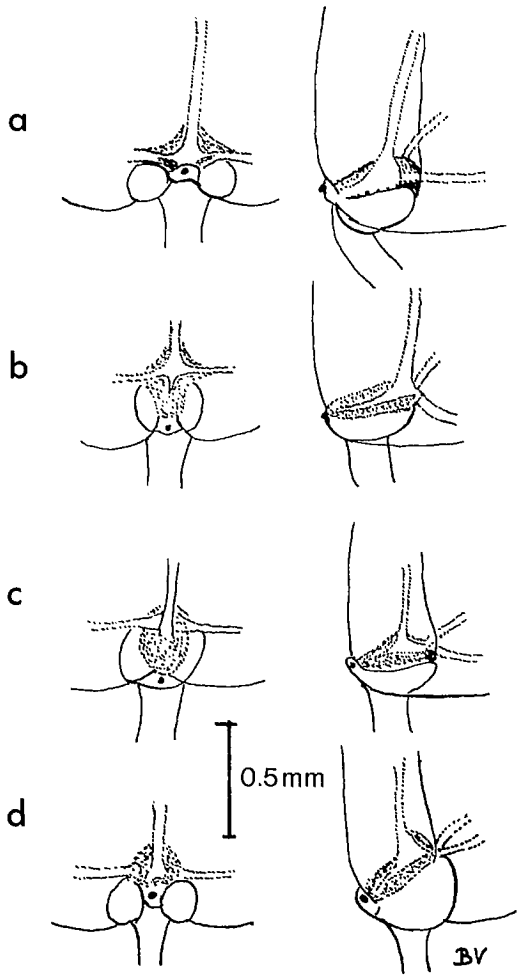


Fig. 9. *Sarsia*. Details of marginal bulbs; frontal and lateral views. a. *S. apicula;* b. *S. princeps;* c. *S. tubulosa;* d. *S. sp.*

Description of medusa: Umbrella nearly one half higher than wide; up to 15 mm high, 10 mm wide. Apical chamber on average shorter than that of *S. princeps*. Manubrium up to 2½ times the height of the umbrella.

Hydroid: work in progress, to be published elsewhere.

Discussion of taxonomy: This species is distinguished from *S. tubulosa* through its triangular bell, which is a rather constant feature in living specimens. The pinkish color of the tentacles and manubrium also distinguishes it from the typical blue *S. tubulosa* of the research area. It is distinguished from *S. princeps* through its shorter apical canal (average of several specimens), the relation of height to width of the umbrella and the shape of the marginal nematocyst pads (Fig. 9).

Murbach and Shearer (1903) discuss the possibility that this species may be identical with *Coryne rosaria*. However, they conclude, as we have discussed above, that the descriptions by Agassiz (1865) and Fewkes (1889a, 1889b) of *C. rosaria* are too vague for specific identification. Sverdrup (1921) tentatively designated a specimen from Norway as *S. apicula;* however, this was an incorrect identification as his plate shows a rounded rather than triangular bell.

Distribution:

British Columbia and Puget Sound;
Puget Sound (Murbach and Shearer 1902; 1903); Victoria Harbour (Murbach and Shearer 1902; 1903; present work); Sooke Harbour (present work).

Notes: Seasonal occurrence is from May to July. Physiological papers dealing with "*Sarsia tubulosa*" from British Columbia or Puget Sound waters may often in fact be based on *Sarsia apicula* specimens. At Sooke, *S. apicula* occurred in various collections together with the very blue form of *S. tubulosa*.

Sarsia japonica (Nagao, 1962) comb. nov.

Stauridiosarsia japonica Nagao, 1962: 176; Rees, 1975: 112, 156, 166, pl. 22-23, 35-40.

Specific characters: Umbrella bell-shaped, up to 5 mm high. Apical chamber short, conical or round. Manubrium one-third to two-thirds height of subumbrella, yellowish-grey to lemon yellow. Gonads flask-shaped, leaving short upper and distal portion of manubrium free. Nematocyst pads of marginal bulbs thick, slightly narrower viewed from front than from side. Marginal bulbs orange with reddish black ocelli.

Description of medusa: Umbrella up to 5 mm high, 4.5 mm wide. Exumbrellar nematocysts of young medusae concentrated in eight adradial zones, disappearing at about 30 days. Endoderm in radial canals thin, giving radial canals a hair-like appearance.

Hydroid: described by Nagao (1962) and Rees (1975). With scattered capitate tentacles and a whorl of small filiform tentacles.

Discussion of taxonomy: Our records of this species are based on two adult specimens from Ucluelet Inlet, on the west coast of Vancouver Island. We have not collected or raised the hydroid stage.

Distribution:

British Columbia and Puget Sound;
Ucluelet Inlet (present work).

Pacific Ocean;
Bodega Harbor, California (Rees 1975); Akkeshi Bay, Hokkaido (Nagao 1962, reared from hydroid).

Notes: Nematocysts of adult medusae are stenoteles and desmonemes (Rees 1975); young medusae also possess microbasic mastigophores (Nagao 1962).

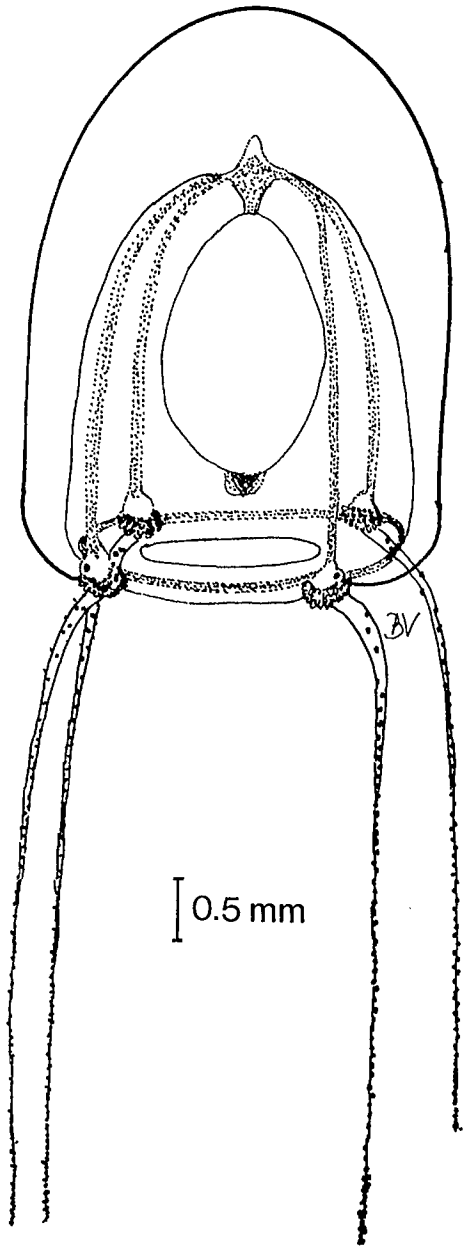


Fig. 10. *Sarsia japonica*, Ucluelet Inlet.

Sarsia princeps (Haeckel, 1879)

Codonium princeps Haeckel, 1879: 13, pl. 1; Grönberg, 1898: 458, Fig. 1, 2.
Sarsia princeps Haeckel, 1879: 655; Browne, 1903: 8, pl. 1, 3; Hartlaub, 1907: 47; Bigelow, 1909b: 303, pl. 30; 1913: 5; 1920, 4H, pl. 1; Kramp, 1926: 2, pl. 1; 1932: 5; Dunbar, 1942: 72; Kramp, 1942: 12; 1955a: 150; 1959a: 79; 1961: 29.
Coryne princeps Naumov, 1955a: 52, pl. 7; 1960: 255; Zelickman, 1970: 82; 1976: 202.
Coryne (=*Sarsia*) *princeps* Naumov, 1956a: 37.

Specific characters: Umbrella conical, up to 40 mm high. Apical chamber often very long. Manubrium pink or violet and tentacles pink. Gonads tapering off at upper and distal portion of manubrium. Nematocyst pads of marginal bulbs thicker viewed from side than front (Fig. 9). Marginal bulbs pink with small, dark red or black ocelli.

Description of medusa: Umbrella conical, up to twice as high as wide, up to 40 mm high (specimens in present collections up to 20 mm high, 10 mm wide). Apical chamber on average double the length of *S. tubulosa* blue variety, often widened at its upper end. Manubrium two times the height of the umbrella or longer, but often shortening to 1/3 the umbrella height during preservation. Umbrella often with a pink tinting.

Hydroids: work in progress, to be published elsewhere. Naumov (1951) raised the primary hydranths.

Discussion of taxonomy: Jagged radial canals are often mentioned as a typical character of this species. However, as noted by Bigelow (1920), there are various degrees of waviness independent of specimen size. Grönberg (1898) who described *S. princeps* from living specimens showed smooth radial canals in his drawings. We also find that living specimens have smooth radial canals and that the jagged canals occur in both *S. tubulosa* and *S. princeps* in deteriorating specimens. With this character removed as a diagnostic character it is very difficult to identify *S. princeps* from single preserved specimens, distribution records usually giving sufficient data to make a positive identification only if accompanied by a good, original drawing. We found that the most constant features for *S. princeps* are the "narrow" marginal bulbs (Fig. 9) and the high triangular umbrella. Foerster (1923) lists three specimens from Departure Bay and Dodds Narrows based on jagged radial canals. These specimens (No. 63, 64, 65) were found in the Pacific Biological collection and examined but they were in too poor a condition for specific identification (Brinckmann-Voss 1974). It is probable that they were not all *S. princeps* due to the short apical chamber of two specimens. Uchida (1933) also described bell-shaped specimens from Kamchatka which probably do not belong to this species. Kramp (1942) tentatively designated these specimens as *S. tubulosa* but definite identification is not possible from the description given.

Distribution:
British Columbia and Puget Sound;
Departure Bay (present work); Brentwood Bay (present work); Bamfield Inlet

Fig. 11. *Sarsia princeps*, preserved specimen, 10.6 mm high, Departure Bay, Photo. M. N. Arai.

(present work); Ucluelet Inlet (present work); Kyuquot Sound (present work, reexamination Pacific Biological Station specimen No. 40).

Pacific Ocean;

Southern Bering Sea (Bigelow 1913); Ishikari Bay, off Takashima, Hokkaido (Uchida 1927a); Busse Lagoon, Aniva Bay (Zelickman 1976).

Atlantic Ocean;

See Kramp (1920a, 1926, 1942), Dunbar (1942), Peterson (1957), Lacroix (1961) and Semenova (1962) for details.

Arctic Ocean;

See Kramp (1926, 1942, 1955a), Bernstein (1934), Ranson (1936), Yashnov (1939), Dunbar (1942), Vibe (1950), MacGinitie (1955), Kamshilov and Zelickman (1958), Grainger (1962), Zelickman (1972), Zelickman and Golovkin (1972), Grainger (1975), Grainger and Grohe (1975), Grainger and McSween (1976) and Shih and Laubitz (1978) for details.

Notes: Linko (1900) examined the ocelli of *S. princeps* and Kramp (1926) describes the histology of various other structures. Fraser (1969) showed that the feeding selectivity of *S. princeps* for copepods rather than fish

larvae depends on the inability of the medusa to retain hold of anything larger than a copepod while actively pulsating.

We have collected *S. princeps* April to June, with *S. tubulosa* but in much smaller numbers.

Sarsia tubulosa (M. Sars, 1835)

Oceania? tubulosa M. Sars, 1835: 25, pl. 5; Gould, 1841: 348.
Syncoryna Sarsii Lowen, 1836: 176, pl. 8; M. Sars, 1846: 2, pl. 1.
Sarsia tubulosa Lesson, 1843: 333; Forbes, 1848: 55, pl. 6 (in part); Schulze, 1873: 14, pl. 2, 3; Haeckel, 1879: 16 (in part); Hartlaub, 1907: 19; Mayer, 1910: 52 (in part); Hartlaub, 1917: 383; Kramp, 1926: 8, pl. 1 (in part); 1927: 24 (in part); 1928: 28; Russell, 1953: 55, pl. 1, 2 (in part); Kramp, 1961: 31 (in part); Mackie and Mackie, 1963: 64 (in part); Edwards, 1978: 301.
Syncoryna decipiens Dujardin, 1845: 275, pl. 14, 15.
Coryne sarsii Johnston, 1847: 43; Broch, 1916: 14 (in part); Kühl, 1962: 214 (in part).
Sarsia mirabilis L. Agassiz, 1849: 224, pl. 4, 5; Haeckel, 1879: 17; Fewkes, 1881: 141, pl. 3; Hartlaub, 1907: 37 (in part); 1917: 384; Foerster, 1923: 18 (in part).
Coryne mirabilis L. Agassiz, 1862: 185, pl. 17, 18, 19 (hydroid in part, and medusa).
Syncoryne sarsii Allman, 1864: 357; Hincks, 1868: 52, pl. 7 (in part); Allman, 1872: 275; Schulze, 1873: 2, pl. 1, 3.
Syncoryne mirabilis Allman, 1864: 357; 1872: 278 (in part); C. Hargitt, 1905: 30; Fraser, 1944: 41, pl. 4 (in part).
Syncoryne decipiens Hincks, 1868: 56, pl. 10; Hartlaub, 1916: 93.
Sarsia decipiens Hartlaub, 1907: 30.
Sarsia litorea Hartlaub, 1907: 32.
Sarsia tubulosa var. *Sarsia mirabilis* Mayer, 1910: 53, pl. 3, 4 (in part).
Coryne tubulosa Rees, 1941: 129; Hamond, 1957: 299; Naumov, 1960: 233 (in part).
Coryne (=*Sarsia*) *tubulosa* Werner, 1963: 468.

Specific characters: Umbrella round, dome-like, higher than wide, up to 18 mm high. Apical chamber short. Manubrium and tentacles blue, green, brown, peach, or colorless (in present collections usually sky blue). Gonads leaving short upper and distal portion of manubrium free. Nematocyst pads of marginal bulbs of same thickness viewed from side or front (Fig. 9). Marginal bulbs blue, green, brown, yellow, or white (in present collections blue or white only) with large dark red or black ocelli.

Description of medusa: Umbrella bell-shaped. Velum broad. Apical chamber on average half the length of that of *S. princeps*. Manubrium cylindrical, 3 times the height of the umbrella or longer, often contracted to ½ the umbrella height. Mouth simple tube-like. Gonads encircling manubrium in a thick ring.

Hydroid: work in progress, to be published elsewhere. Hartlaub (1916) described the hydroid (as *Syncoryne decipiens* Dujardin) and discussed the confused synonymy of hydroids tentatively correlated with *Sarsia tubulosa* by

Fig. 12. *Sarsia tubulosa*, preserved specimen, 5.3 mm high, Departure Bay, Photo. M. N. Arai.

previous authors. Rees (1941) described asexual budding. Werner (1963) and Edwards (1978) described the effect of temperature on growth, form, and the release of medusae.

Discussion of taxonomy: This is a highly variable species with a confused synonymy. Kramp (1926) investigated the color varieties present in Greenland and European waters and concluded that there were insufficient morphological differences present to divide the main color varieties into separate species. His 'blue' and 'brown' varieties are relatively uncontroversial. His 'scarlet' form characterized by apical knob and marginal tentacle bulbs of brilliant scarlet, is however, more controversial [see discussions by Kramp (1926), and Russell (1953)]. It differs not only in color but in such characters as a longer proximal portion of the manubrium free from gonad and apical chamber filled with a plug of endodermal cells to form an apical knob. We have therefore followed a conservative approach in the above synonymy, excluding the 'scarlet' variety and the possibly related forms *Sarsia pulchella* Forbes, 1848, *S. erythrops* Romanes, 1876a, *S.*

pattersoni Haddon, 1886 and *S. densa* Hartlaub, 1907.

Large recent collections convinced us that the 'blue'variety, characterized by manubrium and tentacles of pure sky blue, is most common in our research area. Elsewhere the 'blue' variety has been described from the Kattegat and Baltic (Kramp 1926, 1927), the Hebrides (Nicol 1936) and Strait of Dover (Kramp 1930). In addition to the sky blue specimens, more greenish specimens have been obtained from Brentwood and lighter blue from Departure Bay in early spring (beginning of April). Occasional peach-colored specimens are collected in Departure Bay. Such variation in color may be due to diet as suggested by Edwards (1978).

Previous records of *Sarsia tubulosa* in the present research area must be treated with varying degrees of skepticism. Foerster (1923) included *S. apicula* as a possible synonym and includes specimens with long apical chambers as well as some with short. His locations should therefore be rechecked with abundant living material. Re-examination of his specimens in the Pacific Biological Station collection allowed us only to confirm his identification of Departure Bay and Dodds Narrows specimens, but he also listed Banks Island, Bull Harbour, off Snake Island, off Newcastle Island, north of Entrance Island, Northumberland Channel, Round Island, Vesuvius Bay and Saltspring Island. Mackie and Mackie (1963) also synonymized *S. tubulosa* with *S. apicula*. We rechecked some specimens sent by Mackie to the National Museum, Ottawa. The color had been lost so positive identifications could not be made. As the shapes of the preserved specimens are partly round, partly triangular, the collection probably included both *S. tubulosa* and *S. apicula*. Other papers, mostly physiological, which report collection of specimens from Friday Harbor (Johnson and Snook 1927; Hyman 1940; Jha and Mackie 1967; Mackie and Passano 1968; Passano 1973) do not give sufficient data for taxonomic identification. However Kramp (1928) gave a brief description of *S. tubulosa* specimens from Ruxton Passage. In view of his shortly preceding extensive work on European specimens (Kramp 1926) it is probable that his identification is reliable.

Similarly, reports of *Sarsia tubulosa* in the remainder of the Pacific area must be carefully checked. Uchida (1927a, 1930, 1938b and c, 1940, 1958) listed *S. mirabilis* or *S. tubulosa* in various locations in Japan. The most complete description is given in his 1927 paper. These specimens are not *S. tubulosa* since the gonad is present only on the distal portion of the manubrium. The brief description given in the 1940 paper is consistent with the specimens being *S. tubulosa* (the gonads are shown as extending most of the length of the manubrium), although description of such features as the nematocyst pads of the marginal bulbs is not included. The remaining papers include listings only. Kakinuma (1966) raised, from a presumed *Sarsia tubulosa* hydroid, mature medusae with a short proximal portion of the manubrium free of gonad but with an orange apical knob, manubrium and marginal bulbs. Against this background the identification of the specimens used by Nagao (1969b) may also be questioned since morphological data on the medusae are lacking.

The exact distribution of the species in the Atlantic may be questioned in some locations but its presence on the Atlantic coasts of Europe and North American is well documented. The extent of its penetration into Arctic waters is more controversial. For example Dunbar (1942) and Grainger (1962) list it as present in the eastern Canadian Arctic. However, they do not give

morphological or color data and Kramp (1942) describes scarlet specimens from off Kap Farvel, Greenland, the nearest location for which clear data are given. Similarly, the species has been listed by a number of authors in the Barents and White Sea areas. It is difficult to find clear descriptions of the form present (see Wagner 1885; Birulya 1896; Linko 1899, 1904; Naumov 1960) but it is probable that at least some of the specimens described truly belong to this species.

Distribution:

British Columbia and Puget Sound;
Deep Bay (present work); French Creek boat basin (present work); Departure Bay (Foerster 1923; present work); Dodds Narrows (Foerster 1923, re-examination Pacific Biological Station specimen No. 49); Ruxton Passage (Kramp 1928); Ladysmith Harbour (present work); Brentwood Bay (present work); Victoria Harbour (present work); Sooke Harbour (present work); Bamfield Inlet (present work); Ucluelet Inlet (present work); Masset Harbour (present work).

Pacific Ocean;
See discussion of taxonomy.

Atlantic Ocean;
See Hartlaub (1907), Kramp (1926, 1927, 1930), Nicol (1936), Russell (1953) and Calder (1971) for details.

Arctic Ocean;
See discussion of taxonomy.

Notes: "*Sarsia tubulosa*" has been extensively used for experimental work especially on neural and non-neural conduction and behavior. Although it is not clear whether all this work has actually been done on *Sarsia tubulosa* specimens, the following paragraphs summarize such work without speculation on individual papers as to whether they were done on correctly identified material (see discussion of taxonomy). It is unlikely that most data obtained would differ significantly in related species, but where conflicting details arise the possibility of specific variability should be borne in mind.

The swimming, feeding, and "crumpling" behavior have been described by L. Agassiz (1849, 1862), Romanes (1876b, 1877b, 1880, 1885), Henschel (1935), and Hyman (1940). Rice (1964) showed that pressure decrease caused decreased activity and consequent sinking, whereas increased pressure enhanced movement toward the light source, i.e., normally upward. Hansen (1951) described aggregation in or near the discontinuity layer of Oslo fjord and Arai (1973, 1976) showed active aggregation and increased fishing activity at temperature and salinity discontinuities in laboratory chambers. Gladfelter (1973) briefly discussed the functions of eight adradial mesogloeal joints and exumbrellar creases in locomotion. Linko (1900), Jha and Mackie (1967), and Mackie (1971) described the histology and ultrastructure of the ocelli and nervous system, particularly the marginal nerve rings. Mackie and Passano and their co-workers have extensively investigated the control of behavior (Passano 1965; Mackie, Passano, and Pavans de Ceccatty 1967; Passano, Mackie, and Pavans de Ceccatty 1967; Mackie and Passano 1968; Mackie 1971; Passano 1973, 1976). Of particular interest is the demonstration of neuroid and myoid conduction in simple epithelia and myoepithelia, respectively. The swimming muscle in the subumbrella is a myoid conducting tissue, whereas the exumbrellar epithelium is a neuroid epithelium involved in the "crumpling" response.

Sarsia tubulosa is known to feed on copepods, mysids, amphipods, nauplii

of cirripedes and euphausids, *Sagitta*, and occasionally other medusae such as *Aurelia* (Forbes 1848, L. Agassiz 1849, 1862, Linko 1899, Lebour 1922, 1923; Plotnikova 1961, Sveshnikov 1963). Lebour (1922, 1923) stated it would not feed on fish even when confined in small chambers with them but Plotnikova (1961) and Sveshikov (1963) reported feeding on larvae of herring, capelin and flatfish. Feeding reactions can be stimulated by solutions of peptone, glycine or 3-methylindole (Henschel 1935). Ingestion and digestion are rapid (Plotnikova 1961).

Sarsia tubulosa is common in May and June although we have collected immature specimens in April at Departure Bay and mature forms to mid-July in Sooke Harbour.

Sarsia viridis Brinckmann-Voss, 1980

Sarsia viridis Brinckmann-Voss, 1980: In press.

Specific characters: Umbrella dome-like, or slightly conical, up to 8 mm high. Apical chamber short. Apical chamber, base of manubrium and marginal bulbs iridescent green with black ocelli. Gonads leaving at least proximal ½ of manubrium free. Nematocyst pads of marginal bulbs of same thickness viewed from side or front.

Description of medusa: Height of umbrella (adult specimens) 5-8 mm, width 4-6 mm. Manubrium longer than bell cavity. Tentacles whitish; umbrella transparent.

Hydroid: not known.

Discussion of taxonomy: This species is distinguishable from the other species in the research area by its small size, large gonad-free portion of manubrium, and iridescent green marginal bulbs.

Distribution:
British Columbia and Puget Sound;
Departure Bay (present work); Brentwood Bay (Brinckmann-Voss 1980; present work); Friday Harbor (Brinckmann-Voss 1980; R. Miller personal communication); Sooke Harbour (Brinckmann-Voss 1980; present work); Ucluelet Inlet (Brinckmann-Voss 1980).

Notes: Cnidocysts are stenoteles and desmonemes (Brinckmann-Voss 1980).

Sarsia sp.

Specific characters: Umbrella conical, 10 mm high. Apical chamber short. Manubrium and marginal bulbs bright orange with dark red ocelli. Gonads encircling manubrium completely, leaving less than ¼ of upper manubrium free. Nematocyst pads of marginal bulbs very thick, of same thickness viewed from side or front (Fig. 9).

Description of medusa: Height of umbrella 10 mm, width 8 mm. Manubrium longer than umbrella. Adaxial part of marginal nematocyst pads thicker than in *S. apicula*, *S. princeps*, *S. tubulosa* or *S. viridis*.

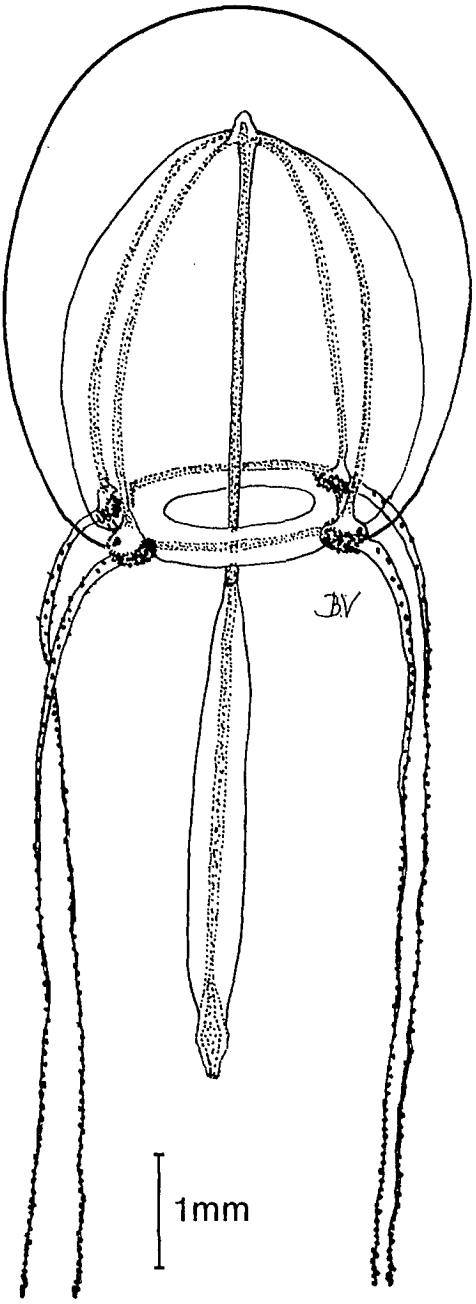


Fig. 13. *Sarsia viridis*, Sooke Harbour.

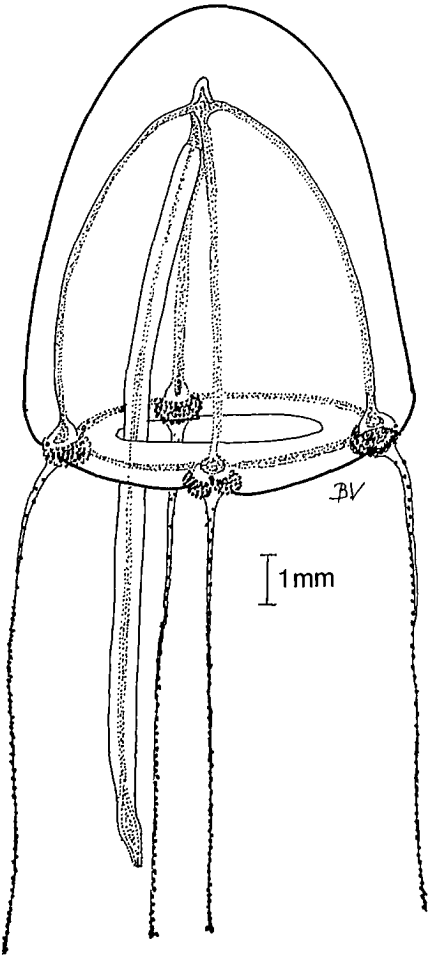


Fig. 14. *Sarsia* sp., Brentwood Bay. The manubrium was 2 times the length of the umbrella in the living specimen.

Hydroid: not known.

Discussion of species: We have found only two specimens of this species. It is clearly distinguished from the other known British Columbia species by the very thick nematocyst pads and the bright orange marginal bulbs and manubrium.

Distribution:
British Columbia and Puget Sound;
Departure Bay (present work); Brentwood Bay (present work).

Family Cladonematidae

Creeping and swimming Anthomedusae; with mouth with oral tentacles armed with nematocyst clusters; with stomach with radial pouches; with variable number of radial canals, bifurcated or simple; with variable number of hollow, branching marginal tentacles, each furnished with organs of adhesion; with ocelli. Hydroids with oral whorl of capitate tentacles, and usually with an aboral whorl of small filiform tentacles.

Genus *Cladonema* Dujardin, 1843

Cladonematidae with simple, unbranched oral tentacles; without an apical cavity above stomach.

Type species: *C. radiatum* Dujardin, 1843.

Cladonema californicum Hyman, 1947

Cladonema californica Hyman, 1947: 262.
Cladonema californicum Mackie and Mackie, 1963: 67; Rees, 1979b: 295.

Specific characters: Manubrium carrying 6 (rarely 7) gonads as elongated, rounded protrusions in a whorl. Nine (rarely 11) simple, straight radial canals. Tentacles same number as radial canals, with one sucker-branch and 1 or 2 branches with nematocysts.

Description of medusa: Umbrella rounded, up to 3 mm wide. Velum wide, muscular. Manubrium of adult can be extended beyond velum, ridged above ring of gonads, smooth distally with six dark pigment strips and six very short oral tentacles, each terminating in a nemotocyst cluster. Each tentacle with a tentacular bulb, forking slightly distally into one branch terminating in a sucker and one or two branches with clusters of nematocysts. Ocelli reddish.

Hydroid: was raised from planulae by Rees (1979b).

Distribution:
British Columbia and Puget Sound;
Haro Strait, off Vancouver Island between Oak Bay and Cadboro Bay (Mackie and Mackie 1963); Ucluelet Inlet (present work).
Pacific Ocean;
Tomales Bay, California (Hyman 1947); Bodega Harbor, California (Rees 1979b).

Notes: The histology of the gonads and suckers was briefly described by Hyman (1947). The nematocysts are desmonemes and two sizes of stenoteles (Hyman 1947, Rees 1979b).

Family Rathkeidae

Anthomedusae with four or eight radial canals; with mouth with four lips;

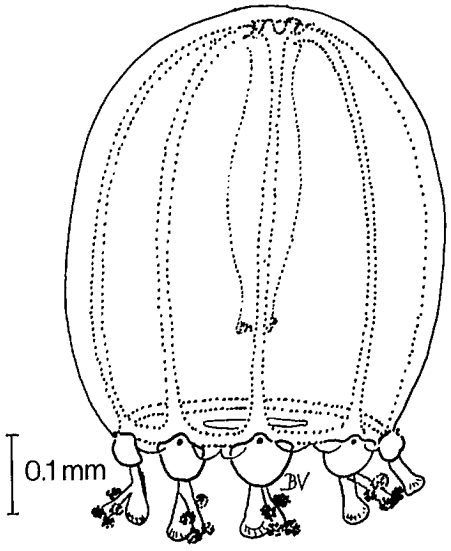


Fig. 15. *Cladonema californicum*, Ucluelet Inlet.

with or without medusa buds on stomach walls; with solid marginal tentacles arranged in eight groups; without ocelli.

Genus *Rathkea* Brandt, 1837

Rathkeidae with four (in rare abnormal specimens six or eight) radial canals; with the four corners of the mouth drawn out so as to form four oral arms with terminal (and with or without lateral) clusters of nematocysts.

Type species: *R. octopunctata* (M. Sars, 1835).

Rathkea octopunctata (M. Sars, 1835)

Cytaeis octopunctata M. Sars, 1835: 28, pl. 6; 1846: 10, pl. 4; Linko, 1899: 140.
Oceania Blumenbachii Rathke, 1835: 321.
Rathkia Blumenbachiana Brandt, 1837: 187.
Hippocrene octopunctata Forbes, 1841: 84.
Bugainvillia octopunctata Lesson, 1843: 292.
Lizzia octopunctata Forbes, 1846: 286; 1848: 64, pl. 12; L. Agassiz, 1862: 345; Böhm, 1878: 186, pl. 4, 5, 6; Bigelow, 1909b: 306, pl. 31.
Rathkia Blumenbachii L. Agassiz, 1862: 345.
Lizzia grata A. Agassiz, 1862: 99; 1865: 161; Fewkes, 1881: 142, pl. 1; Nutting, 1901a: 376; C. Hargitt, 1905: 39.
Margellium octopunctatum Haeckel, 1879: 95; Browne, 1895: 270; 1896: 477; 1900: 710; 1903: 15; 1910: 21.
Margellium gratum Haeckel, 1879: 95.

Fig. 16. *Rathkea octopunctata*, preserved specimen, 1.7 mm high, Departure Bay. Photo. M. N. Arai.

Rathkea blumenbachii Haeckel, 1879: 96; Mayer, 1910: 177; Hartlaub, 1911: 229; Neppi and Stiasny, 1913: 56, pl. 2; Bigelow, 1913: 11; 1914: 9; Hartlaub, 1917: 408; Uchida 1925: 86.

Rathkea octopunctata Haeckel, 1879: 97; Giard, 1888: 317, pl. 21; Garstang, 1894: 213; Chun, 1896: 15, pl. 2; Birulya, 1896: 340 (in part); Mayer, 1910: 177, pl. 20; Kramp, 1913a: 266; 1914: 408; Uchida, 1923: 211; Ranson, 1925: 461 (in part); Kramp, 1926: 58; Uchida, 1927a: 224; Russell, 1953: 137, pl. 7; Naumov, 1960: 212 (in part); Kramp, 1961: 72.

Lizzia blondina Wagner, 1885: 73, pl. 2 (non *L. blondina* Forbes, 1848: 67).

Rathkea octopunctata var. *grata* Mayer, 1910: 179, pl. 18; Littleford, 1939: 1070.

Lizzia shimiko Kishinouye, 1910: 25, pl. 5.

Specific characters: Eight marginal bulbs, four perradial each with two to five tentacles, four interradial each with one to three (rarely to five) tentacles depending on stage of development. In older stages, oral lips bifurcated at distal end, each branch with a terminal nematocyst knob, and with one or two pairs of lateral nematocyst clusters proximal to the bifurcation.

Description of medusa: Umbrella up to 4 mm high, 4 mm wide, somewhat globular, with rounded apical process. Stomach short, four sided, on well developed conical peduncle, not reaching umbrella margin. Smallest specimens with four simple, unbranched oral lips each terminating in a single cluster of

nematocysts; increasingly larger specimens with lips bifurcated at distal end, each branch terminating in a cluster of nematocysts, following which one or two pairs of lateral clusters appear proximal to the bifurcation and may become stalked. Finally there may be a central nematocyst cluster between the two terminal branches of the lips when fully developed. Gonads completely surrounding stomach; asexual reproduction by budding from stomach wall. Color of marginal bulbs yellow, red, brown or black, and of stomach pink, yellow, or brown.

Hydroid: The hydroid was first reared by Rees and Russell (1937). Further details were added by Werner (1956, 1958).

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (Fulton 1968); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Brentwood Bay (present work); Sooke Harbour (present work); Pacific Ocean, off Esperanza Inlet (McMurrich 1916).

Pacific Ocean;
Bodega Bay, California (Rees 1975); Bodega Harbor (Rees 1975); Yaquina Bay, Oregon (McCormick 1969); Dutch Harbour, Aleutian Islands (Bigelow 1913); South Bering Sea (Naumov 1956a); 51°33'N, 156°20'E, Okhotsk Sea off Kuril Islands (Uchida 1933); Okhotsk Sea (Naumov 1956); Akkeshi Bay, Hokkaido (Uchida 1940, Hada 1972); Mutsu Bay, off Asamushi (Uchida 1927a, 1927b, 1930, 1938b); Sagami Bay, off Misaki (Kishinouye 1910); Hamana Inlet (Kishinouye 1910); Tanabe Bay, off Seto Marine Biological Laboratory (Uchida 1927a, Yamazi 1958); Omura Bay (Kishinouye 1910); Ishikari Bay, off Oshoro, Hokkaido (Uchida 1925, 1927a, Ikeda 1974); Northern Sea of Japan (Naumov 1956a, 1960); Coasts of Korea (Uchida 1938b, 1940); Yellow Sea (Chow and Huang 1958).

Atlantic Ocean;
See Hartlaub (1911), Ranson (1925), Bigelow (1926), Fish (1925), Pinhey (1926), M'Intosh (1926), Kramp (1926, 1927, 1930), Sanderson (1930), Watson (1930), Runnström (1932), Künne (1935), Thiel (1935b), Kramp (1942), Kändler (1950), Berrill (1952), Deevey (1952), Vannucci (1956), Werner (1958, 1959), Porumb (1959), Kühl (1962, 1965, 1967), Lacroix (1963), Teissier (1965), Beyer (1968), Allwein (1968), Razouls and Thiriot (1968), Berhaut (1969), Calder (1971), Kühl (1971), Kühl and Mann (1971, 1973), Goy (1972), Boyd et al (1973) and Linkletter et al (1977) for details.

Arctic Ocean;
See Linko (1913), Kramp (1926), Bernstein (1934), Yashnov (1939), Dunbar (1942), Kramp (1942), Hand and Kan (1961), Zelickman (1966, 1972), Zelickman and Golovkin (1972), Mohammed and Grainger (1974), and Grainger and McSween (1976) for details.

Notes: *Rathkea octopunctata* has excited most interest as a species which reproduces both asexually by manubrial budding and sexually. Details of the budding have been described by Böhm (1878), Fewkes (1881), Chun (1896), Braem (1908), and Bouillon (1961). The manubrial buds have been shown to be purely ectodermal in origin in contrast to the medusa buds of the hydroid which are (as is usual) of both ectodermal and endodermal origin (Chun 1896, Braem 1908), Bouillon 1961, Bouillon and Werner 1965). The change from asexual budding to sexually reproducing individuals is primarily a response to rising temperature both in field and laboratory conditions (Kramp 1927, Berrill 1952, Werner 1956, 1958, 1961, 1962, Zelickman 1972, Skinner 1975). Sexes are usually separate but hermaphroditic specimens have been found (Kulikova 1957).

Russell (1938a) found microbasic euryteles and desmonemes in the tentacles.

Rathkea octopunctata is a nonselective polyphage which has been observed feeding on a number of animals including *Phialidium*, *Pleurobrachia*, rotifers, cladocera, copepods, various nauplii, trochophores of Aphroditidae, crab zoeae and eggs, *Sagitta*, tunicates especially *Oikopleura*, and fish larvae, especially herring, sprat, flatfishes and capelin (Lebour 1922, 1923, Hollowday 1947, Plotnikova 1961, Kühl 1962, Sveshnikov 1963, Zelickman et al 1969). Plotnikova (1961) lists ingestion and digestion times for various prey and describes storage of food substances for up to 10 days. Zelickman et al (1969) suggest that in areas of high population density, the larger food may be depleted and the medusae may be able to utilize bacteria, protozoa or dissolved organic matter. Ikeda (1974) found a respiratory rate of 3.02 µL O_2/(mg dry wt . h) at 14.5-17.5°C.

Rathkea octopunctata is a eurythermal, euryhaline species. Penetration into estuaries has been described in most detail by Kühl and Mann in northern Germany (Kühl 1962, 1965, 1967, 1971, Kühl and Mann 1971, 1973). It also may survive in highly polluted water, as for example in Oslo fjord (Beyer 1968). Local populations forming aggregations as dense as 250 medusae per 1 m^3 in sheltered bays or fjords have been described in most detail in the Barents Sea area (Zelickman 1969, 1972, Zelickman et al 1969). Such aggregations have not yet been recorded in the present research area, although the species is very common in Departure Bay in March and April.

Family Bougainvilliidae

Anthomedusae with simple tubular mouth with simple or dichotomously branching oral tentacles inserted above the mouth opening; with four radial canals; gonads interradial or adradial, or completely surrounding stomach; with two, four or more solitary marginal tentacles, or with 4, 8 or 16 large marginal bulbs each with a group of solid tentacles; with or without ocelli. Hydroids with a single whorl of filiform tentacles.

Genus *Bougainvillia* Lesson, 1836

Bougainvilliidae, with four perradial, dichotomously branching oral tentacles, each branch terminating in a nematocyst knob; with four perradial clusters of marginal tentacles each cluster arising from a marginal bulb, the tentacles of each cluster being all of one kind and similar in structure, gonads on stomach interradial or adradial, rarely perradial.

Type species: *B. macloviana* Lesson, 1836.

