

THE CARLSBERG FOUNDATION'S  
OCEANOGRAPHICAL EXPEDITION ROUND THE WORLD 1928—30  
AND PREVIOUS "DANA"-EXPEDITIONS  
UNDER THE LEADERSHIP OF THE LATE PROFESSOR JOHANNES SCHMIDT

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DANA-REPORT No. 72.

THE HYDROMEDUSAE OF  
THE PACIFIC AND INDIAN OCEANS  
SECTIONS II AND III.

BY

P. L. KRAMP  
Zoological Museum, Copenhagen.

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WITH 367 FIGURES IN THE TEXT

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*PUBLISHED BY THE CARLSBERG FOUNDATION*

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## INTRODUCTION

**T**he first section of the present paper was issued in the Dana-Report no. 63, 1965, comprising a systematic account of the Hydromedusae collected by the "Dana" and the "Galathea" Expeditions during their passages through the Pacific and Indian Oceans, besides various minor collections from these waters.

As in the previous treatment of the Atlantic collections in the Dana-Report no. 46, 1959, the systematic account of the collected material was to be followed by the two sections which are herewith presented: Section II, a survey of all the Hydromedusae known from the Indian and Pacific Oceans, with diagnoses, figures, and keys for identification, and Section III, Zoogeography, first considerations on the zoogeographical characters of the species occurring within the Indo-Pacific waters, to be followed by a comparison with the Atlantic fauna.

In the explanations of the figures W. P. means that the figure has been redrawn by Mr. POUL H. WINTHER, E. L. redrawn by Mr. E. LEENDERS. "The Oceans": H. U. SVERDRUP, M.W. JOHNSON & R. H. FLEMING: The Oceans, 1955. PL. SH. means the Plankton Sheets edited by the "Conseil International pour l'Exploration de la Mer".

## SECTION II. A SURVEY OF THE HYDROMEDUSAE OCCURRING IN THE INDIAN AND PACIFIC OCEANS

In conformity with the paper on the Atlantic Hydromedusae (KRAMP 1959) the following survey will contain brief diagnoses of the families, genera and species accompanied by keys for identification of the species which may be considered as valid; doubtful or obsolete species are just mentioned. A summarized account of the geographical distribution of each species will be given, and also the most indispensable references to the literature. A complete bibliography up to 1910 may be found in A. G. MAYER: *Medusae of the World*, vol. I–III, 1910 and, for the Antho- and Leptomedusae, in M. BEDOT: *Matériaux pour servir à l'histoire des Hydroïdes*, I–VII, 1901–1925. A new complete bibliography for the period 1910–1959 is given in P. L. KRAMP, *Synopsis of the Medusae of the World*, Journal of the Marine Biological Association of the United Kingdom, Vol. 40, Plymouth 1961.

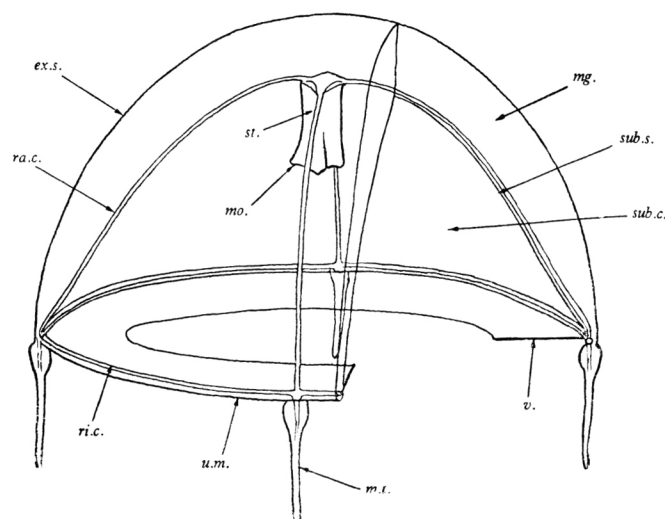


Fig. 1. Diagram of a medusa with one quadrant cut away. *ex. s.* exumbrella surface; *mg.* mesogloea; *mo.* mouth; *m. t.* marginal tentacle; *ra. c.* radial canal; *ri. c.* ring canal; *st.* stomach; *sub. c.* subumbrellar cavity; *sub. s.* subumbrellar surface; *u. m.* umbrella margin; *v.* velum. (After RUSSELL).

As far as the terminology is concerned I shall refer to the adjacent figure (fig. 1) which may facilitate determination for those who are not specially acquainted with the morphology of the medusae, but some knowledge of the animals is, of course, indispensable. When picked out from plankton samples medusae are frequently more or less mutilated, and it may be difficult to identify the species, but I have tried to accentuate such characters, which are usually retained even in badly preserved material; identification of young developmental stages is usually extremely difficult, unless a complete series is available, and an attempt to include them in the diagnoses here presented would be an overwhelming task and fall outside the scope and the expenditure of this work.

More or less doubtful species are retained, mainly in order to call attention to them in case they might be rediscovered and perhaps be recognized on future occasions.

### Key to the Orders of Hydromedusae.

- Gonads only on stomach, or occasionally both on stomach and extending for a short distance along radial canals; no statocysts ..... Anthomedusae
- Gonads only on radial canals, but occasionally contiguous with base of stomach; with or without statocysts, statocysts velar ectodermal when present ..... Leptomedusae
- Gonads either only on stomach, or both on stomach and extending for a short distance along radial canals, or only on radial canals; with or without statocysts; statocysts in form of enclosed sensory clubs with endodermal axes when present ..... Limnomedusae
- Umbrella margin entire; with radial canals; gonads usually only on radial canals; with statocysts in form of free or enclosed sensory clubs with endodermal axes ..... Trachymedusae
- Umbrella margin lobed; gonads only on stomach; without true radial canal system; with statocysts in form of free sensory clubs with endodermal axes ..... Narcomedusae

## I. 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.

### Key to the families of Anthomedusae.

1. Mouth simple and tubular ..... 2  
Mouth with four lips ..... 10
2. Reduced medusae with four permanently rudimentary tentacles ..... Pennariidae  
Medusae with one or more well-developed tentacles ..... 3
3. Without oral tentacles ..... 4  
With oral tentacles ..... 9
4. Marginal tentacles simple ..... 5  
Marginal tentacles branched or with stalked nematocyst capsules ..... 7
5. Marginal tentacles solitary ..... 6  
Marginal tentacles in four groups ..... Margelopsidae
6. Tentacle bulbs with abaxial ocelli ..... Corynidae  
Tentacle bulbs without ocelli ..... Tubulariidae
7. Marginal tentacles branched ..... 8  
Marginal tentacles unbranched, but with stalked capsules containing nematocysts ..... Zancleidae
8. Marginal tentacles bifurcating ..... Eleutheriidae  
Marginal tentacles with several branches ..... Cladonematidae
9. Oral tentacles simple, situated on mouth rim ..... Cytaeidae  
Oral tentacles simple or branched, inserted above mouth opening ..... Bougainvilliidae
10. Mouth with four lips with clusters of nematocysts ..... 11  
Mouth with four simple or folded lips without clusters of nematocysts ..... 13
11. Lips with continuous row of nematocyst clusters along margin ..... Clavidae  
Lips elongated to form tentacles each with one or a few nematocyst clusters ..... 12
12. Marginal tentacles solitary ..... Hydractiniidae  
Marginal tentacles in eight groups ..... Rathkeidae
13. With simple, pointed oral tentacles inserted above mouth opening; marginal tentacles in groups... Russelliidae  
Without oral tentacles, marginal tentacles solitary ..... 14
14. Gonads sausage-like or spiral ..... Polyorchidae  
Gonads in walls of stomach, rarely extending perradially on subumbrella ..... 15
15. No marginal cordylus-like structures ..... 16  
With marginal cordylus-like structures ..... Tiarannidae
16. Marginal tentacles with basal swelling, without terminal nematocyst cluster ..... Pandeidae  
Marginal tentacles without basal swelling, with terminal cluster of nematocysts ..... Calycopsidae

## Family Corynidae.

Anthomedusae with a simple circular mouth; with four radial canals; with gonads completely surrounding the manubrium; with 2–4 hollow marginal tentacles; with ocelli on the abaxial side of the tentacle bulbs.  
—Hydroids *Coryne*-like.

### Key to the genera of Corynidae represented in Indo-Pacific waters.

1. Gonad divided into two or more rings ..... *Dipurena*  
Gonad undivided ..... 2
2. With two well-developed and two rudimentary tentacles ..... *Dicodonium*  
With four equally developed tentacles ..... 3
3. Hydroid with capitate and reduced filiform tentacles ..... *Stauridiosarsia*  
Hydroid without filiform tentacles ..... *Sarsia*

*Sarsia* LESSON 1843. Corynidae with four similar, perradial tentacles; with gonad forming a single continuous ring or cylinder surrounding the manubrium. Hydroid with capitate tentacles only.

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

*Stauridiosarsia* MAYER 1910. Medusa similar to *Sarsia*. Hydroid with some filiform tentacles on proximal part of the hydranth.

Type species: *S. producta* (WRIGHT).

**Key to the Indo-Pacific species of *Sarsia* and *Stauridiosarsia*.**

1. Manubrium much longer than the height of the bell cavity ..... *tubulosa*  
    Manubrium short, rarely projecting slightly below the velar opening ..... 2
2. Manubrium with a distinct apical canal widened in its upper end; umbrella large, conical ..... *princeps*  
    Apical canal simple or absent; umbrella bell- or egg-shaped ..... 3
3. With a simple apical canal ..... 4  
    Without an apical canal ..... 7
4. Apical canal long; manubrium about half as long as bell cavity, swollen, distal part free of gonad ..... *conica*  
    Apical canal short; manubrium about as long as bell cavity ..... 5
5. Manubrium spindle-shaped, gonad leaving both ends free; umbrella with a small apical projection ..... *rosaria*  
    Manubrium entirely surrounded by gonad ..... 6
6. Tentacles ringed with prominent nematocyst swellings, distal end swollen; apex pointed ..... *cocometra*  
    Tentacles with a small terminal knob; apex rounded, with a conical apical chamber .... *Stauridiosarsia producta*
7. Tentacles with a distinct terminal knob ..... 8  
    Tentacles without a distinct terminal knob ..... 9
8. Manubrium spindle-shaped, about half as long as bell cavity, proximal and distal portions free of gonad; tentacles short, with 6-7 rings of nematocysts ..... *nipponica*  
    Manubrium cylindrical, about as long as bell cavity, entirely surrounded by gonad; tentacles with round nematocyst warts ..... *eximia*
9. Tentacle bulbs triangular, each with five ocelli; tentacles with "remarkable" nematocyst clusters; manubrium short and wide ..... *polyocellata*  
    Tentacle bulbs each with one ocellus; tentacles very short, nematocysts uniformly distributed; manubrium wide at base, narrow distally, about half as long as bell cavity ..... *resplendens*

*Sarsia tubulosa* (M. Sars 1835). Up to 18 mm high, somewhat higher than wide, dome-like, walls moderately thick. Manubrium very long, tubular, both ends free of gonads; distinct, globular apical chamber.

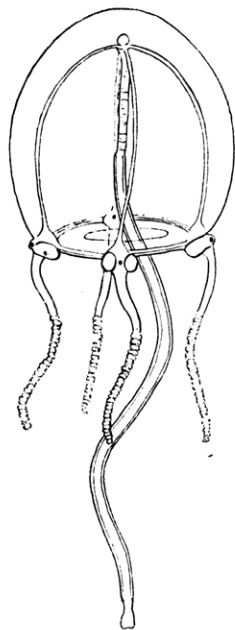


Fig. 2. *Sarsia tubulosa* (from Pl. Sh.).

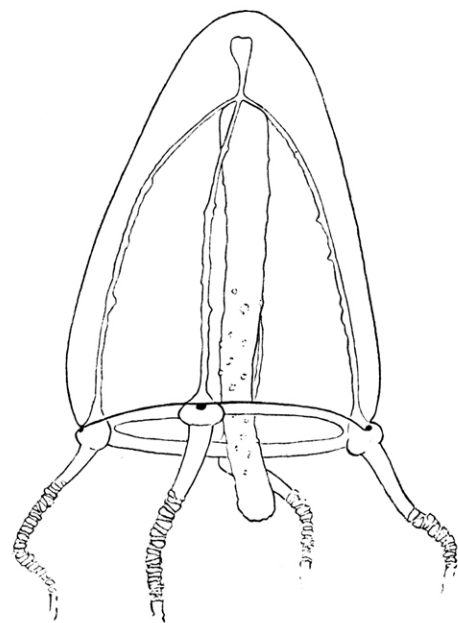
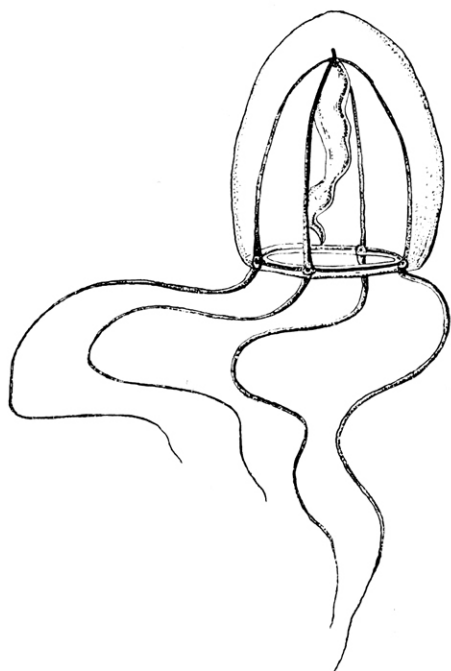
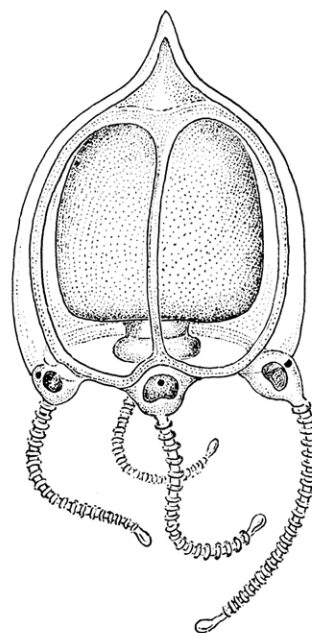


Fig. 3. *Sarsia princeps* (from Pl. Sh.).

Fig. 4. *Sarsia rosaria* (from HARTLAUB 1907).Fig. 5. *Sarsia coccometra* (from BIGELOW 1909, redrawn by P. W.).

Tentacles with broad bulbs, very long, densely beset with with spangles and groups of nematocysts, no terminal knob. — Very common in boreal and subarctic coastal waters, Atlantic and Pacific, circumpolar. (MAYER 1910 pp. 52–57, figs.; KRAMP 1926 p. 8, Pl. 1, figs. 5–7, textfigs. 6–16).

*Sarsia princeps* (HAECKEL 1879). Up to 40 mm high, somewhat conical. Manubrium about as long as bell cavity, almost completely covered by gonad; a distinct apical canal, widened in its upper end; radial canals with jagged edges. Tentacles long, with numerous prominent clasps of nematocysts; tentacle bulbs well developed, ocelli small. — Arctic, circumpolar. (MAYER 1910 p. 60, fig. 22; KRAMP 1926 p. 2, Pl. 1 figs. 1–4, textfigs. 1–5; KRAMP 1961 p. 29). Synonym: *Codonium princeps* HAECKEL 1879.

*Sarsia conica* (HAECKEL 1880). 12 mm high, 4 mm wide, barrel-shaped with large, conical apex. Manubrium half as long as bell cavity; stomach subspherical, swollen by encircling gonad; short cylindrical throat-tube free of gonads. Long axial canal. Four tentacles with small oval bulbs. — Indian Ocean. (MAYER 1910 p. 58; KRAMP 1961 p. 27). Synonym: *Codonium conica* HAECKEL 1880; only seen by HAECKEL.

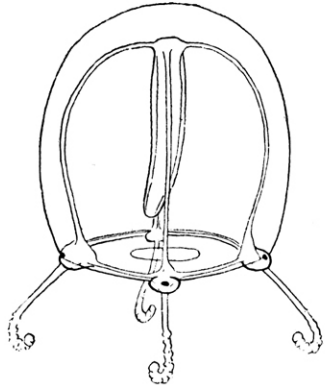
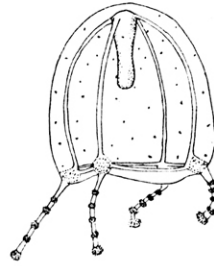
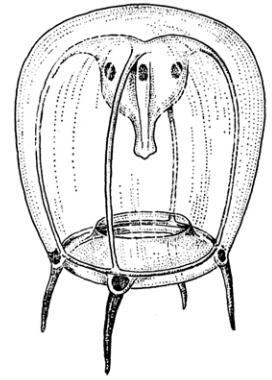
*Sarsia rosaria* (L. AGASSIZ 1862). 15–30 mm high, 10–15 mm wide, fairly thick walls, a small conical apical projection. Manubrium short, spindle-shaped, about as long as bell cavity; a short apical canal; gonad leaving both ends free. Tentacle bulbs large, flanked by two large nematocyst pads. — West coast of North America; Kurile Islands. (HARTLAUB 1907 p. 17, fig. 9, as *Sarsia apicula*, p. 50, fig. 45 as *S. rosaria*; KRAMP 1961 p. 31).