Dicussion of genus: The genus *Bougainvillia* is represented in British Columbia by two species, *B. multitentaculata* Foerster and *B. superciliaris* (L. Agassiz). Mackie and Mackie (1963) reported *B. principis* but their specimens have been reexamined and referred to *B. multitentaculata* (see below). *B. muscoides* was reported (as *B. nordgaardi*) from one specimen by Foerster (1923). This specimen was found in the collection of the Pacific Biological Station, Nanaimo and rechecked. We could not confirm the identification of

B. muscoides. The specimen is in very poor condition but is probably *B. superciliaris*. Therefore we agree with Edwards (1964) that the record of *B. muscoides* for the Pacific remains doubtful until it is found again.

Bougainvillia multitentaculata Foerster, 1923

Bougainvillia multitentaculata Foerster, 1923: 27; Vannucci and Rees, 1961: 73.
Bougainvillia principis Mackie and Mackie, 1963: 68 (non *Margelis principis* Steenstrup, in Lutken 1850: 35).

Specific characters: Gonads interradial, sometimes with interradial furrow. Medusa with up to 50 tentacles per tentacle bulb.

Description of medusa: Umbrella up to 10 mm high and wide, rounded at the top, with thick mesogloea. Very broad peduncle indicated in some specimens, not in all. Oral tentacles branch dichotomously 6-7 times. Gonads interradial, often with an adradial concentration but always connected interradially. Marginal tentacle bulbs shape of deeply cleft, wide, inverted V; each with up to 50, rarely to 60, tentacles per tentacle bulb, arranged on bulb in a zigzag row. Red-brown ocellus at base of each tentacle in newly preserved specimens.

Hydroid: not known.

Discussion of taxonomy: A portion of the collection from Banks Island on which Foerster (1923) based his original description of *B. multitentaculata* was obtained from the University of British Columbia. Comparison of the specimens which Mackie and Mackie (1963) designated as *B. principis* and deposited in the National Museum of Natural Sciences, Ottawa (No. 239) showed that they also belong to *B. multitentaculata*. All these specimens possess four broad interradial gonads rather than the eight adradial swollen gonads typical of *B. principis*. Young *B. superciliaris* and *B. multitentaculata* are very similar so that younger specimens can be easily misidentified.

Distribution:
British Columbia and Puget Sound;
Deep Bay (present work); Departure Bay (Brinckmann-Voss 1974; present work); Brentwood Bay, Saanich Inlet (present work); Friday Harbor (Mackie and Mackie 1963, Szollosi 1969; Singla 1972); Sooke Harbour (present work); Ucluelet Inlet (present work); Hecate Strait off Banks Island (Foerster 1923; Vannucci and Rees 1961; present work); Prince Rupert (present work).

Notes: Szollosi (1969) has described the unusual eggs of *Bougainvillia multitentaculata* which are spawned with an envelope consisting of a single layer of cnidocytes. Gladfelter (1973) analyzed the actions of muscle and mesogloea in swimming and turning. Singla (1972, 1974) described (as *B. principis*) the structure of the ocelli and the electrical events accompanying the burst of swimming which follows turning off a blue-green light.

B. multitentaculata has been collected May to July in Friday Harbor and British Columbia waters.

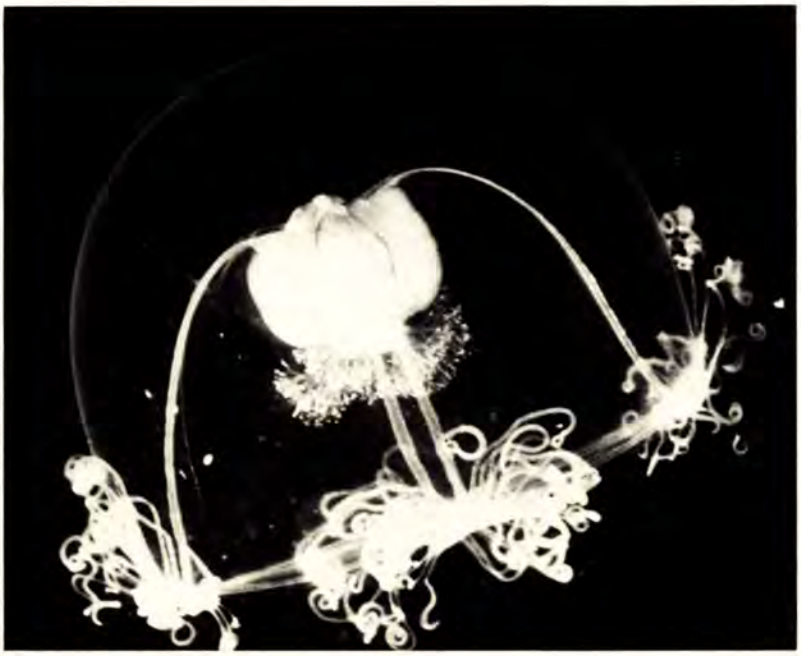


Fig. 17. *Bougainvillia multitentaculata*, live specimen, 9.1 mm high, Departure Bay. Photo M. N. Arai.

Bougainvillia superciliaris (L. Agassiz, 1849)

Hippocrene Bugainvillii Brandt, 1835: 39 (in part, non *Cyanea Bugainvillii* Lesson, 1830: 118); Brandt, 1838: 393, pl. 20 (in part).
Hippocrene superciliaris L. Agassiz, 1849: 273, pl. 1-3; Haeckel, 1879: 92; Birulya, 1896: 339.
Margelis superciliaris Mörch, 1857: 24.
Bougainvillia superciliaris L. Agassiz, 1862: 291, 344 (in part, medusa non hydroid); A. Agassiz, 1865: 153 (in part, medusa non hydroid); Hartlaub, 1897: 466, pl. 16 (in part); Hartlaub, 1909: 464 (in part); Mayer, 1910: 162, pl. 17 (in part); Hartlaub, 1911: 171 (in part, non hydroid and young medusa); Foerster, 1923: 28 (in part); Kramp, 1926: 44 (in part); 1930: 13 (in part); Dunbar, 1942: 73; Kramp, 1942: 29; Russell, 1953: 169 (in part); Naumov, 1960: 197 (in part); Uchida and Nagao, 1960b: 249; Hand and Kan, 1961: 7; Werner, 1961: 206; Vannucci and Rees, 1961: 85 (in part); Edwards, 1966a: 136; Kramp, 1968c: 32 (in part).
Bougainvillia Mertensii L. Agassiz 1862: 344; A. Agassiz 1865: 152 (in part, medusa non hydroid).
Bougainvillia paradoxa Mereschkowsky, 1878: 323; 1879: 177, pl. 20.
Hippocrene Mertensii Haeckel, 1879: 92.
Bougainvillea superciliaris Wagner, 1885: 73, pl. 2; Bigelow, 1909b: 305, pl. 31; 1913: 9.
Hippocrene (Bougainvillia) superciliaris Maas, 1893: 69; 1904a: 9, pl. 1.
Bougainvillia bougainvillei Hartlaub, 1911: 159 (in part); Foerster, 1923: 27 (in part); Kramp, 1968c: 34 (in part).

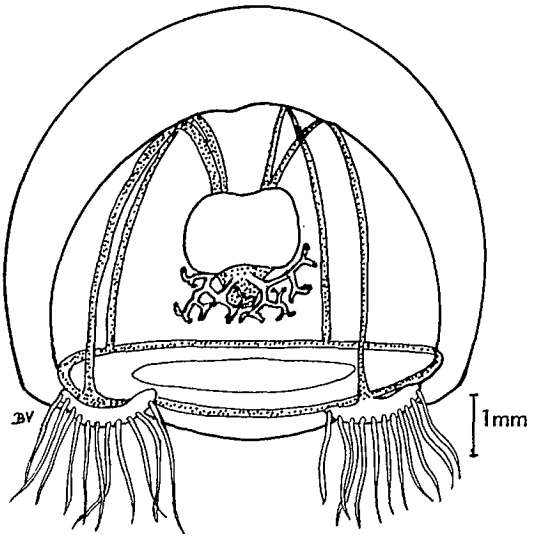


Fig. 18. *Bougainvillia superciliaris*. Brentwood Bay.

Specific characters: Peduncle present. Gonads interradial. Usually 11 to 15 tentacles on each marginal bulb.

Description of medusa: Umbrella almost globular, up to 12 mm high, with thick mesogloea. Stomach short, with broad base, cruciform in section. Well developed broad peduncle. Oral tentacles branch dichotomously, usually 4-5 (rarely 6-7) times. Gonads interradial, planulae develop in situ within capsules. Marginal tentacle bulbs crescent shaped to heart shaped, less than half as wide as the interradial space; with 11-15 (up to 22) tentacles per tentacle bulb. Ocelli large, one on base of each tentacle. Color of living specimens, stomach brown to reddish brown; marginal bulbs chestnut brown; ocelli reddish brown to black.

Hydroid: Described by Uchida and Nagao (1960b), Werner (1961), and Nagao (1964), (following incorrect descriptions by earlier authors). Gerd (1892) described egg segmentation.

Discussion of taxonomy: Murbach and Shearer (1903) reported a single poorly preserved specimen of this species from Victoria Harbour (as *Hippocrene Mertensii*). The description is too incomplete for identification, but the specimen was probably not *Bougainvillia superciliaris* since it lacked a peduncle.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (L. Agassiz 1862; A. Agassiz 1865); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Brentwood Bay (present work); Port Townsend Harbor (A. Agassiz 1865).

Pacific Ocean;
San Francisco Harbor (A. Agassiz 1865); off Attu Island, Aleutian Islands (Bigelow 1913); Bering Sea, off St. Matthew Island (Brandt 1835; 1838); Okhotsk Sea (Naumov 1960); Akkeshi Bay, Hokkaido (Uchida and Nagao 1960b; Nagao 1964); Yellow Sea (Chow and Huang 1958).

Atlantic Ocean;
See Hartlaub (1911), Kramp (1914, 1926, 1927, 1939, 1942, 1948, 1955a), Fish (1925), Bigelow (1926), Dunbar (1942), Künne (1952), Werner (1962), Edwards (1968), Russell (1970) and Skinner (1975) for details.

Arctic Ocean;
See Hartlaub (1911), Kramp, (1914, 1926, 1942), Dunbar (1942), Vibe (1950), Hand and Kan (1961), Grainger (1962), Sveshnikov (1963), Zelickman (1966, 1972), Zelickman and Golovkin (1972), and Mohammed and Grainger (1974) for details.

Notes: Linko (1900) described the histology of the ocelli of *Bougainvillia superciliaris* and associated nerve cells. The medusae use the oral tentacles to capture herring larvae, euphausid nauplii and polychaete trochophores in preference to various other crustacea (Sveshnikov 1963, Fraser 1969). Werner (1961, 1962) described the restriction of the North Sea population to low temperatures, especially for budding of medusae from the polyp in falling temperatures below 7-5°C, both in culture and as deduced from collecting records. Zelickman (1972) has questioned this conclusion for the Barents Sea population. Werner (1961) also noted two types of nematocysts present (desmonemes and microbasic euryteles) and that the chromosome number is 2n=30.

In the Strait of Georgia region specimens have been collected March to May.

Family Pandeidae

Anthomedusae with apical projection in most genera. Four-cornered mouth (or eight in *Octotiara*) with more or less folded or crenulated lips, without nematocyst clusters. Four radial canals (except eight of *Octotiara*), either smooth and jagged. Gonads situated adradially or interradially on stomach wall, rarely on perradii on subumbrella. Tentacles filiform with marginal bulb. Hydroids, where known, with single whorl of filiform tentacles.

Discussion of family: The Pandeidae are a family in which species with diverging morphological characters are lumped together, because they do not fit in the other families, and there is hesitancy to establish too many new families. As an intermediate solution, the establishment of subfamilies is followed here. Russell (1953) proposed a division into subfamilies based on number of tentacles. The present division is based on number of tentacles and presence or absence of a peduncle. The Pandeidae would thus be divided into four subfamilies:

With more or less conspicuous peduncle	Stomotocinae
Without conspicuous peduncle	
not more than two tentacles	Amphineminae
four tentacles	Protiarinae
six or more tentacles	Pandeinae

(These definitions apply for the adult medusae only. Newly liberated Pandeidae usually have two tentacles only and are nearly impossible to identify).

The genus *Halimedusa*, previously regarded as a Pandeid (Kramp 1961), should be placed in a separate family because of its mouth structure and grouping of marginal tentacles. The genus *Endocrypta* is invalid as the adult medusa belongs to the genus *Bythotiara*, family Calycopsidae.

Subfamily Stomotocinae

Pandeidae with more or less conspicuous peduncle.

Genus *Stomotoca* A. Agassiz, 1862

Stomotocinae with two opposite, perradial tentacles and numerous marginal warts. Stomach on broad peduncle, extending beyond bell margin. Gonads in eight adradial rows, well separated.

Type species: *S. atra* A. Agassiz, 1862.

Stomotoca atra A. Agassiz, 1862

Stomotoca atra A. Agassiz, (in L. Agassiz) 1862: 347; 1865: 168; Bigelow, 1909a: 201; Vanhöffen, 1913: 14, pl. 2 (in part); Bigelow, 1918: 370; Foerster, 1923: 239.

Specific characters: Bell-shaped. Mouth-rim smooth, not crenulated; gonads simple, transverse folds.

Description of medusa: Bell up to 35 mm high, 39 mm diameter. Usually about 20 small rudimentary tentacles in each quadrant; rarely up to 30. Living specimens, manubrium white or light yellow, gonads dark brown, tentacles light brown.

Hydroid: The hydroid of this species has not been raised beyond the planula (Strong 1925), although the fine structure of the first cleavage furrow has been described (Schroeder 1968).

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (A. Agassiz (in L. Agassiz) 1862; 1865); Deep Bay (present work); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Nanaimo Region (Fraser 1932); Forwood Channel (present work); Ladysmith Harbour (present work); Long Harbor, Saltspring Island (present work); Cowichan Bay (present work); Brentwood Bay (present work); San Juan Archipelago (Fraser 1932); Friday Harbor (Child 1918; Bovard and Osterud 1918; Harvey 1921; Foerster 1923; Strong 1925; Hyman 1940; Davenport and Nicol 1955; Mackie and Mackie 1963; Lenhoff 1964; Schroeder 1968; Mackie and Singla 1975); Rosario Strait (Agassiz 1865); Puget Sound, near Port Townsend (Agassiz 1865); Victoria Harbour (present work); Sooke Harbour (present work); Ucluelet Inlet (present

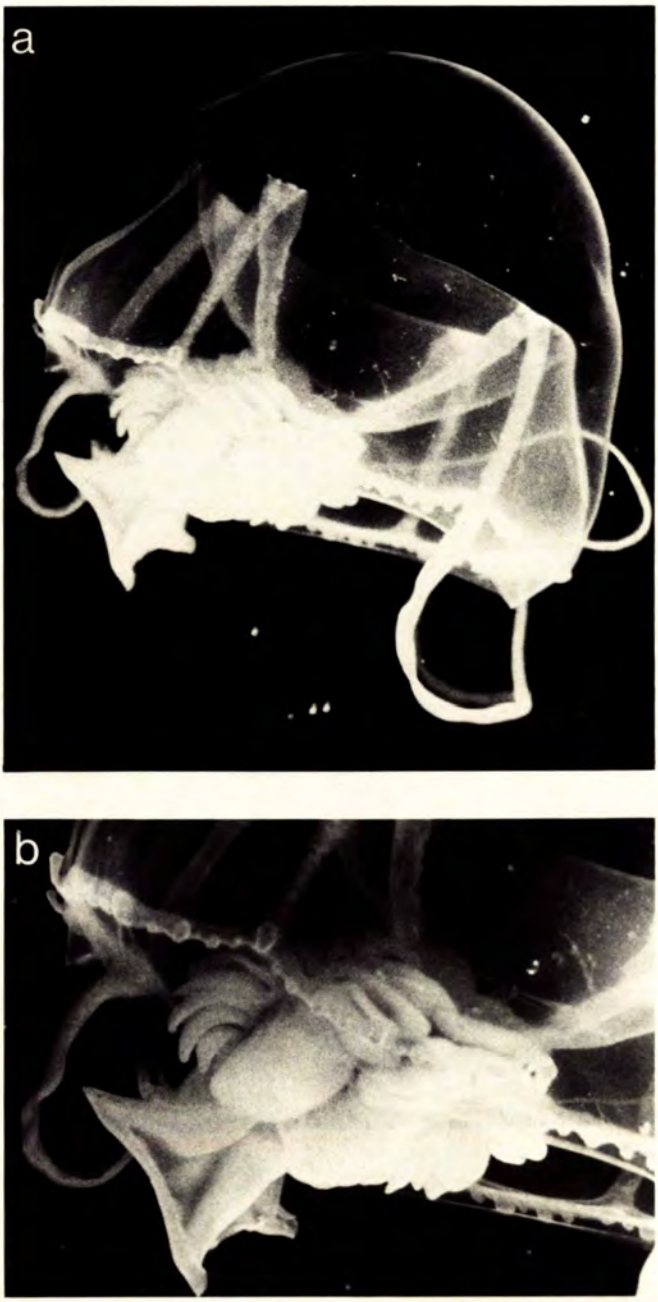


Fig. 19. *Stomotoca atra*, preserved specimen, 14.7 mm high, Departure Bay. a. whole animal. b. detail of gonads. Photos M. N. Arai.

work); Kyuquot Sound (Brinckmann-Voss 1974); Laredo Channel (Foerster 1923; Brinckmann-Voss 1974); Houston Stewart Channel (Brinckmann-Voss 1974); Ikeda Cove, Moresby Island (Foerster 1923; Brinckmann-Voss 1974); Masset Harbour (present work).

Indian Ocean;
See Navas (1971) for details.

Notes: *Stomotoca atra* is weakly luminescent (Harvey 1921; Davenport and Nicol 1955). It is an active swimmer with marginal creases and strong swimming muscle (Gladfelter 1973). Other medusae, such as *Phialidium*, are caught by bending the manubrium and grasping the food with the lips (Hyman 1940). Extracts of mesogloea of *Aequorea*, *Halistaura*, *Sarsia*, or *Phialidium* and even the presence of a specimen of *Aequorea* in the same dish cause increased activity of the manubrium and strong contraction of the velum, resulting in temporary cessation of swimming (Lenhoff 1964). Mackie and Singla (1975) identified nerves and muscles involved in swimming, crumpling (protective involution due to contraction of radial muscles), and tentacle shortening and pointing (unilateral reciprocal flexions of the manubrium and margin). Mackie (1975) used suction electrodes to record the electrical events accompanying these behavior patterns and noted that swimming was inhibited by crumpling. Schwab (1977) investigated the electrical events resulting from stimulation with *Aequorea* mesogloeal extract and found both crumpling and pointing responses.

King and Packard (1975) found a low ratio of respiratory oxygen consumption to respiratory electron transport activity.

In British Columbia waters *Stomotoca atra* is common May to July, and has been collected April to September.

Subfamily Pandeinae

Pandeid medusae with bell-shaped umbrella with round or pointed apical projection in most genera. Without conspicuous peduncle. Gonads developing on adradial sides of stomach, either forming interradial bridges or remaining separate in adult stages, with or without isolated interradial pits. Six or more marginal tentacles with tapering conical or round marginal bulbs.

Genus *Catablema*

Pandeinae of rather broad shape with dome-like apical projection often as high as bell in living specimens; however often damaged and collapsed in preserved specimens. Stomach with large broad base; with upper part of stomach attached for various lengths to radial canals (to form structures often called "mesenteries"). Radial canals broad, denticulate. Gonads adradial with interradial connection; with irregular or parallel folds which run in either vertical or perpendicular direction.

Type species: *C. vesicarium* (A. Agassiz, 1862).

Catablema multicirrata Kishinouye, 1910

Catablema multicirrata Kishinouye, 1910: 24; Bigelow, 1913: 19, pl. 1; Kramp, 1926: 91, pl. 2; Uchida, 1927a: 213; 1933: 130; 1940: 286; 1969: 286.
Catablema eurystoma Kramp, 1913a: 267 (in part, non *Catablema eurystoma* Haeckel 1879: 64).
Perigonimus (=Catablema) multicirrata Naumov, 1956a: 37.
Perigonimus multicirratus Naumov, 1960: 187.
Catablema multicirratum Kramp, 1961: 96.

Specific characters: Adult specimens with at least 80 tentacles.

Description of medusa: Umbrella diameter up to 60 mm, rarely to 80 mm; height up to 30 mm without apical projection. Huge dome-like apical projection almost as high as bell. Stomach with very broad, quadrangular base, gonadal folds running mostly vertical. Adult specimens with up to 160 tentacles, rarely to 240 (80-126 for B.C. specimens); without marginal bulbs between tentacles in adult specimens. Stomach and marginal bulbs light orange in living specimens.

Hydroid: not known.

Fig. 20. *Catablema multicirrata*, live specimen, 32 mm high, Bamfield Inlet. Photo M. N. Arai.

Distribution:

British Columbia and Puget Sound;
Ladysmith Harbour (present work); Bamfield Inlet (present work; No. NMCICI 980-32 National Museum of Natural Sciences, Ottawa, Canada).

Pacific Ocean;
Prince William Sound, off Orca, Alaska (Bigelow 1913); Dutch Harbor, Unalaska Island (Bigelow 1913); Pacific Ocean, off Paramushir Island, Kuril Islands (Kishinouye 1910); 51°52'N, 156°17'E, Okhotsk Sea off Kuril Islands (Uchida 1933); Akkeshi Bay, Hokkaido (Uchida 1940); Pacific Ocean, off Kushiro, Hokkaido (Uchida 1927a); Mutsu Bay (Uchida 1930; 1938b); Busse Lagoon, Aniva Bay (Zelickman 1976).

Atlantic Ocean;
See Kramp (1942) for details.

Arctic Ocean;
See Kramp (1942) and Uchida (1969) for details.

Catablema nodulosa comb. nov.

Catablema vesicarium var. *nodulosa* Bigelow, 1913: 17, pl. 1.
Catablema vesicarium Hartlaub, 1914: 315 (in part, non *Catablema vesicarium* Haeckel, 1879: 64); Foerster, 1923: 242; Kramp, 1926: 87 (in part).
Catablema vesicaria Brinckmann-Voss, 1974; (non *Turris vesicaria* A. Agassiz, 1862: 97).

Specific characters: With 8 to 16, rarely 32 tentacles.

Description of medusa: Umbrella diameter not more than 20 mm in living specimens, gonads with perpendicular to vertical folds, with one to three marginal bulbs between adjoining tentacles, gonads and manubrium gold-brown or peach color in living specimens.

Hydroid: not known.

Discussion of taxonomy: Hartlaub (1914) united *C. vesicarium* and *C. vesicarium* var. *nodulosa*. However numerous specimens found in Brentwood Bay with very little intraspecific variation clearly show differences in tentacle number and maximum bell size between *C. vesicarium* sensu strictu and *C. vesicarium* var. *nodulosa*, the latter being the species found in British Columbia. The latter is therefore considered a separate species and designated *C. nodulosa* n. comb. The shape of gonad folds is very variable and should not be used as a character to distinguish the species. *C. vesicarium* is apparently an Atlantic and Arctic species and holds morphologically an intermediate position between *C. nodulosa* and *C. multicirrata*. Bigelow found *C. nodulosa* in Dutch Harbor, Alaska. It is not possible from published reports to determine whether *Perigonimus vesicarius* of Naumov (1956a, 1960) collected in the Sea of Okhotsk is *C. vesicarium* or *C. nodulosa*.

Distribution:

British Columbia and Puget Sound;
Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Dodd Narrows (Foerster 1923); Cowichan Bay (present work); Brentwood Bay, Saanich Inlet (present work); Friday Harbor (present work).

Fig. 21. *Catablema nodulosa*, live specimen, 11.5 mm high, Brentwood Bay. Photo M. N. Arai.

Pacific Ocean;
Dutch Harbor, Unalaska Island (Bigelow 1913).

Genus *Halitholus* Hartlaub, 1914

Pandeinae with large, dome-like apical projection. Manubrium not round - rather square in cross-section; radial canals connected with stomach wall only in upper part or entering from above (i.e. mesenteries absent); radial canals smooth or slightly jagged. Eight adradial folded gonads with interradial smooth connections. Eight or more tentacles.

Type species: *H. pauper* Hartlaub, 1914.

Halitholus pauper Hartlaub, 1914

Tiara conifera Levinsen, 1893: 144 (in part, non *Tiara conifera* Haeckel,

1879: 59).
Turris conifera Mayer, 1910: 128 (in part).
Halitholus pauper Hartlaub, 1914: 272; Kramp, 1914: 413; Kramp, 1926: 71, pl. 2; Uchida, 1933: 128; 1940: 285; Kramp, 1942: 37.
Tiara pileata Kramp 1913a: 266 (in part, non *Medusa pileata* Forskal, 1775: 110).
Catablema campanula Kramp 1913a: 267 (in part, non *Catablema campanula* Haeckel, 1879: 63); 1914: 415 (in part).
Catablema eurystoma Kramp 1913a: 267 (in part, non *Catablema eurystoma* Haeckel, 1879: 64).
Perigonimus (=Halitholus) pauper Naumov 1956a: 37.

Specific characters: Radial canals jagged. Adradial gonads, with 4-6 perradially directed folds, with conspicuous interradial connection. Marginal bulbs round, not laterally compressed. Ocelli present.

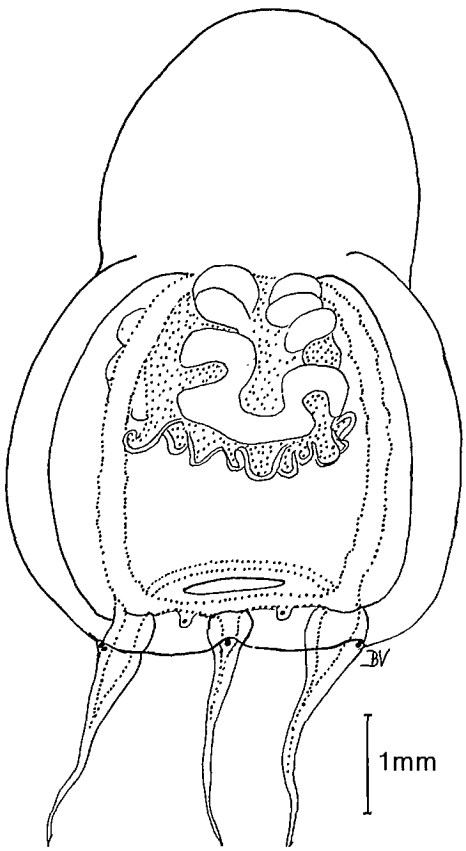


Fig. 22. *Halitholus pauper*, Deep Bay.

Description of medusa: Umbrella up to 12 mm high, 9 mm wide, with round apical projection only about half of the height of the exumbrella. Stomach flask shaped; radial canals entering stomach from aboral side, leaving no trace of mesenteries. Lips moderately crenulated. Eight tentacles (four perradial and four interradial), with ocelli, with one to three rudimentary bulbs between each two of them. Ocelli pink or reddish-orange, centre part of gonadal folds orange or reddish-orange in living specimens.

Hydroid: not known.

Discussion of taxonomy: Foerster (1923) reported *Halitholus pauper* from Departure Bay. The description and figure do not correspond to *H. pauper* since the radial canals were smooth and more than eight tentacles were appearing. The description is not sufficiently detailed to allow definite referral to another species.

Distribution:

British Columbia and Puget Sound;
Deep Bay (present work); Departure Bay (present work); Pacific Ocean off Ucluelet (present work).

Pacific Ocean;
51°52'N, 156°17'E, Okhotsk Sea off Kuril Islands (Uchida 1933); Akkeshi Bay, Hokkaido (Uchida 1940; Hada 1972).

Atlantic Ocean;
See Kramp (1926, 1942, 1943), Dunbar (1942) and Shih (1977) for details.

Arctic Ocean;
See Kramp (1926, 1942), Dunbar (1942), and Grainger and McSween (1976) for details.

Halitholus species I.

Leuckartiara octona Mackie and Mackie, 1963: 68 (in part; non *Geryonia octona* Fleming, 1823: 298).
Halitholus sp. Brinckmann-Voss, 1974: 12 (Acc. No. 75, 76, 77).
Neoturris pileata Brinckmann-Voss, 1974: 88 (in part; Acc. No. 88) (non *Medusa pileata* Forskal, 1775: 110).

Specific characters: Radial canals smooth. Adradial gonads, with 2-6 perradially directed folds, with indistinct interradial connection. Marginal bulbs triangular. Ocelli present.

Description of medusa: Umbrella with apical projection of varying size; up to 10 mm high (exumbrella 6 mm, apical projection 4 mm), 5 mm wide. Stomach with fairly straight sides, often with 4 definite perradial ridges. Subumbrella extending in four pouch-like apical projections in some specimens. Lips folded or only slightly curved. Four perradial tentacles, with one to three interradial tentacles between each two perradial tentacles and with one or two rudimentary marginal bulbs between each 2 adjacent tentacles. Short abaxial spurs may be present in perradial (=oldest) tentacles. Color of living specimens; center of folds and interradial connections of gonads bright red, ocelli with dark red or orange centers tapering off to lighter color on their periphery, fading soon after preservation.

Fig. 23. *Halitholus* sp. I, preserved specimen, 6.5 mm high, Departure Bay. Photo. M. N. Arai.

Hydroid: With single whorl of filiform tentacles (Brinckmann-Voss, unpublished).

Discussion of taxonomy: This species looks similar to an immature *Leuckartiara nobilis*. However, as it lacks mesenteries it is not a *Leuckartiara*. The attachment of the perradial sides of the stomach to the subumbrella gives the impression of small mesenteries in some specimens. Mackie and Mackie (1963) reported *L. octona* from Friday Harbor. Rechecking of this material, deposited in the National Museum of Natural Sciences, Ottawa (No. 194), showed that it included one specimen of this species of *Halitholus*.

The variation in this form is very wide even within a single collection. Analysis of anatomical characters indicate the probable presence of two similar species, the present one and *Halitholus* species II. However, there may be only one species or more than two species involved. Extensive rearing experi-

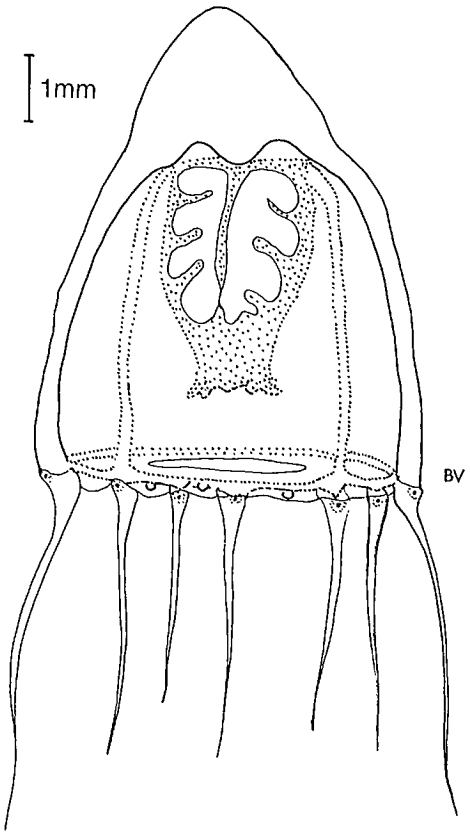


Fig. 24. *Halitholus* sp. I., Departure Bay.

ments will be necessary to fully clarify the speciation. Such a study has been begun and will be published elsewhere at a future date.

Distribution:
British Columbia and Puget Sound;
Departure Bay (Brinckmann-Voss 1974; present work); Stuart Channel (present work); Brentwood Bay (present work); Friday Harbor (Mackie and Mackie 1963).

Halitholus species II

Neoturris pelagica Foerster, 1923: 25, pl. II, Fig. 4. (non *Turris pelagica* Agassiz and Mayer 1902: 142).
Leuckartiara octona Brinckmann-Voss, 1974 (Acc. No. 78) (non *Geryonia octona* Fleming, 1823: 298).
Halitholus pelagica Brinckmann-Voss, 1974 (Acc. No. 85).

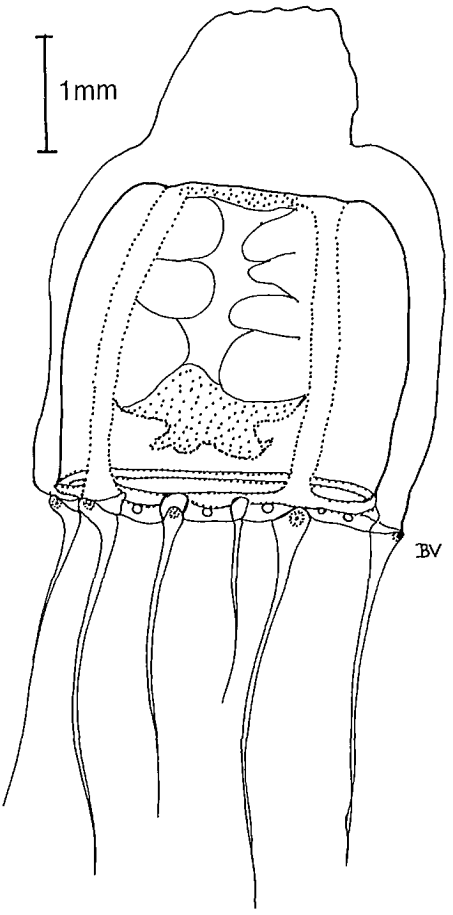


Fig. 25. *Halitholus* sp. II., Departure Bay.

Specific characters: Radial canals smooth or slightly jagged. Eight rather bulbous adradial gonads occupying more than two-thirds of the manubrium, with 3-4 interradially directed folds, with interradial connection not as thick as adradial parts. Marginal bulbs laterally compressed. Ocelli present.

Description of medusa: Umbrella (including apical projection) 4.5 - 6 mm high, 3-4 mm wide (in alcohol preserved specimens). Manubrium occupying about two-thirds of subumbrella. Stomach flask shaped. Lips faintly crenulated. Eight to 10 tentacles with one or two rudimentary marginal bulbs between each two of them.

Hydroid: not known.

Discussion of taxonomy: This species may be only a variation of *Halitholus* species I but has been provisionally kept separate because of the larger gonads until more material can be obtained. This species was described and figured by Foerster (1923) as *Neoturris pelagica*. His specimen was re-examined by Brinckmann-Voss (1974) (Acc. No. 85). It was well preserved and it was found that the "*Neoturris* pits" were actually eggs.

Distribution:
British Columbia and Puget Sound;
Departure Bay (Foerster 1923; Brinckmann-Voss 1974); Dodds Narrows (Brinckmann-Voss 1974); Cowichan Bay (present work); Brentwood Bay (present work).

Genus *Leuckartiara* Hartlaub, 1914

Pandeinae with apical projection of varying shape and extent. With upper part of stomach attached for various lengths to radial canals (to form structures often called "mesenteries"). Folded adradial gonads with interradial connections which vary greatly in extent. Six to 48 marginal tentacles; marginal bulbs with ocelli.

Type species: *L. octona* (Fleming, 1823).

Discussion of genus: The genus *Leuckartiara* is represented in British Columbia by *Leuckartiara nobilis* Hartlaub, 1914, *L. foersteri*, and a new species which is provisionally referred to as *Leuckartiara* species. *Leuckartiara breviconis* is transferred to the genus *Neoturris* (see discussion of species). *Leuckartiara octona* has not been found present. Foerster (1923, p. 240, pl. 1) reports and figures several specimens he identified as *L. octona* stating, "The specimens resemble so closely those figured by Hartlaub that there can be no doubt as to their identity." However, the figure does not show mesenteries, i.e., it is either a very young *Leuckartiara* which could not be identified at the specific level, or an adult specimen of another genus. Mackie and Mackie (1963) reported *L. octona* but their specimens have been reexamined and referred to another species of *Leuckartiara* and to *Halitholus* (see under appropriate designations).

The species of *Leuckartiara* show clear-cut differences in some specimens but gliding characters in others. The variation is so great that it is often extremely difficult to distinguish the species and even to distinguish them from *Halitholus*, a distinction that depends only on the length of the mesenteries. (A paper dealing with the variations and their possible causes in the family Pandeidae is in preparation).

Leuckartiara foersteri Arai and Brinckmann-Voss, 1980

Leuckartiara octona Brinckmann-Voss, 1974 (Acc. No. 74, 79) (non *Geryonia octona* Fleming, 1823: 298).
Leuckartiara foersteri Arai and Brinckmann-Voss, 1980: In press.

Specific characters: Marginal tentacles without abaxial spurs. Gonads with even parallel folds, situated on adradial sides of cross-shaped stomach with no distinct interradial connection.

Fig. 26. *Leuckartiara foersteri*, immature live specimen, 7.8 mm high, Departure Bay. Photo. M. N. Arai.

Description of adult: Umbrella bell-shaped; bell approximately 5 mm high, 7 mm wide, with dome shaped apical projection up to same height as bell. Stomach cross-shaped seen from aboral side of medusa; lower part much narrower than upper part; mesenteries up to approximately one-third subumbrella length. Folds of gonads vary from the typical angle of 45° to main axis of the animal to a more downward direction. Lips slightly crenulated, drawn out in four perradial corners. Radial canals wavy or smooth. Four perradial, 4 interradial, and 1-8 adradial tentacles with 1-3 marginal bulbs between each two adjacent tentacles. Abaxial ocelli orange; gonads reddish; depth of coloration (as in other pandeidae) dependent on length of preservation especially in alcohol.

Hydroid: not known.

Distribution:

British Columbia and Puget Sound;
Deep Bay (present work); Departure Bay (Arai and Brinckmann-Voss 1980; present

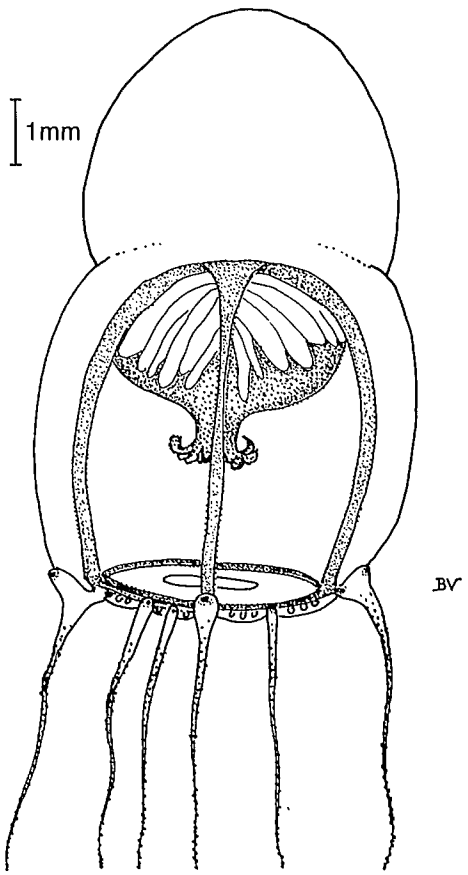


Fig. 27. *Leuckartiara foersteri*, Ladysmith Harbour.

work); Stuart Channel (Arai and Brinckmann-Voss 1980); Ladysmith Harbour (present work); Brentwood Bay (Arai and Brinckmann-Voss 1980).

Notes: The nematocysts are microbasic mastigophores and microbasic euryteles (Arai and Brinckmann-Voss 1980). The species has been collected April to September in Departure Bay.

Leuckartiara nobilis Hartlaub, 1914

Tiara pileata var. *coccinea* Haeckel, 1879: 58, pl. iii, Fig. 6.
Tiara pileata Browne, 1900: 712 (in part; non *Medusa pileata* Forskal, 1775).
Leuckartiara nobilis Hartlaub 1914: 308; Foerster 1923: 24, pl. 1; Kramp 1926: 83, pl. 2; Ranson 1936: 77; Kramp 1965a: 31.

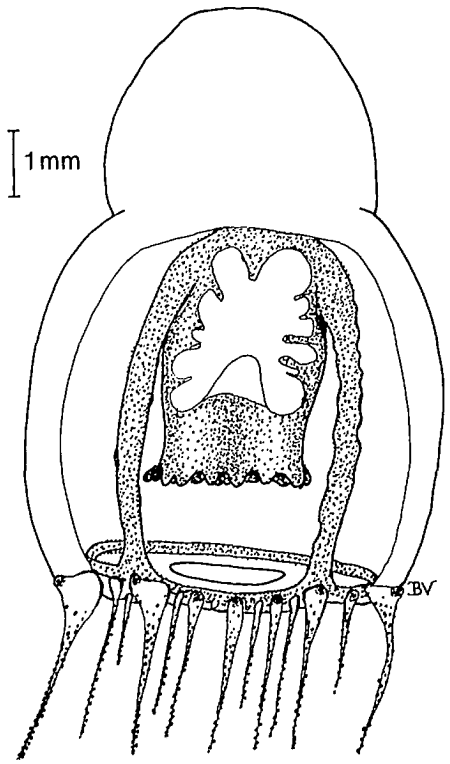


Fig. 28. *Leuckartiara nobilis*, Naples.

Specific Characters: Marginal tentacles without definite abaxial spurs; fewer marginal bulbs than tentacles. Adradial gonads deeply folded with interradial bridge, folds radiating from interradial connections.

Description of adult: Medusae deep bell-shaped with apical projection; height of bell to 22 mm (most specimens over 10 mm); diameter to 20 mm; height of apical projection not exceeding 1/3 height of bell. Stomach flask-shaped; mesenteries approximately 1/2 length of stomach. Lips complexly folded. Up to 40 tentacles with very few marginal bulbs between them; no or faintly developed abaxial spurs. Marginal tentacle bulbs with abaxial ocelli. In living specimens manubrium and gonads dark red; ocelli dark red or purple; tentacle bulbs and tentacles pale yellow.

Hydroid: not known.

Discussion of taxonomy: It is probable that the same Laredo Channel specimens were reported by Foerster (1923) and Brinckmann-Voss (1974), as the specimens identified by her had been originally identified by him.

Distribution:

British Columbia and Puget Sound;

Ucluelet Inlet (present work); Laredo Channel (Foerster 1923; Brinckmann-Voss 1974; No. NMCICI 980-33 National Museum of Natural Sciences, Ottawa, Canada).

Pacific Ocean;

30-32°N, 135-146°E, Pacific Ocean southeast of Japan (Kramp 1965a).

Atlantic Ocean;

See Kramp (1926, 1927, 1955a), Ranson (1936), Petersen (1957) and Goy (1972) for details.

Notes: Fraser (1969) showed *L. nobilis* to be a voracious feeder even on animals considerably larger than itself. In the laboratory it caught fish larvae, copepods, amphipods, *Aglantha*, *Sarsia*, and *Clione*.

Leuckartiara species

Leuckartiara octona Mackie and Mackie, 1963; 68 (in part; non *Geryonia octona* Fleming, 1823: 298).

Specific characters: Marginal tentacles with very long abaxial "spurs". Adradial gonads in horizontal folds, without distinct interradial connections.

Description of adults: Height of bell 8-10 mm; diameter 5-7 mm; with pointed apical projection about 1/3 height of medusa. Stomach flask shaped; mesenteries 1/3 or less stomach length. Manubrium extending 1/2 to 1/3 of subumbrella. Adradial gonads consisting of 5-7 prominent horizontal ribs connected by a smooth part on the interradial portion of stomach not showing distinct gonadal material. Lips faintly crenulated. Twelve to 15 marginal tentacles with 1-2 rudimentary marginal bulbs between each two adjacent tentacles. Abaxial spurs lengthening to longitudinal ribs; up to 1/3 of exumbrella in perradial tentacles.

Hydroid: not known.

Discussion of taxonomy: Mackie and Mackie (1963) reported *L. octona* from Friday Harbor. Mackie and Mackie mentioned, however, that the nematocyst measurements did not correspond with the ones for *L. octona* given by Russell (1938a). Rechecking the Friday Harbor material, deposited in the National Museum of Natural Sciences, Ottawa (No. 194), revealed that it is not *L. octona* but includes three specimens of the present species of *Leuckartiara* and one specimen of *Halitholus*. The present species is distinguished from *L. octona* by gonad shape (compare Fig. 29 and Fig. 30), and the prolongation of the abaxial spurs of the tentacles, better called here ectodermal canals (compare Fig. 29 and Fig. 30). This species lies in its morphological characters between *L. zacae* Bigelow and *L. octona*. The *L. zacae* specimens so far described have longer ectodermal canals (Bigelow 1940, Kramp 1965a, Fagetti 1973) but since the range of variation is not yet known for *L. zacae* or the present form, it is not desirable to name a new species at this time.

Distribution:

British Columbia and Puget Sound;

Friday Harbor (Mackie and Mackie 1963).

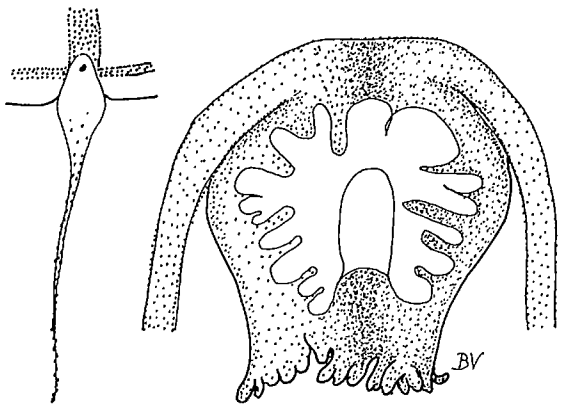


Fig. 29. *Leuckartiara octona*, details of abaxial spurs and gonads, Naples.

Genus *Neoturris* Hartlaub, 1914

Pandeinae with apical projection of varying shape and extent. Manubrium large and wide, with mesenteries at least one-third length. Gonads with adradial folds and with few or numerous interradial pits. Adult medusae with more than 50 marginal tentacles (B.C. species only); with laterally compressed marginal bulbs; few or none (depending on age) rudimentary marginal bulbs. No ocelli.

Type species: *N. pileata* (Forskal, 1775).

Neoturris breviconis (Murbach and Shearer, 1902) comb. nov.

Turris breviconis Murbach and Shearer, 1902: 73; 1903: 170, pl. 18.
Tiara pileata Kramp, 1913a: 266 (in part, non *Medusa pileata* Forskal, 1775: 110); 1914: 411.
Leuckartiara brevicornis Hartlaub, 1914: 304; 1917: 410; Uchida, 1938c: 49.
Leuckartiara breviconis Foerster, 1923: 241; Kramp, 1926: 80, pl. 2; Hand and Kan, 1961: 9.
Perigonimus brevicornis Naumov, 1955a: 53, pl. 7.
Perigonimus (=Turris) breviconis Naumov, 1956a: 37.
Perigonimus breviconis Naumov, 1960: 204.
Neoturris sp. Brinckmann-Voss, 1974 (Acc. No. 73).

Specific characters: Gonads with variable number of interradial pits. Adult medusae with 90 or more marginal tentacles.

Description of medusa: Medusa up to 45 mm high and 45 mm wide; with a rather low, rounded apical projection (seldom cubical as reported Hartlaub 1914). Manubrium broad, usually half to one-third height of subumbrella;

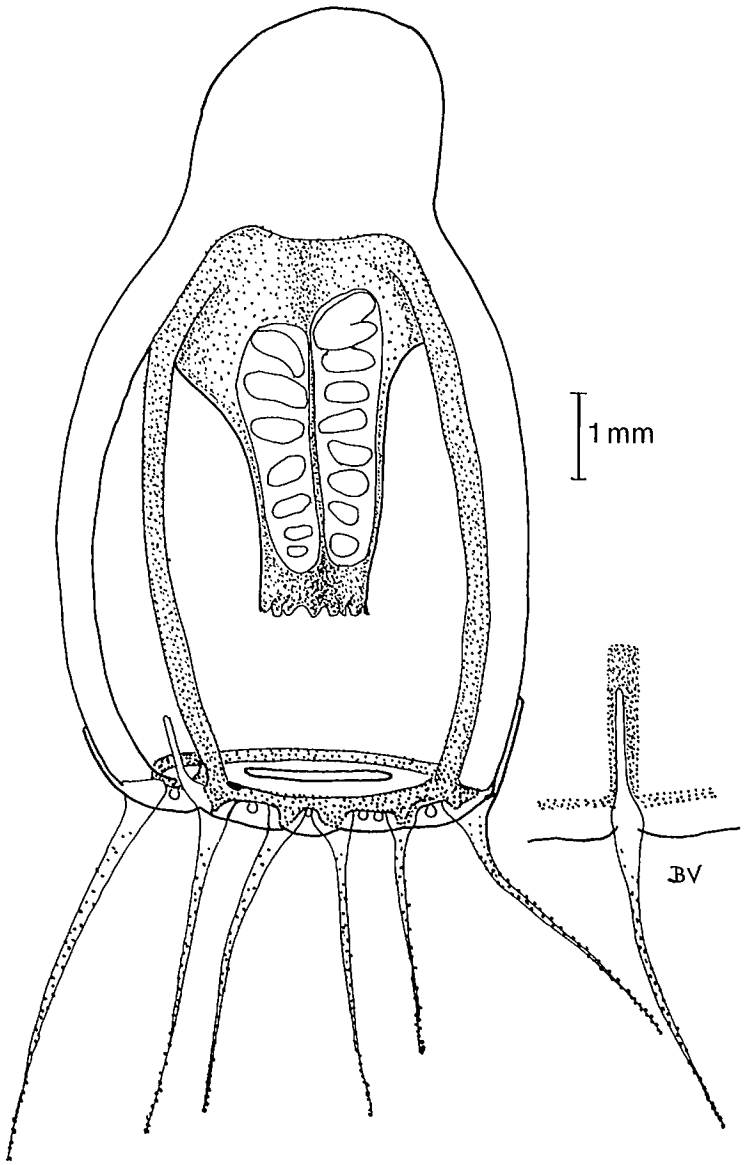


Fig. 30. *Leuckartiara* sp., Friday Harbor. Note the long abaxial spurs. (Coll. G. Mackie).

Fig. 31. *Neoturris breviconis*, live specimen, 12.1 mm high, Brentwood Bay. Photo. M. N. Arai.

mesenteries variable in length; lips crenulated or finely folded. Gonads horseshoe-shaped with oblique adradial folds; often with small pit-like folds in the interradial connection. Radial canals jagged, broad. Ring canal smooth, broad. Up to 140 tentacles, densely crowded. Marginal tentacle bulbs elongated, grasping margin but with variable abaxial spur. Color of living specimens, gonads and manubrium pale orange, deep pink or dark red.

Hydroid: not known.

Discussion of taxonomy: The similarity of *N. breviconis* and *N. pileata* makes it advisable to place *N. breviconis* in the genus *Neoturris*, rather than *Leuckartiara*. *N. breviconis* agrees with *N. pileata* in the absence of ocelli, in the numerous tentacles with laterally compressed marginal bulbs, and in the absence of reduced marginal bulbs in adult specimens. It is distinguished from *N. pileata* by the broader shape of the exumbrella, the smaller number of interradial pits of the gonads, and the maximum number of tentacles.

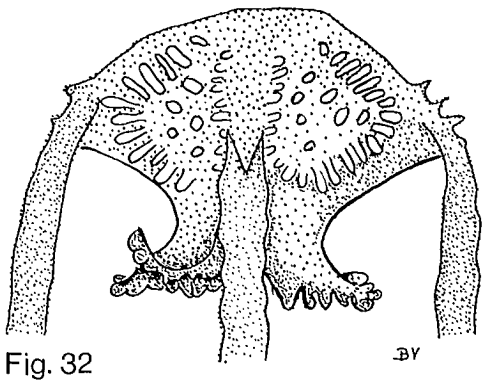


Fig. 32

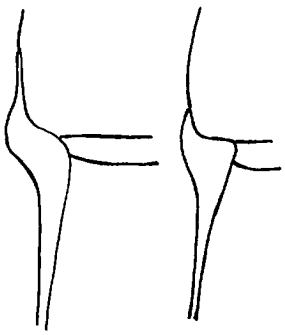


Fig. 33

Fig. 32. *Neoturris breviconis*, detail of gonads of not quite mature specimen, Brentwood Bay.

Fig. 33. *Neoturris breviconis*, variation of abaxial spurs on marginal bulbs.

Neoturris pileata was tentatively reported from Departure Bay by Foerster (1923) on the basis of a single very small specimen. As noted by Edwards (1965) the description and figures are inadequate for critical determination. Brinckmann-Voss (1974) examined the Pacific Biological Station collection including specimens identified by Foerster. Specimen No. 73 from Loredo Channel, identified originally by Foerster as *Leuckartiara breviconis*, tentatively named by Brinckmann-Voss as *Neoturris* sp. probably *pileata*, is *N. breviconis*. On the other hand the identification by Foerster of specimens 86, 87 and 88 from Departure Bay as *Neoturris pileata* was retained by Brinckmann-Voss (1974). These specimens have now been reexamined and are not *Neoturris pileata*, specimen 88 being *Halitholis* sp. I, specimens 86 and 87 in very poor condition. Therefore, the distribution record of *N. pileata* by Foerster (1923) is probably incorrect.

Distribution:

British Columbia and Puget Sound;
Departure Bay (Foerster 1923); Strait of Georgia, northeast of Five Finger Island (present work); Brentwood Bay (present work); Friday Harbor (Mackie and Mackie 1963); Laredo Channel (Foerster 1923, Brinckmann-Voss 1974).

Pacific Ocean;
Bering Sea, off St. Paul Island, Pribilof Islands (Murbach and Shearer 1902; 1903); Okhotsk Sea (Naumov 1955a); Pacific Ocean, off Kuril Islands (Naumov 1960); Okati Bay, Honshu (Uchida 1938c).

Atlantic Ocean;
See Kramp (1926, 1939, 1942), Petersen (1957), Russell (1970) and Boyd et al (1973) for details.

Arctic Ocean;
See Hand and Kan (1961), Zelickman (1972), and Zelickman and Golovkin (1972) for details.

Notes: Mackie and Mackie (1963) found microbasic mastigophores and microbasic euryteles to be the nematocysts present.

Genus *Pandea* Lesson, 1843

Pandeinae with umbrella with or without conical apical projection; with mesenteries; with gonads forming an irregular network of ridges with pits between them.

Type species: *P. conica* (Quoy et Gaimard, 1827).

Pandea rubra Bigelow, 1913

Pandea rubra Bigelow, 1913: 14, pl. 2; Kramp, 1926: 96, pl. 2; Bigelow, 1938: 107; Kramp, 1957a: 18; 1965a: 41.

Specific characters: Manubrium deep brownish red, color extending to tentacles and subumbrella in large specimens; no exumbrellar nematocyst tracks.

Description of medusa: Umbrella bell-shaped, up to 75 mm high and wide, with fairly thin, soft walls, no apical projection. Manubrium wide, half as long as bell cavity, attached to perradii for 4/5 of the length of the radial canals; mouth-rim cruciform, very complexly folded; gonads close network on entire interradial areas. Radial canal margins wavy or jagged. Up to 24 large tentacles; large conical bulbs.

Hydroid: not known.

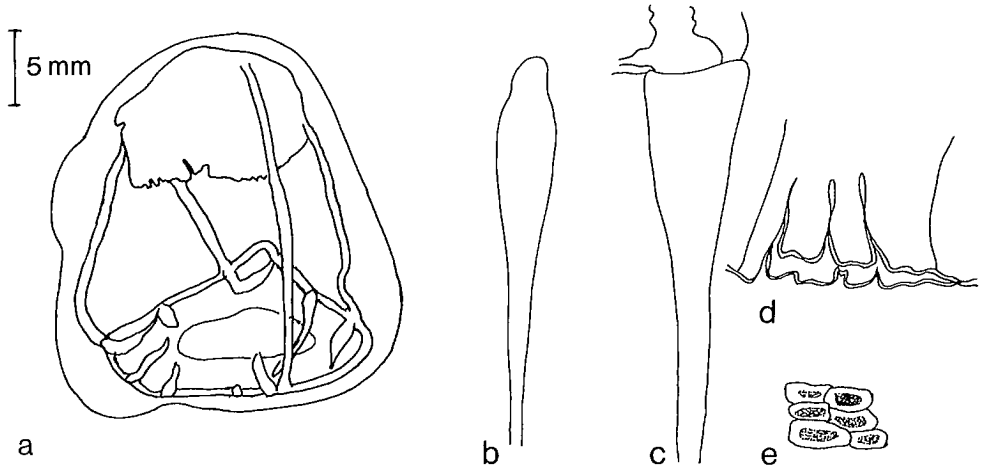


Fig. 34. *Pandea rubra*, a. young specimen (after Bigelow 1913, modified); b. marginal tentacle, frontal; c. marginal tentacle, lateral; d. part of fringed lips; e. part of gonad pits; b-d. "Discovery collections", Copenhagen.

Distribution:

British Columbia and Puget Sound;
52°02'N, 132°53'W, west of Cape St. James, Queen Charlotte Islands (Bigelow 1913).

Pacific Ocean;
53°53'N, 144°53'W, Gulf of Alaska (Bigelow 1913); 39°43'N, 167°55'W, Pacific Ocean (Kramp 1965a); 52°37'N, 158°50'E, off Staritschkof Island, Kuril Islands (Bigelow 1913); 49°06'N, 153°06'E, off Chirinkotan I., Kuril Islands (Bigelow 1913); 45-46°N, 152-153°E, Kurile-Kamchatka Trench (Naumov 1971).

Atlantic Ocean;
See Kramp (1957a), Russell (1970) and Fraser (1974) for details.

Indian Ocean;
See Kramp (1957b, 1965a) and Vannucci et al (1970) for details.

Notes: *Pandea rubra* is an apparently bathypelagic form which has been obtained in significant numbers only from the central north Pacific (Kramp 1965a) and from an area of upwelling in the Indian Ocean (Vannucci et al 1970).

Family Halimedusidae fam. nov.

Anthomedusae with four radial canals; with subumbrella protruding into stomach giving a peduncle-like appearance; mouth cruciform with row nematocysts; with four perradial tentacles and four interradial groups of tentacles, each hollow and lacking adhesive organs; with marginal bulbs with abaxial ocelli.

Discussion of family: When Bigelow described the genus *Halimedusa* in 1916, he placed it in the family Pandeidae. Unfortunately this family has served as a collection box for the unusual for over half a century. Endeavoring to define the Pandeidae better, we removed the genus *Halimedusa* from it. We feel that the structure of the lips and the interradial grouping of the tentacles separate *Halimedusa* sufficiently from all known Pandeidae to justify placing it in a new family - Halimedusidae.

Genus *Halimedusa* Bigelow, 1916

Halimedusidae with characters of the family.

Type species: *H. typus* Bigelow, 1916.

Halimedusa typus Bigelow, 1916

Halimedusa typus Bigelow, 1916: 91, pl. 1.

Specific characters: This is the only species of the genus.

Description of medusa: Umbrella up to 16 mm high, 13 mm wide; with thick mesogloea, at apex about one third of the height of the bell. Radial and ring canals narrow. Stomach with four large perradial folds, narrowing to the oral portion. Lips with a thick row of nematocysts either in clusters or forming a continuous folded ribbon. Gonads smooth, occupying the whole upper inter-

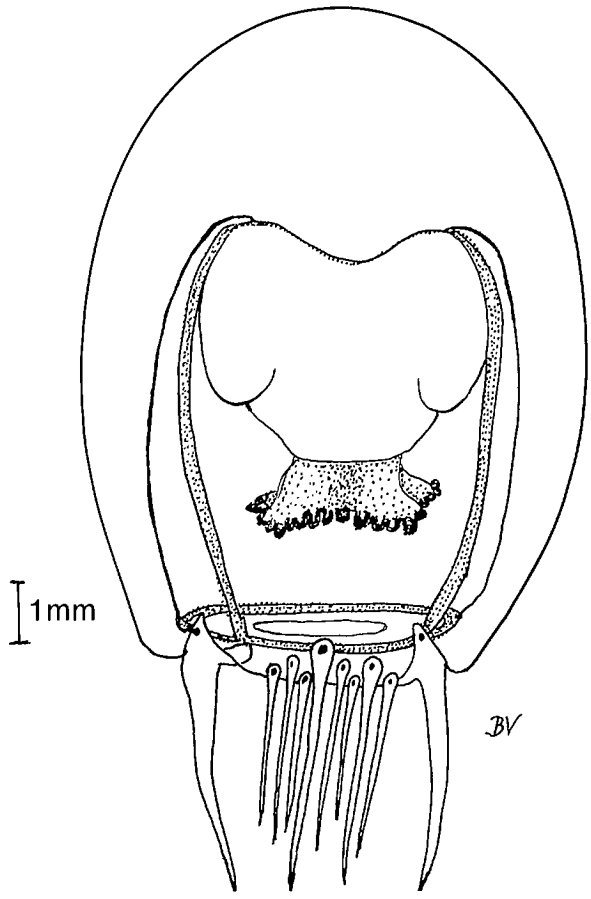


Fig. 35. *Halimedusa typus*, Yaquina Bay, Oregon. (Coll. R. J. Larsen).

radial space of the manubrium but leaving the oral part free. Interradial tentacle group with tentacles situated at various levels above margin. Color of living specimens; bell transparent, tentacles cream white, ocelli purple-black, gonads greenish, white, or salmon-color.

Hydroid: not known.

Distribution:
British Columbia and Puget Sound;
Pacific Ocean, off Amphitrite Point (Bigelow 1916).
Pacific Ocean;
Bodega Bay, California (Rees 1975); Bodega Harbor (Rees 1975).

Family Calycopsidae

Anthomedusae with four simple or crenulated lips; with four or eight simple or branched radial canals; with or without centripetal canals; with four or more hollow marginal tentacles without basal swelling ("marginal bulb") but with more or less prominent terminal nematocyst cluster, which may be knob-shaped or oblong, with or without rudimentary tentacles; with or without ocelli.

Genus *Bythotiara* Gunther, 1903

Calycopsidae with four narrow simple or bifurcate radial canals; without centripetal canals. Gonads with transverse furrows; with or without secondary tentacles.

Type species: *B. murrayi* Gunther, 1903.

Bythotiara depressa Naumov, 1960

Bythotiara depressa Naumov, 1960: 191.

Specific characters: Four unbranched radial canals, eight tentacles.

Description of medusa: Umbrella up to 20 mm high, with thick mesogloea especially at apex, laterally flattened, with two radial canals passing through greatest diameter of cross section and two through smallest diameter. Manubrium half length of bell cavity or less; stomach walls folded and hence gonads folded. Eight tentacles thick at base becoming very thin and thread-like before terminal nematocyst clusters; without secondary tentacles.

Discussion of taxonomy: The single specimen which we have collected was obtained in a plankton haul at 47°45'N, 125°15'W, in the Pacific Ocean off the Washington State coast just south of our research area. The species is included, however, because it is a rare oceanic species which is likely to be found off the Canadian west coast when more extensive collections are made.

Naumov (1960) described the species based on 31 specimens from 20 locations. In our single specimen the manubrium extends about half the length of the bell cavity rather than being very short as described by Naumov. The terminal nematocyst clusters of the perradial tentacles were more spherical, and the clusters of the interradial tentacles smaller than shown in Naumov's figure. These differences are probably developmental as our specimen was only 8 mm high. The manubrium of the living specimen was yellow.

Hydroid: not known.

Distribution:
Pacific Ocean;
47°45'N, 125°15'W, Pacific Ocean off Washington (present work); Bering Sea (Naumov 1960); Pacific Ocean off Commander Islands (Naumov 1960); Pacific Ocean off Kuril Islands (Naumov 1960); 45-46°N, 152-156°E, Kuril-Kamchatka Trench (Naumov 1971); Okhotsk Sea (Naumov 1960).

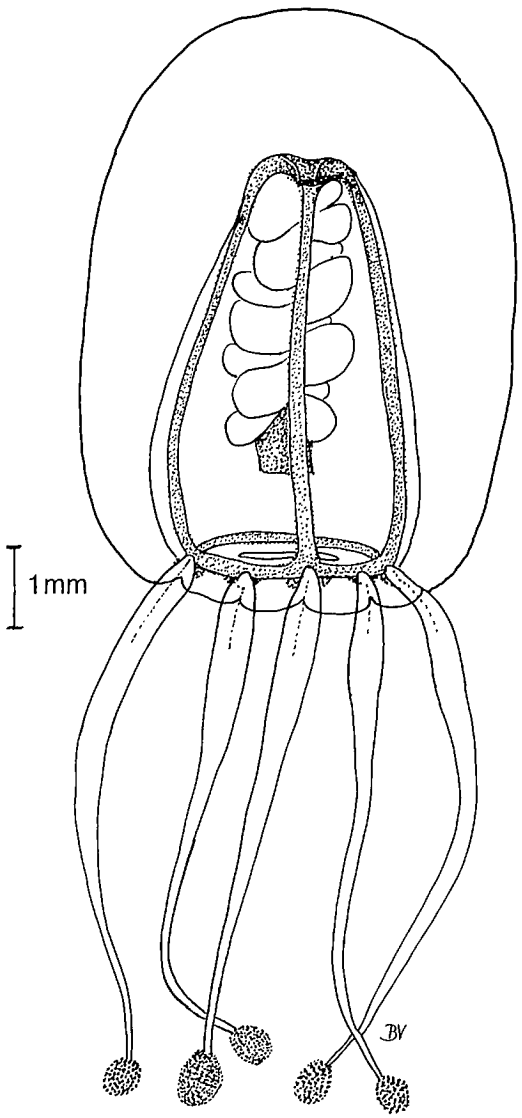


Fig. 36. *Bythotiara depressa*, Lat. 47°45'N, Long. 125°15'W.

Notes: Most of the specimens described by Naumov (1960, 1971) were collected at depths of over 1000 m, although they have been obtained as near the surface as in a 200-0m haul. Our specimen was collected in a 400-0m vertical haul.

Bythotiara huntsmani (Fraser, 1911)

Crypta huntsmani Fraser, 1911: 19, pl. 1.
Endocrypta huntsmani Fraser, 1912: 216; 1914: 109, pl. 1.
Bythotiara huntsmani Brinckmann-Voss, 1979: 1226.

Specific characters: Umbrella deep bell-shaped in adult specimens. Four unbranched radial canals. Eight adradial gonads with variable degree of folding. Four perradial tentacles with terminal cnidocyst clusters not thicker than diameter of contracted tentacles.

Description of medusa: Umbrella up to 7.1 mm high, up to 6.5 mm wide, with scattered cnidocysts on exumbrella. Stomach occupying about half of subumbrella cavity. Lips four cornered with numerous cnidocyst patches. Radial and ring canals smooth. Without ocelli. Manubrium, junction of radial canals and ring canal, and tentacle tip orange to dark brown. Gonads of male specimens milk white, female more transparent. Remainder of medusa colorless.

Discussion of taxonomy: This medusa has not yet been collected in the field. The newly liberated medusa was described by Fraser (1914). The mature medusa was reared by Brinckmann-Voss (1979) and identified as a species of *Bythotiara*.

Hydroid: The hydroid has been described by Fraser (1911, 1914) and Brinckmann-Voss (1979). It has four to five irregular whorls of filiform tentacles. It lives in the prebranchial zone of the ascidians *Ascidia paratropa* and *Halocynthia aurantium*.

Distribution:
British Columbia and Puget Sound;
The medusa has been reared from hydroids collected in Nanoose Bay (Fraser 1914); Strait of Georgia, off Five Finger Island (Brinckmann-Voss 1979); Departure Bay (Fraser 1914; Brinckmann-Voss 1979; present work); off Protection Island (Fraser 1914); Friday Harbor (Fraser 1914).

Notes: The medusa is not known in the sea. It is suspected to invade deeper waters during its development (Brinckmann-Voss 1979). It prefers colder water (down to 1°C) and thrives on fish and decapod larvae. Gladfelter (1973) states that the medusa possesses 12 interradial and adradial joints of deformable mesogloea used in swimming movements. Brinckmann-Voss (1979) found microbasic mastigophores and microbasic euryteles.

Genus *Calycopsis* Fewkes, 1882

Calycopsidae with four primary radial canals which may branch plus more centripetal canals with or without blind ending. Base of stomach cruciform. All tentacles hollow, with nematocysts only in terminal knob.

Type species: *C. typa* Fewkes, 1882.

Fig. 37. *Bythotiara huntsmani*, 1.6 mm high, newly released from hydroid collected Departure Bay. Photo. M. N. Arai.

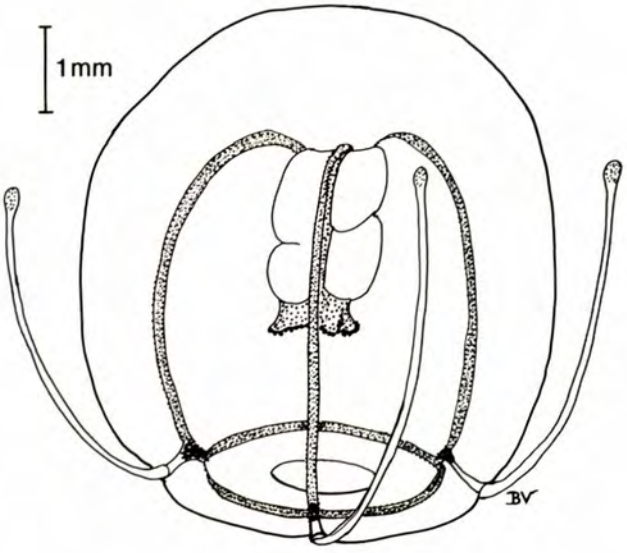


Fig. 38. *Bythotiara huntsmani*, raised from hydroid collected Departure Bay.

Calycopsis nematophora Bigelow, 1913

?Sibogita simulans Bigelow, 1909a: 213 (in part).
?Calycopsis typa Vanhöffen, 1911: 214, pl. 22 (in part, non *Calycopsis typa* Fewkes, 1882: 301, pl. 1).
Calycopsis nematophora Bigelow, 1913: 23, pl. 2, 3; 1940: 290; Naumov, 1956a: 37; Kramp, 1959a: 21; Renshaw, 1965: 841.
Perigonimus nematophora Naumov, 1955a: 53, pl. 7.

Specific characters: Four primary radial canals emerging from stomach, each forking into 3 to 5 branches a short distance from the stomach. Mouth with labial nematocyst clusters. Without ocelli.

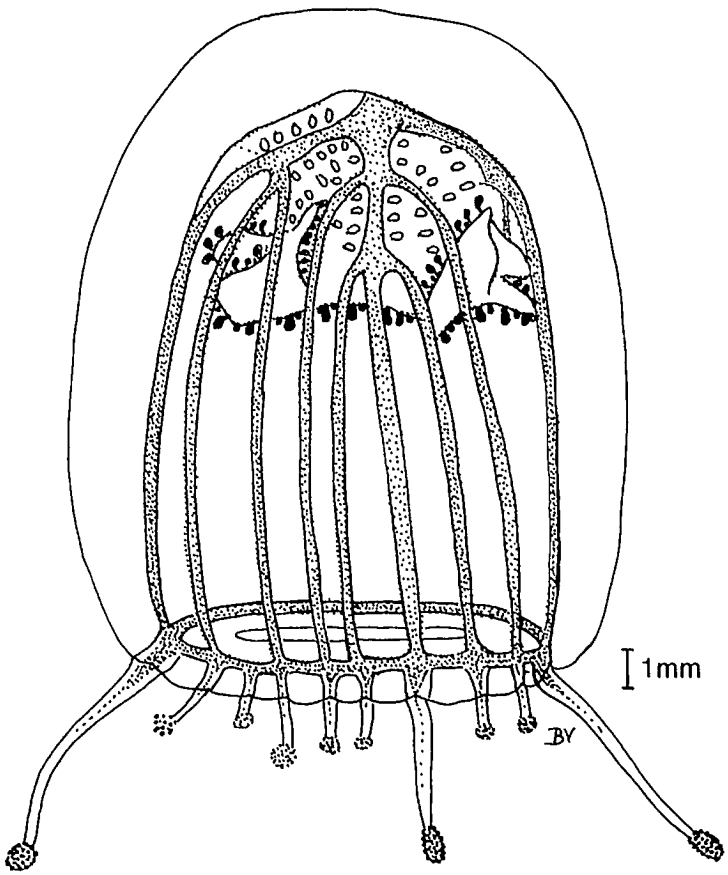


Fig. 39. *Calycopsis nematophora*, Lat. 50°N, Long. 145°W, "Station P".

Description of medusa: Umbrella up to 30 mm high, nearly as wide as high. Mesogloea about 1/5 - 1/4 diameter of exumbrella. Stomach thick in upper part connected to subumbrella, necklike in lower part with fringed much folded lips. Lips carrying a line of cnidocyst clusters, the larger of them oblong and stalked. Gonads smooth, interradial, each bearing four rows of slit-like identations mostly running parallel to radial canals. Radial canals thick, trunk-like at their base, forking into thinner canals a short distance from the stomach. Up to 60 tentacles of different sizes, those corresponding to the central radial canal of each group of radial canals being the largest with an elongated terminal cnidocyst cluster. Interradial tentacles shortest (probably youngest), each with a spherical cnidocyst cluster. Remaining tentacles intermediate in size (larger tentacles often damaged in preserved specimens). Gonads and manubrium including labial cnidocyst clusters dark red to purple in living specimens.

Hydroid: not known.

Distribution:
British Columbia and Puget Sound;
Friday Harbor (W. Schwab personal communication).
Pacific Ocean;
Pacific Ocean off Oregon (Pearcy 1972); 44°39' - 46°14'N, 125°15' - 127°00'W, Pacific Ocean off Oregon (Renshaw 1965); 50°N, 145°W, "Station P", Gulf of Alaska (present work); 55°20'N, 143°26'W, Gulf of Alaska (present work); 55°00'N, 155°00'W, Gulf of Alaska (Renshaw 1965); Lat. 49°46' - 49°50'N, 160°48' - 160°50'W, Pacific Ocean (Renshaw 1965); 52°00'N, 166°20'W, Pacific Ocean, south of Aleutian Is. (Renshaw 1965); 53°57'N, 168°06'W, off Bogosloff Islands, Aleutian Islands (Bigelow 1913); 53°20'N, 171°W, off Yunaska I., Aleutian Islands (Bigelow 1913); 52°38'N, 174°49'W, off Kaniuji I., Aleutian Islands (Bigelow 1913); 49°00' - 51°18'N, 175°27' - 178°09'W, Pacific Ocean south of Aleutian Islands (Renshaw 1965); 53°02' - 55°09'N, 169°57' - 174°37'W, Bering Sea (Renshaw 1965); Bowers Bank, Bering Sea (Bigelow 1913); 58°02' - 58°12'N, 179°57' - 180°00'W Bering Sea (Renshaw 1965); 52°39'N, 173°22'E, off Attu I., Aleutian Is. (Bigelow 1913); 54°48'N, 164°54'E, off Bering Island (Bigelow 1913); 46°42'N, 151°47'E, off Simushir I., Kuril Islands (Bigelow 1913); 44° - 46°N, 149° - 155°E, Kuril-Kamchatka Trench (Naumov 1971); 48°25'N, 145°30'E, Okhotsk Sea (Bigelow 1913).

Note: Nematocysts of labial and tentacle clusters are desmonemes (Renshaw 1965).

Genus *Heterotiara* Maas, 1905

Calycopsidae with four simple radial canals; without centripetal canals; gonads purely interradial, without definite transverse folds; without secondary tentacles.

Type species: *H. anonyma* Maas, 1905.

Heterotiara anonyma Maas, 1905

Heterotiara anonyma Maas, 1905: 19, pl. 3; Bigelow, 1909a: 216, pl. 41;

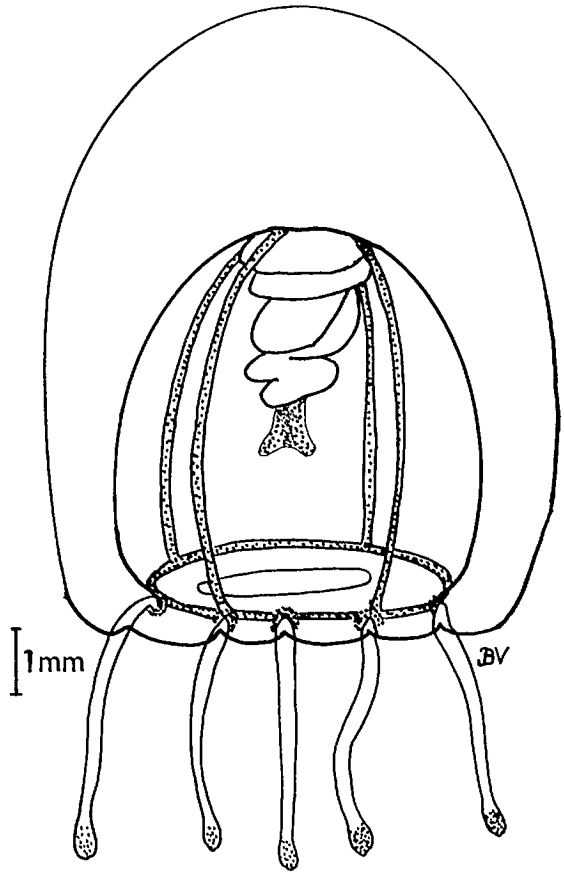


Fig. 40. *Heterotiara anonyma*, off Mona Island, Puerto Rico. (Coll. R. J. Larsen).

Vanhöffen, 1911: 211, pl. 22; Bigelow, 1913: 25; 1918: 382; 1919: 287; Kramp, 1948: 21; 1959a: 17; 1965a: 41; Schmidt, 1973: 22.

Specific characters: with 6-12 tentacles.

Description of medusa: Umbrella up to 22 mm high and 20 mm wide with rather thick walls, deep, rather narrow bell cavity. Manubrium barrel-shaped; mouth with four simple lips. Gonads occupying entire interradial areas, from base of manubrium to close to lip. Terminal nematocyst knobs of tentacles bright orange-red; gonads opaque yellowish.

Hydroid: not known.

Discussion of taxonomy: Bigelow (1909a) showed a specimen without terminal nematocyst clusters in plate 41, figure 13. This figure was copied by Hartlaub (1914) and Kramp (1968c), leading to some confusion. However,

according to Bigelow's own description (1913, 1918) spherical terminal knobs are present. This is confirmed by Kramp (1948, 1965a) and Schmidt (1973).

Distribution:

Pacific Ocean;

30°30'N, 120°00'W, off San Diego, California (Alvariño 1967); 53°05'N, 138°31' W, Gulf of Alaska (Bigelow 1913); 53°57'N, 168°06'W, off Bogoslof Islands, Aleutian Islands (Bigelow 1913); 52°38'N, 174°49'W, off Kaniuji Island, Aleutian Islands (Bigelow 1913); Bowers Bank, Bering Sea (Bigelow 1913); 54° 48'N, 164°54'E, off Bering Island (Bigelow 1913); 52°37'N, 158°50'E off Staritschkof Island, Kuril Islands (Bigelow 1913); 15°22'N, 115°20'E, South China Sea (Kramp 1965a); Sulu Sea (Kramp 1965a); Surigao Strait, off Dinagat, Philippines (Kramp 1965a); Bali Sea (Kramp 1965a); Banda Sea (Kramp 1965a); Molucca Sea (Kramp 1965a); Halmahera Sea (Maas 1905, van Soest 1975); Pacific Ocean, off Aguja Point, Peru (Bigelow 1909a).

Atlantic Ocean;

See Kramp (1959a) for details.

Indian Ocean;

See Vanhöffen (1911), Kramp (1965a), Schmidt (1973), and Vannucci and Navas (1973b) for details.

Notes: *Heterotiara anonyma* has been included, although it has been found only in the Gulf of Alaska somewhat outside the research area, because it is a fairly rare form which will probably be found when more collecting is done off our coasts. It has been collected in widely scattered areas of the warmer oceans, typically at less than 600 m (Bigelow 1909a, Kramp 1959a, 1965a, Alvarino 1967).

Russell (1940) found desmonemes and possibly euryteles in the terminal cluster of a tentacle.

Family Polyorchidae

Anthomedusae deep bell-shaped; with no peduncle in young specimens, but more or less pronounced peduncle in adults; with manubrium with four-cornered mouth which develops fringed lips in adult stages; with four radial canals with or without lateral branches; gonads sausage shaped or spiral.