*Sarsia coccometra* BIGELOW 1909. 5 mm high, 4 mm wide; thin walls, pointed apex; short apical canal. Manubrium as long as bell cavity, entirely encircled by gonad; eggs very large. Tentacles ringed with prominent nematocyst swellings, distal end swollen, knob-like; bulbs swollen, with ocelli. — Pacific coast of Central America. (BIGELOW 1909 p. 179, Pl. 7, fig. 8, Pl. 40 fig. 1, Pl. 43 figs. 8–9; KRAMP 1961 p. 26).

*Sarsia eximia* (ALLMAN 1859). 3–4 mm high, a little higher than wide, bell-shaped; manubrium cylindrical, about as long as bell cavity, entirely surrounded by gonad, females with few and large eggs; no apical chamber; tentacles with large, oval bulbs, each with a large ocellus; tentacles with many round nematocyst warts and usually with a distinct terminal knob. — North-western Europe; Chile; California and Alaska. (MAYER 1910 p. 57, figs. 19–21; RUSSELL 1953 p. 50, Pl. 2 fig. 3, textfigs. 17 A, 18 A, B).

*Sarsia nipponica* UCHIDA 1927. 1.2 mm high 0.9 mm wide, nearly spherical; exumbrella with nematocyst clusters. Manubrium spindle-shaped, half as long as bell cavity, encircled by gonad except in proximal and distal



Fig. 6. *Sarsia exima* (from Pl. Sh.).Fig. 7. *Sarsia nipponica* (from UCHIDA).Fig. 8. *Sarsia resplendens* (from UCHIDA, redrawn by P. W.).

portions. Tentacle bulbs large; four stout tentacles, half as long as bell height, with 6–7 rings of nematocysts and a larger terminal knob. — Southern Japan and Chefoo in China. (UCHIDA 1927 p. 183, Pl. 10 fig. 1).

*Sarsia resplendens* BIGELOW 1909. 2.2 mm high, 2 mm wide; no apical projection. Manubrium half as long as bell cavity, wide at base, narrow distally, mouth four-sided; gonad surrounding entire manubrium, except short mouth tube. Tentacles with swollen bulbs with large ocelli, very short, with uniformly distributed nematocysts. — Pacific coast of Mexico; southern Japan. (BIGELOW 1909 p. 181, Pl. 7 fig. 1, Pl. 40 fig. 8; UCHIDA 1927 p. 184, Pl. 10 fig. 2 a, b).

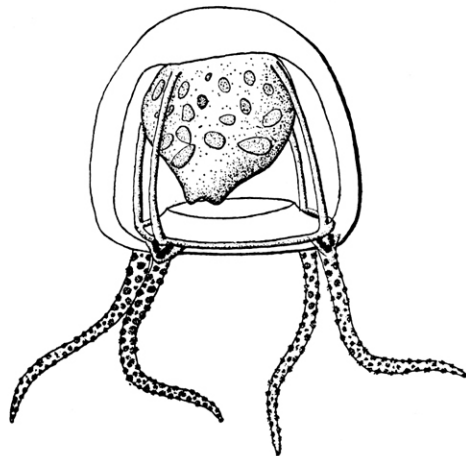
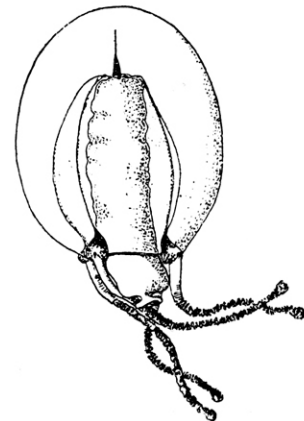
*Sarsia polyocellata* UCHIDA 1927. 2 mm high, 2.2 mm wide; no apical elevation, soft, equally thick throughout. Manubrium short and wide, mouth small; gonads "separate" on manubrium. Tentacle bulbs triangular, each with five ocelli; tentacles with remarkable nematocyst clusters on the whole length. — Southern Japan. (UCHIDA 1927 p. 182, fig. 25).

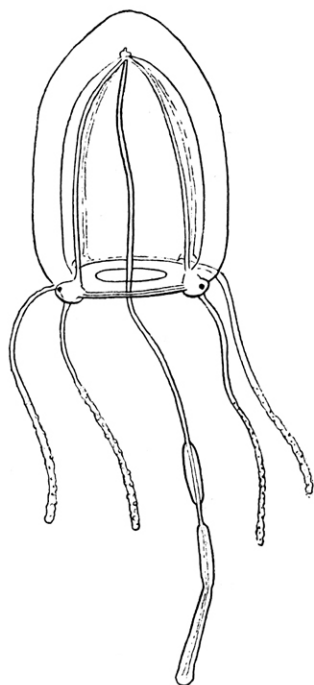
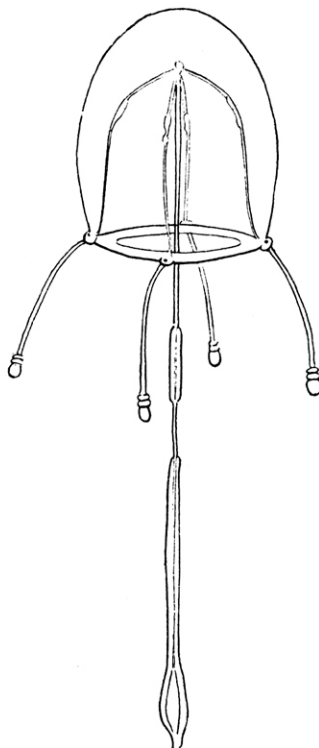
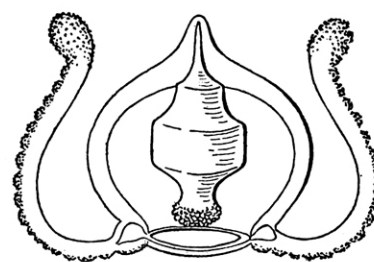
*Stauridiosarsia producta* (WRIGHT 1858). Up to 10 mm high and 7 mm wide, with thick walls; manubrium cylindrical, about as long as bell cavity, usually with a conical apical chamber; tentacles fairly long, with a small terminal knob and with large bulbs, each with an ocellus. — Ochotian Sea. North-western Europe, White Sea; Brazil. (MAYER 1910 p. 65, figs. 28–30; RUSSELL 1953 p. 64, figs. 26 A–C, 27 A, B). Synonym: *Stauridia producta* WRIGHT 1858, *Stauridium productum* HARTLAUB 1917.

Remarks on the species of *Sarsia* and *Stauridiosarsia*, see Dana Report 46, KRAMP 1959 p. 81.

*Dipurena* MCCRADY 1857. Corynidae with four similar, perradial tentacles; with gonad divided into two or more distinct rings surrounding the manubrium; tentacle bulbs with abaxial ocelli. Synonym: *Slabberia* FORBES 1848, preoccupied.

*Dipurena ophiogaster* HAECKEL 1879. 5 mm high, higher than wide; manubrium, when extended, very long; gonads with 2–6 or more segments surrounding manubrium; distinct apical chamber; tentacles with

Fig. 9. *Sarsia polyocellata* (from UCHIDA).Fig. 10. *Stauridiosarsia producta* (from HARMLAUB).

Fig. 11. *Dipurena ophiogaster* (from Pl. Sh.).Fig. 12. *Dipurena halterata* (from Pl. Sh.).Fig. 13. *Dicodonium cornutum*  
(from MAYER).

irregularly distributed clusters of nematocysts. — Southern Japan; Palao Islands; New Guinea (new record); Ceylon; Pacific coasts of Mexico and Chile. Mediterranean Sea and north-western Europe. (RUSSELL 1953 p. 71, Pl. 1 fig. 5, Pl. 2 fig. 4, text-figs. 25 E, 30 A, B, 31). Synonyms: *Purena brownei* BIGELOW 1909 (specimens from Ceylon and Mexico Pacific).

*Dipurena halterata* (FORBES 1846). Up to 8 mm high and 6 mm wide, bell-shaped; manubrium very long; gonads with two or more segments surrounding manubrium, leaving upper half free; distinct apical chamber; a small swelling in the middle of each radial canal; tentacles each with a large terminal knob and 3–6 distinct rings immediately above. — Victoria Harbor in Pacific coast of North America. Great Fishbay, west coast of Africa. Adriatic Sea; British coasts; Florida. (RUSSELL 1953 p. 67, Pl. 1 fig. 3, Pl. 2 fig. 2, textfigs. 28, 29). Synonyms: *Slabberia catenata* FORBES & GOODSIR, *Dipurena picta* MAYER 1900.

*Dicodonium* HAECKEL 1879. Corynidae with two well-developed and two rudimentary tentacles; no meridional lines of nematocysts. Remarks, see "Dana Report 46," KRAMP 1959 p. 83.

*Dicodonium cornutum* HAECKEL 1879. 4 mm high and wide; bulging sides and pointed apex; manubrium spindle-shaped, shorter than bell cavity; axial canal well developed; gonad swollen, around middle 1/3 of manubrium; two large tentacles curled upwards, with adaxial clusters of nematocysts; no rudimentary bulbs; no ocelli. — Red Sea. (MAYER 1910 p. 46, fig. 12).

*Dicodonium dissonema* HAECKEL 1879. Size unknown; bell-shaped to egg-shaped with blunt conical apex; apical canal present; Manubrium spindle-shaped, wide in middle; large, swollen gonad; two long tentacles with very large bulbs with adaxial ocelli; rudiments? — Australia. (MAYER 1910 p. 45).

## Family Tubulariidae.

Anthomedusae with a simple circular mouth; with four radial canals; with manubrium not extending beyond umbrella margin; with gonad completely surrounding manubrium; with four or fewer marginal tentacles, usually hollow; without ocelli on marginal bulbs. — Hydroids *Tubularia*-like or *Corymorpha*-like.

**Key to the genera of Tubulariidae represented in Indo-Pacific waters.**

1. Gonad with four sausage-like processes from the interradial sides of the stomach (with one thick, hollow tentacle with a round terminal knob) ..... *Gotoea*  
     Gonad simple, annular ..... 2
2. Exumbrella with longitudinal tracks of nematocysts ..... 3  
     Exumbrella without nematocyst tracks ..... 4
3. With two or four tentacles; eight tracks of nematocysts ..... *Ectopleura*  
     With one tentacle, or a cluster of two or three arising from a common bulb; five tracks of nematocysts .... *Hybocodon*
4. One or four tentacles, each terminating in a large knob of nematocysts ..... 5  
     Tentacles without a large terminal knob ..... 6
5. Four tentacles ..... *Plotocridae*  
     One tentacle ..... *Hybocodon forbesi*
6. Three short or rudimentary tentacles and one long differing from the others in structure ..... *Euphysora*  
     1-4 tentacles of equal structure, though sometimes of unequal length ..... 7
7. Four equally developed tentacles with clusters of nematocysts in a single row ..... 8  
     1-4 tentacles unequally developed, with nematocysts in rings or in uniformly distributed groups; stomach tubular 9
8. Tentacles with adaxial clusters of nematocysts, stomach quadrangular ..... *Euphysilla*  
     Tentacles with abaxial clusters of nematocysts, stomach circular in transverse section ..... *Euphysomma*
9. Umbrella with a pointed apical projection containing an apical canal; one tentacle ..... *Steenstrupia*  
     Umbrella without a pointed apical projection; 1-4 tentacles ..... *Euphysa*

*Euphysa* FORBES 1848. Tubulariidae without apical projection to umbrella; without exumbrellar nematocyst tracks; without apical canal; with 1-4 tentacles unequally developed but all of the same structure; tentacles usually moniliform.

**Key to the Indo-Pacific species of *Euphysa*.**

1. With one tentacle, nematocysts in rings (moniliform) ..... *aurata*  
     With more than one tentacle ..... 2
2. Four tentacles, all alike in adult ..... 3  
     One long and three small tentacles, with warts of nematocysts ..... *tetrabrachia*
3. Tentacles with groups of nematocysts, all alike in adult but developed in succession ..... *flammea*  
     Tentacles moniliform, all alike, also in young stages ..... *japonica*

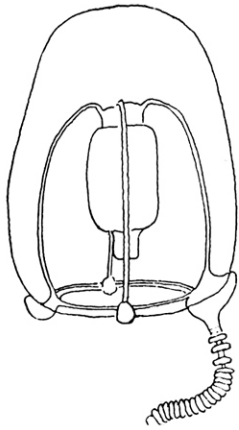
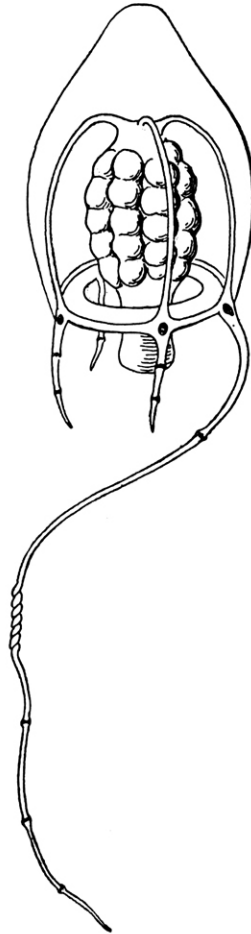
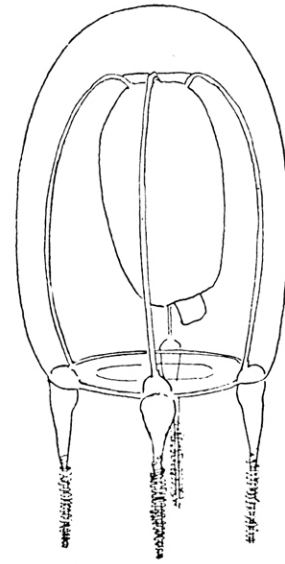
*Euphysa aurata* FORBES 1848. About 4 mm high, higher than wide, bell-shaped, jelly thick, especially in apical region; manubrium shorter than bell cavity; gonad encircling almost whole stomach; one tentacle, moniliform. — Chile; Chefoo in China; Philippines; east coast of Malacca. Mediterranean and Adriatic Sea; north-western Europe; northern Norway, Murman coast, and White Sea; west coast of Greenland; Massachusetts Bay in North America; Patagonia. (RUSSELL 1953 p. 90, Pl. 3 fig. 2, text-figs. 35 E, 38, 39).

*Euphysa tetrabrachia* BIGELOW 1904. 4 mm high, about half as wide, with well developed, blunt apical projection, lateral walls thin; manubrium spindle-shaped, about as long as bell cavity; mouth tube free of gonad; one long tentacle with warts of nematocysts, and three short tentacles all alike. — Maldives Islands. (BIGELOW 1904 p. 251, Pl. 1 fig. 1).

*Euphysa flammea* (LINKO 1905). 12 mm high, 7 mm wide, bell-shaped, walls fairly thin; manubrium about two-thirds as long as bell cavity, in whole length encircled by gonad; four tentacles with scattered groups of nematocysts, all like in adult, but developed in succession, youngest stages with only one tentacle, the others added successively. — Arctic, circumpolar; Ochotian Sea, Bering Sea, Vancouver Island region in northern Pacific. In the Atlantic southwards to Newfoundland. (KRAMP 1926 p. 19, Pl. 1 figs. 12-14). Synonym: *Sarsia flammea* LINKO 1905, HARTLAUB 1907.

*Euphysa japonica* (MAAS 1909). 8 mm high or more, cylindrical, walls fairly thick; manubrium broad, barrel-shaped or cylindrical, as long as bell cavity, surrounded by gonad in almost entire length; tentacles moniliform, all alike, also in young stages. — Northern Japan; Kamchatka; Aleutians; Vancouver. (MAAS 1909 p. 6, Pl. 1 fig. 1; KRAMP 1928 p. 30, figs. 2-7). Synonym: *Sarsia japonica*.

Doubtful species: *Euphysa australis* VON LENDENFELD 1884 (Australia); *Euphysa* sp. UCHIDA 1927 (Japan); see KRAMP 1961 pp. 37, 38.

Fig. 14. *Euphysa aurata* (from Pl. Sh.).Fig. 15. *Euphysa tetrabrachia* (from MAYER).Fig. 16. *Euphysa flammea* (from Pl. Sh.).

*Steenstrupia* FORBES 1846. Tubulariidae with a pointed apex and a well developed apical canal; without exumbrellar nematocyst tracks; with one moniliform tentacle.

*Steenstrupia nutans* (M. SARS 1835). 5–6 mm high, 3–4 mm wide, with a high, conical apical projection and a long, narrow apical canal; manubrium about as long as bell cavity, upon a short, broad gelatinous peduncle; one moniliform tentacle, very long, and three rudimentary bulbs. — A doubtful record from Bombay in India. Black Sea; Mediterranean and Adriatic Sea; north-western Europe, northwards to Lofoten in Norway; south coast of Iceland. (RUSSELL 1953 p. 84, Pl. 3 fig. 1, textfigs. 35 A-D, 36, 37 A-C). Synonyms: *rubra* FORBES 1848, *flaveola* FORBES 1848, *lineata* LEUCKART 1856, *cranoides* HAECKEL 1864, *galanthus* HAECKEL 1879.