Genus *Polyorchis* A. Agassiz, 1862

Polyorchidae with lateral branches on radial canals in adult specimens; gonads sausage-shaped, hanging down from the junction points of the radial canals with the manubrium in developing specimens or from the peduncle in fully mature specimens; tentacles around the whole bell margin, not in clusters.

Type species: *P. penicillatus* (Eschscholtz, 1829).

Polyorchis penicillatus (Eschscholtz, 1829)

Melicertum penicillatum Eschscholtz, 1829: 106, pl. 8.
Aglaura penicillata de Blainville, 1834: 283, pl. 33.

Fig. 41. *Polyorchis penicillatus*, immature live specimen, 12.6 mm high, Departure Bay. Photo. M. N. Arai.

Polyorchis penicillata A. Agassiz (in L. Agassiz), 1862: 349; 1865: 119; Fewkes, 1889b: 103, pl. 4; Maas, 1904b: 442 (in part); Mayer, 1910: 218 (in part); Little, 1914: 307 (in part); Foerster, 1923: 250 (in part); Kramp, 1928: 60; non Bigelow, 1940: 296.
Polyorchis penicillatus Haeckel, 1879: 150; Skogsberg, 1948: 118; Brinckmann-Voss, 1977: 93.
Polyorchis minuta Murbach and Shearer, 1902: 72; 1903: 174, pl. 19, 22; Mayer, 1910: 219.
Polyorchis minutus Skogsberg, 1948: 113.
?Polyorchis montereyensis Skogsberg, 1948: 114.
Polyorchis sp. Rees, 1975: 139.

Specific characters: Lateral branches on radial canals each with not more than four secondary branches; gonads simple or bifurcate, rarely with more than one branch.

Description of medusae: Adult medusae (with mature gonads) 8 to 60 mm high; with 48 to 120 (rarely more) tentacles each with a dark red or purple abaxial ocellus surrounded by an orange-red pigmented zone which increases with the age of the tentacle; with 4 to 45 (usually 4 to 15) gonads on each radial canal occupying 1/3 or more of the subumbrella; with peduncle short in small specimens, up to 1/3 of the subumbrella in largest specimens. Smallest medusae with 4 tentacles only; stomach four sided, nearly tubular.

Hydroid: described by Brinckmann-Voss (1977).

Discussion of taxonomy: The decision to unite *P. minutus*, *P. montereyensis* and *P. penicillatus* is based on detailed measurements of the different possible diagnostic characters (length/width ratio of the umbrella; spacing, length and ramifications of the lateral branches of the radial canals; number, state and length of gonads; number of tentacles; color variations) from more than 80 specimens from Queen Charlotte Islands to Puget Sound. Special attention was given to the variation within single populations. It was found that it is impossible to allocate the different variations to different groups of specimens because there are intermediate stages between any of them.

Skogsberg (1948) claimed, based on Foerster's (1923) description of the purple color, that *P. minutus* Murbach and Shearer should be kept as a separate species (although Foerster placed it in synonymy with *P. penicillatus*). However, we found that even within a single population there may be two color variations - one deep orange to purple, one pale yellow - with equal sizes and no morphological differences (observation of living specimens from the Strait of Georgia off French Creek).

Comparison of the specimens of the British Columbia coast with the published description of *P. montereyensis* (Skogsberg 1948) showed that the range of number and length of gonads may be greater in specimens from Monterey Bay, California (the type locality of *P. montereyensis*). We have observed a maximum of 15 gonads on each radial canal whereas Skogsberg (1948) mentions specimens with from 6 to 45 gonads. However, this is the only difference. Skogsberg's type specimens have apparently been lost (Rees 1975). Rees (1975) also questions the distinction between the species based on collections from Bodega Harbor and San Francisco Bay, California and Yaquina Bay, Oregon. A separate species does not seem to be justified only on the basis of greater range of gonad number but this can not be finally decided until further collections can be made in Monterey Bay.

Nagao (1970) studied the development of *P. karafutoensis* and observed that *P. karafutoensis* goes during its development through stages which correspond to the "species" *P. haplus*, *P. penicillatus* and *P. montereyensis*. Although the differences between *P. penicillatus* and *P. karafutoensis* seem to be merely numerical, *P. karafutoensis* representing a more developed stage than *P. penicillatus*, we leave *P. karafutoensis* as a separate species, because it is restricted to the Western side of the Pacific. It should be noted however that partially developed stages of *P. karafutoensis* cannot be distinguished from *P. penicillatus*. *P. pinnatus* Haeckel from the Hawaiian Islands is also not included in *P. penicillatus* because it may be either a *P. penicillatus* or an immature *P. karafutoensis*.

Distribution:

British Columbia and Puget Sound;

Strait of Georgia (A. Agassiz in L. Agassiz 1862, 1865); Strait of Georgia, off French Creek (present work); Departure Bay (Foerster 1923, Brinckmann-Voss 1974, 1977, present work); Strait of Georgia, off Newcastle Island (Foerster 1923); Nanaimo Region (Kramp 1928; Fraser 1932); Brentwood Bay (Brinckmann-Voss 1977, present work); San Juan Archipelago (Fraser 1932); Friday Harbor (Bovard and Osterud 1918, Mackie and Mackie 1963); Puget Sound (Murbach and Shearer 1902, 1903, Skogsberg 1948); Victoria Harbour (present work); Pedder Bay (Singla 1978b); Sooke Harbour (Brinckmann-Voss 1977, present work); Strait of Juan de Fuca (Agassiz 1865); Barkley Sound (Brinckmann-Voss 1974); Bamfield Inlet (Brinckmann-Voss 1974, Spencer 1978, present work); Grapple Inlet (Spencer 1978); Ucluelet Inlet (Brinckmann-Voss 1974); Browning Passage, off Tofino (Brinckmann-Voss 1974, present work); Nuchatlitz Inlet, off Port Langford (Brinckmann-Voss 1974); Kyuquot Sound (Brinckmann-Voss 1974); Bunsby Anchorage, Checleset Bay (present work); Quatsino Sound (Brinckmann-Voss 1974); Sea Otter Cove, San Josef Bay (Foerster 1923); Bull Harbour (Gladfelter 1972, Brinckmann-Voss 1974); Alert Bay (Brinckmann-Voss 1974); Masset Harbour (present work).

Pacific Ocean;

Santa Barbara Channel (Fewkes 1889a, b); off Santa Cruz, California (Fewkes 1889b); Monterey Bay (Fewkes 1889b, Skogsberg 1948, Gladfelter 1972); San Francisco Bay (A. Agassiz in L. Agassiz 1862, 1865, Fewkes 1889b, Bancroft 1904, Little 1914, Skogsberg 1948, Eakin and Westfall 1962, Gladfelter 1972, Lichtenfels 1974, Rees 1975); off California, probably San Francisco Bay (Eschscholtz 1829); Bodega Bay (Gladfelter 1972, Rees 1975); Bodega Harbor (Rees 1975); Pacific Ocean, off Bodega Head (Rees 1975); Yaquina Bay (McCormick 1969, Rees 1975).

Notes: *Polyorchis penicillatus* swims actively using the alternating antagonistic action of the subumbrellar swimming muscles and the elastic mesogloea. Most of the mesogloea remains firm at water contents above 76% of normal (Hargens 1977). Eight adradial joints of highly deformable mesogloea lack visible fibers, allowing bending or folding of the mesogloea around these joints under the action of the muscle (Gladfelter 1972, 1973). Contraction can be influenced by electric current (Bancroft 1904), ions (Loeb 1906) or organic compounds (MacCallum 1907). The medusae possess well developed ocelli, the structure of which has been described by Little (1914) and Eakin and Westfall (1962, 1964). It was therefore particularly interesting when Anderson and Mackie (1977) demonstrated that directly light-induced depolarizations and hyperpolarizations of neurons in the inner nerve ring could cause variations in swimming activity. Singla (1978b) and Spencer (1978) have continued to analyze the morphological and electrical correlates of swimming, crumpling and postural changes.

McCormick (1969) found the food to consist largely of copepods. Lichtenfels (1974) found larval trematodes, *Contracaecum* sp., present near the radial canals of two specimens.

Cnidocysts of the tentacles and manubrial margin are stenoteles and desmonemes (Mackie and Mackie 1963, Brinckmann-Voss 1977). The exumbrellar cnidocyst patches of the very young medusae contain microbasic mastigophores. Brinckmann-Voss (1977) suggests that a fourth type of cnidocyst may be present.

Although specimens of *P. penicillatus* have been captured at various localities in this region and at all times of the year, they have been found abundantly only in the harbors of the outer coast of Vancouver Island and the Queen Charlotte Islands in summer or fall (Gladfelter 1972, present work).

Family Trichydridae

Anthomedusae without exumbrellar nematocyst tracks; with four simple or slightly pleated lips; with four radial canals; tentacles solid, each with a single row of endodermal cells most of their length; no ocelli.

Genus *Trichydra* Wright, 1858

With the characters of the family.

Type species: *T. pudica* Wright, 1858.

Trichydra pudica Wright, 1858

Trichydra pudica Wright, 1858: 111; 1862a: 50, pl. 6; Rees, 1941: 135; Russell, 1953: 148; Edwards, 1973b: 87.
Pochella polynema Hartlaub, 1917: 414; Russell, 1938b: 425; 1953: 394.
Proboscidactyla polynema Foerster, 1923: 30.

Specific characters: Stomach lacking peduncle; radial canals often with exceedingly fine branches; more than 24 tentacles in mature medusae.

Description of medusa: Umbrella bell-shaped or hemispherical, to 4 mm in diameter, jelly thick. Exumbrella with scattered nematocysts. Stomach large, four-sided, about 2/3 as long as bell cavity. Mouth with four lips, simple in small specimens, becoming slightly pleated in larger specimens. Up to 48 tentacles. Manubrium, gonads and tentacle bulbs light yellowish brown.

Hydroid: *Trichydra pudica*, first described by Wright (1858), was identified as the hydroid of *Pochella polynema* Hartlaub (1917) by Edwards (1973b). Further details of the life cycle are given in Rees (1941), and Russell (1953).

Distribution:
British Columbia and Puget Sound;
Deep Bay (present work); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Ladysmith Harbour (present work); Cowichan Bay (present work); Brentwood Bay, Saanich Inlet (present work); Bamfield Inlet (present work).
Atlantic Ocean;
See Russell (1953), Edwards (1973b) and Fraser (1974) for details.

Notes: The medusa has been obtained March to June in Departure Bay, the only British Columbia locality where the medusa has been extensively collected.

Fig. 42. *Trichydra pudica*, live specimen, 3.6 mm high, Departure Bay. Photo. M. N. Arai.

ORDER LEPTOMEDUSAE

Hydromedusae with hemispherical or flattened umbrella; with gonads on radial canals; marginal sense organs, when present, in form of cordyli or marginal vesicles of ectodermal origin; occasionally with ocelli. Hydroids with single whorl of more than 8 filiform tentacles.

Family Dipleurosomatidae

Leptomedusae with stomach with narrow base; with gonads on radial canals separated from stomach; without statocysts or cordyli; with or without ocelli.

Genus *Dipleurosoma* Boeck, 1866

Dipleurosomatidae with three or more radial canals either irregularly branching or originating directly from the stomach; with numerous tentacles.

Type species: *D. typicum* Boeck, 1866.

Dipleurosoma typicum Boeck, 1866

Dipleurosoma typica Boeck, 1866: 131.
Dipleurosoma stuvitzii Boeck, 1866: 131.
Ametrangia hemispherica Allman, 1873: 73.
Dipleurosoma typicum Haeckel, 1879: 155; Browne, 1900: 696, 715, pl. 20, 21; Maas, 1904b: 441 (in part); Russell, 1953: 251.
Dipleurosoma irregulare Haeckel, 1880: 636.
Dipleurosoma hemispherica Haddon, 1886: 526.
Dipleurosoma hemisphaericum Browne, 1898, 1898: 826, pl. 48.

Specific characters: Five to 18, usually 7 to 13, radial canals; more than 100 tentacles in adult specimens; without club-shaped appendages between tentacles.

Description of medusa: Umbrella up to 12 mm wide, flatter than a hemisphere, with thin mesogloea. Stomach of varying shape; small lips varying according to shape of stomach but never pointed. Radial canals either all originating from stomach or branching a short distance from stomach. Gonads situated along radial canals nearer to stomach than to ring canal. Tentacles with a bulbous base, with adaxial ocelli which fade after prolonged preservation. Medusae colorless except for blackish lips and base of stomach (Pacific specimens), or pale yellowish-brown, brown or reddish brown stomach and tentacle bulbs (Atlantic specimens); ocelli black.

Hydroid: A detailed description of the hydroid has not yet been published, although the hydroid was raised by the Misses Delap (Browne 1900), and medusae were raised from the hydroid by Edwards (Russell 1970).

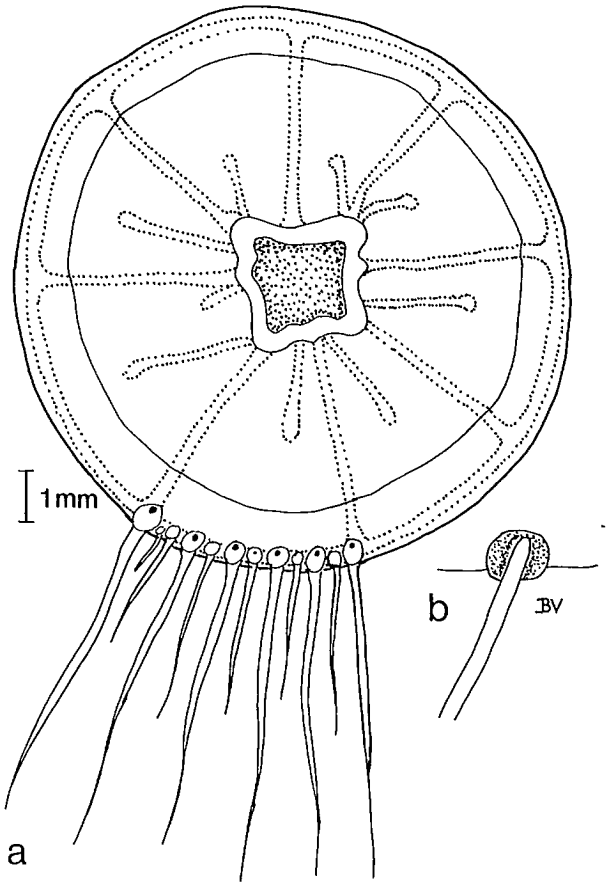


Fig. 43. *Dipleurosoma typicum*, Departure Bay, a. whole animal, oral view; b. marginal bulb, abaxial view.

Distribution:

British Columbia and Puget Sound;
Departure Bay (present work); Friday Harbor (Claudia Mills, personal communication).

Atlantic Ocean;
See Russell (1953) and Fraser (1974) for details.

Notes: *Dipleurosoma typicum* is very variable (Browne 1898, 1900, Russell 1953). This may be partly due to its ability to undergo transverse fission to daughter medusae (Edwards 1973c). The Friday Harbor specimen (8 mm fixed diameter) was collected in March, the two Departure Bay specimens (8 and 9 mm) were collected in May and June. All were without gonads. Only every second or third radial canal reached the ring canal, also an indication of immaturity.

Russell (1940) tentatively identified the nematocysts as microbasic euryteles.

Family Melicertidae

Leptomedusae with wide base of stomach; adults with eight simple or bifurcating radial canals; with hollow marginal tentacles; without marginal or lateral cirri; without marginal sense organs; with or without ocelli.

Genus *Melicertum* L. Agassiz, 1862

Melicertidae without peduncle; with simple radial canals; with gonads on radial canals separated from stomach.

Type species: *M. octocostatum* (M. Sars, 1835).

Melicertum octocostatum (M. Sars, 1835)

Oceania octocostata Sars, 1835: 24, pl. 4.
Melicertum campanulatum Ehrenberg, 1837: 190, 255, pl. 8 (non *Medusa campanulata* Chamisso and Eysenhardt, 1821: 359, pl. 30).
Aequorea octocostata Lesson, 1843: 312.
Thaumantias milleri Landsborough, 1847: 265 (as quoted Forbes, 1848: 30).
Stomobrachium octocostatum Forbes, 1848: 30, pl. 4; Green, 1857: 244; Wright, 1867: 42, pl. 1; Romanes, 1876a: 526.
Melicertum campanula L. Agassiz, 1862: 349 (in part, non *Medusa campanula* Fabricius, 1780: 366); A. Agassiz, 1862: 96; 1865: 130 (in part); Haeckel, 1879: 137; Linko, 1904: 218; Bigelow, 1909b: 308 (in part); Mayer, 1910: 207, pl. 23, 24; Kramp, 1919: 57; Foerster, 1923: 31 (in part); Uchida, 1927b: 220; Naumov, 1960: 324; Zelickman, 1976: 205.
Melicertum pusillum L. Agassiz, 1862: 349 (in part, non *Actinia pusilla* Swartz 1788 as quoted Eschscholtz, 1829: 106).
Melicertum georgicum A. Agassiz (in L. Agassiz), 1862: 349; 1865: 135; Haeckel, 1879: 137; Mayer, 1910: 209; Foerster, 1923: 31; Kramp, 1968c: 63.
Melicertidium octocostatum Haeckel, 1879: 138; Hartlaub, 1894: 192; Browne, 1895: 277; 1905a: 762, Table 1, 2; Gemmill, 1920: 459; 1921: 339; Ranson, 1933: 316.
Melicertidium campanula Browne, 1905a: 766.
Melicertidium georgicum Browne, 1905a: 766.
Melicertum octocostatum Mayer, 1910: 208; Kramp, 1919: 52, pl. 1, 3; Sverdrup, 1921: 22, pl. 4; Kramp, 1933a: 237; 1933b: 562; Künne, 1935: 65; Uchida, 1938b: 41; Kramp, 1942: 57; Russell, 1953: 245, pl. 13; Kramp, 1959a: 134; 1961: 136; Mackie and Mackie, 1963: 69; Rees and Thursfield, 1965: 64; Kramp, 1968c: 63.
Gymnoblastic hydroid Robson, 1914: 104, pl. 1, 2.
Milercertium campanula Fish, 1925: 123.

Specific characters: Adult medusae with more than 50 tentacles; without ocelli.

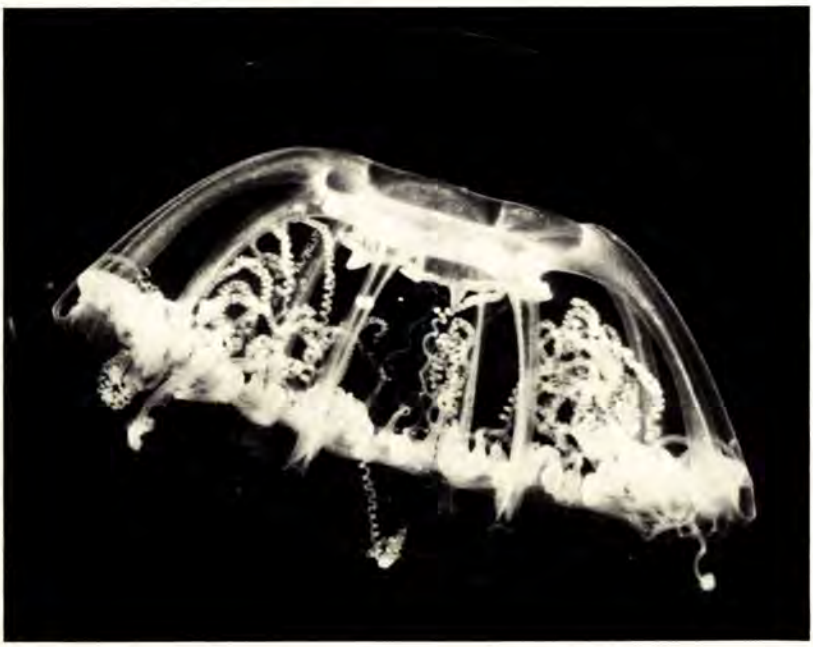


Fig. 44. *Melicertum octocostatum*, live specimen, 6.4 mm high, Departure Bay. Photo. M. N. Arai.

Description of medusa: Umbrella up to 20 mm wide, deep lens-shaped, height about 1/3 to more than equal to width; mesogloea thickened in apical region. Stomach broad, about 1/3 to 1/4 height of subumbrella. Mouth with eight simple or slightly undulating lips. Subumbrella with three to seven strands of tissue per octant running centripetally, lacking or with varying numbers of cnidocysts. With eight broad radial canals when adult, four radial canals in young stages; four secondary canals arising from stomach. Gonads sinuous; extending up to almost entire length of radial canals; usually considerably thicker near umbrella margin than near manubrium. With up to 88 large hollow marginal tentacles with laterally compressed marginal bulbs; smaller marginal tentacles approximately alternating with larger ones, sometimes becoming almost as large. Manubrium, radial canals, gonads and marginal tentacle bases white, orange yellow or yellowish brown.

Hydroid: The hydroid has been described by Robson (1914) and Gemmill (1921) and redescribed by Rees and Thursfield (1965). An earlier description by A. Agassiz (1865) is questionable (see discussion of taxonomy).

Discussion of taxonomy: The genus *Melicertum* has been a very controversial one, both with respect to the generic name and to the specific identity of the common forms on the two sides of the Atlantic. With respect to the generic name we have followed Kramp (1919) in considering *Melicertum*, as redefined by L. Agassiz (1862) to include medusae with 8 radial canals, as a valid genus. This has been generally accepted by more recent authors.

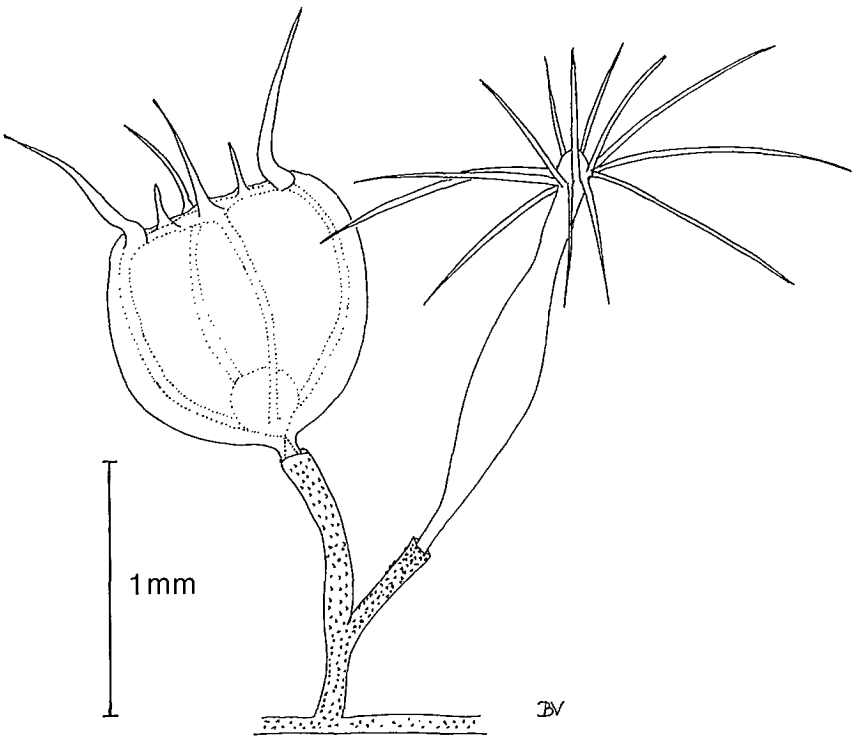


Fig. 45. *Melicertum octocostatum*, hydroid, St. John's Harbour, Newfoundland.

The specimens from off the New England coast described by A. Agassiz (1865) and subsequent authors as *Melicertum campanula* have been reported to differ from *M. octocostatum* of Europe in lacking subumbrella nematocyst tracks. Kramp (1933b) examined specimens from both sides of the Atlantic and concluded that the species were identical. We find that in specimens from the present research area the character is variable. Strands of tissue are present but most specimens lack cnidocysts or possess very few. As pointed out by Russell (1953), A. Agassiz (1865) reared hydroids from American *M. campanula* in which the tentacles were described as webbed at their bases. Such webbing was not found in hydroids reared from Scottish *M. octocostatum* by Gemmill (1921) and redescribed by Rees and Thursfield (1965). However, one of us (A.B.-V.) has seen hydroids which also lack webbing growing on scallops in Newfoundland waters (Fig. 45). She raised the medusae until they could be identified as *M. octocostatum*. Until hydroids can again be reared from *Melicertum* from New England we conclude that it is best to follow Kramp (1933b, 1961, Naumov 1960) in uniting *M. campanula* with *M. octocostatum*. The species name *octocostatum* then has priority over *campanula* since it was first applied to the medusa with eight radial canals by Sars

(1835) and earlier descriptions of *campanula* refer to a form with four radial canals (see Kramp 1919 for history).

Melicertum georgicum was described by A. Agassiz (in L. Agassiz 1862, 1865) from the Strait of Georgia and has not been collected since. He considered it to differ from the Atlantic form in "the pointed spherosome, the smaller number of circular tentacles, the longer actinostome and the termination of the genital organs somewhat above the circular tube". Comparison of Fig. 215 of *M. georgicum* with Fig. 202 of "*M. campanula*" in A. Agassiz (1865) does not show a substantially longer actinostome (manubrium). The spherosome (umbrella) is slightly pointed but no more than might be due to fixation. The number of tentacles shown in side view is slightly less (about 30) than in "*M. campanula*" (about 45) but in both cases is considerably less than if all tentacles were represented in an adult *M. octocostatum*. The gonads of *M. octocostatum* may terminate somewhat above or very near the ring canal. In 1862 A. Agassiz noted that *M. georgicum* has 4 lips but this was probably a mistake as Fig. 216 of his 1865 paper shows eight "constrictions of the lips" in a dorsal view. We therefore consider, as previously suggested by Mayer (1910) and Kramp (1933a), that *M. georgicum* is a synonym of *M. octocostatum*.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (A. Agassiz in L. Agassiz 1862, 1865); Deep Bay (present work); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Ladysmith Harbour (present work); Cowichan Bay (present work); Brentwood Bay (present work); Friday Harbor (Mackie and Mackie 1963); Hecate Strait, off Banks Island (Foerster 1923; Brinckmann-Voss 1974).

Pacific Ocean;
Bering Sea (Naumov 1956a); Okhotsk Sea (Naumov 1956a); Akkeshi Bay, Hokkaido (Uchida 1940); Uchiura Bay, off Muroran, Hokkaido (Uchida 1938b); Mutsu Bay (Uchida 1927b); Busse Lagoon, Aniva Bay (Zelickman 1976).

Atlantic Ocean;
See Bigelow (1909b, 1926), Kramp (1919, 1942, 1961), Fish and Johnson (1937), Alvariño (1956), Fraser (1969, 1974), Thiel (1970) and Boyd et al (1973) for details.

Arctic Ocean;
See Linko (1904), Kramp (1942), McLaren (1969), Zelickman (1972), Grainger (1975) and Grainger and Grohe (1975) for details.

Notes: *Melicertum octocostatum* possesses a relatively weak swimming muscle (Gladfelter 1973) and in aquaria may periodically rest on the bottom (Zelickman 1976). Feeding on copepods, polychaetes, and fish larvae appears to be by random contact (Russell 1953, Fraser 1969). Gemmill (1920) suggested that the ciliation of the subumbrellar surface and inturned tentacles may aid in gathering of food.

Nematocysts of *M. octocostatum* are basitrichous haplonemes and atriches (Russell 1940; Mackie and Mackie 1963).

This is a neritic species, rarely caught more than 30 km from land (Kramp 1919, Bigelow 1926). It may penetrate into brackish water in such areas as the Norwegian fiords and the Baltic Sea (Kramp and Damas 1925, Mankowski 1962, Thiel 1970). In Departure Bay specimens have been collected

March to October, most commonly in May and June.

Family Laodiceidae

Leptomedusae with four or more simple or branched radial canals; with hollow marginal tentacles; with or without marginal cirri; without marginal vesicles; with marginal cordyli; with or without ocelli.

Genus *Ptychogena* A. Agassiz, 1865

Laodiceidae with four radial canals giving rise to lateral diverticula, in which the gonads are placed; stomach with funnel-shaped perradial lobes; without marginal cirri; without ocelli.

Type species: *P. lactea* A. Agassiz, 1865.

Ptychogena lactea A. Agassiz, 1865

Ptychogena lactea A. Agassiz, 1865: 137; Haeckel, 1879: 147; Browne, 1907: 473; Mayer, 1910: 215; Bigelow, 1913: 28; Kramp, 1913a: 268; 1919: 31, pl. 3; 1942: 52; 1955a: 157; Naumov, 1960: 321 (Medusa; ? hydroid); Calder (1970: 1512 (?hydroid).
Ptychogena pinnulata Haeckel, 1879: 148; 1882: 7, pl. 2; Grönberg, 1898: 465; Linko, 1913: 10.
Ptychogena pinnulata var. *intermedia* Linko, 1904: 217.

Specific characters: Radial canals with up to 30 lamelliform lateral diverticula on either side, in their entire length attached to subumbrella.

Description of medusa: Umbrella up to 30 mm high, 90 mm wide, very thick. Stomach short, quadrangular, mouth rim slightly crenulated, four short lips. Up to 500 tentacles, occasionally with short abaxial spurs. Club-shaped cordyli without nematocysts; in larger specimens cordyli approximately alternating with marginal tentacles, in smaller specimens 1-8 usually 4-5, cordyli between each pair of tentacles, arising from marginal bulbs. Gonads, radial canals and tentacles milk-white.

Hydroid: A polyp has been tentatively linked with *P. lactea* on zoogeographical and ecological basis only (Naumov 1960, Calder 1970).

Discussion of taxonomy: *Ptychogena californica* Torrey 1909 was described from two immature and poorly preserved specimens from off San Diego (Torrey 1909). It is possible, as suggested by Kramp (1919) and Thiel (1932) that these were young *P. lactea*. However, as *P. lactea* has not been collected and clearly described south of Friday Harbor, and is a largely Arctic species, we have not placed *P. californica* in synonymy.

Distribution:
British Columbia and Puget Sound;
Strait of Georgia, northeast of Entrance Is. (present work); Friday Harbor (Mackie and Mackie 1963).

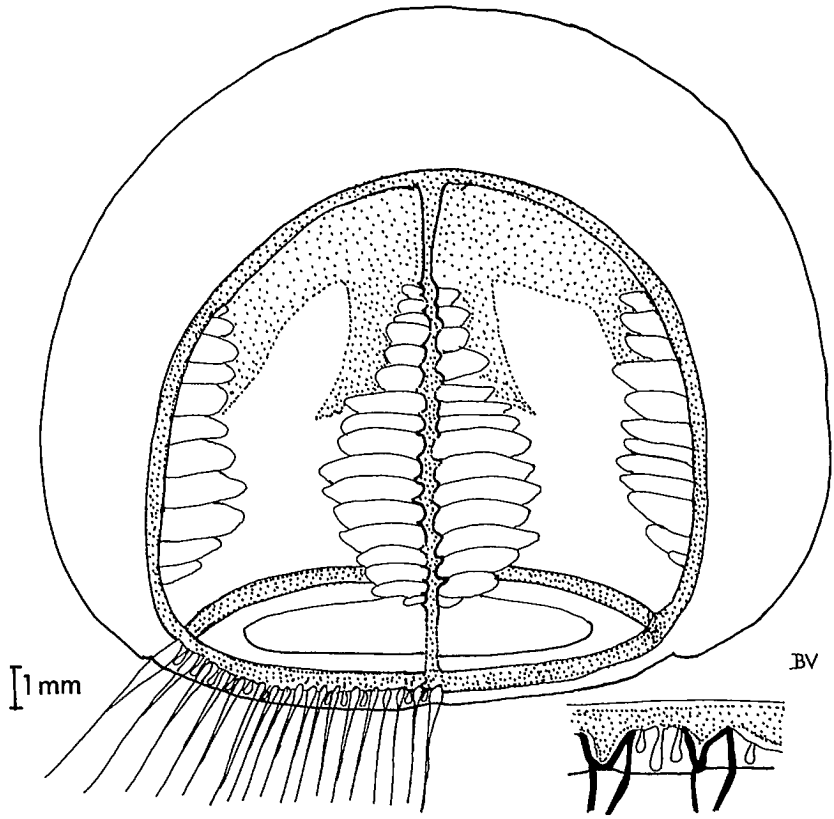


Fig. 46. *Ptychogena lactea*, Friday Harbor (Coll. G. Mackie).

Pacific Ocean;
Bowers Bank, Bering Sea (Bigelow 1913); 54°48'N, 164°54'E, off Bering Island (Bigelow 1913); northwest Pacific Ocean (Naumov 1956a); 46°42'N, 151°45'E, off Simushir Is., Kuril Islands (Bigelow 1913); 44°-46°N, 149°-153°E, Kuril-Kamchatka Trench (Naumov 1971); 46°29'N, 145°46'E, Okhotsk Sea (Bigelow 1913); 42°10'N, 142°15'E, off south Hokkaido (Bigelow 1913).

Atlantic Ocean;
See Whiteaves (1901), Kramp (1919, 1942), Bigelow (1926), Préfontaine and Brunel (1962), and Fraser (1974) for details.

Arctic Ocean;
See Linko (1913), Kramp (1919, 1942), Kamshilov and Zelickman (1958) and Grainger (1965) for details.

Notes: *Ptychogena lactea* is a rare circumboreal species which is most often collected at depths of over 250 m (Naumov 1960, 1971) but may be found near the surface where the water is very cold (e.g. Kramp 1919).

Mackie and Mackie (1963) found mastigophores in the tentacles and manubrium.

Genus *Staurophora* Brandt, 1835

Laodiceidae with four radial canals forming open grooves of the cross-shaped stomach; with gonads hanging in branched diverticula from the radial canals; without marginal cirri; with adaxial ocelli.

Type species: *S. mertensi* Brandt, 1835.

Discussion of genus: *Staurophora purpurea* Foerster, 1923 has been removed from the genus and placed in the Family Mitrocomidae where it is discussed.

Staurophora mertensi Brandt, 1835

Staurophora mertensii Brandt, 1835: 30; 1838: 400, pl. 24, 25; Haeckel, 1879: 149; Browne, 1907: 471; Mayer, 1910: 291, 725, pl. 26; Bigelow, 1913: 27; Kramp, 1914: 420; 1919: 39, pl. 1-3; 1939: 11; Russell, 1953: 239; Kramp, 1957a: 29; 1961: 148; Rutherford, 1962: 199; Hamond, 1964: 665; Russell, 1970: 253.
Staurophora laciniata L. Agassiz, 1849: 300, pl. 7, 8; A. Agassiz, 1862: 89; 1865: 136; Wagner, 1885: 80, pl. 4; Hartlaub, 1897: 484, pl. 16, 22; 1904: 103; Browne, 1907: 472.
Oceania multicirrata Sars, 1851: 158.
Staurophora vitrea Sars, 1863: 399.
Staurophora keithii Peach, 1867: 358, pl. 2.
Staurostoma laciniata Haeckel, 1879: 130; C. Hargitt, 1905: 43.
Staurostoma arctica Haeckel, 1879: 131; Birulya, 1896: 342; Linko, 1900: 4, pl. 2.
Thaumantias melanops M'Intosh, 1890: 40, pl. 8 (non *T. melanops* Forbes, 1848: 45).
Staurophora arctica Browne, 1907: 471.
Staurophora falklandica Browne, 1907: 472; 1908: 235, pl. 1.
Staurophora discoidea Kishinouye, 1910: 29.
Cuspidella humilis Naumov, 1951: 747. (?*C. humilis* Hincks, 1868: 209, pl. 39).
Cuspidella mertensii Naumov, 1960: 300; Zelickman, 1970: 83.

Specific characters: This is the only species of the genus.

Description of medusa: Umbrella up to 300 mm, commonly to 200 mm wide, adult flatter than a hemisphere; mesogloea thick. Four long slit-like arms of mouth with much folded marginal lips. Open portions of radial canals above stomach with numerous short lateral branched diverticula; closed portions of radial canals running to ring canal very short, straight and narrow. Velum very narrow. Numerous short hollow marginal tentacles often spirally coiled; with elongated conical basal bulbs and narrow pointed endodermal spurs. Marginal cordyli approximately alternating with marginal tentacles, with narrow stems, without nematocysts. Gonads, radial canals, and ring canal white or brown; marginal tentacles white or rosy; mouth-lips rosy or yellowish; remainder of umbrella transparent sometimes with bluish tinge; ocelli dark violet or dark brown.

Hydroid: Naumov (1951, 1956b, 1960) designated the hydroid of *Staurophora*

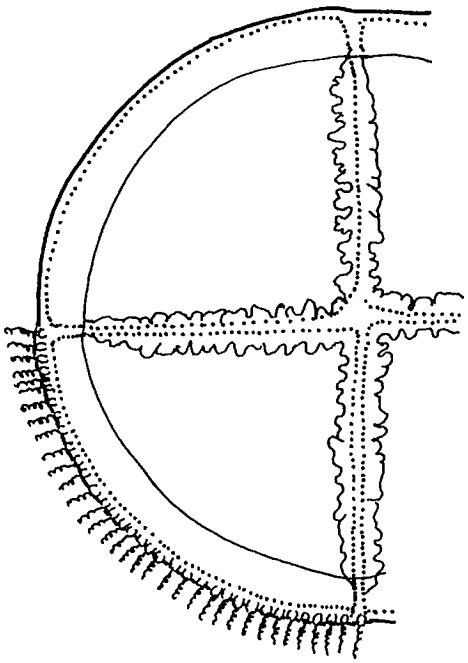


Fig. 47. *Staurophora mertensi* (After Kramp 1968, modified).

mertensi first as *Cuspidella humilis* and then as *Cuspidella mertensii*. As noted by Calder (1970), it is uncertain whether this *Cuspidella* is identical with *C. humilis* Hincks 1868 since other medusae have been raised from very similar hydroids.

Distribution:

British Columbia and Puget Sound;
Friday Harbor (present work, coll. K. Catula and L. Price, Friday Harbor Laboratories).

Pacific Ocean;
Norfolk Sound (i.e. Sitka Sound, S. Alaska) (Brandt 1835; 1838); Pacific Ocean between Sitka and the Aleutian Islands (Brandt 1835; 1838); Prince William Sound (Bigelow 1913); 54°15'N, 158°58'W, Pacific Ocean south of Alaska Peninsula (Murdoch 1885); off Unalaska Island (Brandt 1838); Dutch Harbor, Unalaska Island (Bigelow 1913); off Paramushir Island, Kuril Islands (Kishinouye 1910); Akkeshi Bay, Hokkaido (Uchida 1940; Hada 1972); Busse Lagoon, Aniva Bay (Zelickman 1976); off Chippesani, Sakhalin (Kishinouye 1910); off Chivo, N. Sakhalin (Uchida 1925).

Atlantic Ocean;
See Kramp (1919), Bigelow (1926), Kramp (1939, 1942, 1947, 1955a, 1957a),

Petersen (1957), Lacroix (1963), Edwards (1968), Fraser (1969), Russell (1970) and Fraser (1974) for details.

Arctic Ocean;
See Kramp (1919), Naumov (1960), Uchida (1969), Zelickman (1972) and Kashkin (1976) for details.

Notes: *Staurophora mertensi* is a bipolar neritic species which is usually collected at depths of less than 50 metres.

The movement of the medusa has been described by Brandt (1838), L. Agassiz (1849), Romanes (1876b, 1885) and Rutherford (1962). In addition to the usual symmetrical beat of the undisturbed circular animal, a disturbed specimen may go into "spasm" with strong contraction of the radial muscles to form four distinct lobes or other quadrate configurations. Romanes showed that this "spasm" was not blocked by section of the margin as is the usual beat of hydromedusae. Linko (1900) described the ocelli but also marginal vesicles which have not been found by subsequent investigators (Browne 1908, Kramp 1919).

Feeding behavior has been described by L. Agassiz (1849), Rutherford (1962) and Fraser (1969). Food is ingested anywhere along the cruciform mouth, and digested in that portion of the stomach. *S. mertensi* has been observed feeding on small medusae such as *Sarsia* and young *Aurelia* (L. Agassiz 1849), copepods (Hartlaub 1897, Bigelow 1926, Fraser 1969), and fish larvae (Fraser 1969).

Russell (1940) found microbasic mastigophores on the mouth lips and marginal tentacles.