*Steenstrupia* sp. UCHIDA 1947 p. 300. Palao Islands, central Pacific. No description.

*Hybocodon* L. AGASSIZ 1862. Tubulariidae without pointed apical process to umbrella; with or without exumbrellar nematocyst tracks; with umbrella at oblique angle; with one simple or compound marginal tentacular bulb with 1–3 tentacles; remaining three perradial bulbs rudimentary.

#### Key to the Indo-Pacific species of *Hybocodon*.

1. One tentacle with terminal swelling; no exumbrellar tracks of nematocysts ..... *forbesi*  
No terminal swelling on tentacle ..... 2
2. Without tentacles; one nematocyst band from base of longest radial canal ..... *alentaculatus*  
With 1–3 tentacles on tentacle bulb ..... 3
3. With five lines of nematocysts ..... *prolifer*  
Umbrella with scattered nematocysts; one tentacle, basal bulb small, between two large swellings of nematocysts ..... *unicus*

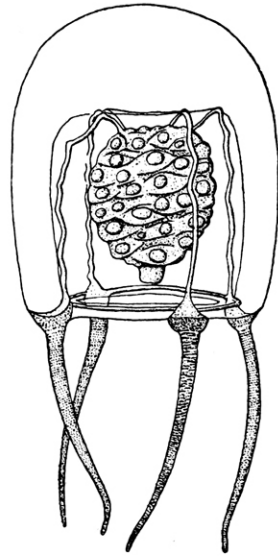


Fig. 17. *Euphysa japonica* (from UCHIDA).

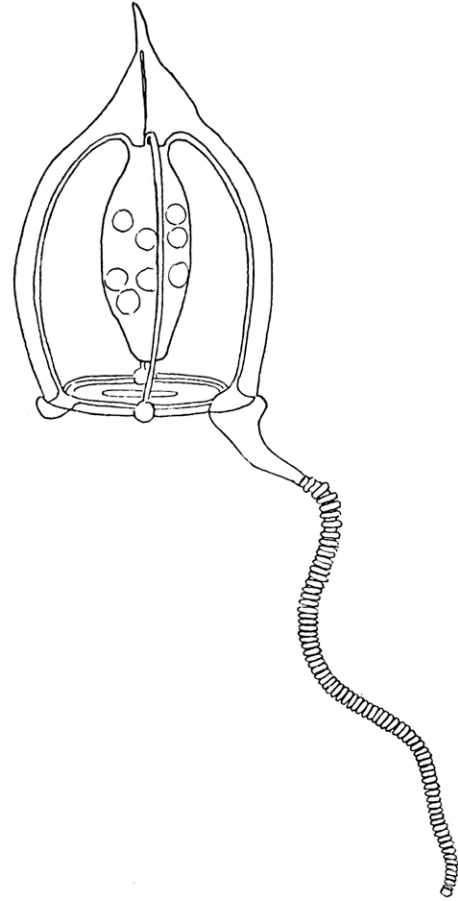


Fig. 18. *Steenstrupia nutans* (from Pl. Sh.).

*Hybocodon profiler* L. AGASSIZ 1862. 4 mm high, 3 mm wide, bell-shaped; exumbrella with five meridional nematocyst tracks, two of which issue from the tentacular bulb; stomach large, cylindrical, mounted upon a short gelatinous peduncle, mouth surrounded by a ring of nematocyst batteries; gonad completely surround-

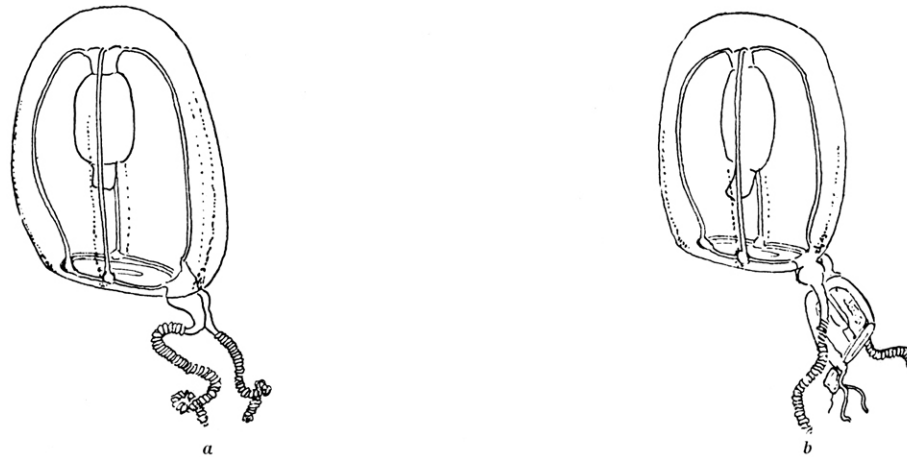


Fig. 19. *Hybocodon prolifer*, a without, b with medusa buds (from Pl. Sh.).

ing stomach, leaving peduncle and mouth free; the tentacular bulb with one or more moniliform tentacles and with medusa-buds, at least in immature stages. — Northern Japan, Kamchatka, Bering Sea, Aleutian Islands, Vancouver. North-western Europe, Barents Sea, Iceland, west coast of Greenland, Newfoundland,

Massachusetts Bay in America. (MAYER 1910 p. 38, Pl. 2 fig. 1, Pl. 3 fig. 3, text-fig. 10; RUSSELL 1953 p. 79, Pl. 3 figs. 3-4, text-fig. 34).

*Hybocodon unicus* (BROWNE 1902). 3 mm high, 2 mm wide, bell-shaped, umbrella margin slightly oblique; exumbrella with scattered nematocysts, not arranged in lines; manubrium mounted upon a short peduncle; stomach in almost whole length surrounded by gonad; one solitary tentacle, moniliform, on a very small bulb placed between two large swellings of nematocysts on bell margin; no medusa buds. — Coasts of India. Falkland Islands in south-western Atlantic. (BROWNE & KRAMP 1939 p. 273, Pl. 15 figs. 2, 3).

*Hybocodon atentaculatus* UCHIDA 1947. 23 mm high, 25 mm wide, globular, very thick walls, subumbrellar cavity only  $10 \times 8$  mm; manubrium flask-shaped; four radial canals asymmetrical in length; a short nematocyst

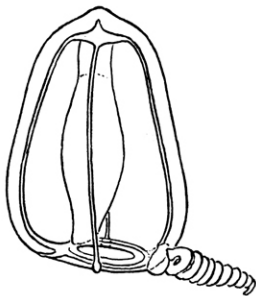


Fig. 20. *Hybocodon unicus* (from BROWNE & KRAMP, redrawn by P. W.).

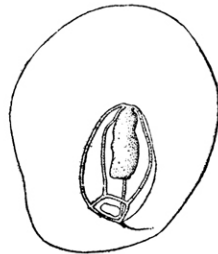


Fig. 21. *Hybocodon atentaculatus* (from UCHIDA).

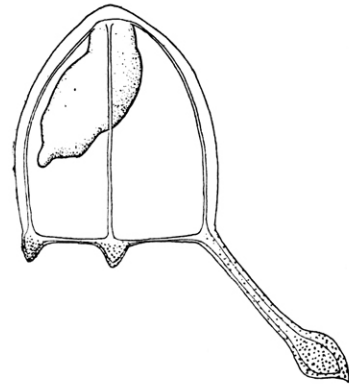


Fig. 22. *Hybocodon forbesi* (from UCHIDA).

band from base of longest radial canal tapering upwards on exumbrella; no tentacles. Systematic position uncertain. — Sagami Bay, Japan. (UCHIDA 1947 b p. 333, fig. 1).

*Hybocodon forbesi* MAYER 1894. 3 mm high, ellipsoidal, oblique, of uniform thickness; no lines of nematocysts on exumbrella; manubrium spindle-shaped, swollen; a single well developed tentacle at the base of the longest radial canal, with a small basal bulb and a large terminal swelling with nematocysts, no medusa buds; Systematic position doubtful. — Coasts of India, Vietnam and southern Japan. Bahamas and Tortugas, Florida. (MAYER 1910 p. 42, Pl. 1 fig. 8, Pl. 2 fig. 3; UCHIDA 1927 p. 193, fig. 30; NAIR 1951 p. 50, Pl. 1 fig. 1).

*Ectopleura* L. AGASSIZ 1862. Tubulariidae with two or four simple tentacles; with eight longitudinal rows of nematocysts on exumbrella, extending from the four tentacle bulbs to apex.

#### Key to the Indo-Pacific species of *Ectopleura*.

1. Gonad with four large, interradian sac-shaped pouches ..... *sacculifera*  
Gonad simple, ring-shaped..... 2
2. With four equally developed tentacles ..... *dumortieri*  
With two tentacles and two rudimentary bulbs ..... *minerva*

*Ectopleura dumortieri* (VAN BENEDEN 1944). 2-3 mm high, bell nearly spherical, gelatinous substance very thick; manubrium short and blunt, apical canal sometimes present; mouth-rim with nematocysts; eight longitudinal tracks of nematocysts, issuing in pairs from the four marginal bulbs, reaching apex; four tentacles with large basal bulbs and with prominent nematocyst clusters on abaxial side. — Pacific coast of Mexico; Chefoo in China, coasts of Vietnam and India. West coast of Africa; Mediterranean Sea; Portugal; north-western Europe; North America from Cape Cod to South Carolina; Cape Frio in Brazil. (MAYER 1910 p. 68, Pl. 5 figs. 4, 5, Pl. 6 figs. 1, 2; RUSSELL 1953 p. 76, Pl. 3 figs. 5, 6, text-fig. 33 A-C).

*Ectopleura minerva* MAYER 1900. 2.5 mm high, pear-shaped, with a well-developed, blunt apical projection; manubrium pear-shaped, about two-thirds as long as bell cavity; a short, conical apical canal; eight tracks of nematocysts on exumbrella; two tentacles and two small rudimentary bulbs, each tentacle with 6-9 nema-

tocyst swellings on the abaxial side. — Coast of Malacca; Nicobars; Trivandrum Coast in India. Tortugas, Florida. (MAYER 1910 p. 70, Pl. 5 fig. 3).

*Ectopleura sacculifera* KRAMP 1957. 3 mm high, slightly conical, jelly thick; exumbrella with eight nematocyst tracks issuing in pairs from the four marginal bulbs, continued to apex along the edges of eight very prominent ridges; manubrium half as long as bell cavity; the gonad surrounds the stomach and has four large interradiat sac-shaped pouches; two opposite moniliform tentacles and two rudimentary marginal bulbs. — Off Ecuador in South America. (KRAMP 1957 pp. 7, 96, 105, Pl. 2 figs. 1–3).

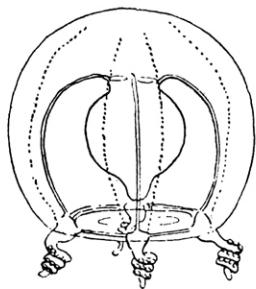


Fig. 23. *Ectopleura dumortieri*  
(from Pl. Sh.).

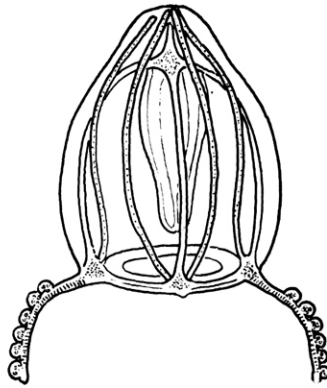


Fig. 24. *Ectopleura minerva* (from  
MAYER, redrawn by P. W.).

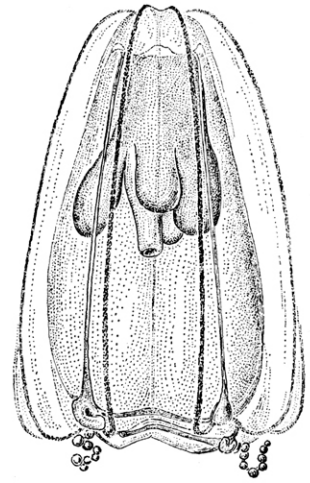


Fig. 25. *Ectopleura sacculifera* (from  
KRAMP, redrawn by P. W.).

*Euphysora* MAAS 1905. Tubulariidae with three short or rudimentary tentacles and one long tentacle which differs from the others not only in size, but also in structure.

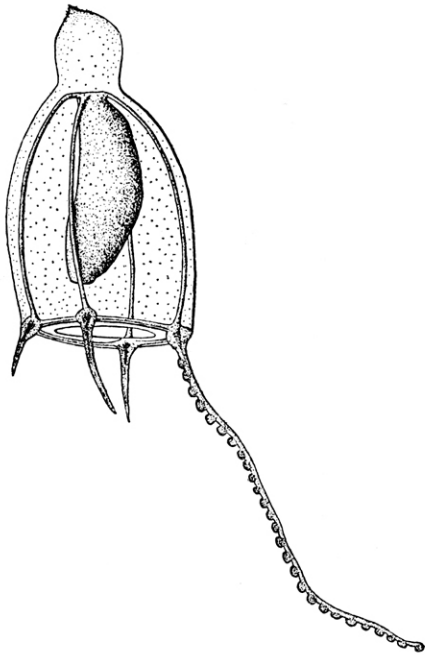
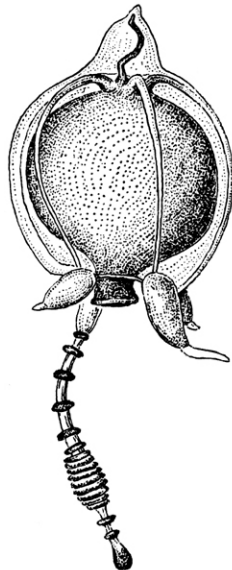
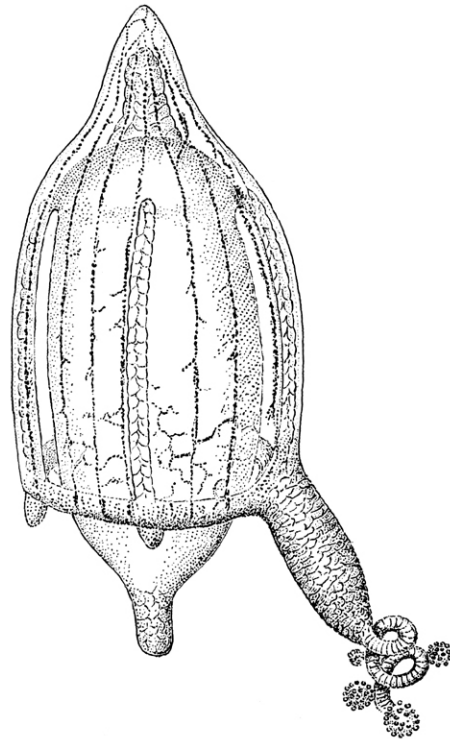
#### Key to the Indo-Pacific species of *Euphysora*.

1. With only one tentacle, very long and thin, with several bifurcated lateral branches; bell globular . . . . . *gigantea*  
With one long and three small or rudimentary tentacles . . . . . 2
2. Terminal end of principal tentacle twice bifurcated . . . . . 3  
Principal tentacle unbranched . . . . . 4
3. Principal tentacle long, the four terminal branches each with a knob of nematocysts; opposite this a fairly long filiform tentacle . . . . . *furcata*  
Principal tentacle short, without knobs of nematocysts, the three other tentacles all alike, short . . . . . *valdiviae*
4. Principal tentacle moniliform, with numerous rings of nematocysts, the three other tentacles cone-shaped . *annulata*  
Principal tentacle with a single row of nematocyst knobs . . . . . 5
5. Principal tentacle long, with an abaxial row of prominent nematocyst knobs; three other tentacles rudimentary . . . . . *abaxialis*  
The row of nematocyst knobs on principal tentacle adaxial or lateral . . . . . 6
6. Principal tentacle long, the row of nematocyst knobs adaxial . . . . . *bigelowi*  
Principal tentacle short, with three lateral knobs of nematocysts and a large terminal knob . . . . . *normani*

*Euphysora bigelowi* MAAS 1905. Up to 13 mm high, with pointed apex at the end of which is a collection of small papillae; principal tentacle long, with several large nematocyst knobs in a unilateral, adaxial position and a distinct terminal knob, the three other periradiat bulbs each with a short, pointed tentacle without nematocyst clusters. — Indo-Malayan Region, coasts of India, off the east coast of Africa; southern Japan and Chefoo in China; north-east Australia. A record from Chile is probably erroneous. (MAAS 1905 p. 7, Pl. 1 figs. 1–3; UCHIDA 1927 p. 189, Pl. 10 fig. 3, text-fig. 28).

*Euphysora annulata* KRAMP 1928. 2 mm high, 1.4 mm wide, barrel-shaped, with thin walls and a pointed apex with an apical canal; stomach wide, as long as bell cavity; principal tentacle long, moniliform, with



Fig. 26. *Euphysora bigelowi* (from UCHIDA).Fig. 27. *Euphysora annulata* (from KRAMP, redrawn by P. W.).Fig. 28. *Euphysora normani* (from BROWNE, redrawn by P. W.).

numerous rings of nematocysts, three short cone-shaped tentacles, the one opposite the main tentacle longer than the two others. — Sunda Strait; Madras in India; North-East Australia. (KRAMP 1928 p. 39, fig. 13).

*Euphysora normani* (BROWNE 1916) 2.5 mm high, 1.25 mm wide; apical chamber high and conical; principal tentacle with a large, sac-like bulb and with three lateral knobs of nematocysts projecting from the tentacle, and a large terminal knob. — Indian Ocean north of Chagos Islands. (BROWNE 1916 p. 174, Pl. 39 fig. 1, as *Steenstrupia normani*).

*Euphysora abaxialis* KRAMP 1962. Up to 3 mm high and 2.4 mm wide; dome-shaped, the rounded apex with a patch of small papillae; jelly thick, no apical canal; stomach almost entirely filling the bell cavity; the principal tentacle long, mounted upon a large basal bulb and provided with numerous prominent clusters of nematocysts in one row along the abaxial side; three other marginal bulbs quite rudimentary. — Indo-Malayan Region. (KRAMP 1962 p. 309, figs. 2–4).

*Euphysora furcata* KRAMP 1948. Up to 8 mm high and 6.5 mm wide, with pointed apex and fairly thin walls; stomach barrel-shaped, with broad, conical apical chamber; canals with large, vacuolated endoderm cells; principal tentacle long, in terminal part twice bifurcated, with four knobs of nematocysts; opposite this a fairly long, filiform tentacle, two lateral tentacles short and conical. — Oceanic; widely distributed in the Indian Ocean and in the western Pacific, northwards to Japan, eastwards to Tahiti; recently also recorded from Chile (FAGETTI & FISCHER 1964 p. 163). Widely distributed in the Atlantic Ocean between 40° N. and 40° S. (KRAMP 1948 p. 19, Pl. 1 figs. 7, 8; KRAMP 1957 pp. 5, 97, 125).

*Euphysora valdiviae* VANHÖFFEN 1911. 6.5 mm high, 5 mm wide; with a large, conical apical chamber; exumbrella with anastomosing tracks of nematocysts; principal tentacle short, twice bifurcated, without clusters of nematocysts; three other tentacles short, conical, all alike. — West of Sumatra (VANHÖFFEN 1911 p. 198, figs. 2, 2a; KRAMP 1957 p. 5, discussion).

*Euphysora gigantea* KRAMP 1957. Up to 26 mm high and wide, globular, jelly very thick, bell cavity very narrow. Only one tentacle, very long and thin, carrying several bifurcated lateral branches separated by long intervals. — Antarctic. (KRAMP 1957 pp. 6, 98, Pl. 1 figs. 3, 4).

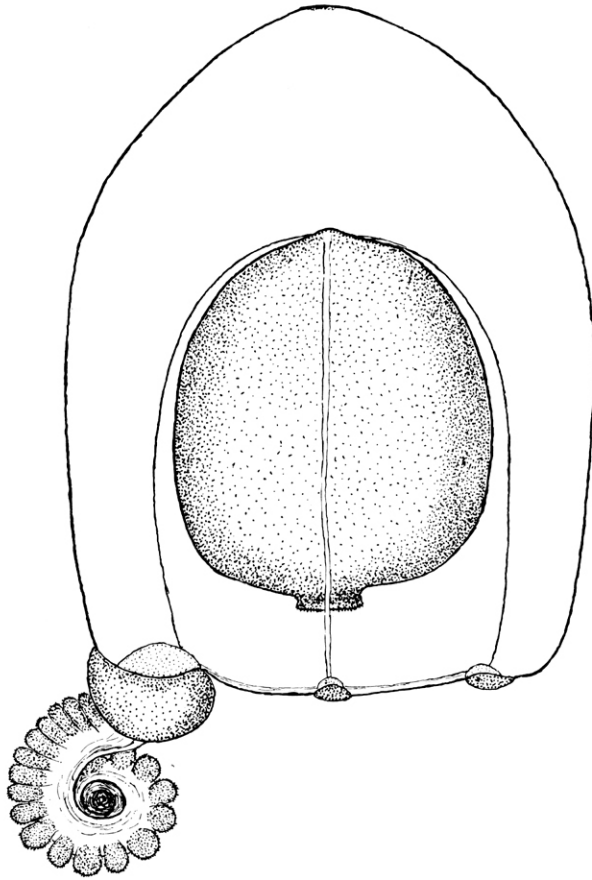


Fig. 29. *Euphysora abaxialis* (from KRAMP).

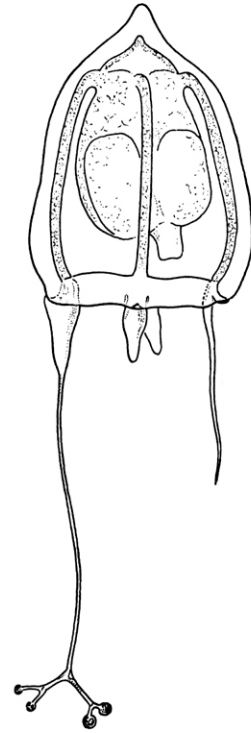


Fig. 30. *Euphysora furcata* (from KRAMP, redrawn by P. W.).

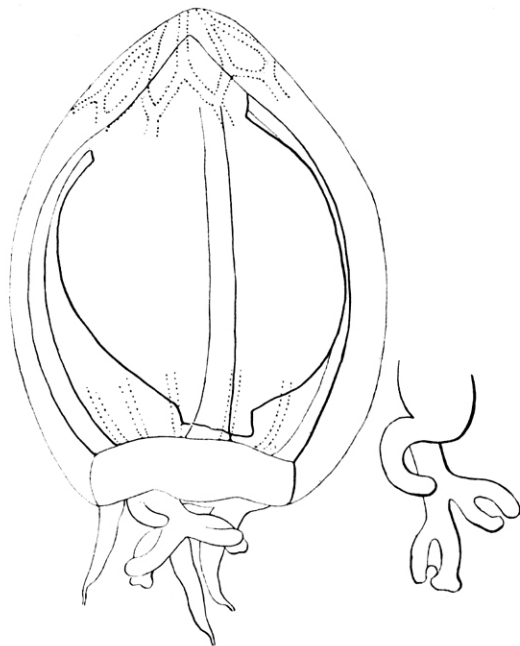


Fig. 31. *Euphysora valdiviae* (from VANHÖFFEN).

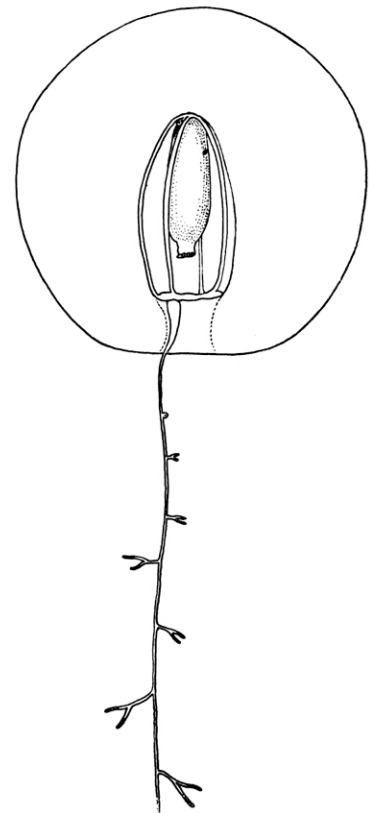


Fig. 32. *Euphysora gigantea* (from KRAMP, redrawn by P. W.).

*Euphysilla* KRAMP 1955. Tubulariidae without exumbrellar nematocyst tracks; with four equally developed tentacles with adaxial clusters of nematocysts; without a stomachal peduncle.

*Euphysilla pyramidata* KRAMP 1955. Diameter 2.3 mm, about the same height; stomach pyramidal, with a broad, quadrate base, completely surrounded by gonad; four tentacles, rather short and stout, each provided with 5–7 prominent transversal clasps of nematocysts on their adaxial side and a spherical terminal knob; no ocelli. — West of Madagascar. Gulf of Guinea on the west coast of Africa. (KRAMP 1955 p. 245, Pl. 1 fig. 1, Pl. 2 fig. 3).

*Euphysomma* KRAMP 1962. Tubulariidae without exumbrellar nematocyst tracks; with broad stomach surrounded by a ring-like gonad circular in transverse section; mouth rim simple, studded with nematocysts; with four hollow, perradial tentacles provided with abaxial clusters of nematocysts; without ocelli.

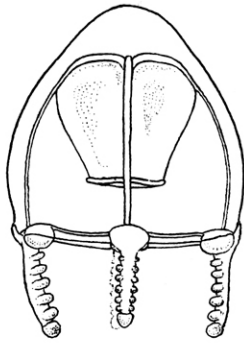


Fig. 33. *Euphysilla pyramidata* (from KRAMP, redrawn by P. W.).

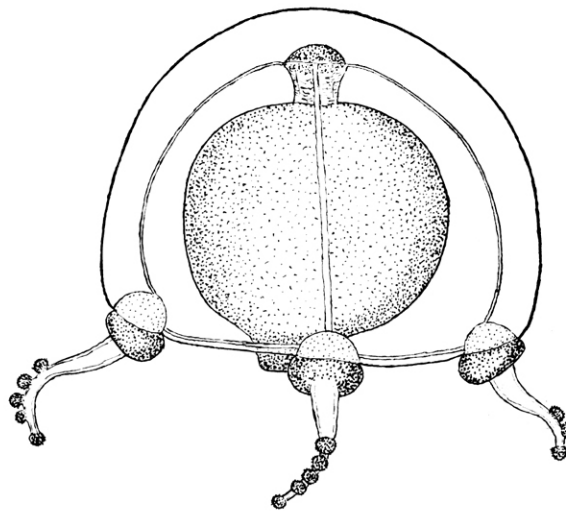


Fig. 34. *Euphysomma brevia* (from KRAMP).

*Euphysomma brevia* (UCHIDA 1947). About 1 mm high and wide, almost globular; manubrium as long as bell cavity, bulged, voluminous; small, round mouth; four tentacles with conspicuous basal bulbs; tentacles short, with 2–4 abaxial clusters of nematocysts and a terminal cluster. — Palao Islands and Vietnam. (UCHIDA 1947 p. 299, fig. 1; KRAMP 1962 p. 306, fig. 1). Synonym: *Sarsia brevia* UCHIDA 1947.

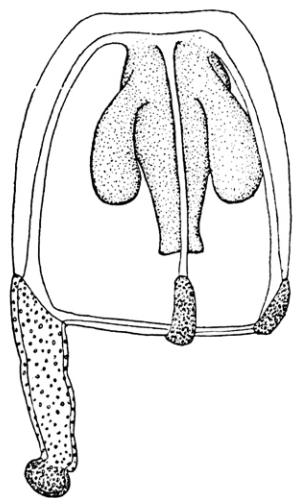
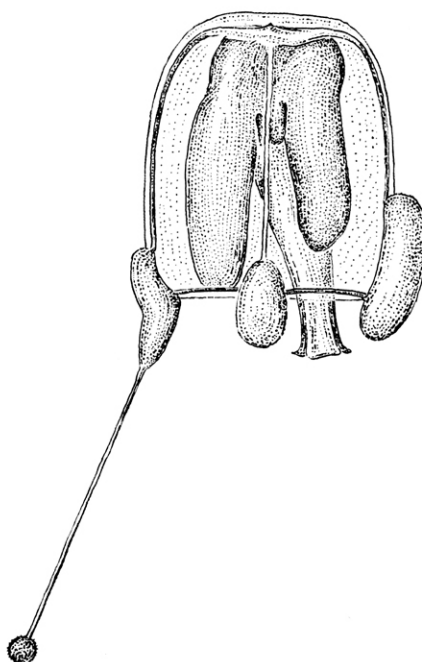
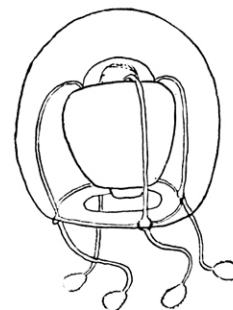
*Gotoea* UCHIDA 1927. Tubulariidae with four radial canals, one well developed, hollow tentacle and three exumbrellar nematocyst pads at the bases of the radial canals without tentacles; no ocelli; manubrium simple and without lips; gonad encircling stomach but with sausage-like processes in the interradii.

*Gotoea typica* UCHIDA 1927. 3.3 mm high, 2.8 mm wide, nearly pyriform, flat-topped; thin walls; manubrium large, about three-quarters as long as bell cavity; gonad with four interradii sausage-like, pendent protuberances; one tentacle, about half as long as bell height, thick, with a round terminal knob. — Southern Japan. (UCHIDA 1927 p. 195, fig. 31).

*Gotoea similis* KRAMP 1959. About 3.5 mm high, 3 mm wide; similar to *G. typica*, but the tentacle is long and thin, with a large terminal knob, and the perradial nematocysts pads much larger. — Bali; Madagascar and Mozambique Channel. Atlantic Ocean near St. Helena. (KRAMP 1959a p. 5, Pl. 2 fig. 1).

*Plotocnide* WAGNER 1885. Tubulariidae with scattered nematocysts on exumbrella; with four solid tentacles, each with a large terminal knob of nematocysts.

*Plotocnide borealis* WAGNER 1885. 3 mm high and almost as wide, apex rather thick, rounded; manubrium about half as long as bell cavity, with a broad, dome-shaped apical chamber; without a peduncle; gonad a thick ring; tentacle bulbs well developed; tentacles with solid endoderm and an oval terminal swelling studded with nematocysts. — Arctic and subarctic, circumpolar; Kamchatka. (YASHNOV 1939 pp. 108, 113, figs. 1–4; KRAMP 1942 p. 22, figs. 5, 6; NAUMOV 1960 p. 221 fig. 110). Synonym: *Sarsia inabai* UCHIDA 1933.

Fig. 35. *Gotoea typica* (from UCHIDA).Fig. 36. *Gotoea similis* (from KRAMP, redrawn by P. W.).Fig. 37. *Plotocnide borealis* (from Pl. Sh.).

## Family Margelopsidae.

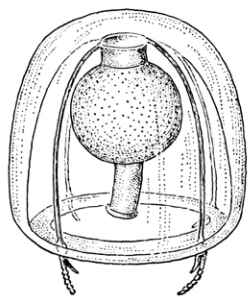
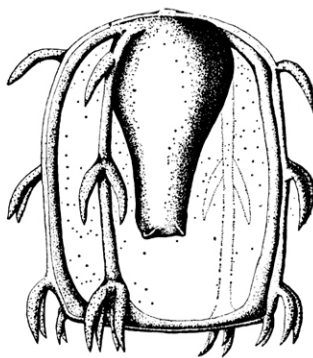
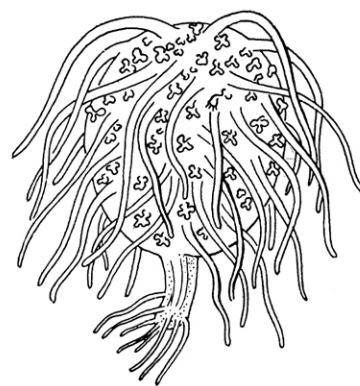
Anthomedusae without exumbrellar nematocyst tracks; with simple circular mouth without oral tentacles; with gonads completely surrounding stomach; with four radial canals; with solid, moniliform tentacles in perradial clusters on margin, or at different levels on exumbrella; without ocelli. Hydroids, where known, aberrant pelagic tubularians.

*Margelopsis* HARTLAUB 1897. Margelopsidae with four perradial clusters of tentacles on bell margin. Eggs develop into actinulae on manubrium.

*Margelopsis australis* BROWNE 1910. 1–3 mm high and wide, almost globular; manubrium cylindrical, almost as long as bell cavity; gonad a globular swelling around middle portion of manubrium; four marginal bulbs very small, each with two tentacles placed one behind the other. — Antarctic, apparently circumpolar. (BROWNE 1910 p. 11, Pl. 4 fig. 7; VANHÖFFEN 1912 p. 356, Pl. 24 fig. 1). According to VANHÖFFEN the tentacles are not moniliform.

*Margelopsis* spp. GANAPATI & NAGABHUSHANAM 1958 pp. 92, 94. — Vizagapatam Coast, India.

*Climacocodon* UCHIDA 1924. Margelopsidae with pairs of tentacles at several levels; actinulae develop on manubrium.

Fig. 38. *Margelopsis australis* (from BROWNE, redrawn by P. W.).Fig. 39. *Climacocodon ikarii* (from UCHIDA).Fig. 40. *Pelagohydra mirabilis* (from MAYER).

*Climacocodon ikarii* UCHIDA 1924. 1.1 mm high, 0.6 mm wide; in each perradius seven short tentacles at four levels. — Northern and southern Japan; Vietnam. (UCHIDA 1927 p. 197, Pl. 10 fig. 5).

*Pelagohydra* DENDY 1902. Pelagic hydroid with medusa buds.

*Pelagohydra mirabilis* DENDY 1902. Medusa: 1 mm wide; four radial groups of marginal tentacles, each with five tentacles, the median smallest; manubrium pyriform. Hydroid pelagic, medusae not seen free. — New Zealand. (DENDY 1902 p. 1, Pl. 12; MAYER 1910 p. 83, fig. 40 a).