Family Mitrocomidae

Leptomedusae with four or more radial canals; with or without marginal cirri; with oval open marginal vesicles; with or without ocelli.

Discussion of family: Changes were necessary at the generic level within this family. *Halistaura cellularia* (A. Agassiz 1865) was the type species of the genus *Halistaura* Bigelow 1913. This genus differed from the genus *Mitrocoma* only in the absence of cirri. However, we have confirmed the observation of Mackie and Mackie (1963) that young stages of *Halistaura cellularia* have cirri between adjacent tentacles which are lost in older stages. We have therefore placed the species in the genus *Mitrocoma*, thereby abolishing the genus *Halistaura*. Navas (1969) described *Halistaura bruuni*, the only other species of *Halistaura*, from the Indian Ocean. It is made the type species of a new genus *Foersteria* with characters similar to those previously ascribed to *Halistaura:* four radial canals, numerous marginal vesicles with no ocelli, and lack of marginal cirri.

The species *Staurophora purpurea* Foerster (1923) was found to possess open marginal vesicles characteristic of the family Mitrocomidae and to lack cordyli characteristic of the family Laodiceidae in which it had been placed. It is also placed in the new genus *Foersteria* as it possesses the generic characters.

Genus *Foersteria* gen. nov.

Mitrocomidae with four radial canals; with numerous marginal vesicles; without ocelli; without marginal cirri.

Type species: *F. bruuni* (Navas, 1969).

Foersteria purpurea (Foerster, 1923) comb. nov.

Staurophora purpurea Foerster, 1923: 32, pl. 4; Kramp, 1961: 149.
Staurophora sp. Brinckmann-Voss 1974 (Acc. No. 169).
?Cosmetirella davisi Brinckmann-Voss, 1974 (Acc. No. 246) (non *Tiaropsis davisii* Browne, 1902).

Specific characters: Gonads curtain-like, split longitudinally. Lips highly folded.

Description of the species: Umbrella up to 30 mm wide, hemispherical. Stomach small, hanging on short peduncle, with four perradially elongated highly folded lips. Margin with about 120 tentacles and more than 40 open marginal vesicles. Color of living specimens, manubrium, stomach and lips dark purple, radial canals and gonads light purple.

Hydroid: not known.

Discussion of taxonomy: Foerster (1923) described this species and placed it in the family Laodiceidae because of some similarity to *Staurophora mertensi*. Kramp (1961) left it provisionally in the Laodiceidae with the remark "systematic position doubtful". The specimen which Foerster described was found in the Pacific Biological Station collections in very poor condition (Brinckmann-Voss, 1974 Acc. No. 169). Neither Foerster's description nor his specimen show the marginal cordyli typical for the Laodicidae. Foerster included a drawing showing what he believed to be statocysts of this specimen. However, the size of these structures in relation to the tentacles seems to indicate that they were not statocysts at all, but broken tentacles. Unfortunately, the single specimen was so damaged that the statocysts could not be found on reexamination. We got four specimens in recent collections in the same central area of the Strait of Georgia which, apart from statocysts, match the text of Foerster's description of *Staurophora purpurea*. However, the statocysts in our specimens were clearly of the "open" type of the Mitrocomidae. For reasons given in the discussion of the family, this species is placed in a new genus *Foersteria*, the type species of which is *Foersteria bruuni* (Navas 1969) n. comb.

Distribution:
British Columbia and Puget Sound;
Strait of Georgia, northeast of Five Finger Is. (present work); Strait of Georgia, north of Entrance Is. (Foerster 1923; Brinckmann-Voss 1974); Skidegate Channel (Brinckmann-Voss 1974).

Note: The five specimens collected in the Strait of Georgia were all obtained in tows to over 350 m in July and August.

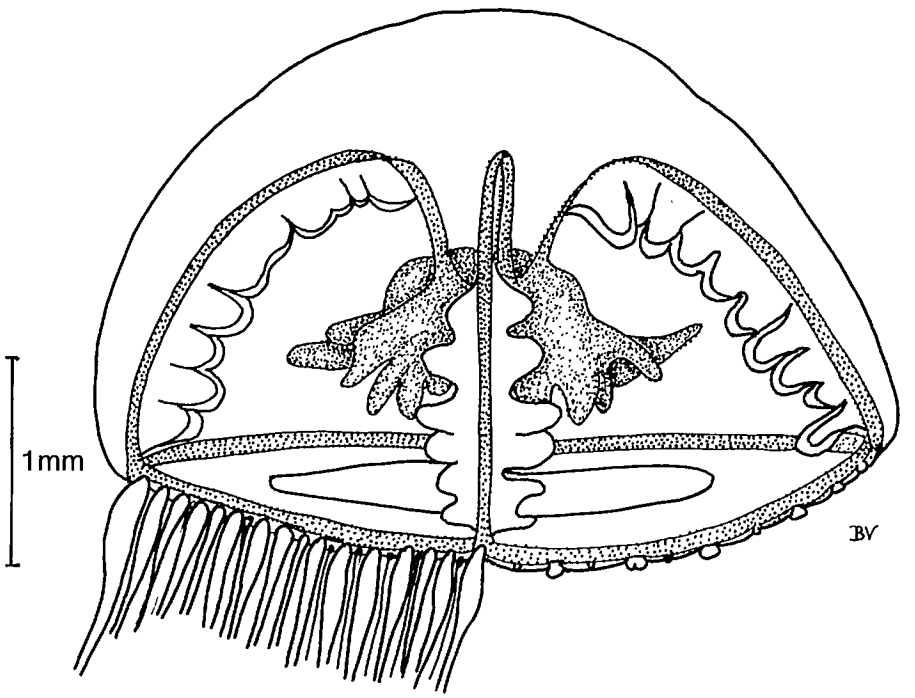


Fig. 48. *Foersteria purpurea*, Strait of Georgia.

Genus *Mitrocoma* Haeckel, 1864

Mitrocomidae with four radial canals; with numerous marginal vesicles; without ocelli; with marginal cirri which coil spirally.

Type species: *M. annae* Haeckel, 1864.

Mitrocoma cellularia (A. Agassiz, 1865)

Laodicea cellularia A. Agassiz (in L. Agassiz), 1862: 350; 1865: 127.
Thaumantias cellularia Haeckel, 1879: 129; Murbach and Shearer, 1903: 172, pl. 17.
Halistaura cellularia Bigelow, 1913: 30; Foerster, 1923: 254, pl. 5; Kramp, 1932: 362; Mackie and Mackie, 1963: 71.
Mitrocoma cellularia Harvey, 1921: 280.
Mitrocoma discoidea Foerster, 1923: 253 (in part, non *M. discoidea* Torrey, 1909); Kramp, 1932 (in part); Brinckmann-Voss 1974 (Acc. No. 166).

Specific characters: 1 to 3 cirri between marginal tentacle bulbs in young stages; perradial, very elongated lips; up to 60 statocysts, normally 16-24.

Fig. 49. *Mitrocoma cellularia*, umbrella margin. Photo. M. N. Arai.

Description of species: Umbrella near watch glass shape, up to 100 mm wide. Stomach small, quadrangular, with slender, very elongated crenulated lips. Gonads on nearly entire length of radial canals, starting as thin enlargements and becoming mature only with a bell diameter of 40 to 50 mm. Marginal tentacles number up to 340. With one to three spiral cirri between marginal tentacles or developing tentacles in young stages, lost except for small "stumps" when the animal reaches maturity. Number of statocysts variable, ranging from 0 to 6, rarely to 15 per quadrant, total complement per medusa being most commonly 16 to 24. Living animals varying from almost colorless with a blue-white tinting of the gonads to a pale blue umbrella with manubrium, gonads and tentacular bulbs of deeper shades of violet-blue.

Hydroid: not known.

Discussion of taxonomy: Taxonomic workers examining the statocysts of *Mitrocoma cellularia* with light microscopy found that the species possessed the open marginal vesicles characteristic of the family Mitrocomidae (Bigelow

1913). Singla (1975) using electron microscopic methods found that although the *M. cellularia* statocysts resemble those of *Tiaropsis multicirrata* and *Mitrocomella polydiademata* in being covered on the outside by vacuolated cells, they are closed by a thin epithelium. Since relatively few members of the family have as yet been examined by electron microscopy it is premature to separate species based on closed vesicles as seen by these methods and we have therefore retained *Mitrocoma cellularia* in the Mitrocomidae.

As noted above in the discussion of the family, Mackie and Mackie (1963) showed that young specimens possess cirri between adjacent tentacles which are lost in mature specimens. We have confirmed this observation. The species has therefore been placed in the genus *Mitrocoma*, from which it was previously separated only by a lack of marginal cirri.

As previously noted by Kramp (1932) *Mitrocoma cellularia* resembles *Mitrocoma discoidea* Torrey 1909. We have reexamined the specimens of *Mitrocoma discoidea* described by Foerster (1923) in the Pacific Biological Station collections and can find no characters to distinguish these specimens from *Mitrocoma cellularia*. We have hesitated, however, to fully synonymize *Mitrocoma discoidea*. Torrey's (1909) original description of *M. discoidea* was based on specimens from California. The description is brief but the diagram shows lips which are shorter than those typical of *M. cellularia*, where the very elongated lips are one of the most characteristic features. He also mentions a yellow-green ring canal, which has not been observed in *M. cellularia*. In the absence of Californian specimens *M. discoidea* of Torrey (1909) is therefore kept tentatively as a separate species.

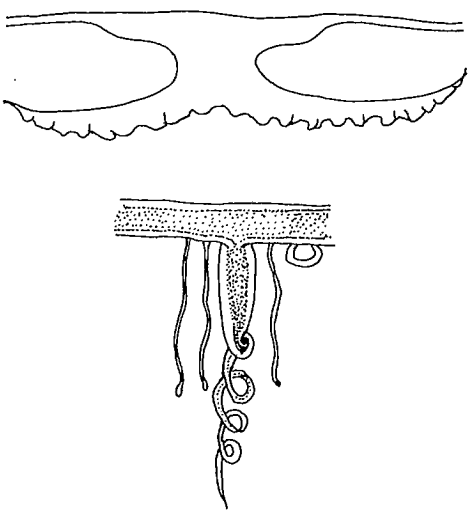


Fig. 50. *Mitrocoma cellularia*, details of mouth and margin.

MacGinitie (1955) extends the range of this species from the Pacific Ocean into the Arctic Ocean at Point Barrow, Alaska. However, no morphological data are given and the color is described as "with peach colored canals" so this identification must be treated with caution.

Distribution:

British Columbia and Puget Sound;

Strait of Georgia (A. Agassiz in L. Agassiz 1862, 1865); Strait of Georgia, off Mitlenatch Island (Brinckmann-Voss 1974); Strait of Georgia, north of Five Finger Island (Foerster 1923); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); off Nanaimo (Kramp 1932); off Gabriola Island (Foerster 1923); Ladysmith Harbour (present work); Porlier Pass (Brinckmann-Voss 1974); Strait of Georgia, north of Active Pass (Brinckmann-Voss 1974; present work); Cowichan Bay (present work); Tod Inlet, Saanich Inlet (Foerster 1923; Brinckmann-Voss 1974); Friday Harbor (Murbach and Shearer 1903; Bovard and Osterud 1918; Harvey 1921; Foerster 1923; Johnson and Snook 1927; Hyman 1940; Davenport and Nicol 1955; Mackie and Mackie 1963; Shimomura et al 1963c; Lenhoff 1964; Mackay 1969; Singla 1972; Brinckmann-Voss 1974; present work); Puget Sound (Murbach and Shearer 1903; Bigelow 1913); Puget Sound off Port Townsend (Agassiz 1865); Victoria Harbour (Murbach and Shearer 1903); Sooke Harbour (present work); Juan de Fuca Strait, off Sheringham Point (Brinckmann-Voss 1974); Pacific Ocean 5.5 km south of Swiftsure Bank (Brinckmann-Voss 1974); Barkley Sound (Brinckmann-Voss 1974); Pacific Ocean, off Rafael Point, Flores Island (Brinckmann-Voss 1974); Pacific Ocean, off Nootka Sound (present work); Forward Inlet, Quatsino Sound (present work); Quatsino Sound, off Drake's Island (Brinckmann-Voss 1974); Houston Stewart Channel (present work); Skidegate Channel (Brinckmann-Voss 1974); Cartwright Sound, off Marble Island (Brinckmann-Voss 1974).

Pacific Ocean;

Pacific Ocean off Oregon (Pearcy 1972); Pacific Ocean, 47°45'N; 125°15.8'W (present work); Pacific Ocean, 47°44.7'N; 125°15.6'W (present work); Pacific Ocean, off Southern Alaska (Bigelow 1913).

Notes: Child (1918) showed decrease in pulsation rate and susceptibility to HCl and KNC with increasing age for *Mitrocoma discoidea* from Friday Harbor i.e. probably *Mitrocoma cellularia*. Gladfelter (1973) noted the broad bell with marginal creases and the weak swimming muscle. Even a light touch may induce "crumpling" behavior (Hyman 1940).

The margin of the bell shows bluish-green bioluminescence arising from a nearly continuous line of yellowish tissue near the circular canal (Harvey 1921, Davenport and Nicol 1955). The response is local, elicited by direct mechanical or electrical stimulation. The bioluminescent protein halistaurin has been extracted, purified, its spectra characterized, and shown to be activated by calcium or strontium ions (Shimomura et al 1963c).

Puget Sound specimens contain 96.5 to 96.6% water (Hyman 1940). The sulphate ion concentration of the mesogloea is maintained lower than that of seawater (Mackay 1969).

The only data on feeding is the observation of Hyman (1940) that specimens may be caught containing small polychaetes. Nematocysts include large and small basitriches and large and small atriches (Mackie and Mackie 1963).

Specimens of *M. cellularia* have been collected May to December. During June to August it is one of the most common and conspicuous medusae for the research area. However, it is very delicate and difficult to keep in the laboratory.

Genus *Mitrocomella* Haeckel, 1879

Mitrocomidae with four radial canals; with 8-16 marginal vesicles; without ocelli; with marginal cirri which coil spirally.

Type species: *M. polydiademata* (Romanes, 1876).

Mitrocomella polydiademata (Romanes, 1876)

Tiarops polydiademata Romanes, 1876a: 525.
Tiaropsis polydiademata Romanes, 1876b: 274; 1877a: pl. 15.
Mitrocomella polydiadema Haeckel, 1879: 185; Browne, 1895: 279; 1910: 33.
Mitrocomella fulva Browne, 1903: 17, pls. 1, 3 (in part).
Mitrocomella polydiademata Browne, 1905a: 767; Kramp, 1932: 346, pl. 10; 1961: 156; Mackie and Mackie, 1963: 73; Yashnov, 1970: 1780; Edwards, 1973a: 601.
Mitrocoma polydiademata Mayer, 1910: 290; Kramp, 1919: 59.
Mitrocoma cruciata Bigelow, 1915b: 320 (non *Halopsis cruciata* A. Agassiz, 1865); 1926: 348.
Mitrocoma (Mitrocomella) fulva Sanderson, 1930: 226.
Cuspidella polydiademata Naumov, 1960: 302.

Specific characters: Gonads not divided longitudinally, occupying most of the radial canals leaving only upper one-third to one-fifth of radial canals gonad free. Adult specimens with 25-48 marginal tentacles (to 64 in NW Atlantic waters); 4-20 marginal cirri between adjacent tentacles; 10-19 (usually 16) marginal vesicles.

Description of medusa: Umbrella flat bell-shaped, adults commonly 9-20 mm, rarely to 30 mm wide. Stomach small. Mouth with four elongated, slightly folded lips. Gonads not divided longitudinally; however, a thin median line can be seen. One to two marginal bulbs between adjacent tentacles. Cnidocysts along whole length of marginal cirri. Manubrium, gonads and marginal tentacle bases rosy to purplish, or (less often) yellowish brown in living specimens.

Hydroid: Raised from medusae by Edwards (1973a).

Distribution:

British Columbia and Puget Sound;
Departure Bay (present work); Cowichan Bay (present work); Brentwood Bay, Saanich Inlet (present work); Friday Harbor (Mackie and Mackie 1963; Singla 1972); Sooke Harbour (present work).

Atlantic Ocean;
See Kramp (1919, 1932, 1947), Bigelow (1926), Sanderson (1930), Runnström (1932), Werner (1959) and Fraser (1974) for details.

Arctic Ocean;
See Yashnov (1970), Zelickman (1972) and Shih and Laubitz (1978) for details.

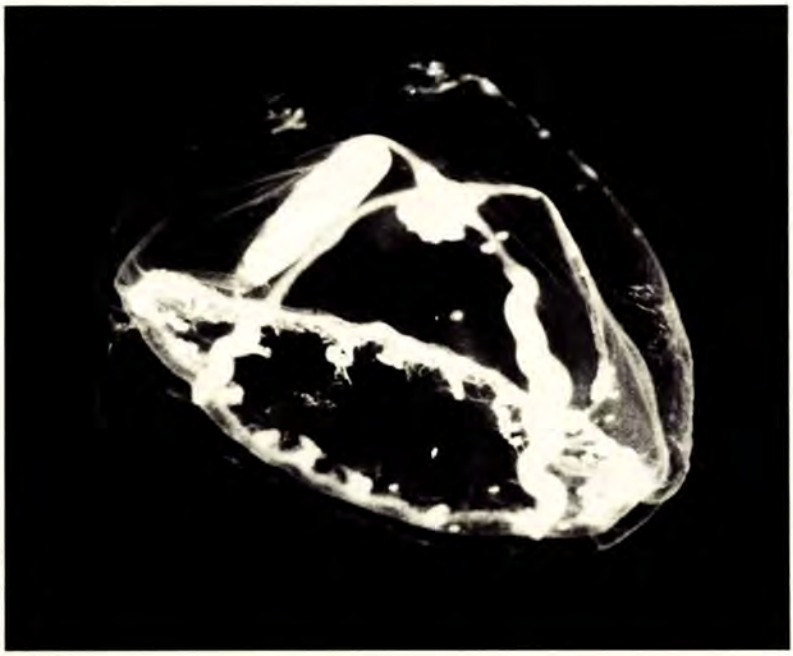


Fig. 51. *Mitrocomella polydiademata*, preserved specimen, 9.1 mm diam., Departure Bay. Photo. M. N. Arai.

Notes: Romanes (1876a) and Browne (1895) noted that *Mitrocomella polydiademata* is luminescent around the margin of the umbrella when stimulated. The swimming muscle is weak (Gladfelter 1973), and the animal contracts in response to light stimulation (Romanes 1885). The structure of the open statocysts was described by Singla (1975).

Mackie and Mackie (1963) found large and small basitrichs and large and small atrichs.

In British Columbia waters *Mitrocomella polydiademata* has been collected April to July, being most frequently present late May to early June.

Mitrocomella sinuosa (Foerster, 1923)

Mitrocoma sinuosa Foerster, 1923: 35, pl. 4; Brinckmann-Voss 1974 (Acc. No. 167).
Mitrocomella sinuosa Kramp, 1932: 343.

Specific characters: Gonads divided longitudinally, along distal half of radial canals. About 50 marginal tentacles; 3-5 marginal cirri between adjacent tentacles; 12 marginal vesicles.

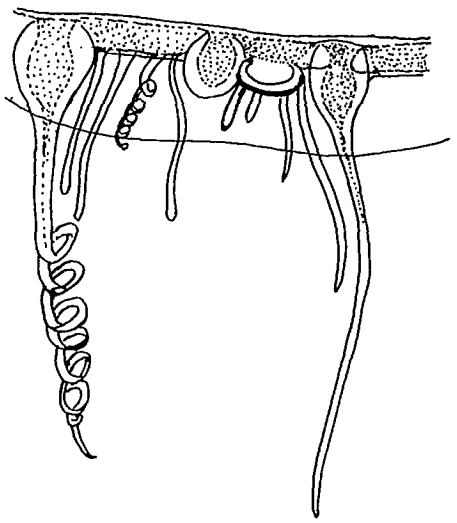


Fig. 52. *Mitrocomella polydiademata*, detail of margin.

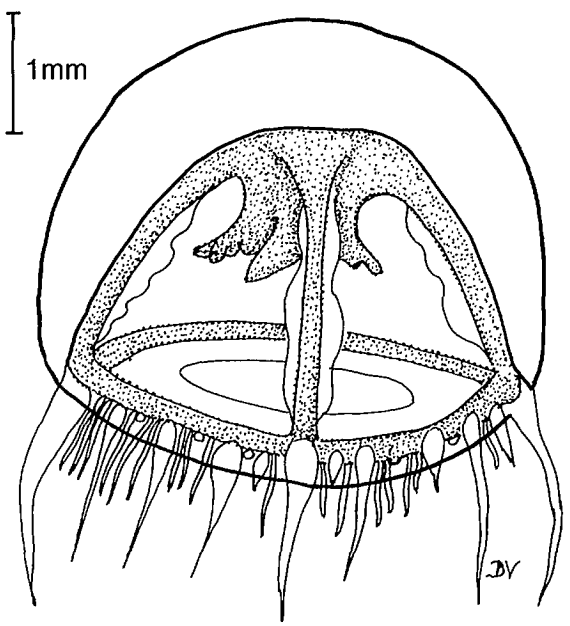


Fig. 53. *Mitrocomella sinuosa*, Strait of Georgia, north of Five Finger Island.

Description of medusa: Umbrella 4 mm wide. Stomach wide. Mouth with four recurved lips. Tentacles with thick, conical basal bulbs.

Hydroid: not known.

Discussion of taxonomy: Foerster (1923) based this species on a single specimen. Brinckmann-Voss (1974) reexamined the same specimen from the Pacific Biological Station collection. Although the specimen is in poor condition we could see the divided gonads which distinguish this species from other species of *Mitrocomella*.

Distribution:
British Columbia and Puget Sound;
Strait of Georgia, north of Five Finger Is. (Foerster 1923; Brinckmann-Voss 1974).

Notes: The single specimen was obtained June 27, 1921.

Genus *Tiaropsidium* Torrey, 1909

Mitrocomidae with four or more (up to 16) radial canals; with 8, 16 or 48 marginal vesicles, each with an ocellus; with two kinds of tentacles; without marginal cirri.

Type species: *T. kelseyi* Torrey, 1909.

Tiaropsidium kelseyi Torrey, 1909

Tiaropsidium kelseyi Torrey, 1909: 19; Foerster, 1923: 255; pl. 4; Kramp, 1932: 370.
Tiaropsis kelseyi Browne, 1910: 33; Mayer, 1910: 494.

Specific characters: Medusae with 8 marginal vesicles; with 8 tentacles; with 12-32 rudimentary tentacles per quadrant.

Description of medusa: Umbrella about two to three times as broad as high, to 50 mm wide. Manubrium small, short, with thin walls and slightly fringed lips. Gonads narrow, curtain-like, much folded in larger specimens, and along nearly entire length of radial canals. Four large perradial and four similar interradial tentacles with bulbous bases. Manubrium and gonads pale yellow, ocelli black.

Hydroid: not known.

Discussion of taxonomy: In addition to the structures described by Torrey (1909) after examining many specimens, Foerster (1923) noted numerous hollow, coiled "tentacular" processes from the proximal part of each radial canal. Foerster (1923) based his description on a single specimen, which is no longer present in the Pacific Biological Station collections (Brinckmann-Voss 1974). We have not collected any specimens of this species so we are not able to evaluate whether these were abnormal structures as suggested by Kramp (1932).

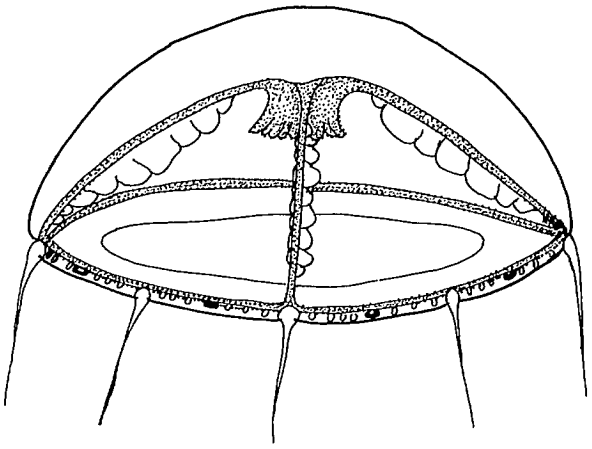


Fig. 54. *Tiaropsidium kelseyi* (after Torrey 1909, modified).

Distribution:
British Columbia and Puget Sound;
Tod Inlet, Saanich Inlet (Foerster 1923).
Pacific Ocean;
Pacific Ocean, off San Diego to Monterey (Torrey 1909).

Genus *Tiaropsis* Agassiz, 1849

Mitrocomidae with four radial canals; with eight marginal vesicles each with a basal ocellus; with only one kind of tentacle; without marginal cirri.

Type species: *T. multicirrata* (M. Sars, 1835).

Tiaropsis multicirrata (M. Sars, 1835)

Thaumantias multicirrata Sars, 1835: 26, pl. 5.
Thaumantias melanops Forbes, 1848: 45, pl. 10.
Tiaropsis diademata L. Agassiz, 1849: 289, pl. 6; 1862: 308, pl. 31; A. Agassiz, 1862: 92; 1865: 69; Haeckel, 1879: 178; Linko, 1899: 143, 154, pl. 1; Mayer, 1910: 258, pl. 31, 32; Bigelow, 1913: 33.
Thaumantias pattersonii Green, 1857: 245, pl. 14.
Tiaropsis multicirrhata L. Agassiz, 1862: 355.
Tyaropsis scotica Allman, 1871: 140.
Tiaropsis scotica Böhm, 1878: 183, pl. 2.
Thaumantias eschscholtzii Haeckel, 1879: 129, pl. 8.
Tiaropsis multicirrata Haeckel, 1879: 179; Browne, 1895: 278; 1905a: 773, table 2; Mayer, 1910: 259; Le Danois, 1913a: 22; Kramp, 1919: 77, pl. 4; Sanderson, 1930: 227; Kramp, 1932: 364; Rees, 1941: 138; Russell,

Fig. 55. *Tiaropsis multicirrata*, live specimen, 18.3 mm diam., Departure Bay. Photo. M. H. Arai.

1953: 278, pl. 17; Kramp, 1955a: 156; Chow and Huang, 1958: 178, pl. 2; Naumov, 1960: 328; Zelickman et al 1969: 167; Zelickman, 1972: 259.
Cuspidella mollis Spasskii, 1929: 13, pl. 2.

Specific characters: This is the only species of the genus.

Description of medusa: Relaxed umbrella of adult flatter than a hemisphere, up to 24 mm wide. Stomach short. Mouth with perradial, elongated, much folded lips. Gonads occupying nearly whole length of radial canals in older specimens, only the center part of radial canals in younger specimens. Margin with up to 330 equal tentacles. Two black ocelli per quadrant with an oval shaped statocyst beneath each ocellus. Color of living specimens, stomach, gonads and marginal tentacle bases dull yellow tinged with varying amounts of black (which fades in preserved specimens).

Hydroid: Originally described as *Cuspidella mollis* by Spasskii (1929), the primary hydroid has been reared from planulae by Korsakova (1949) and Naumov (1951, 1960). Rees (1941) also found the polyps with gonangia and established their identity based on a medusa released from a gonotheca.

Distribution:
British Columbia and Puget Sound;
French Creek boat basin (present work); Departure Bay (present work); Pedder

Bay (Singla 1972).

Pacific Ocean;

Dutch Harbor, Aleutian Islands (Bigelow 1913); off Agattu Island, Aleutian Islands (Bigelow 1913); Okhotsk Sea (Yashnov 1948); Yellow Sea (Chow and Huang 1958).

Atlantic Ocean;

See Kramp (1919), Fish (1925), Pinhey (1927), Sanderson (1930), Watson (1930), Kramp (1932), Runnström (1932), Fish and Johnson (1937), Russell (1938b), Kramp (1942), Künne (1952), Russell (1953), Petersen (1957), Hamond (1964), Lacroix (1966), Boyd et al (1973) and Fraser (1974) for details.

Arctic Ocean;

See Kramp (1919), Yashnov (1939), Grainger (1959, 1962), Zelickman (1972) and Grainger and Grohe (1975) for details.

Notes: The variation in form from very flat to globular during swimming of *Tiaropsis multicirrata* was first described by L. Agassiz (1849) and related to the muscular system. It was more recently redescribed by Zelickman (1969) who emphasized the subquadrate appearance of the strongly contracted medusa. Zelickman (1969) also noted a highly pronounced positive photokinesis. The structure of the eight ocelli and statocysts have been investigated by several authors (L. Agassiz 1849, 1862, Agassiz and Mayer 1899, Linko 1899, Singla 1974, 1975). Each ocellus consists of an endodermal cup of pigment cells over ectodermal receptor cells connected to the subumbrellar nerve ring. The statocysts are of the open type characteristic of the Mitrocomidae.

The medusae have been observed feeding on ephyrae, *Bolinopsis*, *Rathkea octopunctata*, other *Tiaropsis multicirrata*, cladocera, copepods, cyprid larvae, larval molluscs, nectochaetes, larvacea, echinoderm larvae, capelin larvae and decayed animal matter (Agassiz 1849, Plotnikova 1961, Zelickman 1969, Zelickman et al 1969). They have also been shown to assimilate C^{14} - labeled algal metabolites (Erokhin 1971, 1975). Mass aggregations of the medusae in the Jarnyshnaya Fjord of the Barents Sea area have been described by Zelickman and her co-workers (Zelickman 1969, 1972, Zelickman et al 1969). She suggests that dissolved metabolites may act as an additional food source when the zooplankton supply is low but that when particulate food is abundant the growth rate and rate of maturation increase greatly.

Natochin et al (1971) showed that the medusae placed in a variety of solutions were able to concentrate K and Na, and that volume regulation depended on the level of hydration of the mesogloea and the retention of Na.

The hydroid is very common at the wharfs of Departure Bay and French Creek, where it grows on the stems of other hydroids or algae. The youngest stages of the medusae, easily distinguished by the eight ocelli, are very common during the second half of March in Departure Bay, adults being collected to early June.

Family Campanulariidae

Leptomedusae with typical or reduced velum; normally with four simple or dilated radial canals; without excretory pores; with gonads separated from stomach; with or without peduncle which if present never exceeds 1/4 of subumbrellar cavity; without marginal or lateral cirri; with closed marginal

vesicles; gonad without median groove. Hydroid usually with bell-shaped hydrotheca, without operculum, hydranth with club- or trumpet-shaped manubrium.

Genus *Obelia* Peron and Lesueur, 1809

Campanulariidae with almost flat eversible umbrella; with reduced velum; with solid marginal tentacles; with eight lithocytes.

Discussion of genus: Many hydroid and medusae species of *Obelia* have been described. Cornelius (1975) has recently reduced the hydroid species to three very widespread forms; *Obelia bidentata* Clark, 1875, *O. dichotoma* (Linné, 1758) and *O. geniculata* (Linné, 1758). All three have been described from the present research area (see Fraser 1937 for summary of earlier papers). *O. dichotoma* (usually reported as *O. longissima*) is the commonest campanularian in the Vancouver Island region. The medusae of the three hydroid species cannot at present be distinguished (Russell 1953, Cornelius 1975). We have therefore followed the usual practice of more recent systematists such as Kramp (1961) and avoided a specific name for the medusae.

Obelia spp.

As discussed above it is not possible to make a clear distinction between species of *Obelia* medusae. The following therefore simply lists the names under which *Obelia* medusae from the research area have been described;
Obelia longissima Fraser, 1914: 153; Foerster, 1923: 39.
Obelia sp. Foerster, 1923: 40.

Description of medusa: Umbrella up to 6 mm wide, mesogloea thin; velum rudimentary. Stomach short, with quadrangular base, without peduncle. Mouth with four short simple perradial lips. Four straight radial canals. Gonads round, one on middle of each radial canal. Marginal tentacles 16+ on release, numerous in adult specimens, short, solid, somewhat stiff, with axial core of single row of endoderm cells, each with small basal bulb and a short prolongation of endoderm into mesogloea of umbrella margin. Eight adradial lithocytes, each situated on underside of basal bulb of marginal tentacle, each with one concretion. Color of bases of marginal tentacles, gonads and stomach various shades of yellow and brown; in present research area gonads and manubrium often bright green.

Hydroid: see discussion of genus.

Distribution:
British Columbia and Puget Sound;
Deep Bay (present work); French Creek boat basin (present work); Departure Bay (Fraser 1914; Foerster 1923; Smith 1933; present work); Nanaimo Region (Fraser 1932); Dodd Narrows (Foerster 1923; Brinckmann-Voss 1974); Ladysmith Harbour (present work); off Penelakut Spit, Kuper Is. (Smith 1933); Sidney Channel, near Sidney (Smith 1928); San Juan Archipelago (Fraser 1932); Sooke Harbour (present work); Ucluelet Inlet (present work).

Notes: In the Strait of Georgia area *Obelia* medusae have been collected from March to September and are common April to June.

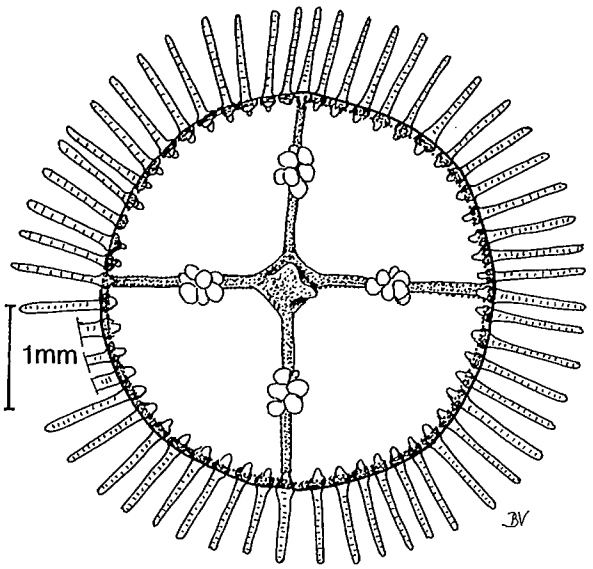


Fig. 56. *Obelia* sp., Sooke Harbour.

Genus *Orthopyxis* L. Agassiz, 1865

Campanulariidae with medusae, when present, very short lived, usually only observed when liberated from hydroids in the laboratory. Medusae without manubrium and without marginal tentacles; with four radial canals with or without lateral dilations; with gonads either situated on lobed protuberances of radial canals or bandlike along radial canals; with eight adradial statocysts. Hydroid unbranched campanularid with hydrotheca with walls thickened to variable degree; often half or more the width of the internal cavity in thickness.

Type species: *O. caliculata* (Hincks, 1853).

Orthopyxis compressa (Clark, 1876)

Campanularia compressa Clark, 1876: 214, pl. 8; ? Hartlaub, 1905: 562; non Jäderholm, 1905: 14, pl. 5; Linko, 1911: 172 (in part); Behner, 1914: 384 (in part); Naumov, 1960: 256 (in part).
Eucopella campanularia von Lendenfeld, 1883: 497, pl. 27-32 (in part).
Campanularia caliculata Calkins, 1899: 351, pl. 2, 6 (non *C. caliculata* Hincks, 1853: 168).
Clytia compressa Nutting, 1901b: 170, pl. 17; non Torrey, 1902: 58, pl. 6; ? Vanhoffen, 1910: 303.
Eucopella caliculata Fraser, 1911: 36; 1914: 147, pl. 14; 1937: 77, pl. 15 (in part).

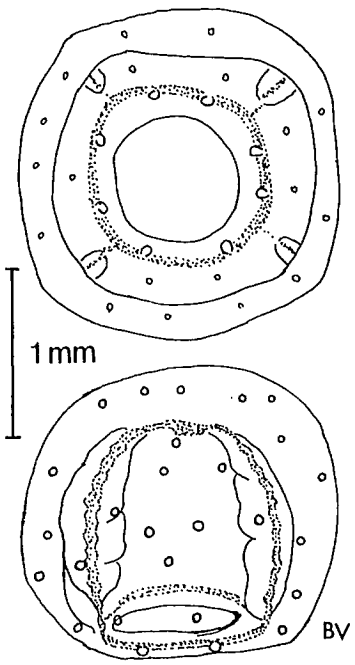


Fig. 57

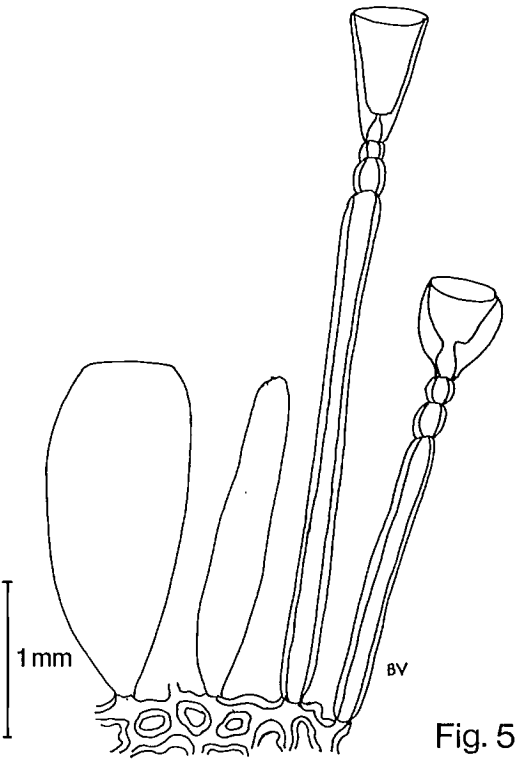


Fig. 58

Fig. 57. *Orthopyxis compressa*, Friday Harbor (Coll. R. Miller).

Fig. 58. *Orthopyxis compressa*, hydroid, Friday Harbor (Coll. R. Miller).

Eucopella compressa Fraser, 1911: 37 (in part); 1937: 78, pl. 16 (in part).
Orthopyxis compressa Bale, 1914: 80; Nutting, 1915: 65, pl. 15 (in part); Stechow, 1919: 69 (in part).
Orthopyxis caliculata Nutting, 1915: 64, pl. 15 (in part, non *O. caliculata* Bale, 1914: 74, pls. 11, 12); Miller, 1978: 385.
Campanularia integra Broch, 1918: 159 (in part, non *C. integra* MacGillivray, 1842: 465).
Orthopyxis pacifica Stechow, 1919: 69.

Specific characters: Medusae with nearly straight radial canals; gonads in thick banks on both sides of radial canals, often filling entire space between them. Hydroids with laterally flattened gonothecae; with long hydrocauli; with stem of hydranth smooth except for up to 3 (rarely to 6) constrictions immediately below hydranth; hydrotheca with smooth margin.

Description of medusa: Umbrella of preserved specimens 1.5 to 1.7 mm wide, nearly globular, with scattered cnidocysts on exumbrella. Velum 1/3

of marginal opening. Ring canal much thinner than radial canals with hardly any connection between ring canal and radial canals. Radial canals filled with yellow pigment granules.

Hydroid: See discussion of taxonomy.

Discussion of taxonomy: The very entangled *Orthopyxis* - group of species is in urgent need of revision. Such a revision is outside the scope of the present work. *Orthopyxis compressa* was first described as *Campanularia compressa* by Clark (1876) from the Shumagin Islands, Alaska. He described gonothecae "very much compressed laterally," hydrothecae with "rim entire" on pedicels "with a single well-marked annulation at the base of the hydrothecae and usually two or three constrictions just beneath the annulation, not annulated at the base." The diagrams show a smooth stem below the constrictions. Since then the specific name has been applied to a number of forms which differ in one or more characters.

In the north Pacific the original form has been recorded from Orca, Alaska (Nutting 1901b), Friday Harbor (present work) and Sakhalin (Linko 1911). However, Torrey (1902, 1904) included California specimens which had hydrothecae with "wavy" or "crenate" margins. Fraser (1948) listed collecting records for California but gave no morphological data.

In the southern Pacific Bale (1914) recorded *Orthopyxis compressa* from Australia which had the characters of the original description.

Jäderholm (1905) described Tierra del Fuego specimens with ringed or twisted peduncles as *Campanularia compressa*. Hartlaub (1905) described specimens with smooth pedicels from Chile but did not observe any gonangia. Vanhöffen (1910) included smooth and ringed specimens from South Africa. Millard (1966) states that the South African material shows intergrading forms between *Campanularia caliculata* and *C. compressa*. It is doubtful that any of these forms are actually *Orthopyxis compressa*.

In the Mediterranean area Müller (1913) reported *Campanularia compressa* var. *napoletana* from Naples. Behner (1914) described *Campanularia compressa* from the same locality with a number of rings on the pedicel of the hydrotheca and with a "breit-oval" gonotheca. He designated the medusa produced by this form *Agastra rubra*. Stechow (1919) notes the similarity of Mediterranean *Orthopyxis compressa* to *O. caliculata* but maintains the two forms separate on the basis of the form of the gonotheca. Stefani (1956) found intermediate gradations in the gonophore shape, therefore considered Mediterranean *O. compressa* synonymous with *O. caliculata*. Our own observations of *Orthopyxis* specimens from Naples support this conclusion.

It is not clear whether *Orthopyxis caliculata* (Hincks 1853) is also present in the present research area. Hincks (1853, 1868) described an Irish form, *Campanularia caliculata*, as having a pedicel "with a single well-marked ring immediately below the calycle, and crenated or faintly annulated from this point to the base", hydrotheca "campanulate with an even rim", gonotheca "of an irregular oval shape, having somewhat wavy outline, truncate at the top, and with a wide aperture". The pedicel could have from 9 to 30 "crenations, rings or slight waves". He believed his species to be synonymous with *Campanularia brevicyphia* Sars 1857 from the Mediterranean and *Clytia*

(Orthopyxis) poterium L. Agassiz, 1862 from Massachusetts. Since then this specific name has been applied to forms in many parts of the world.

Calkins (1899) described, as *Campanularia caliculata*, specimens from Puget Sound which had "one well-marked ring immediately behind the hydrotheca; occasionally one or more irregular segments below the ring - while from here down the stem is perfectly smooth". The gonotheca had a "decidedly flattened form" truncate at the end. Fraser (1911, 1914, 1932, 1936, 1937) listed the common form as *Eucopella caliculata*. He stated the pedicel of the hydranth was "slightly wavy or annulated with a distinct double annulation below the hydrotheca". However, his diagrams (such as Fig. 45, plate XIV, Fraser 1914) show a smooth pedicel below the first few rings. Bale (1914) and Nutting (1915) both questioned whether Calkins (1899) had described *C. caliculata*. Stechow (1919) reexamined specimens of *Eucopella caliculata* from Vancouver sent to him by Fraser. He concluded they differed from *Orthopyxis caliculata* and the *O. compressa* of the Mediterranean. He described a new species *Orthopyxis pacifica* with the same characters as *O. compressa* Clark, i.e., with the pedicel of the hydranth smooth except for constrictions immediately below the hydrotheca and a flattened gonotheca. *O. pacifica* is therefore a junior synonym of *O. compressa* Clark. Miller (1978) included a photograph of a female medusa collected off the Friday Harbor dock which he reported as *Orthopyxis caliculata*. He allowed us to examine specimens of male medusae and hydroids and photographs of female medusae which he had collected June 1977 at Friday Harbor and we identified them as *O. compressa*.

Distribution:
British Columbia and Puget Sound;
Friday Harbor (Miller 1978; present work).

Notes: Lacking manubrium and marginal tentacles, the medusae live only a few hours and die after shedding eggs or sperm. Miller (1978) showed that the egg produces a species-specific sperm attractant.

Genus *Phialidium* Leuckart, 1856

Campanulariidae with normal velum; with hollow marginal tentacles. Adults with more than eight marginal vesicles.

Type species: *P. hemisphaericum* (Linné, 1767).

Phialidium gregarium (A. Agassiz, 1862)

Oceania gregaria A. Agassiz (in L. Agassiz), 1862: 353; 1865: 74.
Phialidium gregarium Haeckel, 1879: 188; Murbach and Shearer, 1903: 179, pl. 20; Strong, 1925: 391, pl. 37; Roosen-Runge, 1962: 15; Kramp, 1962b: 25; Roosen-Runge and Szollosi, 1965: 41; Roosen-Runge, 1970: 217.
Phialidium languidum Murbach and Shearer, 1903: 179 (non *Oceania languida* A. Agassiz (in L. Agassiz), 1862: 353).
Clytia inconspicua Bovard and Osterud, 1918: 128 (?*Campanularia inconspicua* Calkins, 1899: 349, pl. 2; non *Thaumantias inconspicua* Forbes, 1848: 52, pl. 8).
Phialidium languidum var. *gregarium* Foerster, 1923: 41.

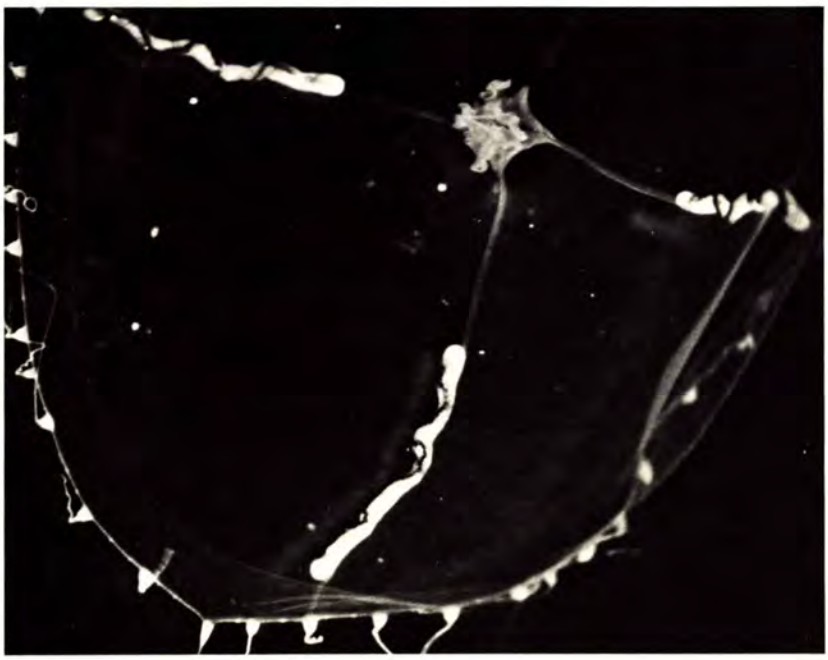


Fig. 59. *Phialidium gregarium*, live specimen showing gonad pigmentation, 16.6 mm diam., Departure Bay. Photo. M. N. Arai.

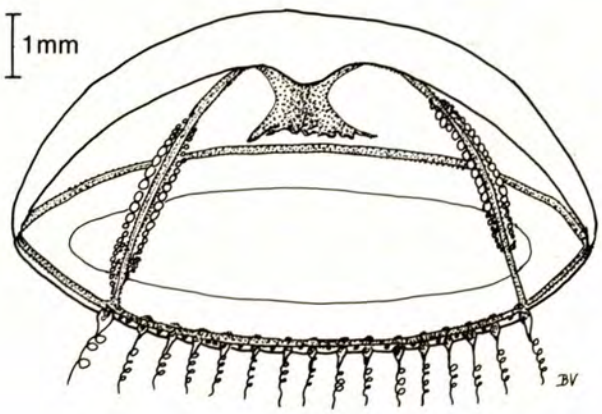


Fig. 60. *Phialidium gregarium*, Departure Bay.

Clytia osterudi Strong, 1925: 389, 391, pl. 37.
Clytia gregaria Roosen-Runge, 1970: 217.

Specific characters: Umbrella deep lens-shaped; manubrium with four rather long, fringed lips; 12 to 19 marginal tentacles plus bulbs per quadrant; margin of lips, gonads, marginal bulbs and ring canal "dusted" with variable amounts of dark pigment in living or freshly preserved specimens.

Description of medusa: Umbrella up to 22 mm wide. Stomach hanging on a very short peduncle; stomach walls drawn out on radial canals, thus showing a cross seen from above. Gonads linear, on up to two-thirds of distal radial canals, not touching the ring canal. Testis elipsoid in cross-section. Tentacles and bulbs standing closely together on the bell margin, averaging 12-19 tentacles and bulbs per quadrant in adult specimens. Marginal bulbs nearly globular. One or two, rarely three statocysts between tentacles or tentacle bulbs. Variable amounts of black or dark brown pigment on margin of lips, gonads, marginal bulbs and ring canal which fades if specimens are preserved longer than a year; gonads pale yellow to salmon.

Hydroid: The hydroid has been raised from the medusae at least three times but has not been clearly identified with any of the *Clytia* species described from field collections in the area. Bovard and Osterud (1918) stated that Mrs. T. C. Frye raised *Clytia inconspicua* but gave no morphological details. *Clytia inconspicua* was recorded in field collections from Puget Sound (Calkins 1899; Fraser 1911, 1914, 1937) but was originally described from Britain where it was raised from *Thaumantias inconspicua*, now considered a synonym of *Phialidium hemisphaericum* (Forbes 1848, Wright 1862b, Russell 1953). This must therefore be considered a doubtful synonym, although the *Clytia inconspicua* form of Calkins and Fraser may not be identical with the British form.

Strong (1925) reared a hydroid with 5-6 teeth on the hydrotheca which he distinguished from *C. inconspicua* (7 teeth) and which he named *Clytia osterudi*. Roosen-Runge (1970) reared a hydroid with 8-13 teeth on the hydrotheca which he was also unable to identify with any of the field collected species and which he named *Clytia gregaria*. Obviously more work needs to be done to clarify the degree of variability of the species. It is probable that more than one of the field collected species of *Clytia* correspond with *Phialidium gregarium*. Further details of the development have been added by Bonner (1955), Roosen-Runge (1962, 1970), Szollosi (1964), Roosen-Runge and Szollosi (1965), and Worthman (1974).

Discussion of taxonomy: Kramp (1962b) made an extensive survey of *P. gregarium* from Friday Harbor. As he noted the original description of *Oceania gregaria* by A. Agassiz (in L. Agassiz 1862) is insufficient for a reliable determination. However, he assumed that this is the same species based on lip length and common occurrence in the area. Murbach and Shearer (1903) gave a clearer description of *P. gregarium*. However, they also described some specimens of the same species with 60 tentacles as *Phialidium languidum*. This greatly confused the subsequent literature as *P. languidum* does not possess 60 tentacles (see discussion of *P. lomae*). Foerster (1923) described the common species of the Strait of Georgia and Friday Harbor as *Phialidium languidum* var. *gregarium*, although he examined Atlantic specimens of *P. languidum* and showed they were definitely distinct. After rechecking Foerster's

material and examining large collections of our own, we agree with Kramp (1962) that *P. gregarium* as described by Murbach and Shearer (1903) constitutes a separate, clearly definable species.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (A. Agassiz in L. Agassiz 1862; 1865); Strait of Georgia off Five Finger Is. (Foerster 1923; Brinckmann-Voss 1974); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Nanaimo Region (Kramp 1965a); Strait of Georgia off north end Gabriola Island (Foerster 1923); Northumberland Channel (Foerster 1923); Stuart Channel off Round Island (Foerster 1923); Ladysmith Harbour (present work); Saanich Inlet (Huntley and Hobson 1978); Brentwood Bay, Saanich Inlet (present work); Friday Harbor (Bovard and Osterud 1918; Child 1918; Harvey 1921; Foerster 1923; Strong 1925; Hyman 1940; Davenport and Nicol 1955; Roosen-Runge 1962; Kramp 1962b; Mackie and Mackie 1963; Szollosi 1964; Roosen-Runge and Szollosi 1965; Mackie and Passano 1968; Mackay 1969; Roosen-Runge 1970; Spaulding 1972; Singla 1972; Worthman 1974; Brinckmann-Voss 1974); Puget Sound (Murbach and Shearer 1903); Victoria Harbour (Murbach and Shearer 1903); Sooke Harbour (present work); Bamfield Inlet (present work); Ucluelet Inlet (present work); Nuchatlitz Inlet, off Port Langford (Brinckmann-Voss 1974); Bull Harbour (Foerster 1923; Brinckmann-Voss 1974).

Pacific Ocean;
Yaquina Bay, Oregon (McCormick 1969); 48°15'N, 125°19'W, Pacific Ocean (present work); Pacific Ocean off Cape Flattery (present work).

Notes: The relatively small size of *P. gregarium* has precluded much work on its physiology in spite of its abundance at Friday Harbor in the summer. Water content varies from 96.5 to 97.2% (Hyman 1940). Specific gravity is regulated by secretion of sulphate ion (Mackay 1969). King and Packard (1975) measured a respiration rate per animal of 1.94 $\mu L\ O_2 h^{-1}$.

P. gregarium shows a local bluish-green luminescence from the tentacular bulbs (Harvey 1921, Davenport and Nicol 1955). The statocysts are closed with a single lithocyte per statocyst (Singla 1975). Behavior patterns include irregular pulsations, crumpling, and feeding in which the bell margin is bent to the manubrium (Hyman 1940). Crumpling, induced by stimulation of the exumbrella, is propagated over the surface of the exumbrella by nonnervous epithelium (Mackie and Passano 1968). Septate junctions between cells of the gastrodermis are permeable to ruthenium red (Leik and Kelly 1970).

P. gregarium medusae largely eat copepods although they may also eat small numbers of other arthropods such as cladocera, cyclopoids, and barnacle and decapod larvae, as well as *Oikopleura* and gastropod larvae (McCormick 1969). Single medusae are present throughout the year but the species is common April to September. Large swarms are often present in July and August, presumably due to an abundant food supply for the hydroid 5 to 6 weeks earlier (Roosen-Runge 1970, Huntley and Hobson 1978).

Phialidium lomae Torrey, 1909

Phialidium lomae Torrey, 1909: 22 (in part, non 66-tentacle specimen); Kramp, 1952: 7 (in part); 1962b: 27 (in part); 1965a: 63; 1966: 6.

Phialidium languidum Mayer, 1910: 269, 495, pl. 33, 34 (in part; ? *Oceania languida* A. Agassiz (in L. Agassiz) 1862: 353); Foerster, 1923: 41 (in part); Brinckmann-Voss 1974: 16 (in part).
?Clytia inconspicua Fraser, 1914: 144.
Phialidium hemisphaericum Roosen-Runge, 1962: 15 (in part; *?Medusa hemisphaerica* L.); 1970: 216 (in part); Roosen-Runge and Szollosi, 1965: 41.
?Clytia attenuata West and Renshaw, 1970: 332.

Specific characters: Umbrella deep lens-shaped; manubrium with four short, rather blunt lips; 7 to 10 marginal tentacles plus bulbs per quadrant.

Description of medusae: Umbrella up to 18 mm wide. Stomach slightly drawn out on radial canals giving the appearance of a blunt cross seen from above. Lips undulating, pointing in four perradial corners. Gonads usually ovate, sometimes elongate in small specimens, becoming elongate in larger specimens, on up to three-quarters of distal radial canals. Testis almost round in cross-section. Marginal bulbs nearly triangular. One or two, rarely three statocysts between adjoining tentacles or tentacle bulbs. Color of tentacle bulbs occasionally slightly brownish but with no black margin of lips or ring canal as in *P. gregarium;* gonads yellowish.

Hydroid: Fraser (1914) states Dr. McMurrich raised *Clytia inconspicua* from *Phialidium hemisphaericum* from this region. However, no details are given to corroborate the identity of the medusa. West and Renshaw (1970) reared medusae from *Clytia attenuata* from Santa Catalina Island, California, which they considered synonymous with *Phialidium lomae.* However, these medusae differed in smaller size, adult gonad shape and smaller number of tentacles. Also under certain conditions the cultured hydroid was indistinguishable from *Clytia cylindrica.* Until *Clytia attenuata* can be reared from typical *Phialidium lomae* medusae the synonymy must be considered tentative.

Roosen-Runge and Szollosi (1965) examined the structure of the testis and gamete release.

Discussion of taxonomy: In addition to the more common *P. gregarium,* a second species of *Phialidium* is present in the research area which differs in having fewer tentacles and shorter lips. It has been described by various previous authors as *Phialidium lomae* Torrey 1909 (originally described from San Diego, California), *Phialidium languidum* (A. Agassiz 1862) (the common species off the northeastern United States), and *Phialidium hemisphaericum* (L.) (the common species of the coasts of Europe). The extent of variation and distribution in all three of these species is controversial, not only with respect to the medusae but also the hydroids. Both the medusa and hydroid stages of *Phialidium* vary in morphology depending on temperature, salinity and nutrition. Examination of our own collections of medusae of *P. lomae,* specimens of *Phialidium languidum* from eastern Canada and the United States of America, and *P. hemisphaericum* from the Mediterranean seem to show that all three species of medusae fall into the variation range of *P. hemisphaericum,* which was already discussed by Kramp (1933a) for *P. hemisphaericum* and *P. languidum.* However, clarification of the taxonomy will occur only when the complete life cycle of the three forms can be raised from the medusae under several identical conditions. Such a study is outside the scope of the present investigation. We have therefore kept the three species apart and restricted the synonymy to *P. lomae* of the west coast of North America.

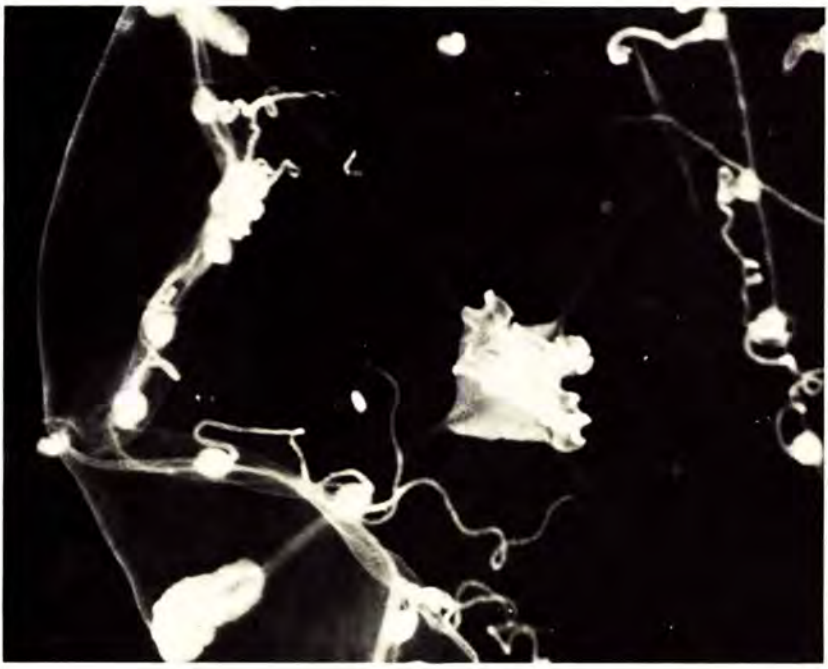


Fig. 61. *Phialidium lomae*, live specimen, 13.2 mm diam., Departure Bay. Photo. M. N. Arai.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (Kramp 1965a); Deep Bay (present work); Departure Bay (Brinckmann-Voss 1974; present work); off San Juan Island (Kramp 1962b); Friday Harbor (Roosen-Runge 1962); Puget Sound (Roosen-Runge 1967); Bamfield Inlet (present work); Kyuquot Sound (Brinckmann-Voss 1974); Quatsino Sound (Brinckmann-Voss 1974).

Pacific Ocean;
Off San Diego, Calif. (Torrey 1909).

Notes: *Phialidium hemisphaericum* has been used extensively for physiological and ecological work in Europe. The only study that can definitely be referred to *P. lomae* is that of Roosen-Runge (1967) who examined the action of flagellae and the muscle of the gastric pounches in circulation through the gastrovacular system.

Family Eirenidae

Leptomedusae with a small or well-developed peduncle; with 4 or 6 simple radial canals; with gonads on radial canals only; with hollow marginal tentacles; with or without lateral or marginal cirri; with more than 8 closed marginal vesicles; without ocelli.

Genus *Eirene* Eschscholtz, 1829

Eirenidae with a well-developed peduncle; without lateral or marginal cirri.

Type species: *E. viridula* (Péron and Lesueur, 1809).

Eirene mollis Torrey, 1909

Irene mollis Torrey, 1909: 26.
Eirene viridula Mayer, 1910: 311 (in part; non *Oceania viridula* Péron and Lesueur, 1809: 346, pl. 48).
Eirene mollis Foerster, 1923: 262; Kramp, 1936: 250; 1965a: 77; 1968c: 91.

Specific characters: With four radial canals; with peduncle short, conical; with up to 180 tentacles, same number or somewhat more statocysts.

Description of medusa: Umbrella up to 20 mm wide, about twice as broad as high. Manubrium with four prominent, frilled lips. Gonads linear, occupying distal half or more of radial canals. Gonads, canals, and manubrium faint yellow; bulbs of tentacles brick-red.

Hydroid: not known.

Distribution:
British Columbia and Puget Sound;
Strait of Georgia (Kramp 1965a).
Pacific Ocean;
Off San Diego, California (Torrey 1909).

Notes: This species may be easily misidentified as young *Eutonina indicans*. It can be clearly distinguished by the presence of only eight statocysts in the latter species.

Family Eutimidae

Leptomedusae with small stomach; with peduncle; with four simple radial canals; without excretory pores; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal cirri; with or without lateral cirri; with closed marginal vesicles; without ocelli.

Genus *Eutonina* Hartlaub, 1897

Eutimidae with eight adradial marginal vesicles; without cirri; without marginal warts; with gonads restricted to subumbrella.

Type species: *E. indicans* (Romanes, 1876).

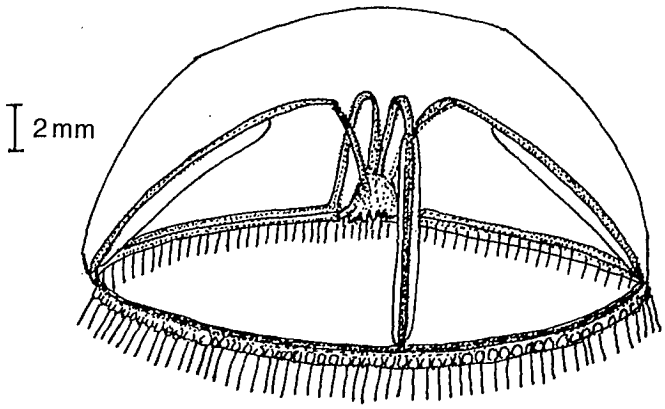


Fig. 62. *Eirene mollis* (after Torrey 1909, modified).

Eutonina indicans (Romanes, 1876)

Tiarops indicans Romanes, 1876a: 525.
Tiaropsis indicans Romanes, 1877a: 194, pl. 15.
Eutimalphes indicans Haeckel, 1879: 195; Hartlaub, 1894: 194.
Thaumantias sp. M'Intosh, 1889: 282, pl. 5; 1890: 40, pl. 8.
Eutonina socialis Hartlaub, 1897: 506, pl. 20, 22; 1904: 103; Apstein, 1913: 611.
Eutimium socialis Mayer, 1910: 306.
Eutonina indicans Bigelow, 1913: 34; Kramp, 1919: 98; 1933b: 585; Russell, 1953: 374, pl. 22; Kramp, 1961: 200.
Eutonia indicans Uchida, 1933: 131.
Eutimium indicans Naumov, 1956a; 37.
Eirene indicans Naumov, 1960: 320; Zelickman, 1976: 204.

Specific characters: Marginal vesicles with up to about 12 concretions. Gonads linear, sinuous along nearly whole length of subumbrellar portion of radial canals.

Description of medusa: Umbrella slightly flatter than hemisphere, to 35 mm, rarely 40 mm, wide: jelly rather thick. Velum narrow. Stomach short, in adult situated on an elongated conical peduncle, reaching a little beyond umbrella margin; mouth with four folded lips. Four straight radial canals; narrow ring canal. Up to 230 marginal tentacles, with conical bases. Color of stomach, gonads and marginal tentacle bases white or bright sepia; remainder colorless.

Hydroid: The primary polyp of *E. indicans* was reared by Hartlaub (1897) and the polyp generation and young medusae by Werner (1968) and Rees (1978).

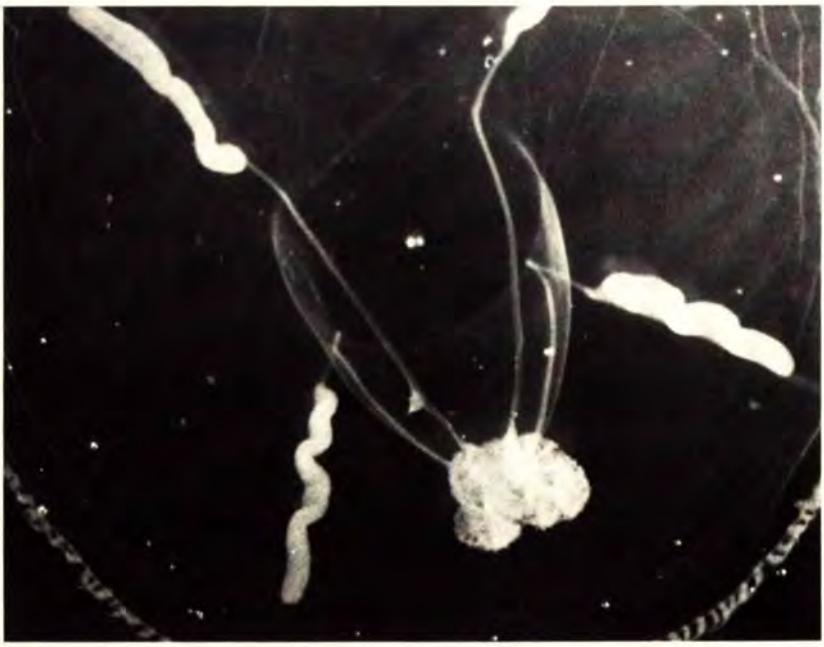


Fig. 63. *Eutonina indicans*, live specimen, 27.6 mm diam., Departure Bay. Photo. M. N. Arai.

Distribution:

British Columbia and Puget Sound;

Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); Strait of Georgia, off Snake Island (Foerster 1923); Strait of Georgia, off Gabriola Island (Brinckmann-Voss 1974); Nanaimo Harbour (present work); Stuart Channel (present work); Kulleet Bay (Brinckmann-Voss 1974); Ladysmith Harbour (present work); Long Harbour, Saltspring Island (present work); Cowichan Bay (present work); Brentwood Bay, Saanich Inlet (present work); Sooke Harbour (present work); Pacific Ocean, 48°29'N, 125°55'W (present work); Bamfield Inlet (present work); Alberni Inlet (present work); Barkley Sound, off Ucluelet (present work); Ucluelet Inlet (present work); Bunsby Anchorage, Chekleset Bay (present work); Southeast Arm, Quatsino Sound (Brinckmann-Voss 1974); Bull Harbour (Foerster 1923; Brinckmann-Voss 1974); Houston Stewart Channel (Brinckmann-Voss 1974); Skidegate Channel (present work); Masset Harbour (present work); Naden Harbour (Brinckmann-Voss 1974).

Pacific Ocean;

Monterey Bay, California (Sassaman 1974); Bodega Bay, California (Rees 1978); Bodega Harbor (Rees 1978); Pacific Ocean, off Bodega Head (Rees 1978); Pacific Ocean off Oregon (Pearcy 1972); Dutch Harbor, Unalaska Island (Bigelow 1913); 51°N, 156°E, Okhotsk Sea off Kuril Islands (Uchida 1933); Akkeshi Bay, Hokkaido (Uchida 1933, 1940); Onagawa Bay, Honshu (Uchida 1938c); Busse Lagoon, Aniva Bay (Zelickman 1976).

Atlantic Ocean;

See Kramp (1919, 1927, 1939), Sanderson (1930), Watson (1930), Runnström

(1932), van der Maaden (1942), Kändler (1950), Russell (1953), Rees (1953), Bossanyi (1957), Howe (1959), Kühl (1965), Allwein (1968), Edwards (1968), Tveite (1969), and Fraser (1974) for details.

Notes: Romanes (1876a) noted that the bell margin of *Eutonina indicans* will luminesce when irritated. He also described the movements of the medusa, particularly the bending of the manubrium towards a site of irritation of the bell (1877b, 1885). This would direct the mouth toward prey, but Horridge (1966) showed that the medusa would turn and swim away from a source of vibration, thus presenting the mouth but ultimately avoiding disturbances.

Werner (1968) and Rees (1978) found only basitrichous haplonemes in the cnidom of the medusa of *E. indicans* but Kubota (1976) found microbasic mastigophores.

Künne (1948) described the transportation of larvae of the actinian *Peachia hastata* on this medusa in the north sea. We found similar unidentified anthozoan larvae on *Eutonina indicans* from Bunsby Anchorage. Sassaman (1974) reported a capacity for development of secondary manubria and Zelickman (1976) found the manubria frequently damaged in the field.

In the Strait of Georgia area *E. indicans* has been collected March to October (Foerster 1923) and is common April to June.

Family Aequoreidae

Leptomedusae with broad short stomach; with or without peduncle; with many simple or branched radial canals; with gonads on radial canals separated from stomach; most species with excretory papillae; without marginal or lateral cirri; with closed marginal vesicles; with or without ocelli.

Genus *Aequorea* Péron and Lesueur, 1809

Aequoridae with or without short peduncle, not more than half the height of the bell; adults with more than eight simple radial canals; subumbrella without rows of papillae; without ocelli.

Type species: *A. forskalea* Péron and Lesueur, 1809.

Aequorea victoria (Murbach and Shearer, 1902)

?Aequorea ciliata Eschscholtz, 1829: 109, pl. 9; Agassiz, 1865: 109.
?Crematostoma flava A. Agassiz (in L. Agassiz), 1862: 360; 1865: 108.
?Zygodactyla coerulescens A. Agassiz, 1865: 108 (non *Zygodactyla coerulescens* Brandt, 1835: 21).
Mesonema victoria Murbach and Shearer, 1902: 72; 1903: 180, pl. 19, 22; Bigelow, 1909a: 174.
Aequorea victoria Maas, 1905: 43; Mayer, 1910: 330; Strong, 1925: 385, pl. 38, 39; Rees, 1939: 439; Kramp, 1961: 209.
Aequorea coerulescens ? Torrey, 1909: 28 (in part; non *Aequorea coerulescens* Bigelow, 1909a: 177, pl. 4, 35); Child, 1918: 49.

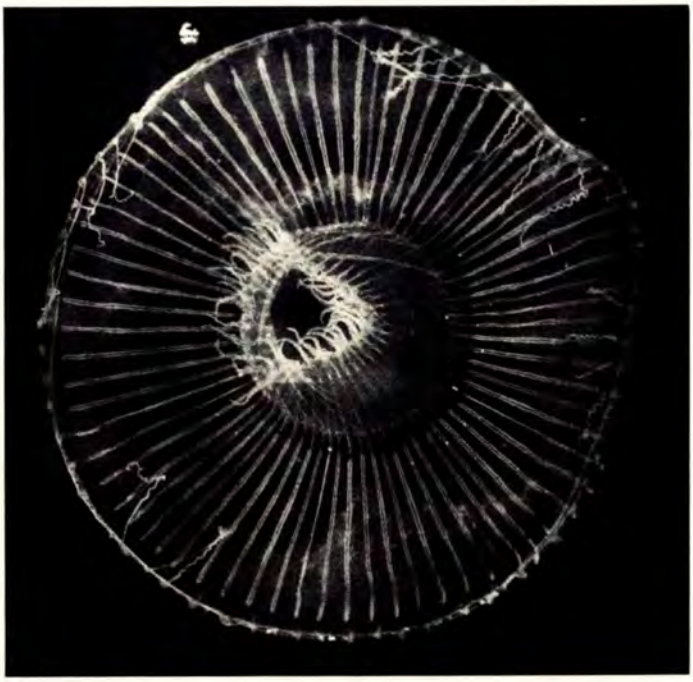


Fig. 64. *Aequorea victoria*, live specimen, approx. 7 cm diam. Departure Bay. Photo. M. N. Arai.

?Campanulina forskalea Fraser, 1911: 43 (in part); 1914: 157 (in part).
Aequorea aequorea var. *aequorea* Bigelow, 1913: 38 (in part; non *Medusa aequorea* Forskal, 1775).
Aequorea forskalea Cameron, 1915: 58 (non *Aequorea forskalea* Péron and Lesueur, 1809: 24); Fraser, 1916: 97; Bovard and Osterud, 1918: 129; Harvey, 1921: 280; Russell, 1953: 342 (in part).
Aequorea aequorea Weese and Townsend, 1921: 117; Foerster, 1923: 263 (in part); Fraser, 1932: 52; Hyman, 1940: 282; Kramp, 1961: 203 (in part); 1965a: 95 (in part).
Campanulina membranosa Strong, 1925: 389.

Specific characters: Bell saucer-shaped to often nearly hemispherical; with thick, lens-shaped part of subumbrella forming a short peduncle. Lips fringed and serrated. Tentacle number approximately half to twice the number of radial canals.

Description of medusa: Umbrella up to 40 mm high, 120 mm wide. Subumbrella forming a thick lens projecting into the stomach cavity which may be almost hemispherical, thus pushing stomach walls to a peripheral circle in preserved specimens. Number of lip lobes from half to same as number of radial canals. Gonads extending along nearly entire length of radial canals. Up to 150 tentacles. Subumbrellar cup-shaped excretory papillae present in older

specimens, one opposite each tentacle bulb, opening into the ring canal. Color of umbrella transparent, bluish or milky white in adult specimens; subumbrella green in very young specimens; gonads opalescent, gray or milky; tentacle bulbs sometimes brown.

Hydroid: Strong (1925) raised the primary hydranth of *Aequorea victoria* from the medusae and designated it as *Campanulina membranosa*. As noted by Rees (1939), this hydroid should bear the same name as the medusa. Fraser (1911, 1914) earlier tentatively named a similar hydroid from field collections in the area *Campanulina forskalea*. These specimens were probably also *Aequorea victoria*.

Discussion of taxonomy: There is considerable confusion about the validity of *Aequorea victoria* as a separate species or as a form of *A. forskalea* Péron and Lesueur 1809. (*A. forskalea* has often been designated *Aequorea aequorea* (Forskal 1775) but Russell (1953) noted that the specific name *aequorea* had been given by Linnaeus and Loefling to an unidentifiable species). The species was described by Murbach and Shearer (1902, 1903) as *Mesonema victoria*. Mayer (1910) listed it as a species separable only on a geographic basis from *A. forskalea*. Most subsequent authors have accepted this suggestion and hence designate the British Columbia and Puget Sound form *A. aequorea* or *A. forskalea*, (see especially Bigelow (1913), Fraser (1916), Foerster (1923), Russell (1953) and Kramp (1965a)), although Kramp (1961, 1968c) listed *A. victoria* as a doubtful species. However Strong (1925) who raised the primary hydranth and saw numerous adult specimens, strongly objects to the opinion that *A. forskalea* and *A. victoria* are synonyms. To decide whether *A. victoria* should be kept separate or not, we examined more than 40 specimens from different areas around Vancouver Island (east, south, southwest and west coasts) and compared them with Mediterranean specimens and the original drawings available in the literature. It was found that *A. forskalea* and *A. victoria* are similar in relation of tentacle number to number of tentacle bulbs and radial canals. However, *A. victoria* has much more regularly serrated mouth lobes than *A. forskalea*. In addition the subumbrella of a *A. victoria* forms a much larger lens in the stomach region, which, as noted by Murbach and Shearer (1903) and Strong (1925), may be almost hemispherical. We have therefore decided to keep the two species separate although intraspecific variation is very wide and identifications should be made from several specimens from one area.

Two descriptions of *Aequorea* in the research area predate Murbach and Shearer's (1902, 1903) description of *A. victoria*. Eschscholtz (1829) described *A. ciliata* from the N.W. coast of North America between 41° and 51°. However, insufficient detail was given to identify the species. A. Agassiz (in L. Agassiz 1862, 1865) described *Crematostoma flava* from the Strait of Georgia. This species corresponds in most details with *A. victoria*; however, Agassiz states that "the digestive cavity hangs always far below the level of the circular tube", a character which he includes in the designation of a new genus. We have not found such a long peduncle in our specimens. Both of these species are therefore only questionable synonyms of *A. victoria*.

There has also been some confusion with *Aequorea coerulescens*. The original description by Brandt (1835, 1838) was of specimens from 35°N i.e. relatively warm water, and with the typical sky-blue coloration of the tent-

acles of the presently accepted *A. coerulescens*, but showed only twice as many tentacles as radial canals in the accompanying plate (1838). The species as redescribed by Bigelow (1909a) and Uchida (1927b) has several times as many tentacles as radial canals and can be clearly distinguished from *A. victoria*. Torrey (1909) however, examined "*Aequorea coerulescens*" specimens from Unalaska and San Diego which may have included some *A. victoria* since he mentions the central broad swelling into the digestive cavity. Child (1918), who gives no morphological details, did physiological work on "*Aequorea coerulescens*" from Friday Harbor which were certainly misidentified since Bovard and Osterud (1918) described "*Aequorea forskalea*" as the abundant species at Friday Harbor in the same summer.

In the distribution list the assumption has been made that all north-eastern Pacific forms listed as *A. forskalea* or *A. aequorea* should be included with *A. victoria*. It is unclear how much farther the range of *A. victoria* may extend. For example Zelickman (1976) lists *A. forskalea* from Aniva Bay, Sea of Okhotsk, which might in fact belong to *A. victoria*, but does not give morphological data on which a decision can be made.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (Foerster 1923; Fulton 1968); Union Bay (Bigelow 1913); Deep Bay (present work); Nanoose Harbour (Brinckmann-Voss 1974); Departure Bay (Fraser 1916; Brinckmann-Voss 1974; present work); Nanaimo Region (Fraser 1932; Kramp 1965a); False Narrows (Cameron 1915); Ruxton Passage (Kramp 1965a); Ladysmith Harbour (present work); Long Harbour, Saltspring Island (present work); Cowichan Bay (present work); Brentwood Bay, Saanich Inlet (present work); San Juan Archipelago (Fraser 1932); Friday Harbor (Bigelow 1913; Bovard and Osterud 1918; Child 1918; Harvey 1921; Weese and Townsend 1921; Strong 1925; Johnson and Snook 1927; Hyman 1940; Davenport and Nicol 1955; Shimomura et al 1962; 1963a; Johnson et al 1962: Mackie and Mackie 1963; Lenhoff 1964; Ridgway and Ashley 1967; Mackay 1969; Hastings et al 1969; Shimomura and Johnson 1969; Johnson 1970; Singla 1972; Johnson and Shimomura 1972; Llinas et al 1972; present work); Puget Sound (Murbach and Shearer 1902); Puget Sound near Port Townsend (Murbach and Shearer 1903); Victoria Harbour (Murbach and Shearer 1902; 1903; present work); Esquimalt Harbour (Murbach and Shearer 1903); Sooke Harbour (present work); Bamfield Inlet (present work); Ucluelet Inlet (Brinckmann-Voss 1974); Pacific Ocean, north-west of Nootka Sound (Brinckmann-Voss 1974).

Pacific Ocean;
Yaquina Bay, Oregon (McCormick 1969); Pacific Ocean, off Washington State (Jawed 1973; present work).

Notes: Adult *Aequorea* are broad with marginal creases of the bell and weak swimming muscle (Gladfelter 1973). The rate of pulsation decreases with age (Child 1918). The medusa may react to adverse conditions of pH, temperature or salinity by inversion and active movement downward (Weese and Townsend 1921). Specimens are relatively insensitive to mechanical stimulation (Hyman 1940). If tilted the medusae show differential pulsation of the top and bottom of the bell. This righting reaction is prevented if the statocysts are removed (Singla 1972, 1975).

A. victoria is a "somewhat indiscriminate feeder" (Hyman 1940). The "gastric juice" includes a protease and a lipase (Hyman 1940). Ingested

carmine particles may circulate through the radial canals and be exuded from the excretory papillae which emit streams of material from the ring canal (Strong 1925; Hyman 1940). The water content of the medusae is about 96.5 - 97% (Hyman 1940) and the sulphate ion is actively regulated (Mackay 1969). The excretory rate of ammonia is very low, even after calculation per unit organic weight (Jawed 1973).