## Family Pennariidae.

Anthomedusae with a simple circular mouth; with four radial canals; with manubrium not extending beyond umbrella margin; with gonad completely surrounding stomach; with four permanently rudimentary tentacles, usually reduced to mere bulbs, with or without ocelli. Hydroids: *Pennaria*.

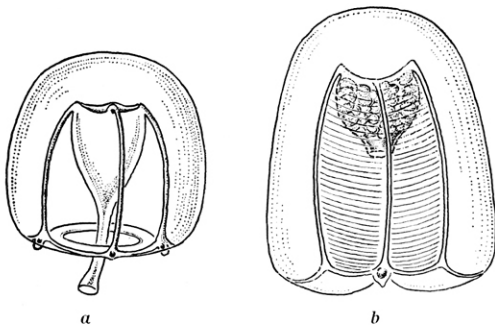


Fig. 41. *Pennaria vitrea* (from AGASSIZ & MAYER, redrawn by P. W.). a male, b female.

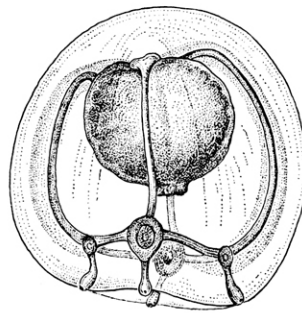


Fig. 42. *Pennaria armata* (from VANHÖFFEN, redrawn by P. W.).

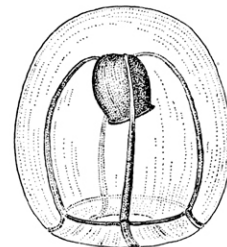


Fig. 43. *Pennaria grandis* (from KRAMP, redrawn by P. W.).

*Pennaria* GOLDFUSS 1820. With the characters of the family. Remarks, see Dana Report 46 p. 93.

Medusae newly liberated from hydroid:

*Pennaria adamsia* VON LEDENFELD 1884. ♂ 1.5 mm high, 0.7 mm wide; four perradial tentacles about as long as diameter of bell, with well developed bulbs with minute ocelli. ♀ 1.5 mm high and wide; tentacles rudimentary, without ocelli; bell cavity filled with eggs. — New South Wales, Australia (VON LEDENFELD 1884 p. 595 Pl. 25 figs. 45–48, Pl. 26 fig. 49).

*Pennaria rosea* VON LEDENFELD 1884. 2 mm high, 1 mm wide; manubrium with ripe gonads fills entire bell cavity; four large rudimentary bulbs with external ocelli. — New South Wales, Australia. (VON LEDENFELD 1884 p. 594, Pl. 24 figs. 40, 42).

Hydroids unknown:

*Pennaria vitrea* AGASSIZ & MAYER 1899. 3 mm high, walls thick and rigid; manubrium flask-shaped in ♂, ♀ with large, pyriform eggs grouped in four interradial clusters; four rudimentary tentacle bulbs; ocelli? — Fiji Islands. (AGASSIZ & MAYER 1899 p. 161, Pl. 1 figs. 1, 2).

*Pennaria armata* VANHÖFFEN 1911. 1.5–1.8 mm high and wide, globular, walls moderately thick; manubrium globular, half as long as bell cavity; two opposite large and two opposite small bulbs without trace of tentacles, but all with an exumbrellal prolongation grasping around margin and terminating with an ocellus. — Nias Island; Great Nicobar, Indian Ocean; Sandwich Islands, Pacific. (VANHÖFFEN 1913 p. 7, Pl. 1 fig. 4).

*Pennaria grandis* KRAMP 1928. 5 mm high, 4.5 mm wide, barrel-shaped, walls thick; manubrium barrel-shaped, 2/5 as long as bell cavity, mouth a wide, simple opening with a narrow, out-turned edge; four equally developed, narrow, perradial bulbs with prolongation grasping around bell margin; no ocelli. — Sunda Strait. (KRAMP 1928 p. 29, fig. 1).

## Codonida incertae sedis.

*Pachycordyle* WEISMANN 1883. Codonida without tentacles, radial canals or circular vessel; manubrium surrounded by a ring-like gonad. Hydroid, where known, *Pachycordyle*. Degenerate forms, possibly of different origin.

*Pachycordyle conica* KRAMP 1959. 1.2 mm high, 1 mm wide, somewhat conical, with thick walls and a large, bluntly pointed apical projection; bell opening very large, velum extremely narrow; manubrium about

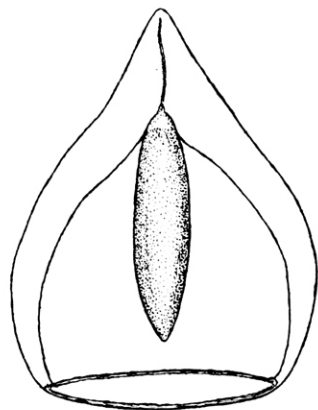


Fig. 44. *Pachycordyle conica* (from KRAMP).

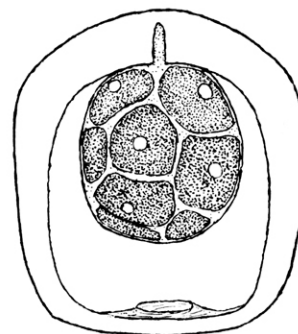


Fig. 45. *Pachycordyle globulosa* (from KRAMP).

as long as the bell cavity, slender, spindle-shaped, without a peduncle, in entire length surrounded by a male gonad; a narrow apical canal reaches almost to the top of the apex. — Gulf of Panama. (KRAMP 1959 *b* p. 226, fig. 3).

*Pachycordyle globulosa* KRAMP 1959. About 1 mm high and wide, almost globular, with thick walls, evenly rounded apically; velum very broad; manubrium broadly oval, 2/3 as long as the bell cavity, completely filled with large, ripe eggs; a short cylindrical apical canal; no peduncle. — Philippines. (KRAMP 1959 *b* p. 225 fig. 1).

*Pachycordyle lineata* KRAMP 1959. About 0.5 mm high and wide, egg-shaped, with thin walls, velum very broad with a narrow opening, subumbrella with ten meridional grooves from bell margin almost to apex,

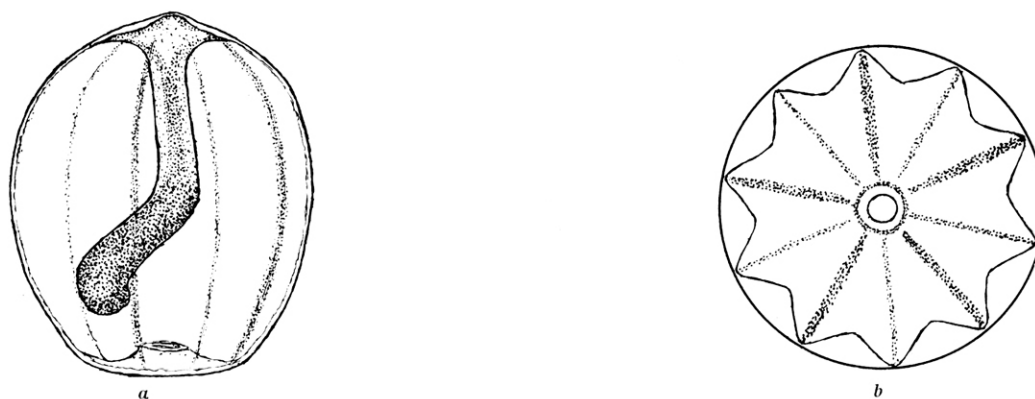


Fig. 46. *Pachycordyle lineata*. *a* lateral view, *b* oral view (from KRAMP).

equidistant, in each groove a black line; manubrium without a peduncle, about as long as the bell cavity, cylindrical, somewhat dilated in apical portion, with black pigmentation throughout the length. — Bali. (KRAMP 1959 *b* p. 225, figs. 2 *a*, *b*).

## Family Zancleidae.

Anthomedusae with, or without, exumbrellar nematocysts confined to specialized tissue in form of oval or club-shaped patches or elongated tracks; with simple circular mouth with or without oral tentacles; with four radial canals (rarely bifurcated); with interradial gonads; with two or four hollow marginal tentacles, each with abaxial stalked capsules (or cnidophores) containing nematocysts, or without marginal tentacles; with or without ocelli.

*Zanclea* GEGENBAUR 1856. Zancleidae with exumbrellar nematocyst armature; without a brood-pouch above stomach; without oral tentacles; with four simple radial canals; with 2–4 marginal tentacles with filiform branches carrying nematocyst capsules; without ocelli.

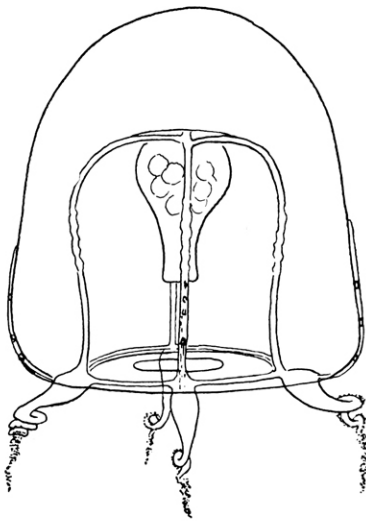


Fig. 47. *Zanclea costata* (from Pl. Sh.).

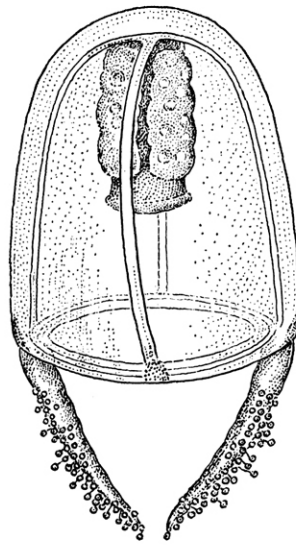


Fig. 48. *Zanclea orientalis* (from BROWNE, redrawn by P. W.).

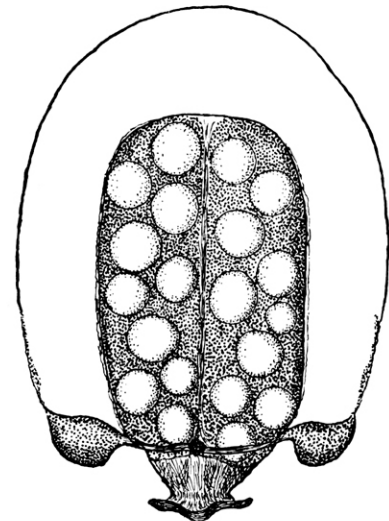


Fig. 49. *Zanclea dubia* (from KRAMP).

*Zanclea costata* GEGENBAUR 1856. Up to 3 mm high and wide; umbrella bell-shaped, jelly moderately thick; exumbrellar nematocysts in oval or club-shaped patches immediately above marginal bulbs or elongated meridional tracks towards summit; manubrium shorter than bell cavity; gonads leaving mouth end free; two opposite or four tentacles with elongated conical bases and with stalked capsules along their abaxial side. — Widely distributed in warm and temperate coastal waters. (MAYER 1910 pp. 87–90, Pl. 6 fig. 7, Pl. 7 fig. 5, Pl. 8 figs. 2–7, text-figs. 41–44; RUSSELL 1953 p. 99, Pl. 4 figs. 1–3, textfigs. 43–48). Synonyms: *gemmosa* McCRADY 1857, *implexa* ALLMAN 1864, *cladophora* A. AGASSIZ 1865.

*Zanclea orientalis* BROWNE 1916. 2 mm high, 1.5 mm wide; rounded summit, thin walls; manubrium cylindrical, half as long as bell cavity, gonads interradial swellings on nearly whole length of stomach; two opposite tentacles and two rudimentary bulbs; four periradial patches of nematocysts upon bell margin, without any groove or streak leading to them. — North of Chagos, Indian Ocean. (BROWNE 1916 p. 176, Pl. 39 figs. 2, 3). Probably identical with *Z. costata*.

*Zanclea dubia* KRAMP 1959. 1.5 mm high, with thick jelly, evenly rounded apically; manubrium very large, completely filling the bell cavity, with four interradial gonads, each with two or three longitudinal rows of large eggs; two large and two rudimentary marginal bulbs, but no tentacles. — Java Sea. (KRAMP 1959 b p. 226, fig. 4). Provisionally regarded as a separate species.

*Pteronema* HAECKEL 1879. Similar to *Zanclea*, but with a brood-sac above stomach; no meridional tracks of nematocysts upon exumbrella.



*Pteronema darwini* HAECKEL 1879. 6 mm high, 4 mm wide, pyriform, with a pointed apex; stomach spindle-shaped, with four simple lips; four radial canals with jagged edges; four tentacles, very long, with an abaxial row of side-branches with terminal nematocyst knobs; no ocelli. — Australia. (HAECKEL 1879 p. 101, Pl. 7 figs. 1, 2).

*Ctenaria* HAECKEL 1879. Zancleidae with four bifurcated radial canals; with two feathered marginal tentacles and simple, unbranched oral tentacles; eight adradial, meridional lines of nematocysts on exumbrella, and a nematocyst track above the base of each marginal tentacle; an apical cavity above stomach.

*Ctenaria ctenophora* HAECKEL 1879. 6 mm high, 5 mm wide; bell three-fourths-egg-shaped. — Japan. (HAECKEL 1879 p. 108, Pl. 7 figs. 5–7).

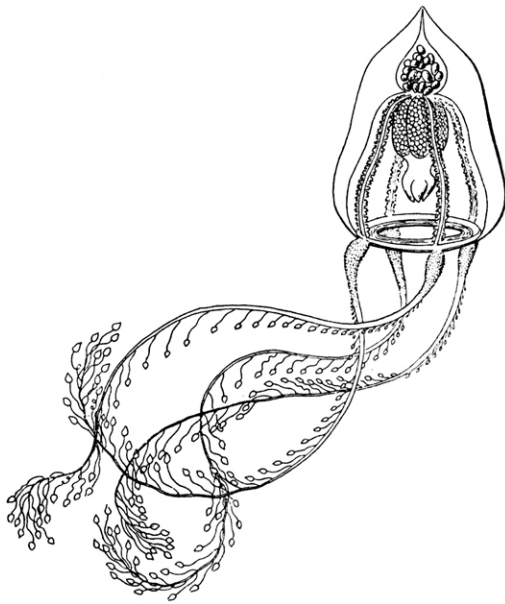


Fig. 50. *Pteronema darwini* (from MAYER).

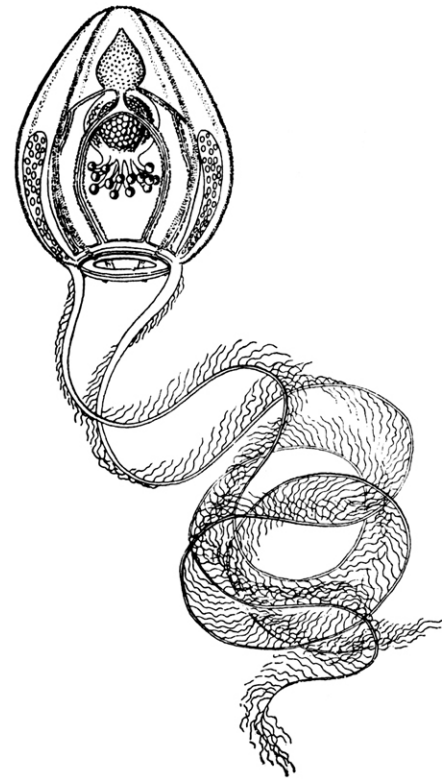


Fig. 51. *Ctenaria ctenophora* (from MAYER).

## Family Cladonematidae.

Creeping and swimming Anthomedusae; mouth with oral tentacles armed with nematocyst clusters; with stomach with radial pouches; with variable number of radial canals, some bifurcated, some simple; with gonads completely surrounding stomach; with variable number of hollow branching marginal tentacles, each furnished with organs of adhesion; with ocelli.

*Cladonema* DUJARDIN 1843. Cladonematidae with simple, unbranched oral tentacles; without an apical cavity above stomach. The distinction between the species is uncertain.

*Cladonema radiatum* DUJARDIN 1843. 4 mm high, 3 mm wide, with fairly thin walls and rounded apex; manubrium about as long as bell cavity; 4 or 5 simple oral tentacles with a terminal knob of nematocysts; gonad completely surrounding stomach, with 4–5 radial sac-like protrusions; 4 or 5 bifurcated radial canals, or 8–10 more simple, or with some bifurcated and some simple canals; 8–10 marginal tentacles, each with 4–6 branches with clusters of nematocysts and 1–4, usually 4, basal branches with adhesive organs; basal bulbs each with an abaxial ocellus. — Japan. North-western Europe; Mediterranean; Black Sea; Florida,

Bermuda and Bahamas. (MAYER 1910 pp. 99 and 101, Pl. 9 figs. 1, 2, 3, textfigs. 43–55; RUSSELL 1953 p. 105, figs. 49–51).