Since it was first described by Harvey (1921) interest of physiologists in *Aequorea* has centered on the luminescence. The luminescent material is contained in an oval mass of yellow cells on either side of the base of each tentacular bulb. A tactile or an electrical stimulus produces a flash or series of flashes of blue-green light localized at the area stimulated (Davenport and Nicol 1955). The luminescence is due to a photoprotein aequorin, which has been extracted and characterized (Shimomura et al 1962, 1963a, Shimomura and Johnson 1969, Kohama et al 1971, Kishi et al 1972, Shimomura and Johnson 1972, 1973a, Calleja 1973, Shimomura et al 1974, Shimomura and Johnson 1975, Prendergast and Mann 1978, Shimomura and Johnson 1978). The luminescence of the extract is bluish since the blue-green reaction of the intact animal depends on the presence of a non-chemiluminescent protein with a greenish fluorescence (Johnson et al 1962, Cormier et al 1973, Morise et al 1974). The luminescent reaction is triggered in the presence of Ca^{++} ions. Although there is some background light emission at low Ca^{++} concentrations, the luminescent reaction is specific for Ca^{++} among substances likely to be found in biological systems, is independent of oxygen and proceeds within the physiological pH range. The rate varies steeply with calcium concentration between 10^{-7} and 10^{-5} Mol/L, and the rise and decay time are in the millisecond region (Shimomura et al 1962, 1963a, Hastings et al 1969, Shimomura and Johnson 1970, Loschen and Chance 1971, Izutsu et al 1972, Shimomura and Johnson 1973b, Izutsu et al 1974a, b, Allen et al 1977). Methods have therefore been developed by which aequorin can be injected into a variety of living cells such as muscle as a very useful indicator of free Ca^{++} (Shimomura et al 1963b, Ridgeway and Ashley 1967, Azzi and Chance 1969, Llinas et al 1972, Izutsu and Felton 1972, Johnson and Shimomura 1972, Blinks 1978). Tons of *Aequorea* have been processed at Friday Harbor to extract the necessary aequorin (Johnson 1970).

Scattered specimens of *Aequorea* have been obtained throughout the year. In the Gulf of Georgia region however, young specimens are most common in May and June and the adults form a very conspicuous component of the plankton in summer and fall.

ORDER LIMNOMEDUSAE

Hydromedusae with lens-shaped to deep bell-shaped umbrella; gonads either on stomach wall with or without perradial lobes extending along radial canals, or on radial canals only; statocysts, if present, internal, provided with endodermal axis. Hydroids with hydranths growing directly from hydrorhiza; often solitary and small; with or without tentacles; endoderm of tentacles in direct connection with that of gastral cavity.

Family Olindiadidae

Limnomedusae with internal marginal vesicles; with gonads on radial canals; with simple, unbranched radial canals; without ocelli. Polyps, where known, very small, with or without tentacles.

Genus *Eperetmus* Bigelow, 1915

Olindiadidae with four radial canals. Most adult specimens with several centripetal, blind canals; oral lips with nematocyst knobs; with numerous tentacles of one kind, not in groups, situated on exumbrella at different heights above bell margin, with rings of nematocysts, without adhesive pads; with numerous statocysts.

Type species: *E. typus* Bigelow, 1915.

Eperetmus typus Bigelow, 1915

Eperetmus typus Bigelow, 1915a: 401, pl. 59; Foerster, 1923: 263; Uchida, 1929: 364, pl. 1; Mackie and Mackie, 1963: 74; Nagao, 1969a: 236; 1973: 89; Mills et al, 1976: 23.
?Eperetmus typus Bigelow, 1920: 9H.
Eperetmus typicus Uchida, 1940: 291.
Aglauropsis sp. Mills et al, 1976: 34.

Specific characters: This is the only species of the genus.

Description of medusa: Umbrella bell-shaped, diameter greater than height. Velum wide, with well-developed muscles. Manubrium short, four-sided. Four cornered oral lips, crenulated, margins with spherical nematocyst knobs arranged in a single row. Four broad radial canals. Ring canal broader than radial canals, sending off up to about 16 centripetal canals in each quadrant which taper inwards. Tentacles more numerous than centripetal canals, arising from bell margin but shifting upwards and projecting from exumbrella at various heights, according to age and hence size, with furrows extending from base to bell margin, armed with thick nematocyst ridges forming complete or incomplete rings. A filament-like extension ending in a cnidocyst cluster present at tip of tentacles in some specimens. Statocysts enclosed, containing one otolith on a stalk nearly alternating with tentacles. Gonads ribbon-like, extending nearly whole length of radial canals, with several transverse folds.

Fig. 65. *Eperetmus typus*, preserved specimen, 14.3 mm diam., Pacific Ocean off Barkley Sound. Photo. M. N. Arai.

Diameter when fully grown up to 45 mm. Color of living specimens: manubrium, gonads and tentacles pale pink or brown, tentacle knobs deep pink, remainder colorless; of formalin preserved specimens manubrium and tentacles pale yellow, gonads yellow, brown or greenish brown.

Hydroid: The polyp generation and development of *E. typus* has been described by Nagao (1969a, 1973).

Discussion of taxonomy: Mills et al (1976) have recently questioned the presence of *Eperetmus typus* in Japan. Bigelow (1915a) first described this species from a single 15 mm diameter specimen with 4-5 centripetal canals per quadrant, the longest reaching "hardly halfway from margin to apex." Two smaller specimens (7 and 9 mm diameter) also from Alaska were poorly preserved and did not show centripetal canals and hence were only tentatively included in the species (Bigelow 1920). Uchida (1929) described three 13-23 mm specimens of *E. typus* from the collections of Takashima Fisheries Station, Hokkaido as possessing 11-16 "rather short" centripetal canals per quadrant. Uchida (1940) reported (as *Eperetmus typicus*, apparently a printing error) numerous specimens from Akkeshi Bay, Hokkaido. He did not mention the centripetal canals. However, Nagao (1969a, 1973) showed that newly liberated *Eperetmus typus* specimens from Akkashi Bay lack the centripetal canals. Mills et al (1976) examined at least 3 specimens (size not noted) which were sent them from Akkashi Bay by Nagao. They could not find the centripetal canals typical for *Eperetmus typus* and therefore conclude that *E. typus* is not present in Japan, but that there is an *Aglauropsis* species present.

Comparison of specimens available in the Pacific Biological Station

collections and our recent material (26 specimens), especially with regard to the centripetal canals, led us to the conclusion that the length and shape of centripetal canals is extremely variable. In British Columbia and Puget Sound waters Foerster (1923) and Mackie and Mackie (1963) examined several 5-45 mm specimens and found 3-6 centripetal canals per quadrant. However, 12 specimens from Sooke (18-40 mm diameter, 10% formalin preserved) included 1 specimen possessing no centripetal canals, 2 specimens with very short and broad centripetal canals, 3 specimens with the shape Uchida described, and the rest as described by Bigelow (1915a) or intermediate stages between Uchida's and Bigelow's specimens. When present there were 4-7 canals per interradius. It may be possible that the material Nagao sent Mills et al was either too young to have centripetal canals or was a different species. Nevertheless, although a higher number of centripetal canals were present in Uchida's specimens than in ours, the shape of the canals he described is the same as found in some of our specimens, and we conclude therefore that *E. typus* is present in Japan.

Mackie and Mackie (1963) reported small lateral extensions at the tip of some mature tentacles in the single specimen they observed. Mills et al (1976) did not find such tentacle tips in the two specimens they examined although they report that R. Larson had found similar structures in Coos Bay specimens. We find that filament like extensions ending in a cnidocyst cluster are present in about 10% of the specimens, especially young ones.

Distribution:

British Columbia and Puget Sound;
Nanaimo Region (Fraser 1932); Strait of Georgia off Snake Island (Foerster 1923); Departure Bay (Foerster 1923; Brinckmann-Voss 1974, present work); Northumberland Channel (Foerster 1923, Brinckmann-Voss 1974); Dodd Narrows (Foerster 1923; Brinckmann-Voss 1974); Pylades Channel (Brinckmann-Voss 1974); Ladysmith Harbour (present work); Tod Inlet off Saanich Inlet (Foerster 1923); Friday Harbor, San Juan Island (Mackie and Mackie 1963); Sooke Harbour (present work); 48°29'N, 125°55.3'W, Pacific Ocean off Barkley Sound (present work); Pacific Ocean off Nootka Sound (Brinckmann-Voss 1974); Flamingo Inlet, Moresby Island (Brinckmann-Voss 1974); Skidegate Channel (Brinckmann-Voss 1974); Masset Harbour (present work).

Pacific Ocean;
Coos Bay, Oregon (Mills et al 1976); Yaquina Bay, Oregon (Mills et al 1976); 3.7 km off Mary Island, Southern Alaska (Bigelow 1915a); Port Clarence, Alaska, off Bering Sea (? Bigelow 1920); off Hokkaido (Uchida 1929); Akkeshi Bay, Hokkaido (Uchida 1940; Nagao 1969a; 1973; Hada 1972).

Notes: Mackie and Mackie (1963) have briefly described the behavior of this medusa. Swimming is forceful, but when it ceases the medusa sinks to the bottom, indicating it is probably essentially bottom living. However, in the present work it was found in the surface water of small bays or inlets.

The nematocysts consist in the adult of microbasic euryteles and a second type described by Mackie and Mackie (1963) as heterotriches but by Nagao (1969a, b, 1973) and Mills et al (1976) as atrichous isorhizes. In the young medusae macrobasic euryteles are also present on the exumbrella.

This species has not been reported as abundant in any British Columbia waters. Although Nagao (1969a) described an annual life cycle in Akkeshi Bay, Japan in which medusae were present May to November, specimens have been

obtained in British Columbia November to February as well as May to July.

Genus *Gonionemus* A. Agassiz, 1862

Olindiadidae with four radial canals; without centripetal canals; with numerous uniform tentacles, all with an adhesive pad near the outer end, and with rings of nematocysts.

Type species: *G. vertens* A. Agassiz, 1862.

Gonionemus vertens A. Agassiz, 1862

Gonionemus vertens A. Agassiz (in L. Agassiz), 1862: 350; 1865: 128; Murbach and Shearer, 1903: 183; Bigelow, 1909a: 105; Thomas, 1921: 287; Broch, 1929: 485; Fraser, 1946: 119; Werner, 1950a: 471; Picard, 1951: 40; Russell, 1953: 398, pl. 23; Kramp, 1959a: 174; Tambs-Lyche, 1964: 1; Kramp, 1965b: 276; Edwards, 1976: 251.
Cosmetira salinarum du Plessis, 1879: 39, pl. 2.
Gonynema vertens Haeckel, 1879: 147.
Halerimita cumulans Schaudinn, 1894: 226.
Gonionemus murbachii Mayer, 1901: 5; Bigelow, 1909a: 105; Thomas, 1921: 287.
Gonionema murbachii Yerkes, 1902b: 181.
Gonionema depressum Goto, 1903: 12, pl. 2, 3.
Gonionemus agassizii Murbach and Shearer, 1902: 73; 1903: 185, pl. 21, 22; Kirkpatrick, 1903: 618, pl. 33; Bigelow, 1909a: 105; Thiel, 1932: 151.
Gonionemus depressum Bigelow, 1909a: 105; Uchida, 1929: 358; 1938a: 146.
Gonionemus vertens var. *depressum* Maas, 1909: 28, pl. 3.
Cladonema sp. Robson, 1913: 27.
Gonionemus vindobonensis Joseph, 1918: 107; 1924: 129; 1925: 374; Werner, 1950a: 472; Kramp, 1965b: 276.
Eleutheria robsonia Lengerich, 1922: 34.
Gonionema murbachi var. *oshoro* Uchida, 1925: 94.
Gonionemus murbachi Broch, 1929: 486; Leloup, 1948: 1; Werner, 1950a: 471; 1950b: 138.
Gonionemus agassizi Broch, 1929: 489.
Gonionemus oshoro Uchida, 1929: 359, pl. 1; Nagao, 1969b: 39.
Gonionemus murbachii var. *chekiangensis* Ling, 1937: 358; Chow and Huang, 1958: 186.
Gonionemus vertens vertens Naumov, 1955b: 102; Mikulich and Naumov, 1974: 11.
Gonionemus vertens vertens var. *oshoro* Naumov, 1955b: 102.
Gonionemus vertens murbachii Naumov, 1955b: 102.
Gonionemus murbachii var. *oshoro* Chow and Huang, 1958: 186, pl. 5.
Gonionemus depressus Yamazi, 1958: 137.
Gonionema oshoro Kakinuma, 1971: 91, pls. 3-7; Kubota, 1976: 240.

Specific characters: Statocysts somewhat fewer than marginal tentacles to almost twice as many; umbrella hemispherical or somewhat flatter; adhesive pads of tentacles not terminal.

Description of medusa: Umbrella hemispherical or somewhat flatter, commonly to 20 mm wide, rarely to 34 mm. Velum very broad. Stomach somewhat shorter to slightly longer than bell cavity. Mouth with four perradial lips

Fig. 66. *Gonionemus vertens*, preserved specimen, 11.2 mm high, Departure Bay. Photo. M. N. Arai.

with crenulated margins. Gonads along greater part of radial canals, folded sinuously on alternate sides of radial canal. When fully grown up to 100 long, rather stiff tentacles, each with many nematocyst clusters, with adhesive pad near distal end, with distal end sharply bent. Closed marginal vesicles, alternating with marginal tentacles, varying in number from somewhat fewer than the marginal tentacles to nearly twice as many, each vesicle embedded in jelly near ring canal and with single endodermal club. Color of living specimens, umbrella transparent or light yellowish green, gonads deep red, violet, orange, or yellowish brown, radial canals yellowish or dark brown, manubrium violet, brownish orange, or brown with lighter lips, sometimes tinged with green, tentacles pink, orange or brown, roots may be bright green.

Hydroid: First described (as *Halerimita cumulans*) by Schaudinn (1894). Further details of the life cycle have been added by Murbach (1895, 1903b), Perkins (1903, 1926), Bigelow (1907), Kinoshita (1916), Joseph (1924, 1925),

Rugh (1929), Komai and Yamazi (1945), Werner (1950b), Komai (1951), Mikulich (1951, 1970), Bodo and Bouillon (1968), and Kakinuma (1971).

Discussion of taxonomy: Kramp (1965b) has described a new species of *Gonionemus*, *G. hamatus*, distinguished in part by the adaxial position of the adhesive pads on the tentacles. This is not a distinctive character since it is often difficult to determine the adaxial or abaxial position in *G. vertens*. For example, Goto (1903) described (as *G. depressum*) specimens from off Yokohama as having suckers on the "inner" (i.e., adaxial) side, but Uchida (1929) describes specimens from the same locality as having them "aboral" (i.e., abaxial). This character should therefore be eliminated, not only from the generic definition as Kramp (1965b) has done, but also as a specific character. *G. hamatus* was incompletely described due to the poor condition of the single specimen. Information on characters such as statocyst number were not given. However, *G. hamatus* differs from *G. vertens* and *G. suvaensis* in the terminal position of the adhesive pads, and in the higher than wide exumbrella with a bluntly conical apical projection. It should therefore be considered a valid species.

Distribution:

British Columbia and Puget Sound;

Strait of Georgia (A. Agassiz in L. Agassiz 1862; 1865); Porpoise Bay, Sechelt Inlet (Mackie and Mackie 1963); Strait of Georgia, off Lasqueti Island (Fraser 1946; Strait of Georgia, off Ballenas Island (Foerster 1923; Fraser 1946); Hammond Bay (Fraser 1946; Brinckmann-Voss 1974; present work); Departure Bay (Foerster 1923; Fraser 1946; Brinckmann-Voss 1974; present work); Horsewell Channel, off Newcastle Island (Fraser 1946); Northumberland Channel, off Duke Point (Fraser 1946); Taylor Bay, Fairway Channel (Fraser 1946); Forwood Channel (present work); Lock Bay, Gabriola Island (Fraser 1946); Pylades Channel, off Gabriola Island (Fraser 1946); off Mudge Island (Foerster 1923; Brinckmann-Voss 1974); Stuart Channel, off Mudge Island (Fraser 1946); Stuart Channel, off Round Island (Foerster 1923); Trincomali Channel, off Cardale Point (Foerster 1923; Fraser 1946); Trincomali Channel, off Galiano Island near Porlier Pass (Fraser 1946); Tod Inlet, Saanich Inlet (Brinckmann-Voss 1974); Brentwood Bay, Saanich Inlet (present work); Strait of Georgia, off Piers Island (Fraser 1946); Stranger Passage, off Krapp Island (Fraser 1946); Roberts Bay (Fraser 1946); Sidney Channel, off Sidney (Fraser 1946); off San Juan Island (Fraser 1962); Mitchell Bay, San Juan Island (Mackie and Mackie 1963); Boundary Passage, off Waldron Island (Fraser 1946); Friday Harbor (Thomas 1921; Hyman 1940; Fraser 1946; Westfall 1970a; 1970b); Argyle Lagoon, North Bay, San Juan Island (Fraser 1946); East Sound, Orcas Island (Fraser 1946); Puget Sound near Port Townsend (Murbach and Shearer 1903); Matsmets Bay (probably Mats Mats Lagoon, near Port Ludlow off Admirality Inlet) (Murbach and Shearer 1903); Oak Bay (Mackie and Mackie 1963); Victoria Harbour (Murbach and Shearer 1903; Fraser 1946); Parry Bay off William Head (Brinckmann-Voss 1974); Bamfield Inlet (present work); Quatsino Sound, off Drake Island (Brinckmann-Voss 1974); Skidegate Channel (Fraser 1946).

Pacific Ocean;

Artificial lagoon, Santa Barbara, California (Todd et al 1966); off Unalaska Island (Murbach and Shearer 1902; 1903); off Kuril Islands (Naumov 1955b; 1960); Okhotsk Sea (Naumov 1956a); Akkeshi Bay, Hokkaido (Uchida 1940; Hada 1972); Uchiura Bay, off Muroran, Hokkaido (Uchida 1940); Mutsu Bay (Uchida 1927b; 1929; 1938b; 1940; Kakinuma 1971); Ommae Bay, near Onagawa (Uchida 1938c); Tokyo Bay, off Yokohama (Goto 1903; Kinoshita 1916; Uchida 1929);

Sagami Bay, off Misaki (Maas 1909; Kinoshita 1916; Uchida 1929; 1930); Tanabe Bay (Yamazi 1958); Naba Bay (Kirkpatrick 1903); Amakusa Bay, Kyushu (Kinoshita 1916; Uchida 1929; 1938a; Komai and Yamazi 1945); Nagasaki Harbour (Naumov 1955b); Sea of Japan, off Wajima, Ishikawa Prefecture (Uchida 1929); Sea of Japan, off Yura, Yamagata Prefecture (Uchida 1929; 1940); Ishikari Bay, off Takashima, Hokkaido (Uchida 1929); Ishikari Bay, off Oshoro, Hokkaido (Uchida 1925; 1929; 1940); off Sakhalin (Uchida 1940); Busse Lagoon, Aniva Bay (Zelickman 1976); Tatar Strait, off S. Sakhalin (Naumov 1955b; 1960); Olga Bay, Sea of Japan (Naumov 1960); Sea of Japan, near Vladivostock (Mikulich 1951; 1961; 1970; Naumov 1960); Yellow Sea (Chow and Huang 1958); East China Sea, off Chengshan, Chekiang (Ling 1937); South China Sea, off Nha Trang, Vietnam (Kramp 1962a).

Atlantic Ocean;
See Bigelow (1914a), Leentvaar (1961), Tambs-Lyche (1964), Russell (1970), and Edwards (1976) for details.

Notes: *Gonionemus* has been frequently used for class demonstrations and the general anatomy is therefore described in many textbooks. The degree of variation, abnormal specimens and potential for manubria, canals, and tentacles to regenerate were investigated by several workers, particularly at the Marine Biological Laboratory, Woods Hole, around the turn of the century (Morgan 1899; Hargitt, C. 1897, 1899, 1900, 1901; Hargitt, G. 1902, 1904; Rugh 1930; Okada 1931).

The histology of the musculature of *Gonionemus vertens* was described by Fraser (1962) and Gladfelter (1973) has described the action of the strong subumbrellar swimming muscle. Bouillon and Coppois (1977) found collagen and elastic fibres in the mesogloea. Hyde (1902) described the nervous system, and the morphological polarization of the synapses and neuro-muscular junctions at the ultrastructural level was established by Westfall (1970a, 1973). Thomas (1921) described the otocysts. Studies of the behavior have been made by several authors (Yerkes 1902a and b, 1904, 1906; Murbach 1903a; Morse 1906, 1907; Terry 1909; Wolf 1928). Among the most characteristic of the behavior patterns is "fishing" behavior in which the animal swims actively to the surface, then turns upside down and floats downward with tentacles widely spread. On contact with seaweed they attach with adhesive pads, at the end of each tentacle, containing columnar glandulomuscular cells surrounded by a collar of microfilament containing epithelial cells (Singla 1977). Although ocelli are not present (Hyman 1940) responses to light have been noted (Yerkes 1902a, 1904, 1906; Yerkes and Ayer 1903; Perkins 1903; Murbach 1903b, 1907, 1909; Morse 1906, 1907; Rugh 1929; Zelickman 1969).

Gonionemus is known to feed on copepods, mysids, isopods, amphipods and fish larvae (Yerkes 1902a; C. Hargitt 1905; Werner 1950a; Russell 1953; Mikulich 1961; Todd et al 1966).

The nematocysts of *G. vertens* are basitrichous or atrichous isorhizes and microbasic euryteles, with macrobasic euryteles also present in the young medusa (Werner 1965; Nagao 1969b; Kubota 1976). Picard (1955a) stated microbasic mastigophores were present in the manubrium but this has not been confirmed by subsequent investigators. Westfall (1970a and b, 1973) has shown that the nematocyte is included in a complex with epithelio-muscular cells and an axon, implying nervous control of nematocyst discharge.

Specimens of this medusa should be treated with great care, although no medical problems have been attributed to it in the northeast Pacific. Japanese (Otsuru et al 1974) and Russian workers have described the effects of contact on humans including immediate burning, edema, and hyperemia followed by muscle weakness or convulsions, disturbed respiration, temporary blindness or deafness, liver manlfunction, and various psychological disorders. Individual reactions are highly variable and it is not normally fatal, most symptoms disappearing in 3 to 4 days. The extensive Russian literature which is difficult to obtain has been summarized by Aznaurian (1964), Pigulevsky and Michaleff (1969), and in a collection of papers edited by Zhirmunskii et al (1974). Liberation of histamine and decrease of blood serotonin have been demonstrated. Various treatments have been tried of which the most successful is intravenous injection of novocain in glucose and in severe cases artificial respiration.

In British Columbia waters *Gonionemus vertens* is often abundant around eelgrass beds May to July, although it has been collected occasionally as late as September.

Family Proboscidactylidae

Limnomedusae without marginal vesicles; stomach with 4-6 or more radial lobes extending along the proximal portions of the radial canals; gonads surrounding stomach and extending onto basal lobes, rarely interradial on stomach wall alone; radial canals generally branched; tentacle bulbs without ocelli. Polyps, where known, with two tentacles, on openings of polychaete tubes.

Genus *Proboscidactyla* Brandt, 1835

Proboscidactylidae with clusters of nematocysts on the exumbrella; with gonads extending onto lobes of stomach; with 4-6 or more branched radial canals; usually without a ring canal.

Type species: *P. flavicirrata* Brandt, 1835.

Proboscidactyla flavicirrata Brandt, 1835

Proboscidactyla flavicirrata Brandt, 1835: 28; 1838: 390, pl. 19; A. Agassiz, 1865: 173; Haeckel, 1879: 159; Browne, 1905b: 725; Foerster, 1923: 29; Uchida, 1940: 288; Uchida and Okuda, 1941: 440; Hand, 1954: 52 (in part); Kramp, 1959a: 177; 1961: 234; Rees, 1979a: 551.
Proboscidactyla flavicirrhata L. Agassiz, 1862: 346.
Proboscidactyla brevicirrata Haeckel, 1879: 160; Murbach and Shearer, 1903: 178.
Willia pacifica Maas, 1909: 17, pl. 3; Uchida, 1927a: 236.
Willsia stellata Uchida, 1925: 88; 1930: 334.
Willia stellata Uchida, 1927a: 235 (non *W. stellata* Forbes, 1846: 268).
Willsia pacifica Uchida, 1930: 334.
Willsia flavicirrata Uchida, 1938b: 40.
Lar flavicirrata Uchida and Okuda, 1941: 431; Yamada, 1950: 6.

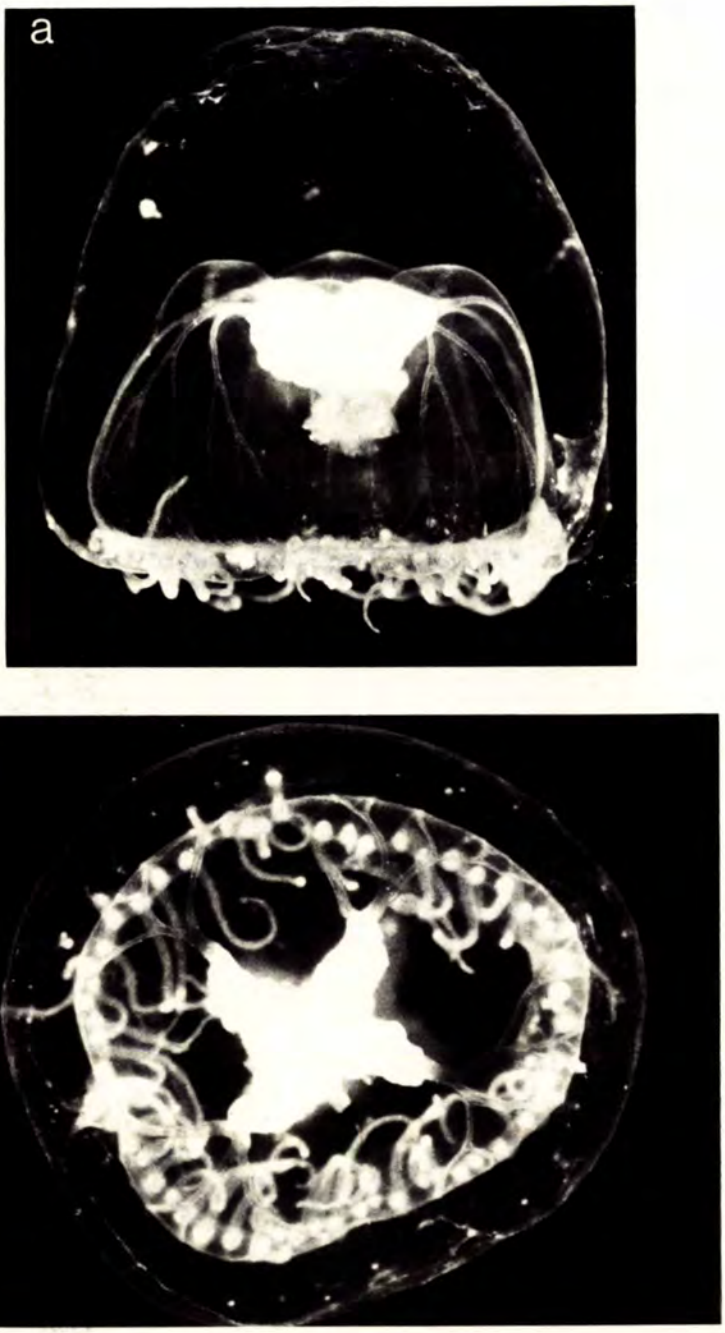


Fig. 67. *Proboscidactyla flavicirrata*, live specimen, 6.2 mm high, Departure Bay. a. lateral view; b. aboral view. Photos. M. N. Arai.

Proboscidactyla pacifica Kramp, 1959a: 177; 1961: 236.
Lar flavicirratus Naumov, 1960: 504 (in part); Zelickman, 1976: 206.

Specific characters: Four, rarely to nine, primary radial canals, with up to 72, rarely to 108, terminal branches and same number of short tentacles; no ring canal in mature specimens.

Description of medusa: Umbrella dome-like, up to 10 mm wide, 10 mm high; cnidothylacies (nematocyst sacs) on exumbrellar surface except above first set of tentacles to develop. Interradial subumbrellar pouches extend the subumbrellar cavity well above the level of the stomach. Gonadal masses interradial on stomach, extending slightly onto radial canals. In larger specimens lips of manubrium highly folded, extending short distance below oral end of gonads. Color in living specimens, stomach and gonads gold-brown (rarely pinkish), tentacle bulbs black or brown.

Hydroid: Described by Uchida and Okuda (1941), Yamada (1950), Hand (1954), Campbell (1968a, and b), Strickland (1971), and Donaldson (1973, 1974a and b). Medusae were raised from the polyp by Rees (1979a).

Distribution:

British Columbia and Puget Sound;

North of Vancouver (Mackie and Mackie 1963); Strait of Georgia (Kramp 1928; Fulton 1968); Deep Bay (present work); French Creek boat basin (present work); Strait of Georgia, north of Five Finger Is. (Foerster 1923; Brinckmann-Voss 1974; present work); Departure Bay (Foerster 1923: Brinckmann-Voss 1974; present work); Strait of Georgia, off Berry Pt., north end Gabriola Island (Foerster 1923; Brinckmann-Voss 1974); Nanaimo Region (Fraser 1932); Nanaimo Harbour (Kramp 1928); Northumberland Channel (Foerster 1923); Dodd Narrows (Foerster 1923; Brinckmann-Voss 1974); Stuart Channel, off Round Island (Foerster 1923; Brinckmann-Voss 1974); Ladysmith Harbour (present work); Vesuvius Bay, Stuart Channel (Foerster 1923); Strait of Georgia, off Galiano Island (A. Agassiz 1865); Tod Inlet, off Brentwood Bay, Saanich Inlet (Foerster 1923); Brentwood Bay, Saanich Inlet (present work); Gulf Islands (Mackie and Mackie 1963); San Juan Archipelago (Fraser 1932); Friday Harbor (Mackie and Mackie 1963; Donaldson 1974b; Spencer 1975); East Sound, Orcas Island (Campbell 1968a); Pleasant Beach, Puget Sound (Murbach and Shearer 1903); Oak Bay (Spencer 1975); Victoria Harbour (Murbach and Shearer 1903; Mackie and Mackie 1963); Sooke Harbour (present work); Bamfield Inlet (present work); Pacific Ocean off Ucluelet (present work); Kyuquot Sound (Brinckmann-Voss 1974); Bull Harbour (Foerster 1923); Massett Harbour (present work).

Pacific Ocean;

Pacific Ocean, between mouth of Columbia River and Cape Blanco, Oregon (Hand 1954); Port of Petropavlovsk, Kamchatka (Brandt 1835; 1838); Aniva Bay, Sea of Okhotsk (Zelickman 1976); Akkeshi Bay, Hokkaido (Uchida 1940; Uchida and Okuda 1941; Yamada 1950); Pacific Ocean, off Kushiro, Hokkaido (Uchida 1927a); Mutsu Bay (Uchida 1930; 1938b); Onagawa Bay (Uchida 1938c); Shibushi Bay, off Biro, Kagoshima (Uchida 1927a); Ishikari Bay, off Takashima, Hokkaido (Uchida 1927a); Ishikari Bay, off Oshoro, Hokkaido (Uchida 1925; 1927a); Yellow Sea (Chow and Huang 1958); Gulf of Arauco, Chile (Fagetti 1973).

Notes: The behavior and electrical activity of the hydroid and medusa have been described by Spencer (1974a and b, 1975). Spencer (1975) described feeding on copepods, cladocera, trochophore larvae, crab zoeae and various

eggs. Electrical activity accompanying swimming and "crumpling" behavior was analyzed.

The nematocysts of *P. flavicirrata* medusae are desmonemes and a second type with a slight dilation toward the tip of the hampe designated by Hand (1954) and Rees (1979a) as macrobasic eurýteles and by Mackie and Mackie (1963) as macrobasic mastigophores.

In the Strait of Georgia area the medusae are common in June and July, and have been collected March to November.

ORDER TRACHYMEDUSAE

Hydromedusae with umbrella margin entire and not divided into lobes; with thickened marginal nematocyst ring; with radial canals; with gonads usually confined to radial canals; with solid marginal tentacles, or with both solid and hollow tentacles, situated on the margin of the umbrella; with sensory clubs with endodermal axis which may be free or enclosed. Without a hydroid stage.

Family Rhopalonematidae

Trachymedusae with narrow stomach with or without peduncle; with usually eight, rarely more, radial canals; centripetal canals absent or very short; with gonads on radial canals, with marginal tentacles evenly distributed, sometimes of two kinds, each tentacle of uniform structure throughout; with free, rarely enclosed, marginal sensory clubs.

Genus *Aglantha* Haeckel, 1879

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

Type species: *A. digitale* (O. F. Müller, 1776).

Aglantha digitale (O. F. Müller, 1776)

Medusa digitale O. F. Müller, 1776: 233; Fabricius, 1780; 366.
Melicerta digitale Péron and Lesueur, 1809: 352.
Dianaea digitala Lamarck, 1816: 507.
Eirene digitale Eschscholtz, 1829: 95.
Circe camtschatica Brandt, 1835: 19; 1838: 354, pl. 1; Agassiz, 1862: 348.
Turris borealis Lesson, 1843: 284.
Circe rosea Forbes, 1846: 286; 1848: 34, pl. 1; Agassiz, 1862: 349.
Turris digitalis Mörch, 1857: 23 (non *T. digitalis* Forbes 1848).
Circe impatiens A. Agassiz (in L. Agassiz), 1862: 349.
Trachynema camtschaticum Agassiz, 1865: 55.
Trachynema digitale Agassiz, 1865: 57; Fewkes, 1881: 160, pl. 2; Nutting, 1901a: 381.
Aglantha digitalis Haeckel, 1879: 272, pl. 16; Maas, 1893: 23; Hartlaub, 1894: 197; Birulya, 1896: 346; Vanhöffen, 1897: 273; Browne, 1903: 22; C. Hargitt, 1905: 55; Maas, 1906: 495; Hartlaub, 1909: 470; Kramp, 1913a: 269; 1913b: 527; Le Danois, 1913a: 27; 1913b: 354; Kramp, 1914: 428 (in part); 1915: 8; Sverdrup, 1921: 27, pl. 4; Uchida, 1928: 79; Kramp, 1955a: 158.
Aglantha camtschatica Haeckel, 1879: 273.
Circe kamtschatica Wagner, 1885: 75, pl. 3.
Circe kamtschatika Schlater, 1891: 342.

Fig. 68. *Aglantha digitale*, preserved specimen, 11.5 mm high, Departure Bay. Photo. M. N. Arai.

Aglantha occidentalis or *A. digitalis* var. *occidentalis* Maas, 1893: 24.
Aglantha digitale var. *occidentalis* Aurivillius, 1896: 194.
Aglantha rosea Browne, 1898: 833, pl. 49; 1903: 23; Bigelow, 1909a: 121; 1909b: 312; Russell, 1925: 786; 1927: 573; Sanderson, 1930: 229; Russell, 1933: 74; 1938b: 433; Beaudoin, 1971: 401.
Aglantha conica C. Hargitt, 1902a: 21; 1905: 56; 1908: 111.
Aglanta digitalis Linko, 1904: 219.
Aglantha digitale Bigelow, 1909a: 121 (in part, non var. *intermedia*); Mayer, 1910: 402, pl. 49; Bigelow, 1913: 43; 1915b: 314; Foerster, 1923: 47; Uchida, 1925: 27; Bigelow, 1926: 352; Uchida, 1927b: 225; Kramp, 1927: 149; Broch, 1929: 512; Thiel, 1932: 154; Ranson, 1936: 177, pl. 2; Kramp, 1942: 81; 1947: 27; Grainger, 1959: 471; McLaren, 1969: 1485; Calder, 1971: 76.
Aglaura hemistoma var. *laterna* Sverdrup, 1921: 26, pl. 3 (non *A. hemistoma* Péron and Lesueur 1809).
Aglantha digitale var. *rosea* Coy, 1924: 56; Peacock, 1924: 60; Kramp, 1927: 152; Russell, 1953: 447; Boyd et al 1973: 397.

Aglantha digitalis var. *rosea* Russell, 1936: 27; 1940: 521.
Aglantha digitale var. *camtschatica* Hand and Kan, 1961: 11.
Aglantha digitale digitale Smedstad, 1972: 112.
Aglantha digitale rosea Smedstad, 1972: 112.

Specific characters: Radial canals on peduncle straight; gonads long, close to base of peduncle.

Description of medusa: Umbrella thimble-shaped, about twice as high as wide, with small conical apical projection, lateral walls thin, subumbrellar muscles strong, up to 40 mm high but often mature at smaller sizes. Velum broad and well developed. Stomach small, at end of conical peduncle, reaching nearly to umbrella margin. Mouth with four small, simple lips. Mature specimens with numerous smooth marginal tentacles in single row. Four to eight marginal sensory clubs situated singly between adjacent radial canals on inner side of ring canal near velum; each with single concretion. Living specimens colorless or with stomach and marginal tentacles delicate or bright pinkish red; gonads milky, yellow, or pale pink.

Hydroid: Trachymedusae do not possess a hydroid stage. The direct larval development has been described by A. Agassiz (1865), Fewkes (1881), Le Danois (1913a, b), G. Hargitt (1917), and Russell (1953). The number of generations per year varies from one to three in different localities (Kramp 1927, Russell 1936, 1938b, McLaren 1969, Smedstad 1972, Arai and Fulton 1973).

Discussion of taxonomy: Local varieties of this wide-ranging species vary in size and color. As seen in the synonymy, this has resulted in many authors distinguishing these varieties as named varieties or as distinct species.

Foerster (1923) described a specimen with 16 statocysts per quadrant. Brinckmann-Voss (1974) reexamined specimens in the Pacific Biological Station collection which had been identified by Foerster and which included specimens from all locations listed by Foerster (1923). No such unusual specimen was found. It is possible Foerster misidentified broken tentacle bases as statocysts.

Distribution:

British Columbia and Puget Sound;
Strait of Georgia (A. Agassiz in L. Agassiz 1862; Fulton 1968; Kramp 1968a); Strait of Georgia, off Mitlenatch Island (Brinckmann-Voss 1974); Deep Bay (present work); Strait of Georgia, off Lantzville (Brinckmann-Voss 1974); Strait of Georgia, northeast of Five Finger Island (Foerster 1923; Brinckmann-Voss 1974; present work); Departure Bay (Foerster 1923; Brinckmann-Voss 1974; present work); East of Newcastle Island (Foerster 1923; Brinckmann-Voss 1974); Nanaimo Region (Fraser 1932); Strait of Georgia, off north end Gabriola Island (Foerster 1923; Brinckmann-Voss 1974); Strait of Georgia, off Galiano Island (A. Agassiz 1865); Saanich Inlet (Arai and Fulton 1973); Tod Inlet, Saanich Inlet (Foerster 1923; Brinckmann-Voss 1974); Boundary Passage (Brinckmann-Voss 1974); San Juan Archipelago (Fraser 1932); Friday Harbor (Mackie and Mackie 1963); Oak Bay (Singla 1978a); Ucluelet Inlet (present work); 52°02'N, 132°53'W, west of Cape St. James, Queen Charlotte Islands (Bigelow 1913).