*Cladonema californicum* HYMAN 1947. 2–3 mm wide, a little shorter than wide; manubrium longer than bell cavity, carrying 6–7 gonads as rounded protrusions in a whorl; with 6 short oral arms; about 9 marginal tentacles, each with one sucker-branch and 1–2 branches with nematocysts. — California. (HYMAN 1947 p. 262, figs. 1–5).

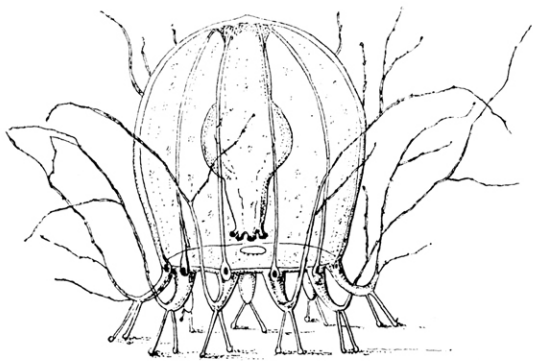


Fig. 52. *Cladonema radiatum* (from NAUMOV).

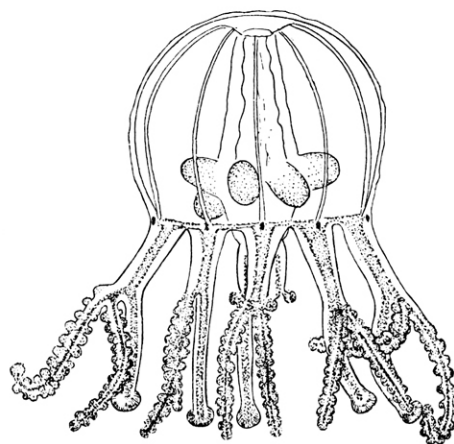


Fig. 53. *Cladonema californicum* (from HYMAN).

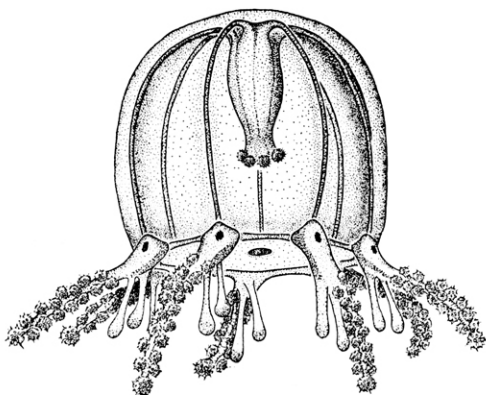


Fig. 54. *Cladonema myersi* (from REES).

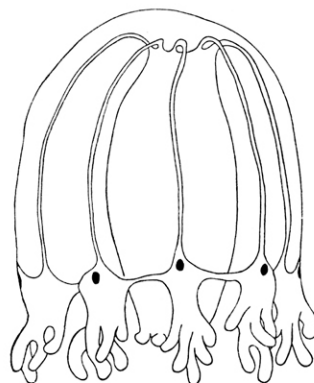


Fig. 55. *Cladonema pacificum* (from NAUMOV).

*Cladonema myersi* REES 1949. Newly liberated medusa 0.7–0.8 mm wide; with 5–6 radial canals; tentacles much branched — California. (REES 1949 pp. 861–5, figs. 1–4; NAUMOV 1960 p. 227, Pl. 29 fig. 5, textfigs. 114–117).

*Cladonema pacificum* NAUMOV 1955. Up to 2 mm high and 2.2 mm wide; manubrium about as long as bell cavity, with six radial protrusions and with 6 spherical oral tentacles; gonads along entire length of stomach; three simple and six paired radial canals issuing directly from base of stomach; 9 marginal tentacles much branched. — Saghalin Island. (NAUMOV 1955 p. 24, figs. 6–8).

## Family Eleutheriidae.

Creeping Anthomedusae with continuous or broken thickened ring of nematocysts around umbrella margin; with simple circular mouth without oral tentacles; with variable number of radial canals which may or may not branch; with gonads on subumbrellar surface or in special dorsal brood pouch; with variable number of hollow, bifurcating marginal tentacles, each furnished with an organ of adhesion; with abaxial ocelli. Velum well developed.

*Staurocladia* HARTLAUB 1917. Eleutheriidae without a brood pouch above stomach; gonads well developed, in ectodermal interradial pockets around stomach, sexes separate; asexual budding may occur; with six or more radial canals; with numerous marginal tentacles, increasing in number with age, bifurcated, lower branch with a terminal adhesive disk, upper branch with one terminal and several other clusters of nematocysts. The distinction between the species is uncertain (see KRAMP, in "Dana" Reports 46, 1959, p. 97).

**Key to the Indo-Pacific species of *Staurocladia*.**

1. The nematocyst clusters on upper branch of tentacles all lateral in position ..... 2  
     Aboral side of tentacles with clusters of nematocysts ..... 3
2. Lateral clusters 5-6 pairs; marginal ring of nematocysts discontinuous ..... *hodgsoni*  
     Up to 8 or 9 pairs of lateral clusters; marginal ring of nematocysts (where described) continuous *charcoti* + *kerguelensis*
3. Nematocyst clusters on oral as well as aboral side of tentacles ..... 4  
     Oral side of tentacles without clusters of nematocysts ..... 5
4. One aboral and two lateral clusters ..... *acuminata*  
     No lateral clusters, aboral clusters meridional in position ..... *haswelli*
5. One cluster on aboral side and two lateral opposite, ..... *bilateralis*  
     Clusters only on aboral side of tentacles ..... 6
6. Clusters in one meridional line ..... *oahuensis*  
     Clusters in two alternating lines ..... *alternata*

*Staurocladia hodgsoni* (BROWNE 1910). Diameter 1.5-2 mm; 6-11 radial canals; 20-32 tentacles, upper branch, when stretched, about as long as lower; no continuous ring of nematocysts, but patches of nematocysts on the basal portion of the tentacles; 5-6 lateral clusters of nematocysts. -- Antarctic: McMurdo Sound, South Georgia, Graham Land. (BROWNE 1910 p. 28, Pl. 3 figs. 1-4).

*Staurocladia charcoti* (BEDOT 1908). 1 mm high, 4 mm wide; about 10 radial canals; about 35 tentacles, upper branch with about 9 pairs of nematocyst clusters, laterally situated, and a terminal cluster; uncertain whether the marginal ring of nematocysts is continuous or interrupted. -- Graham Land in Antarctic. (BEDOT 1908 p. 1, Pl. 1).

*Staurocladia kerguelensis* (GILCHRIST 1918). Diameter up to 5.5 mm, commonly 1-2 mm; 6-10 radial canals; 20-60 tentacles, upper branch shorter than lower; up to 8 pairs of nematocyst clusters, laterally placed; marginal ring of nematocysts continuous. -- Kerguelen Island. (VANHÖFFEN 1911 p. 201, Pl. 22 figs. 1, 2, textfig. 5, as *Eleutheria vallentini*; Lengerich 1920 pp. 527-529, figs. 1-10, as *E. vallentini*).

*Staurocladia acuminata* (EDMONDSON 1930). 0.8 mm wide; radial canals?; up to 24 tentacles; two nematocyst clusters on upper side of tentacle, one on lower side and one on each side, laterally. -- Hawaii; Japan. (EDMONDSON 1930 p. 9 fig. 4 a, b).

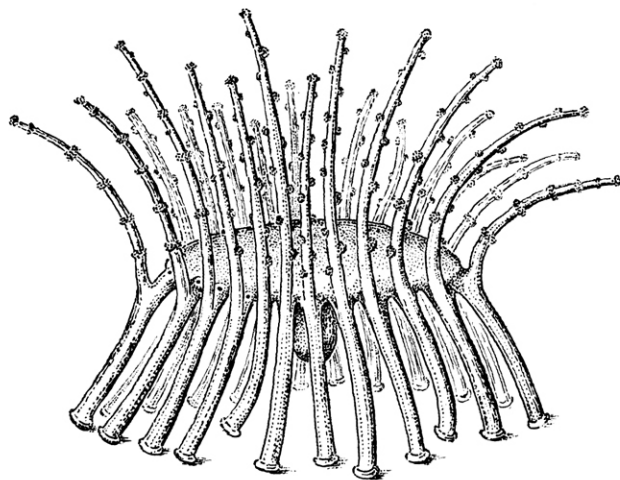


Fig. 56. *Staurocladia hodgsoni* (from BROWNE).

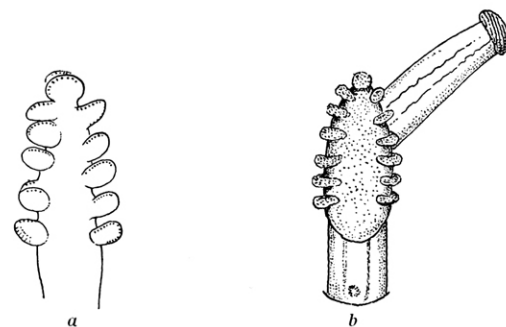


Fig. 57. Tentacles of *Staurocladia*, a *charcoti*, b *hodgsoni* (from KRAMP).

*Staurocladia haswelli* (BRIGGS 1920). 1.2 mm wide; up to 31 tentacles, upper branch shorter than lower; nematocyst clusters meridionally, two to three on upper side and one on lower side; medusa-buds on bell margin. — Port Jackson, Australia. (BRIGGS 1920 p. 97, Pl. 17 figs. 1–5).

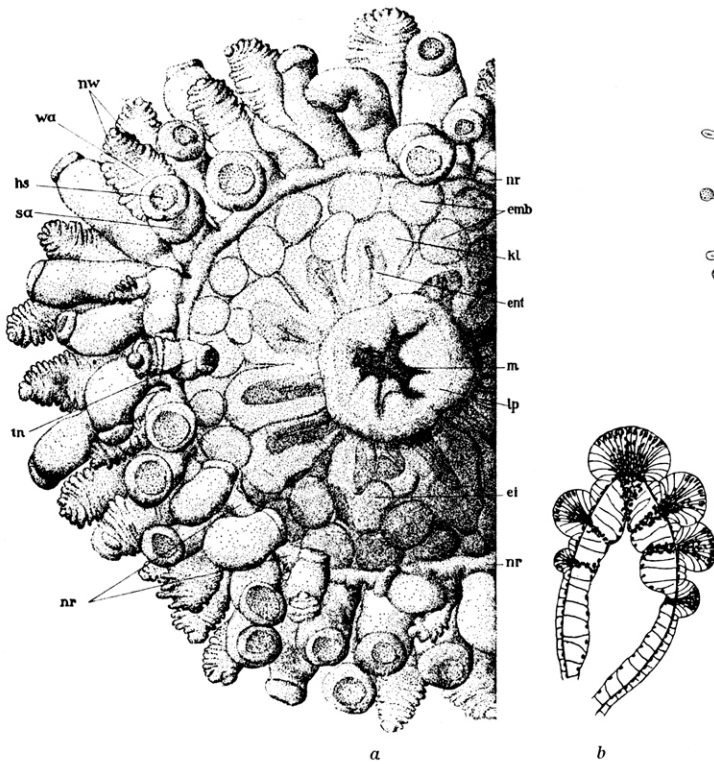


Fig. 58. *Staurocladia kerguelensis* (a from VANHÖFFEN, b from Lengerich).

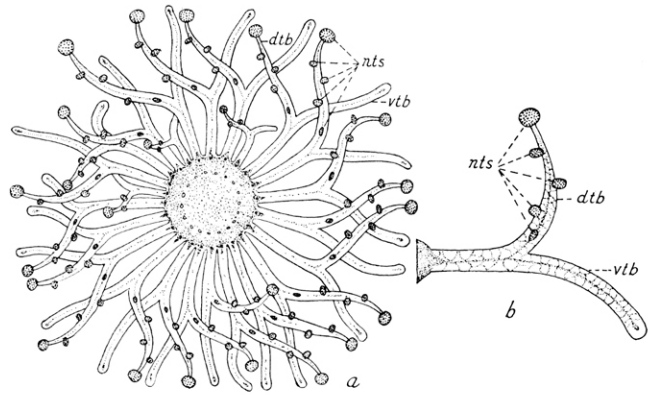


Fig. 59. *Staurocladia acuminata* (from EDMUNDSON).

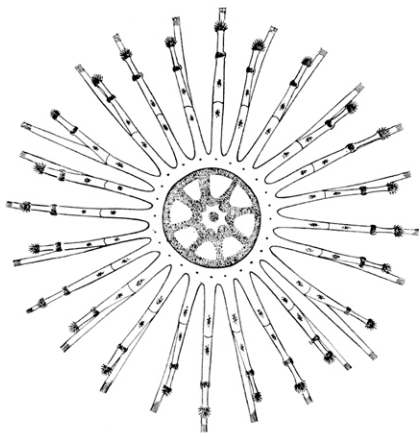


Fig. 60. *Staurocladia haswelli* (from BRIGGS, redrawn by E. L.).

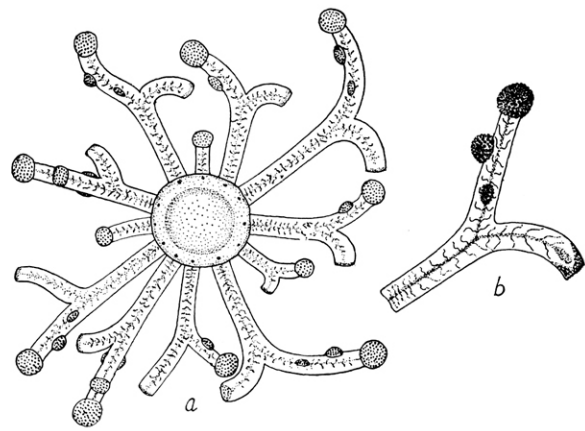


Fig. 61. *Staurocladia bilateralis* (from EDMUNDSON).

*Staurocladia bilateralis* (EDMONDSON 1930). Diameter 0.6 mm; about 12 tentacles, upper branch a little longer than lower; nematocyst clusters on tentacle, one meridional on upper side, two laterally opposite each other, proximal of the meridional cluster; budding. — Hawaii. (EDMONDSON 1930 p. 8, fig. 3 a, b).

*Staurocladia oahuensis* (EDMONDSON 1930). Diameter 0.5 mm; eight radial canals; up to 18 tentacles, upper branch longer than lower; nematocyst clusters meridional, two on upper side, none on underside; propagation by sagittal division. — Hawaii; Chile. (EDMONDSON 1930 p. 3, figs. 1 a, b, 2 a-d).

*Staurocladia alternata* (EDMONDSON 1930). Diameter 0.8 mm; margin of umbrella overhanging base of tentacles; eight radial canals; up to 13 tentacles, upper branch a little longer than lower; six clusters of nematocysts in two alternating lines, only on upper side. — Hawaii. (EDMONDSON 1930 p. 10, fig. 5 a, b).

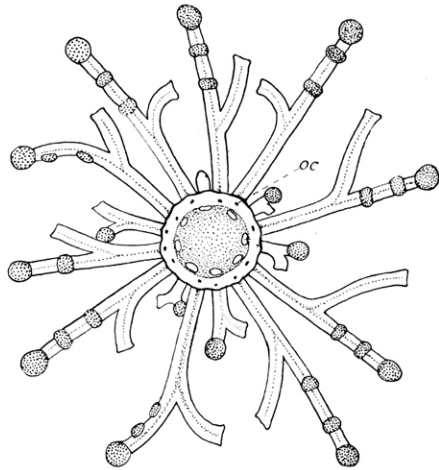


Fig. 62. *Staurocladia oahuensis* (from EDMUNDSON).

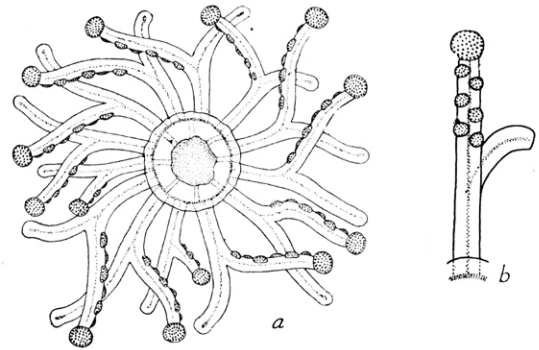


Fig. 63. *Staurocladia alternata* (from EDMUNDSON).

## Family Cytaeididae.

Anthomedusae with simple circular mouth; with simple unbranched oral tentacles; with interradian gonads; with four simple radial canals; with four solid marginal tentacles; without ocelli.

*Cytaeis* ESCHSCHOLTZ 1829. Cytaeididae with four or more simple, unbranched oral tentacles. Only one species of a fully developed medusa is known with certainty, but a number of *Podocoryne*-like hydroids with newly liberated medusae or with medusoid gonophores are described by REES (1962) under the names *C. uchidai* (new name for *C. japonica* KOMAI 1931), *C. nuda*, *C. nassa*, *C. niotha*, and *C. indica*.

*Cytaeis tetrastyla* ESCHSCHOLTZ 1829. 6 mm high, 5 mm wide; stomach very large, numerous medusa-buds on upper half; 8–32 oral tentacles each with a terminal cluster of nematocysts; tentacle bulbs large, pyriform, on exumbrella above the tentacles. — Generally distributed in tropical and subtropical waters, partly oceanic. (MAYER 1910 p. 133, figs. 71–73, as *C. atlantica*). Numerous synonyms.

*Cytaeis vulgaris* AGASSIZ & MAYER 1899. 5 mm high, 3.5 mm wide; stomach oval or spindle-shaped, 1/2–

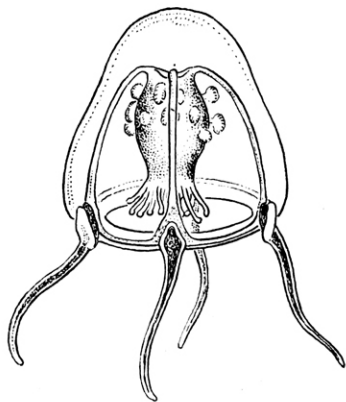


Fig. 64. *Cytaeis tetrastyla* (from BIGELOW, redrawn by P. W.).

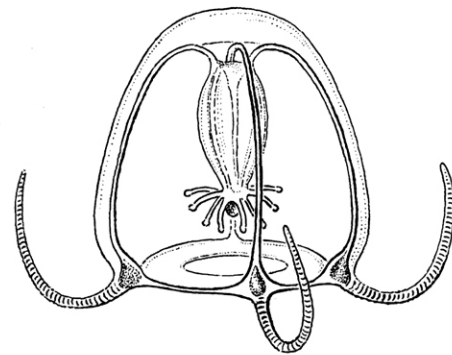


Fig. 65. *Cytaeis vulgaris* (from AGASSIZ & MAYER, redrawn by P. W.).

2/3 as long as bell cavity; short peduncle in young medusae; four interradial, horse-shoe-shaped gonads, with the concavity turned upwards; 32 oral tentacles; tentacle bulbs large, no ectodermal swellings. — Fiji Islands (AGASSIZ & MAYER 1899, p. 161, Pl. 2 figs. 3–5). The medusa from the Fiji Islands may be a valid species, all other records are *C. tetrastyla*.

## Family Clavidae.

Anthomedusae with mouth with four lips with continuous row of nematocyst clusters along margin; with interradial gonads; with four simple radial canals; with numerous solid marginal tentacles, not grouped in clusters; with adaxial ocelli.

*Turritopsis* McCrady 1856. Clavidae in which the walls of the four radial canals, above stomach, consist of highly vacuolated endodermal cells forming a peduncle for the stomach.

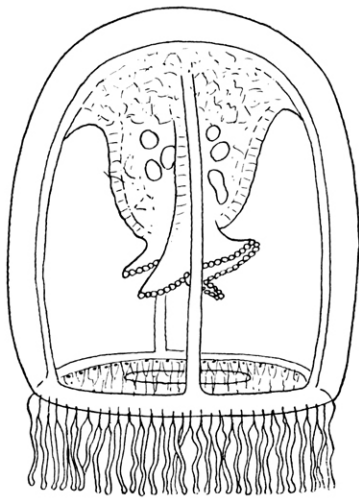


Fig. 66. *Turritopsis nutricula* (from Pl. Sh.).

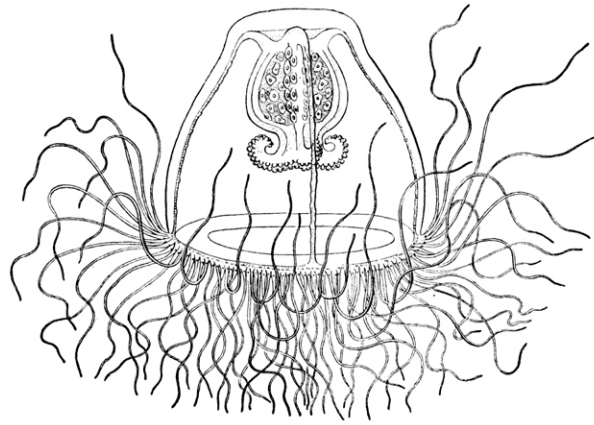


Fig. 67. *Oceania armata* (from MAYER).

*Turritopsis nutricula* McCrady 1856. 4–11 mm high and wide, bell-shaped, walls uniformly thin; stomach large, cross-shaped in transverse section; 80–90 marginal tentacles. — Western Pacific from Japan to New Zealand; Indian Ocean; Red Sea. Mediterranean; eastern Atlantic from the Gulf of Guinea to the North Sea; western Atlantic from Brazil to Cape Cod. (MAYER 1910 p. 143, Pl. 14 figs. 10–13, Pl. 15 figs. 10–13, textfigs 77–79; RUSSELL 1953 p. 115, Pl. 5 figs. 1–5, Pl. 29 figs. 1–3, textfigs. 54–56).

*Turritopsis lata* Lendenfeld 1884. 3.5 mm high, 3 mm wide; with a low, dome-like, apical projection; manubrium on a gelatinous peduncle; proximal parts of radial canals vacuolated; stomach spindle-shaped, 2/3 as long as bell cavity; four recurved lips with stalked nematocyst warts; 60–130 marginal tentacles. — New South Wales, Australia. (Lendenfeld 1884 p. 588, Pl. 22 figs. 36, 36 a). Examination of type-specimen has shown that this is a valid species (Kramp 1953 p. 310).

*Oceania* Kölliker 1853. Clavidae with manubrium upon a simple, solid gelatinous peduncle, not vacuolated.

*Oceania armata* Kölliker 1853. 8–10 mm high and wide, pyriform, flat-topped, with uniform, thin walls; stomach flask-shaped, cruciform in transverse section, upon a short, pyramidal peduncle, not vacuolated; 60–100 marginal tentacles, densely crowded. — Coastal waters in tropical and subtropical parts of the Pacific and Indian oceans. Mediterranean; eastern Atlantic from Portugal to Cape Verde; the Azores; West-Indies.



## Family Hydractiniidae.

Anthomedusae with mouth with four simple or branching lips armed with terminal clusters of nematocysts; with gonads either only on interradial walls of stomach, or on proximal portions of radial canals as well; with four, eight or more solid marginal tentacles; with or without ocelli.

*Podocoryne* M. Sars 1846. Hydractiniidae with four or more simple marginal tentacles, not in groups; with four or eight simple or slightly branched mouth-arms which are dilatations of the mouth-rim.

### Key to the Indo-Pacific species of *Podocoryne*.

1. Mouth-arms divided; numerous marginal tentacles; with adaxial ocelli ..... *ocellata*  
With four simple mouth-arms, each with a terminal cluster of nematocysts; rarely more than eight tentacles;  
no ocelli ..... 2
2. Stomach with medusa buds ..... 3  
No medusa buds ..... 4
3. With four marginal tentacles all alike ..... *minima*  
With two long and two short tentacles ..... *simplex*
4. Umbrella with a bluntly conical apical projection; stomach on a distinct peduncle; four long tentacles .... *apicata*  
No apical projection; no peduncle; 4–8 (rarely 16) tentacles ..... *carnea*

*Podocoryne ocellata* (AGASSIZ & MAYER 1902). 4 mm high and wide, bell-shaped with flat top, walls thin; Manubrium half as long as bell cavity; mouth-arms divided four times; four interradial gonads; about 50 short, stiff tentacles, each with a prominent, adaxial ocellus. — Paumotu, South Pacific Ocean. (MAYER 1910 p. 153, fig. 83, as *Lymnorea ocellata*).

*Podocoryne minima* (TRINCI 1903). 0.3–1 mm high; medusa-buds on stomach; stomach short, on short peduncle; four simple mouth-arms; four marginal tentacles. — Chefoo, China. Mediterranean; English Channel; Brazil. (RUSSELL 1953 p. 134, figs. 63, 64; CHOW & HUANG 1958 pp. 176, 189, figs. 10, 11).

*Podocoryne simplex* KRAMP 1928. 0.75 mm high and wide, dome-shaped, walls thin; stomach on short peduncle, barrel-shaped, circular in cross-section; four simple mouth-arms; medusa-buds on stomach;

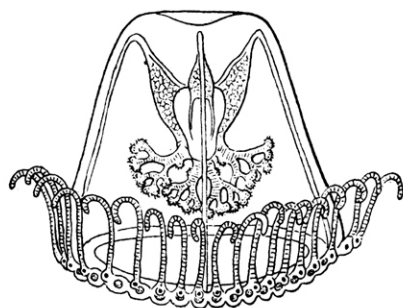


Fig. 68. *Podocoryne ocellata* (from MAYER).

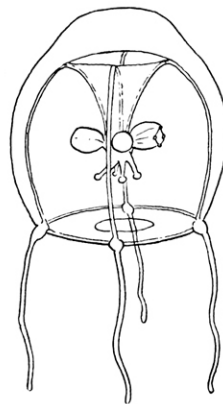


Fig. 69. *Podocoryne minima*  
(from Pl. Sh.).

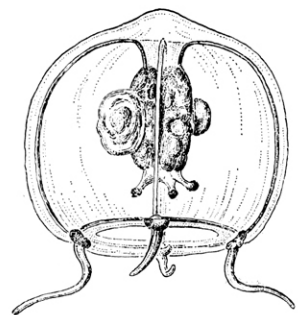
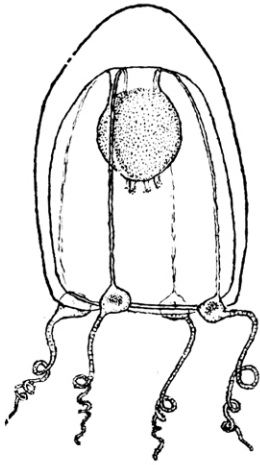
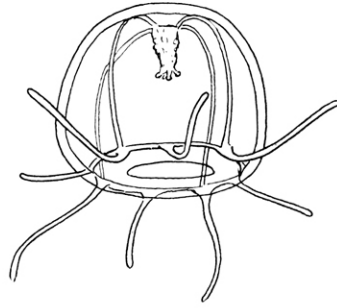
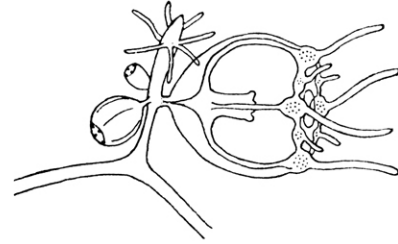


Fig. 70. *Podocoryne simplex* (from  
KRAMP, redrawn by P. W.).

gonads surrounding stomach in its whole length; four marginal tentacles, two larger, two smaller. — Japan; Palao Islands in Central Pacific. (KRAMP 1928 p. 45, fig. 20).

*Podocoryne apicata* KRAMP 1959. Up to 1.2 mm high, somewhat higher than wide, dome-shaped or slightly conical, with a bluntly conical apical projection; stomach barrel-shaped, on a distinct peduncle of varying length, with four interradial gonads completely covering stomach in its entire length; the stomach with its



Fig. 71. *Podocoryne apicalata* (from KRAMP).Fig. 72. *Podocoryne carnea* (from Pl. Sh.).Fig. 73. *Podocoryne bella* (from HAND).

peduncle about half as long as the bell cavity; with four small, simple mouth-arms; four long marginal tentacles with fairly large basal bulbs; each tentacle with a large, circular patch of orange-red pigment on its abaxial side. — Malacca; Gulf of Siam; Vietnam. (KRAMP 1959 *b* p. 228, fig. 5).

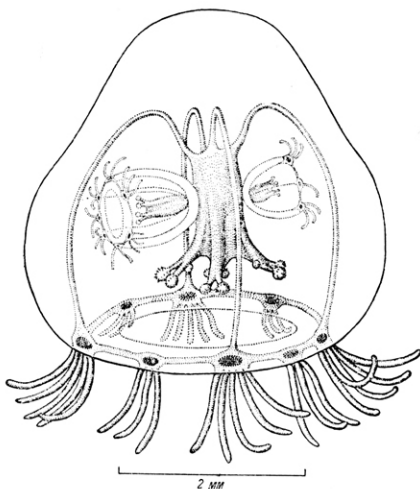
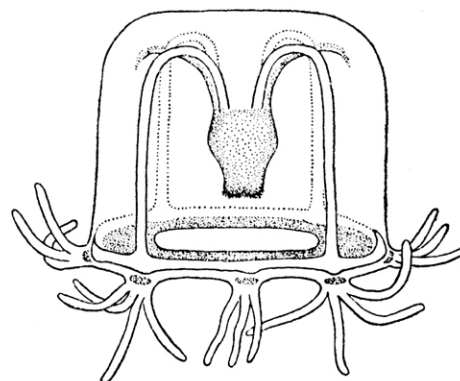
*Podocoryne carnea* M. Sars 1846. Size varying, 1–3.5 mm, in different localities; manubrium flask-shaped; no peduncle; four short, simple mouth-arms; gonads interradiar; no medusa-buds; 4–8 (rarely up to 16) marginal tentacles. — North-western Europe; Iceland (hydroid only); Mediterranean Sea; Black Sea; east coast of North America; South Africa (hydroid). Hydroid with newly liberated medusa described from the coast of Chile as *P. carnea* var. *chilensis*, KRAMP 1952 p. 4, figs. 1, 2. (RUSSELL 1953 p. 121, Pl. 6 figs. 2, 3, textfigs. 57 A, B, 59 B).

*Podocoryne bella* HAND 1961. Hydroid living on the Pigfish, *Congiopodus leucopaecilus*, medusa-buds with up to 8 tentacles not seen liberated. — Otago harbour, New Zealand. (HAND 1961 pp. 91–94, fig. 1).

## Family Rathkeidae.

Anthomedusae with mouth with four lips elongated to form oral arms with terminal, usually also lateral, clusters of nematocysts; with or without medusa-buds on stomach walls; with four (rarely eight) radial canals; with solid marginal tentacles arranged in eight groups; without ocelli.

*Rathkea* BRANDT 1838. Rathkeidae with four radial canals; the four corners of the mouth drawn out so as to form four oral arms with clusters of nematocysts.

Fig. 74. *Rathkea octopunctata* (from NAUMOV).Fig. 75. *Rathkea rubence* (from NAIR).

*Rathkea octopunctata* (M. Sars 1835). 3–4 mm high, 2–4.5 mm wide; pyriform with solid apical projection; stomach short, four-sided, on a well developed peduncle; gonads completely surrounding stomach; with medusa-buds on the stomach before maturation of the gonads; mouth with four lips with 1–2 pairs of nematocyst knobs, when adult with 3–5 marginal tentacles in each perradial, three in each interradial group. — Chefoo in China, Japan, Kamchatka, Aleutian Islands, Bering Sea; Alaska; north coast of U.S.S.R.. Mediterranean Sea; north-western Europe, Iceland, Greenland, Newfoundland, New England, Bermudas. (Mayer 1910 p. 177, Pl. 20 fig. 11; Russell 1953 p. 137; Pl. 7 figs. 3, 4, textfigs. 65 A-E, 66, 67 A, B).

*Rathkea rubence* NAIR 1951. 1.5 mm high, 1 mm wide, top flatly rounded; perradial corners of mouth swollen lobes with nematocysts, mouth pistils absent; no medusa-buds; 3–4 tentacles in each group. — Trivandrum Coast, India. (NAIR 1951 p. 54, Pl. 1 figs. 2, 3).

*Octorathkea* UCHIDA 1927. Rathkeidae with eight radial canals and eight marginal clusters of tentacles; manubrium four-sided with four lips, no oral arms.

*Octorathkea onoi* UCHIDA 1927. 1.5 mm high and wide; gonads not developed; marginal tentacles 5 in each perradius, 3 in each interradius. — Takashima in southern Japan. (UCHIDA 1927 p. 226, fig. 42).

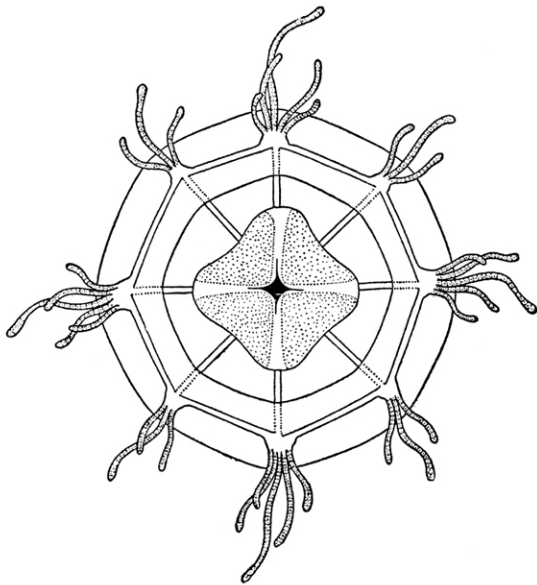


Fig. 76. *Octorathkea onoi* (from UCHIDA).

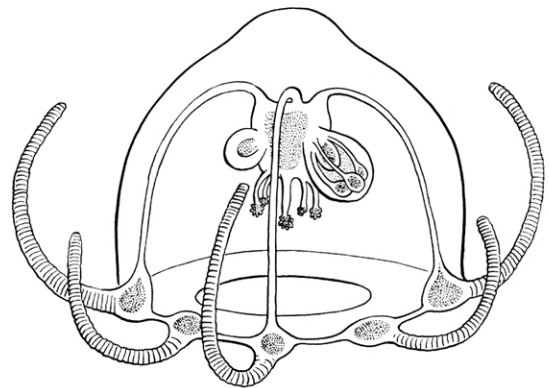


Fig. 77. *Lizzia gracilis* (from MAYER).