Pacific Ocean;
Pacific Ocean off Oregon (Pearcy 1972); Yaquina Bay, Oregon (McCormick 1969); 37°-43°N, 160°-167°W, Pacific Ocean (Kramp 1965a); 50°N, 145°W, "Station P", Gulf of Alaska (Arai and Fulton 1973; Brinckmann-Voss 1974); 53°N, 138°-144°W, Gulf of Alaska (Bigelow 1913); 53°46'N, 164°29'W, off Ugamak Island, Aleutian Islands (Bigelow 1913); Dutch Harbor, Unalaska Island (Bigelow 1913); 53°57'N, 168°06'W, off Bogosloff Islands (Bigelow 1913); 53°20'N, 172°00'W, Bering Sea (Ikeda 1972); 52°38'N, 174°49'W, off Kaniuji Island, Aleutian Islands (Bigelow 1913); Bowers Bank, Bering Sea (Bigelow 1913); 52°55'N - 53°20'N, 170°33'E - 173°30'E, off Attu Is., Aleutian Islands (Bigelow 1913); 54°48'N, 164°54'E, off Bering Island (Bigelow 1913); Karaginsky Bay, Kamchatka (Brandt 1835, 1838); Pacific Ocean, southeast of Kamchatka (Yashnov 1952); 52°37'N, 158°50'E, off Staritschkof Island, Kuril Islands (Bigelow 1913); 51°33'N, 156°20'E, Okhotsk Sea off Kuril Islands (Uchida 1933); 49°06'N, 153°06'E, off Chirnkotan Island, Kuril Islands (Bigelow 1913); Kuril-Kamchatka Trench (Mednikov 1958; Vinogradov 1968; Naumov 1971); 46°29'N, 145°46'E, Okhotsk Sea (Bigelow 1913); 44°33'N, 149°04'E, Pacific Ocean (Bigelow 1913); Akkeshi Bay, Hokkaido (Uchida 1940; Hada 1972); 42°13'N, 144°21'E, off Erimo Cape, Hokkaido (Bigelow 1913), Mutsu Bay (Uchida 1927b; 1928; 1938b); Pacific Ocean, off Enoshima Island (Uchida 1938c); 37°42'N, 147°25'E, Pacific Ocean (Kramp 1965a); Pacific Ocean, east of Choshi (Nakai et al 1966); Tokyo Bay, off Kanazawa (Uchida 1928); Sagami Bay, off Misaki (Uchida 1930); Suruga Bay, off Toi (Uchida 1948); 30°20'N, 138°00'E, Pacific Ocean (Kramp 1965a); 36°41'N, 132°26'E, Sea of Japan, off Oki Islands (Bigelow 1913); Sea of Japan, east of Oki Islands (Furuhashi 1953); New Yamato Bank, Sea of Japan (Yamazi 1953); Toyama Bay (Bigelow 1913); Sea of Japan, off Sado Island (Bigelow 1913; Uchida 1958); Tsugaru Strait (Bigelow 1913; Ikeda 1974); Ishikari Bay, off Takashima, Hokkaido (Uchida 1928); Ishikari Bay, off Oshoro, Hokkaido (Uchida 1925; 1928; Ikeda 1974); 36°32'N, 129°58'E, Sea of Japan, off Korea (Bigelow 1913).

Atlantic Ocean;
See Levinsen (1893), Maas (1906), Kramp (1913b), Bigelow (1926), Kramp (1927, 1947), Wiborg (1955), Alvariño (1956), Kramp (1961), Cronin et al (1962), Kühl (1962), Southward (1962), Hamond (1964), Teissier (1965), Allwein (1968), Beaudouin (1971), Pavshtiks et al (1971), Calder (1971), Shih et al (1971), Smedstad (1972), Boyd et al (1973), van Soest (1973) and Oug (1977) for details.

Arctic Ocean;
See Maas (1906), Kramp (1947, 1961), Hand and Kan (1961), Digby (1961), Grainger (1962, 1965), Uchida (1969), McLaren (1969), Pavshtiks et al (1971), Zelickman (1972), Grainger (1975), Grainger and McSween (1976), Kashkin (1976), Shih and Laubitz (1978), and Kolosova (1978) for details.

Notes: *Aglantha digitale*, with its direct development, is widely distributed in the colder waters of the northern hemisphere. It is common both in the upper 500 m of the open ocean (e.g., Kramp 1913b, Bigelow 1926, Vinogradov 1968) and in landlocked or partially isolated fjords (e.g., McLaren 1969, Smedstad 1972). In some locations diel vertical migration has been observed, whereas in other locations it is apparently absent (Russell 1925, Bogorov 1941, Hansen 1951, Digby 1961, McLaren 1969, Arai and Fulton 1973).

The medusa shows both slow rhythmical swimming and (in response to tactile stimulation) a single very strong contraction which will shoot it forward several body lengths (Gladfelter 1973, Singla 1978a). Singla (1978a)

described a group of giant axons which extend over the striated circular muscle layer and which may control the sudden rapid movement.

Adult *Aglantha digitale* feed primarily on copepods, with a few larvae of other invertebrate groups (Lebour 1922; Smedstad 1972). The smallest medusae may eat phytoplankton (McLaren 1969). The relationships between bell height and dry weight (Mathews and Hestad 1977) or carbon content (McLaren 1969) have been measured. Ikeda (1972) examined moisture, protein, lipid, chitin, carbohydrate and ash content, the largest concentrations being 94.2% moisture, 3.3% protein and 2.3% ash. The pH of the body wall is approximately 7 (Nomura and Kokubo 1934). Ikeda (1974) analyzed nitrogen, carbon and hydrogen content. He found a respiratory rate of 1.37 µL O_2/(mg dry wt . h) at 6.5-7.0°C and of 5.29 µL O_2/(mg dry wt . h) at 14.5-17.5°C.

Russell (1940) found stenoteles and microbasic euryteles near the mouth, with a number of intermediate forms so that he suggested microbasic euryteles might be formed by reduction of the stenoteles.

Genus *Crossota* Vanhöffen, 1902

Rhopalonematidae with or without a short gastric peduncle; with numerous meridional furrows on the exumbrella; with eight or more radial canals; with pendant, sausage shaped gonads on radial canals; with numerous densely crowded tentacles all alike; with free, club-shaped statocysts.

Type species: *C. brunnea* Vanhöffen, 1902.

Crossota rufobrunnea (Kramp, 1913)

Aglantha rufobrunnea Kramp, 1913a: 273.
Crossota brunnea var. *norvegica* Bigelow, 1913: 48 (in part; non *Crossota norvegica* Vanhöffen, 1902: 75).
Crossota norvegica Kramp, 1920b: 5; Broch, 1929: 507 (in part).
Crossota rufobrunnea Kramp and Damas, 1925: 317; Broch, 1929: 506; Ranson, 1936: 162; Kramp, 1942: 79; 1947: 22, pl. 1, 3, 4, 6 (non Uchida, 1948: 338); Yashnov, 1952: 95; Russell, 1953: 444; Kramp, 1961: 257.
Crossota brunnea Thiel, 1936: 20 (in part, non *C. brunnea* Vanhöffen, 1902: 73, pl. 9, 12); Bigelow 1938: 119 (in part); Naumov 1956a: 38; 1960: 558 (in part).

Specific characters: Umbrella up to 22 mm wide; without gastric peduncle; with gonads on eight radial canals near base of stomach; with up to 350 tentacles.

Description of medusa: Umbrella higher than a hemisphere, jelly moderately thin. Stomach bottle-shaped, short, with eight large, deep, longitudinal fissures and above them eight similar small invaginations; mouth with four small outturned lips. Number of statocysts unknown. Subumbrella, stomach, gonads, and tentacles deep reddish-brown; pigmented ectoderm frequently rubbed off preserved specimens.

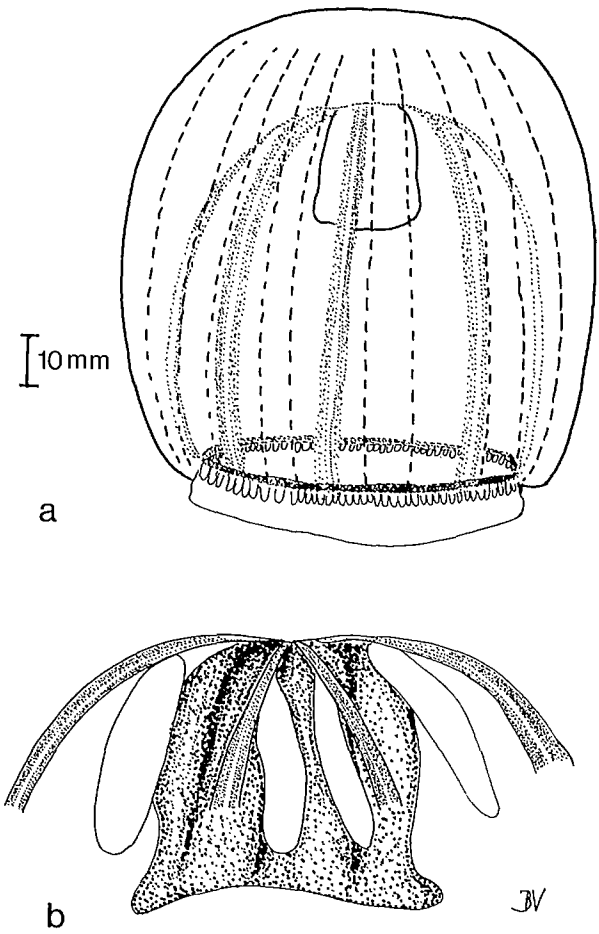


Fig. 69. *Crossota rufobrunnea*, a. whole animal, Lat. 50°N, Long. 145°W, "Station P"; b. detail of stomach and gonads, "Godthaab" collections, Copenhagen.

Discussion of taxonomy: Bigelow (1913) described a *Crossota*, which he called *Crossota brunnea* var. *norvegica*, from the North Pacific. Kramp (1947) reexamined two of these specimens and confirmed that they were *Crossota rufobrunnea*. *C. rufobrunnea* has been found in several locations in the northern Atlantic as far south as about 30°N. It differs from *C. brunnea* of the southern Atlantic chiefly in size and tentacle number. Earlier Bigelow (1909a) collected specimens in the eastern Pacific between 0 and 20°S. These were definitely *C. brunnea* since they were up to 27 mm in diameter, and the smallest specimen with gonads was 17 mm in diameter (Bigelow 1913 p. 49). The distinction between these two species in subsequent collections in the Pacific is often questionable.

Uchida (1948) reported both species off the coast of Japan. The specimens reported as *C. rufobrunnea* differ from the typical form in possessing gonads which are a "protruding mass" and are attached to the manubrium as well as the radial canals, and in being up to 32 mm in diameter. These do not even belong to the genus *Crossota*, presently defined as containing species with pendant, sausage shaped gonads on the radial canals. The specimens reported as *C. brunnea* are not described in sufficient detail to definitely identify. The largest specimen mentioned is less than 22 mm in diameter, so it is possible that these were actually *C. rufobrunnea*. Yashnov (1952) described *C. rufobrunnea* from near Kamchatka. Naumov (1956a, 1960) synonymized the two forms but Kramp (1961) continued to consider them separate species. Since then Pearcy (1972) has reported *C. rufobrunnea* off Oregon, Beklemishev (1961) has reported *C. rufobrunnea* on the 40th parallel west of Oregon, Alvariño (1967) has reported *C. brunnea* off San Diego, California, and Vinogradov (1968) and Naumov (1971) have reported *C. brunnea* from the Kuril-Kamchatka trench, all without any discussion of taxonomy or morphology. Kramp (1965a) reported *C. brunnea* from various locations in the southern Pacific as far north as 14°37'N off the Philippines. In this situation Kramp's (1968c) statement that *C. rufobrunnea* is the species of the northern Pacific and *C. brunnea* is only found slightly north of the equator, must be considered hypothetical until further work can be done.

We have found two specimens from the Strait of Georgia which may belong to this species. They are only about 5 mm wide, without gonads so the identification is very tentative. Although the tentacles were merely stump-like, we counted between 100 and 120 tentacles in each of the specimens.

Distribution:

British Columbia and Puget Sound;
52°02'N, 132°53'W, west of Cape St. James, Queen Charlotte Islands (Bigelow 1913).

Pacific Ocean;
Pacific Ocean off Oregon (Pearcy 1972); 40°N, 133°W, off Oregon (Beklemishev 1961); 50°N, 145°W, "Station P", Gulf of Alaska (present work); 53°N, 138°-145°W, Gulf of Alaska (Bigelow 1913); 53°57'N, 168°06'W, off Bogoslof Islands, Aleutian Islands (Bigelow 1913); 53°20'N, 171°W, off Yunaska Id., Aleutian Islands (Bigelow 1913); 52°38'N, 174°49'W, off Kaniuji Id., Aleutian Islands (Bigelow 1913); Bowers Bank, Bering Sea (Bigelow 1913); 54°48'N, 164°54'E, off Bering Island (Bigelow 1913); Pacific Ocean, southeast of Kamchatka (Yashnov 1952); 52°37'N, 158°50'E, off Staritschkof Island, Kuril Islands (Bigelow 1913); 49°06'N, 153°06'E, off Chirinkotan Island, Kuril Islands (Bigelow 1913).

Atlantic Ocean;
See Kramp (1947), Petersen (1957), van Soest (1973) and Fraser (1974) for details.

Notes: This is a largely bathypelagic species although it has been collected from near the surface to more than 1000 m.

Genus *Pantachogon* Maas, 1893

Rhopalonematidae without a gastric peduncle; with the apical outlines of the subumbrellar muscular fields forming an entire circle; with gonads along

the eight radial canals separated from stomach; with 48 or more tentacles all alike; with free, club-shaped marginal statocysts.

Type species: *P. haeckeli* Maas, 1893.

Pantachogon haeckeli Maas, 1893

Pantachogon haeckelii Maas, 1893: 17, pl. 1.
Pantachogon rubrum Vanhöffen, 1902: 63, pls. 9-11; Kramp, 1913a: 274; Ranson, 1936: 147, pl. 2; Thiel, 1936: 24 (in part).
Pantachogon haeckeli Bigelow, 1913: 44, pl. 3; 1938: 115; Kramp, 1947: 19, pl. 2.

Specific characters: Umbrella without an apical projection; 64 tentacles and 64 statocysts in full grown specimens.

Description of medusa: Umbrella bell-shaped, up to 20 mm high and wide: jelly fairly thin; large specimens with 32 fine exumbrellar meridional furrows; summit of subumbrella transversely truncated and without musculature, remainder of subumbrellar musculature well developed. Velum very broad. Stomach rather short. Mouth with four simple pointed lips. Straight, uniformly narrow radial canals. Gonads initially form discontinuous linear swellings along each side of each radial canal which eventually coalesce and become folded transversely; covering distal two-thirds or almost whole of radial canal. Solid marginal tentacles in one row. Marginal sense organs, one between every two tentacles. Whole medusa colorless with iridescent subumbrella, or with much or all of the animal red, velum excepted.

Distribution:

British Columbia and Puget Sound;
52°02'N, 132°53'W, West of Cape St. James, Queen Charlotte Islands (Bigelow 1913).

Pacific Ocean;
Pacific Ocean off Oregon (Pearcy 1972); 53°53'N, 144°53'W, Gulf of Alaska (Bigelow 1913); 53°57'N, 168°06'W, off Bogoslof Islands, Aleutian Islands (Bigelow 1913); 53°20'N, 171°W, off Yunaska I., Aleutian Islands (Bigelow 1913); 52°38'N, 174°49'W, off Kaniuji I., Aleutian Islands (Bigelow 1913); Bowers Bank, Bering Sea (Bigelow 1913); Pacific Ocean, southeast of Kamchatka (Yashnov 1952); 49°06'N, 153°06'E, off Chirinkotan I., Kuril Islands (Bigelow 1913); Kuril-Kamchatka Trench (Vinogradov 1968; Naumov 1971); 46°29'N, 145°46'E, Okhotsk Sea (Bigelow 1913); Sagami Bay (Uchida 1948); Suruga Bay (Uchida 1948); Southeast Molucca Sea (Maas 1905); West Ceram Sea (Kramp 1965a); Banda Sea, off Ambon (Maas 1905; Kramp 1965a); Banda Trench (Kramp 1965a); Coral Sea, off New Caledonia (Kramp 1965a); South Fiji Basin (Kramp 1965a); 33°30'S, 165°53'E; Tasman Sea (Kramp 1965a); Tasman Sea, off Sydney, Australia (Kramp 1965a); Tasman Sea, east of Bass Strait (Blackburn 1955); 46°43'S, 176°08'E, Pacific Ocean southeast of New Zealand (Kramp 1965a); Pacific Ocean, east of Cook Strait (Kramp 1965a); Kermadec Trench, Pacific Ocean (Kramp 1965a); 69°S, 126°W, Pacific Ocean off Antarctica (Kramp 1957a); 33°-34°S, Pacific Ocean off Chile (Fagetti 1973).

Atlantic Ocean;
See Ranson (1936), Bigelow (1938), Kramp (1947, 1948, 1955, 1957a, 1959a). Fraser (1950, 1955, 1974), Russell (1953), Petersen (1957), Furnestin (1959),

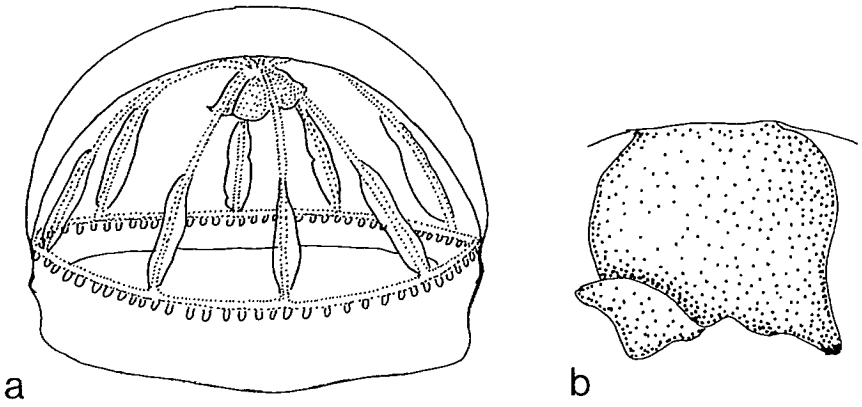


Fig. 70. *Pantachogon haeckeli* a. whole animal (after Vanhöffen 1902, modified); b. detail of stomach, "Dana" collections, Copenhagen.

and van Soest (1973) for details.

Arctic Ocean;

See Kramp (1942), and Zelickman (1972) for details.

Indian Ocean;

See Browne (1916), Kramp (1957a and b, 1965) and Vannucci and Navas (1973b) for details.

Notes: As noted by Gladfelter (1973) *Pantachogon haeckeli* is a very powerful swimmer.

It is a deep-sea oceanic species. In the Kuril-Kamchatka Trench the maximum population lies in the 750 - 1000 m layer but part of the population also descends deeper to 2000 - 3000 m (Vinogradov 1968, Naumov 1971).

ORDER NARCOMEDUSAE

Hydromedusae with sides of umbrella divided by peronial grooves so that umbrella margin may be lobed; with broad stomach with entire circular periphery or with peripheral pouches; without radial canals, and with or without a peripheral canal system; with gonads on stomach walls; with solid marginal tentacles leaving umbrella some distance above margin, and sometimes small secondary tentacles on margin itself; sense organs free sensory clubs with endodermal axis; without true hydroid stage but with parasitic larval development in some species.

Family Aeginidae

Narcomedusae with interradial, divided stomach pouches; with or without peripheral canal system; with primary perradial tentacles leaving umbrella between marginal pouches; pouches extending beyond points of origin of primary tentacles; with or without secondary tentacles on umbrella margin; with or without otoporpae.

Genus *Aegina* Eschscholtz, 1829

Aeginidae with typically 8, occasionally 10 to 12, stomach pouches; with peripheral canal system; with typically four, occasionally three, five or six, primary tentacles and same number of peronia; without secondary tentacles; without otoporpae.

Type species: *A. citrea* Eschscholtz, 1829.

Aegina citrea Eschscholtz, 1829

Aegina citrea Eschscholtz, 1829: 113, pl. 11; Haeckel, 1879: 338, pl. 11; Maas, 1905: 71, pls. 11, 13; Vanhöffen, 1908: 50; Bigelow, 1909a: 73, pls. 1, 14; Mayer, 1910: 451, 726; Bigelow, 1913: 59; Broch, 1929: 530; Ranson, 1936: 209, pl. 2; Bigelow, 1938: 131; Kramp, 1948: 15; Russell, 1953: 467, pl. 28; Kramp, 1957a: 63; Vannucci, 1957: 81; Kramp, 1959a: 61; 1961: 266.

Aegina rosea Eschscholtz, 1829: 115, pl. 10; Haeckel, 1879: 338; Vanhöffen, 1908: 48, pls. 1, 3; Maas, 1909; 35; Vanhöffen, 1912: 388; Bigelow 1913: 59; Uchida, 1928: 91; Broch, 1929: 530; Thiel, 1936: 73; Uchida, 1948: 341; Yashnov, 1952: 96; Yamazi, 1958: 136; Naumov, 1960: 569, pl. 30.

Cunarcha aeginoides Haeckel, 1879: 315; 1882: 24, pl. 9.

Aegina rhodina Haeckel, 1879: 338, pl. 20; Mayer, 1904: 27, pl. 4; Maas, 1905: 71; Bigelow, 1909a: 72; Mayer, 1910: 452, pls. 52, 54.

Aegina canariensis Haeckel, 1879: 339.

Aegina eschscholtzii Haeckel, 1879: 339; Mayer, 1910: 453.

Solmundus tetralinus Haeckel, 1879: 351, pl. 19.

Aegina lactea Vanhöffen, 1908: 50, pl. 1.

Aegina brunnea Vanhöffen, 1908: 51, pl. 1; Mayer, 1910: 453.

Fig. 71. *Aegina citrea*, preserved specimen, 5.3 mm high, Active Pass. Photo. M. N. Arai.

Aegina altermans Bigelow, 1909a: 74, pl. 17; Mayer, 1910: 453.
Aegina pentanema Kishinouye, 1910: 32, pl. 5.
Aegina aeginoides Mayer, 1910: 454.

Specific characters: This is the only species of the genus.

Description of medusa: Umbrella up to 50 mm wide, hemispherical; jelly thick in upper half of umbrella, thin at sides of lower half and margin. Velum well developed. Stomach large, circular, and flattened or dome-shaped dorsally, with typically eight rectangular marginal pounches, sometimes with a small median notch on some or all; lower portion of stomach conical. Mouth simple and circular, not extending beyond umbrella margin. Gonads on walls of stomach pouches, sometimes extending on to main body of stomach. Typically, four large solid marginal tentacles issuing from umbrella at upper ends of peronia in deep exumbrella furrows, at level of top of stomach; with root-like endodermal continuations in substance of apical jelly; length of each marginal tentacle up to twice diameter of umbrella. Numerous marginal statocysts.

Color of stomach, stomach pouches and marginal tentacles yellow, yellowish-brown, brown, pink, green or milky-white to colorless.

Distribution:

British Columbia and Puget Sound;

Strait of Georgia (Fulton 1968); Howe Sound, off Hutt Is. (present work); Nanaimo Region (Fraser 1932); Strait of Georgia, northeast of Five Finger Is. (Foerster 1923; Brinckmann-Voss 1974; present work); Departure Bay (present work); Strait of Georgia, off Berry Pt., north-end Gabriola Island (Foerster 1923; Brinckmann-Voss 1974); Active Pass (Brinckmann-Voss 1974); Strait of Georgia, off Saturna Is. (present work); Friday Harbor (Mackie and Mackie 1963; Singla 1972); Nootka Sound (Brinckmann-Voss 1974); Knight Inlet (Brinckmann-Voss 1974).

Pacific Ocean;

Pacific Ocean off Costa Rica (Bigelow 1940); 30°30'N, 120°00'W, off San Diego, California (Alvariño 1967); Pacific Ocean, off Bodega Head, California (Rees 1975); 39°18'N, 123°58'W, off N. California (Bigelow 1913); Pacific Ocean off Oregon (Pearcy 1972); 53°57'N, 159°31'W, Gulf of Alaska, south of Shumagin Is. (Bigelow 1913); 53°46'N, 164°29'W, south of Aleutian Is. (Bigelow 1913); Bower's Bank, Bering Sea (Bigelow 1913); 53°20'N, 170°33'E, off Attu Is., Aleutian Is. (Bigelow 1913); 54°48'N, 164°54'E, off Bering Is. (Bigelow 1913); Pacific Ocean, southeast of Kamchatka (Yashnov 1952); 52°37'N, 158°50'E, off Staritschkoff Is., Kuril Is. (Bigelow 1913); 44°-46°N, 150°-156°E, Kuril-Kamchatka Trench (Naumov 1971); 44°33'N, 149°04'E, Pacific Ocean (Bigelow 1913); 34°N, 159°E, Pacific Ocean (Eschscholtz 1829); 42°13'N, 144°21'E, off Erimo Cape, Hokkaido (Bigelow 1913); Sagami Bay (Maas 1909; Kishinouye 1910; Uchida 1928, 1948; Kramp 1968a); Suruga Bay (Kishinouye 1910); Lat. 33°25'N, Long. 135°56'E, off Kushino Pt., Wakayama (Bigelow 1913); Tanabe Bay, Wakayama (off Seto Biological Lab.) (Uchida 1928; Yamazi 1958); East China Sea N.E. of Formosa (Kramp 1965a); 6°-14°N, 111°-119°E, South China Sea (Kramp 1965a); Verde Island Passage, Philippines (Bigelow 1919); Sulu Sea (Kramp 1965a); Makassar Strait (Maas 1905); Bali Sea (Kramp 1965a); Gulf of Bone, Celebes (Bigelow 1919); Banda Sea (Maas 1905; Kramp 1965a); Molucca Sea (Maas 1905; Kramp 1965a); West Caroline Basin, off New Guinea (Kramp 1965a); off Ralum, New Britain (Vanhöffen 1908); South Fiji Basin (Kramp 1965a); 27°S-37°S, Tasman Sea (Blackburn 1955; Kramp 1965a); 41°-46°S, 176°E, Pacific Ocean, east of New Zealand (Kramp 1965a); Kermadec Trench, Pacific Ocean (Kramp 1965a); Pacific Ocean, off Samoa (Kramp 1965a); Pacific Ocean, off Tahiti (Kramp 1965a); 7°45'S, 131°22'N, Pacific Ocean east of Marquesas Islands (Kramp 1965a); Pacific Ocean, off Constitucion, Chile (Kramp 1966); Pacific Ocean, 72°-82°W, off Valparaiso, Chile (Fagetti 1973); Peru Basin, off Callao, Peru (Bigelow 1909a); Pacific Ocean, approx. 2°N - 8°S, 87°-116°W, off Galapagos Is. (Bigelow 1909a; Kramp 1965a); Pacific Ocean, off Columbia (Bigelow 1940); Gulf of Panama (Kramp 1959a).

Atlantic Ocean;

See Thiel (1936), Bigelow (1938), Kramp (1947, 1948, 1955b, 1957a, and b, 1959a), Vannucci (1951, 1957), Russell (1953), Petersen (1957), Furnestin (1959), Alvariño (1968), van Soest (1973), and Fraser (1974) for details.

Indian Ocean;

See Vanhöffen (1908, 1912), Browne (1916), and Kramp (1957a, and b, 1958, 1965a) for details.

Notes: The statocysts of *Aegina citrea* have been shown by Singla (1972, 1975) to include a well developed basal cushion and free hanging sensory club

but no sensory papilla.

The nematocysts are apotriches and atriches (Mackie and Mackie 1963).

Aegina citrea is a broadly distributed tropical and temperate species usually obtained in deep or intermediary strata in temperate latitudes but occasionally found in upper layers (Thiel 1935a; Kramp 1947, 1959a; Vannucci 1957; Alvariño 1967). In the Indian Ocean Vannucci and Navas (1973a) have shown it to be a stenohaline but eurythermal and oxygen-tolerant species. It has been obtained March to November in the Strait of Georgia and is probably present throughout the year in deeper waters.

Family Cuninidae

Narcomedusae with perradial and undivided stomach pouches; with or without peripheral canal system; with marginal tentacles leaving umbrella opposite center of each stomach pouch, equal in number to that of pouches; pouches not extending beyond points of origin of tentacles; without secondary tentacles on umbrella margin; with or without otoporpae.

Genus *Solmissus* (Haeckel, 1879)

Cuninidae without peripheral canal system; without otoporpae.

Type species: *S. albescens* (Gegenbaur, 1856).

Solmissus incisa (Fewkes, 1886)

Solmaris incisa Fewkes, 1886: 954.
Solmaris rhodoloma Vanhöffen, 1908: 60, pl. 1 (non *Aequorea rhodoloma* Brandt, 1838: 357, pl. 3).
Solmissus incisa Bigelow, 1909a: 67, pl. 21; 1913: 57; Ranson, 1936: 206; Russell, 1953: 464.

Specific characters: 20-40 stomach pouches, oval in outline, usually somewhat longer than wide; marginal lappets rectangular, about as long as broad, each with 2-5 statocysts.

Description of medusa: Umbrella up to 100 mm diameter, flat and disc-like, with thin and flexible margin, jelly very soft and fragile. Stomach large and circular, covering subumbrellar surface of upper portion of umbrella, with 20-40 marginal pouches, septa between pouches alternating with tentacle roots. Marginal tentacles stiff, tapering, up to slightly longer than diameter of the umbrella, attached to exumbrella at upper ends of peronia separating marginal lappets, with endodermal roots about half as long as septa between marginal gastric pouches. Colorless, or rarely with red gastric pouches.

Discussion of taxonomy: These medusae are extremely fragile and complete specimens have rarely been obtained. For example the presence of a velum was questioned by Russell (1953), although a velum shows clearly in the in situ photograph by Clarke (1961) of a living specimen. Specific characters such as

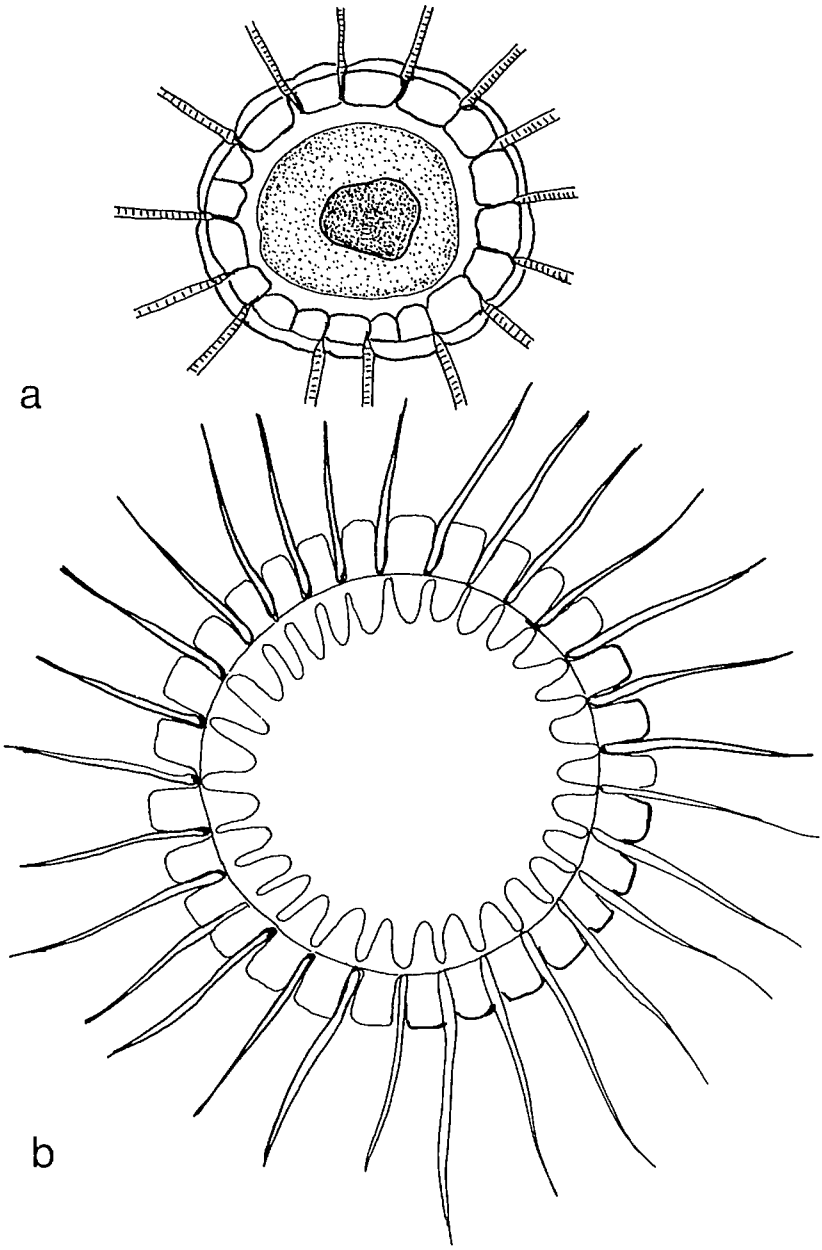


Fig. 72. *Solmissus incisa*, a. small specimen with marginal lappets pointing inwards and therefore hiding stomach pouches; b. larger specimen with marginal lappets pointing outwards with exposed stomach pouches. (After Russell 1953, modified).

shape of stomach pouches and marginal lappets, and number of statocysts can be determined for fragments, however, so all such records have been included in the distribution.

Distribution:

British Columbia and Puget Sound;
52°02'N, 132°53'W, west of Cape St. James, Queen Charlotte Islands (Bigelow 1913).

Pacific Ocean;
Monterey Bay, California (Bigelow and Leslie 1930); Pacific Ocean off Oregon (Pearcy 1972); 53°N, 138°-144°W, Gulf of Alaska (Bigelow 1913); 53°57'N, 168°06'W, off Bogoslof Islands, Aleutian Islands (Bigelow 1913); 52°38'N, 174°49'W, off Koniuji I., Aleutian Islands (Bigelow 1913); Bowers Bank, Bering Sea (Bigelow 1913); 53°20'N, 170°33'E, off Attu Island, Aleutian Islands (Bigelow 1913); 54°48'N, 164°54'E, off Bering Island (Bigelow 1913); 52°37'N, 158°50'E, off Staritschkof Island, Kuril Islands (Bigelow 1913); Sagami Bay (Uchida 1948); Suruga Bay (Bigelow 1913); Pacific Ocean, off Chichi Jima, Bonin Islands (Uchida 1928); 46°43'S, 176°08'E, Pacific Ocean southeast of New Zealand (Kramp 1965a); Pacific Ocean, approx. 0°30'N, 117°W (Bigelow 1909a), Pacific Ocean, approx. 5°30'S, 99°W (Bigelow 1909a); Pacific Ocean, approx. 18°S, 102°W (Bigelow 1909a); Peru Basin, off Callao, Peru (Bigelow 1909a); Pacific Ocean, off Aguja Point, Peru (Bigelow 1909a); 2°06'S, 84°14'W, Pacific Ocean west of Ecuador (Kramp 1968b); Gulf of Panama (Kramp 1959a).

Atlantic Ocean;
See Moore (1949), Russell (1953), Kramp (1955b), Petersen (1957), Kramp (1959a), Clarke (1961), van Soest (1973) and Fraser (1974) for details.

Indian Ocean;
See Vanhöffen (1908) and Kramp (1959a, 1965a) for details.

Notes: This is a deep water oceanic medusa.

Solmissus marshalli Agassiz and Mayer, 1902

Solmissus marshalli Agassiz and Mayer, 1902: 151, pl. 5; Bigelow 1909a: 64, pl. 16, 21; Mayer, 1910: 484; Bigelow, 1919: 329; Uchida, 1928: 89; Kramp, 1957a: 79; Mackie and Mackie, 1963: 79.

Solmaris punctatus Mayer, 1906: 1133 (non *Aequorea punctata* Quoy et Gaimard, 1824: 564, pl. 85).

Solmaris flavescens Vanhöffen, 1908: 58, pl. 2, 3 (non *Pachysoma flavescens* Kölliker, 1853: 322); 1912: 394.

Specific characters: 8-20, usually about 16, rectangular stomach pouches about as long as wide or slightly longer; marginal lappets square, each with up to 15 (rarely 21) statocysts.

Description of medusa: Umbrella up to 62 mm diameter, main portion flat, gelatinous disk thick and rigid, lappet zone very thin. Velum well developed. Stomach wide, with septa between pounches alternating with tentacle roots. Mouth simple round opening. Gonads in walls of stomach pouches, in female consisting of oval swellings each enclosing a single very large egg. Marginal tentacles stiff, tapering, shorter than or as long as bell-diameter. Gonads and tentacles milky in color, remainder colorless.

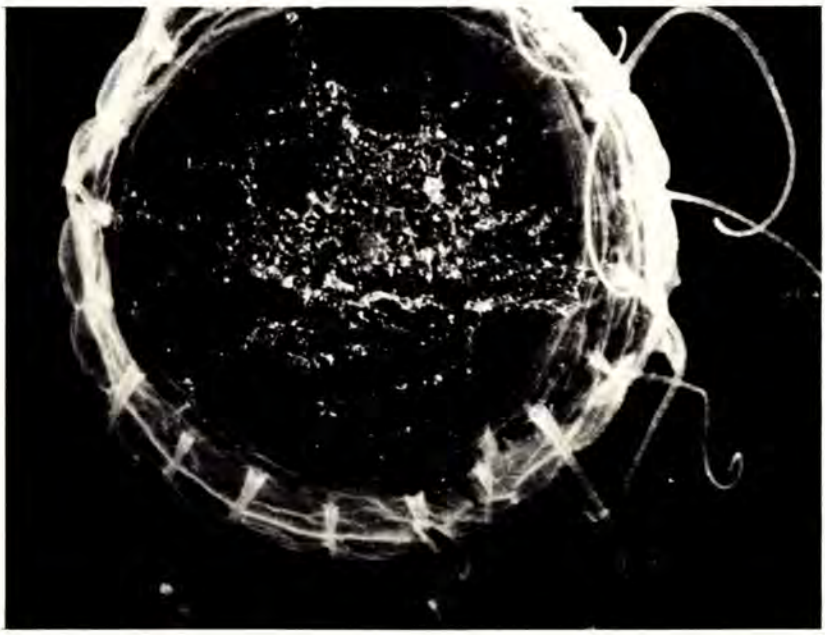


Fig. 73. *Solmissus marshalli*, preserved specimen, 21 mm diam., Becher Bay. Photo. M. N. Arai.

Distribution:

British Columbia and Puget Sound;

Strait of Georgia, northeast of Five Finger Is. (present work); Friday Harbor (Mackie and Mackie 1963; Singla 1972; present work); Becher Bay (present work).

Pacific Ocean;

Pacific Ocean off Oregon (Pearcy 1972); Pacific Ocean, off Molokini Inlet, Hawaiian Islands (Mayer 1906); 29°57'N, 170°50'W, Pacific Ocean northwest of Hawaiian Islands (Kramp 1965a); Pacific Ocean, off Kwajalong Atoll, Marshall Islands (Agassiz and Mayer 1902); 30°-37°N, 135°-160°E, Pacific Ocean east of Japan (Kramp 1965a); Sagami Bay, off Misaki (Uchida 1928); East China Sea, N.E. of Formosa (Kramp 1965a); 19°20'N, 119°48'E, South China Sea (Kramp 1965a); South China Sea, off Hong Kong (Vanhöffen 1913; Bigelow 1919); 7°-15°N, 115°E, South China Sea (Kramp 1965a); off east coast Mindoro, Philippine Islands (Bigelow 1919); Sulu Sea (Kramp 1965a); Mindanao Sea, Philippine Islands (Bigelow 1919; Kramp 1965a); Coral Sea (Blackburn 1955; Kramp 1965a); South Fiji Basin (Kramp 1965a); Tasman Sea (Blackburn 1955; Kramp 1965a); 35°-47°S, 176°E, Pacific Ocean east of New Zealand (Kramp 1965a); 7°45'S, 131°22'N, Pacific Ocean east of Marquesas Islands (Kramp 1965a); Pacific Ocean, off Valparaiso, Chile (Kramp 1966); Peru Basin, off Callao, Peru (Bigelow 1909a); Pacific Ocean, approx. 2°-17°S, 88°-117°W, southwest of Galopagos Islands (Bigelow 1909a); Pacific Ocean, off Colombia (Bigelow 1940).

Atlantic Ocean;

See Vanhöffen (1913), and Kramp (1957a, 1959a, 1959b) for details.

Indian Ocean;
See Kramp (1957a, 1965a), Vannucci and Navas (1973b) and Schmidt (1973) for details.

Notes: *Solmissus marshalli* is a weak swimmer (Mackie and Mackie 1963). The rigid, inflexible central disc of the bell, and the flexible margin and well developed velum allow an unusual motion with upward bending of the latter two areas (Gladfelter 1973). Each statocyst consists of a basal cushion and a free hanging sensory papilla bearing a sensory club (Singla 1972, 1975).

The nematocysts of *S. marshalli* are apotriches and atriches (Mackie and Mackie 1963).

As noted by Kramp (1965a) and earlier authors the vertical distribution of this oceanic medusa is very extensive. At Friday Harbor it appears in the surface water in periods of landward intrusion of the oceanic water mass into the Strait of Juan de Fuca (Mackie and Mackie 1963).

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