## 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 four or eight large marginal bulbs each with a group of solid tentacles; with or without ocelli.

### Key to the genera of Bougainvilliidae.

- |   |                    |
|---|--------------------|
| 1. Oral tentacles simple, unbranched .....  | 2                  |
| Oral tentacles dichotomously branched .....                                       | 3                  |
| 2. Marginal tentacles solitary or in eight unequal groups .....                   | <i>Lizzia</i>      |
| Marginal tentacles in eight groups, all alike with same number of tentacles ..... | <i>Lizzella</i>    |
| 3. Marginal tentacles solitary .....  | <i>Thamnostoma</i> |
| Marginal tentacles in four or eight groups .....                                  | 4                  |
| 4. Marginal tentacles in 8 groups .....   | 5                  |
| Marginal tentacles in 4 groups .....  | 6                  |
| 5. Marginal groups of tentacles cleft .....                                       | <i>Chiarella</i>   |
| Marginal groups of tentacles uncleft .....  | <i>Köllikerina</i> |

6. In each group a median pair of club-shaped tentacles ..... *Nemopsis*  
 Marginal tentacles all alike ..... *Bougainvillia*

*Lizzia*. FORBES 1846. Bougainvilliidae with simple, unbranched oral tentacles; gonads surrounding stomach; with eight marginal bulbs, each with one simple tentacle, or with more tentacles on the perradial than on the interradial bulbs; with a stomachal peduncle; medusa buds develop upon the stomach; no ocelli.

*Lizzia gracilis* (MAYER 1910). 3 mm wide, a little broader than high, with slight apical projection; stomach small, on a slightly developed peduncle; four perradial and four interradial oral tentacles; medusa-buds on stomach; eight stiff marginal tentacles, upward curled, on large basal bulbs. — Malayan Archipelago; Philippines; Fiji Islands. Florida on the east coast of North America. (MAYER 1910 p. 141, Pl. 16 figs. 1–3; KRAMP 1965 p. 14, young stages).

*Lizzella* HAECKEL 1879. Bougainvilliidae with simple, unbranched oral tentacles; with eight marginal bulbs all alike, having same number of tentacles. Systematic position uncertain.

*Lizzella octella* HAECKEL 1879. 15 mm high, 10 mm wide, egg-shaped; stomach spherical or nearly cubical, a conical peduncle as long as stomach; eight simple oral tentacles; gonads four feather-shaped leaves in the stomach wall; eight marginal bulbs each with eight large tentacles. — Japan. (HAECKEL 1879 p. 84; MAYER 1910 p. 180; UCHIDA 1927 pp. 146, 230, ? juv. of *Spirocodon saltatrix*).

*Thamnostoma* HAECKEL 1879. Bougainvilliidae with four or eight (or more) solitary marginal tentacles and four branched oral tentacles above the mouth; gonads interradial.

*Thamnostoma macrostomum* HAECKEL 1879. 8 mm high and wide, cubical; stomach globular, no peduncle; mouth tube three times as long as stomach, extending beyond velar opening; four oral tentacles divided 6–8 times; four gonads; eight similar marginal tentacles with ocelli. — Singapore. (MAYER 1910 p. 153, as *Lymnorea macrostoma*).

*Bougainvillia* LESSON 1836. Bougainvilliidae with four radially placed clusters of marginal tentacles, the tentacles of each cluster being all of one kind and similar in structure; with four perradial, dichotomously branching oral tentacles.

#### Key to the Indo-Pacific species of *Bougainvillia*.

1. With a well developed, distinct, gelatinous gastral peduncle ..... 2  
 Peduncle absent or weakly developed ..... 4
2. Peduncle narrow; gonads interradial, on lateral walls of stomach ..... 3  
 Peduncle broadly conical; gonads extending upwards along perradial sides of peduncle ..... *macloviana*
3. Oral tentacles divided twice; two tentacles in each marginal bulb ..... *bitentaculata*  
 Oral tentacles divided 4–5 (7) times; 11–15 (22) tentacles in each marginal bulb; ocelli large, round .. *superciliaris*
4. Gonads perradial (!); 50–60 tentacles in each marginal bulb ..... *multitentaculata*  
 Gonads adradial or interradial ..... 5
5. Gonads eight adradial ..... 6  
 Gonads four interradial ..... 8
6. Oral tentacles with long basal trunk, divided 4–6 times; ocelli fine transverse lines on basis of marginal tentacles ..... *britannica*  
 Basal trunk of oral tentacles short ..... 7
7. Marginal bulbs broader than interspaces, each with 20–30 (40) tentacles; oral tentacles divided 5–6 times *principis*  
 Marginal bulbs epaulet-shaped, each with 15–20 tentacles; oral tentacles divided 6–8 times; the eight gonads distinctly separated ..... *fulva*
8. Without ocelli; marginal bulbs each with 5–7 tentacles ..... *muscooides*  
 Ocelli present ..... 9
9. Stomach particularly broad and flat, quadrangular; marginal bulbs with 10–13 tentacles; oral tentacles divided 5–6 times immediately from base ..... *platygaster*  
 Stomach not particularly flat; basal trunk of oral tentacles fairly long ..... 10
10. Marginal bulbs with up to 60 tentacles; oral tentacles divided up to 7 times ..... *involuta*  
 Marginal bulbs with 2–4 (rarely more) tentacles; oral tentacles divided 1–2 (rarely slightly more) times; male gonads extending cross-wise on subumbrella ..... *ramosa*

*Bougainvillia macloviana* LESSON 1843. 15 mm high, 13 mm wide, cylindrical, with fairly thick walls and rounded top; manubrium on a broad conical peduncle; oral tentacles with very short trunk divided 5–7 times; gonads extending along perradial lobes of stomach upwards on peduncle; marginal bulbs V-shaped, each with 35–65 tentacles in double row; ocelli yellow, red or brownish-black. — Antarctic and subantarctic, probably circumpolar. North Sea in north-western Europe. (BROWNE & KRAMP 1939 p. 284, Pl. 14 fig. 6, Pl. 15 figs. 7–14; VANNUCCI & REES 1961 p. 69).

*Bougainvillia bitentaculata* UCHIDA 1925. 1 mm high, 0.8 mm wide; oral tentacles short, divided twice; gonads interradial, large, ovoid; only two large tentacles in each perradius; one black ocellus just above and between the tentacle bases. — Japan. (UCHIDA 1925 p. 84, fig. 10; VANNUCCI & REES 1961 p. 60).

*Bougainvillia superciliaris* (L. AGASSIZ 1849). 7–10 (12) mm high and wide, almost globular, walls very thick; stomach short, on broad base, cross-shaped in section, on well-developed peduncle of about same

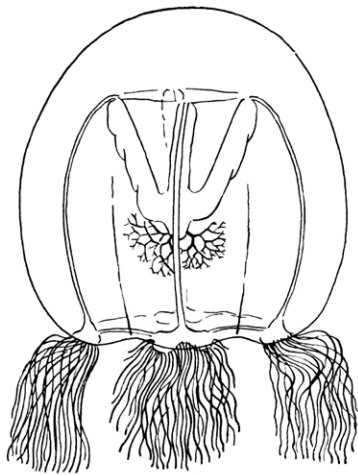


Fig. 78. *Bougainvillia macloviana* (from Pl. Sh.).

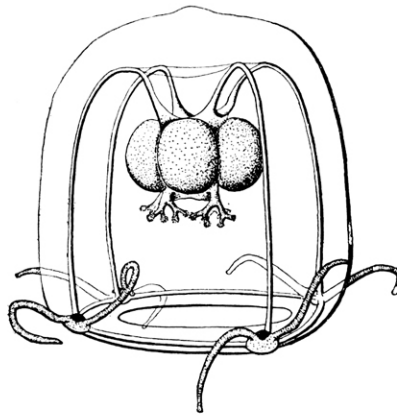


Fig. 79. *Bougainvillia bitentaculata* (from UCHIDA).

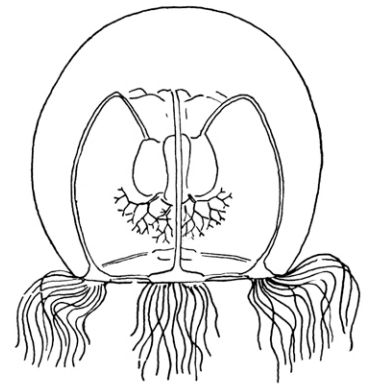


Fig. 80. *Bougainvillia superciliaris* (from Pl. Sh.).

width as stomach; gonads interradial, almost quadratic, on stomach walls only; oral tentacles with short, thick basal trunk, divided 4–5 (rarely 6–7) times, branches short; marginal bulbs crescent-shaped, less than half as wide as interradial spaces, each with 11–15 (up to 22) tentacles; ocelli large, round, black; planulae developing on stomach walls. — From arctic waters southwards to southern Japan. In North Atlantic as far south as Woods Hole in North America and north-western Europe. (MAYER 1910 p. 162, Pl. 17 fig. 1, textfigs. 87, 88; RUSSELL 1953 p. 169, textfigs. 83 A, B, 84 A, B, 85 A–C; VANNUCCI & REES 1961 p. 85).

*Bougainvillia multitentaculata* FOERSTER 1923. 10 mm high and wide, rounded at the top, gelatinous substance quite thick; a low, broad peduncle; gonads probably interradial, but placed along perradial sides of the stomach and the low peduncle; oral tentacles divided 6–7 times; marginal bulbs like a wide, inverted V, each with 50–60 short tentacles; ocelli brown, in a zigzag row. — Vancouver, British Columbia. (FOERSTER 1923 p. 245, Pl. 2 fig. 7, Pl. 3 figs. 1, 2; VANNUCCI & REES 1961 p. 75).

*Bougainvillia britannica* FORBES 1848. 6–8 mm high, globular, walls thick, bell cavity spacious; no peduncle; manubrium short and broad, cross-shaped in cross-section; oral tentacles with long basal trunk, in distal part divided 4–6 times, with small terminal knobs; gonads adradial; marginal bulbs about half as broad as intervals, usually with 12–17, sometimes up to 30 thin tentacles; ocelli a fine transverse black line across the basal part of each tentacle. — Chefoo, China (CHOW & HUANG 1958 pp. 177, 189, Pl. 1 figs. 8, 9). North-western Europe; Gulf of Maine in North America; southern Iceland. (MAYER 1910 p. 161, Pl. 17 fig. 8; RUSSELL 1953 p. 158, Pl. 8 figs. 2, 3, Pl. 9 figs. 1–3, textfigs. 75 A, B, 77 A, B, 78 A, 79 A; VANNUCCI & REES 1961 p. 61).

*Bougainvillia principis* (STEENSTRUP 1850). 10 mm high and wide, globular, jelly moderately thick; manubrium without peduncle, short and broad, with deep interradial furrows; oral tentacles short, divided 5–6

times, almost from base; gonads adradial, swollen; marginal bulbs wider than interspaces, each with usually 20–30, up to 40 tentacles in a single row; ocelli black, on adradial surface of the bulb. — Chefoo, China (CHOW & HUANG 1958 pp. 177, 189, Pl. 2 figs. 12, 13). North of Alaska. Barents Sea; north-western Europe; Iceland; West-Greenland. (RUSSELL 1953 p. 164, Pl. 8 fig. 4, textfigs. 76 A, B, 78 B, 79 B; VANNUCCI & REES 1961 p. 79).

*Bougainvillia fulva* AGASSIZ & MAYER 1899. Up to 14 mm high and 11 mm wide, usually smaller, cylindrical with flatly rounded top, bell-walls thick; manubrium about half as long as bell cavity, no peduncle;

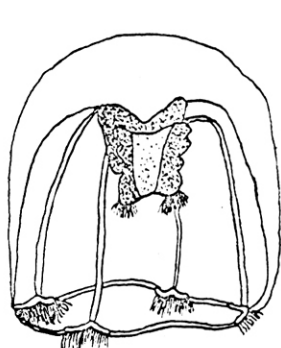


Fig. 81. *Bougainvillia multitentaculata*  
(from FOERSTER).

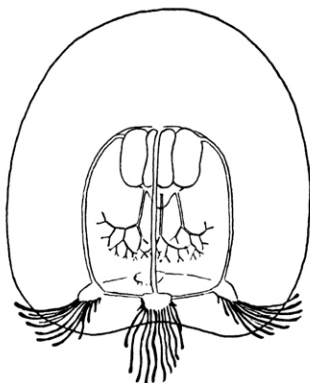


Fig. 82. *Bougainvillia britannica* (from Pl. Sh.).

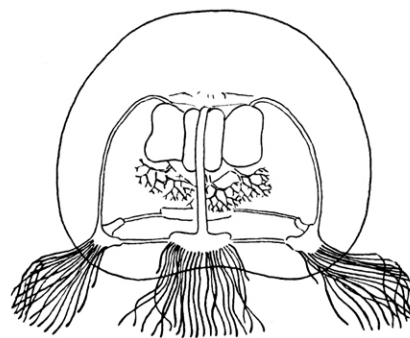
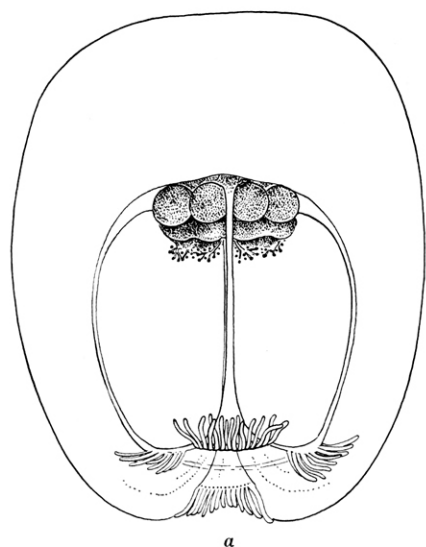
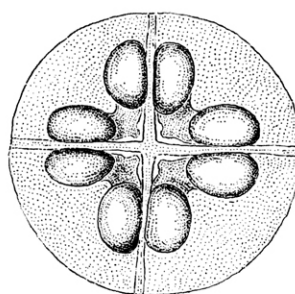


Fig. 83. *Bougainvillia principis* (from Pl. Sh.).



a



b

Fig. 84. *Bougainvillia fulva* (a from MAAS, b from KRAMP, redrawn by E. L.).

oral tentacles divided 6–8 times, basal trunk usually short; eight adradial gonads distinctly separated; marginal bulbs fairly narrow, each with 15–20 short tentacles; ocelli small, black, on the base of the tentacles. Medusa-buds may occur on stomach in eight meridional rows of clusters. — Tropical parts of the Indian and Pacific oceans. (AGASSIZ & MAYER 1899 p. 162, Pl. 2 fig. 6; MAAS 1905 p. 10, Pl. 1 fig. 8, Pl. 2 figs. 9–10; KRAMP 1928 p. 47, figs. 21–23; VANNUCCI & REES 1961 p. 65).

*Bougainvillia muscoides* (M. SARS 1846). 4–5 mm high and wide, oval, walls not very thick; a peduncle may be indicated; manubrium fairly small; oral tentacles divided 4–5 times, basal trunk short but distinct; gonads interrarial, well separated in the perradii but without interrarial furrows; marginal bulbs small, triangular with 5–7 tentacles; no ocelli. — Vancouver in British Columbia; Gulf of Siam. North-western Europe. (MAYER 1910 p. 168, fig. 91; KRAMP & DAMAS 1925 p. 256, figs. 8–12; VANNUCCI & REES 1961 p. 74).  
Synonym: *Bougainvillia nordgårði* BROWNE 1903).

*Bougainvillia platygaster* (HAECKEL 1879). 12 mm high and wide, cubical, with thick walls and flat top; no peduncle; manubrium quadrangular, very flat, being four times as wide as high; oral tentacles short, divided 5–6 times immediately from base; gonads interradial; marginal bulbs triangular, with 10–13 tentacles; ocelli crescent-shaped. Medusa-buds produced either directly from stomach walls or from polypoid structures issuing from stomach walls and provided with mouth and tentacles. — Widely distributed in the tropical parts of the Atlantic and Indian oceans and in the Malayan Archipelago; Fiji Islands. (KRAMP 1957 p. 9, Pl. 3 figs. 1–6; VANNUCCI & REES 1961 p. 78).

*Bougainvillia involuta* UCHIDA 1947. Up to 4 mm high and 4.5 mm wide, jelly thick; manubrium with a short peduncle; gonads interradial, united in large specimens; oral tentacles divided up to 7 times, apparently with short basal trunk; in larger specimens the marginal epaulettes cover the larger part of bell margin,

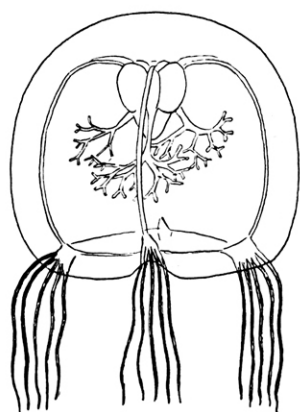


Fig. 85. *Bougainvillia muscoides* (from Pl. Sh.).

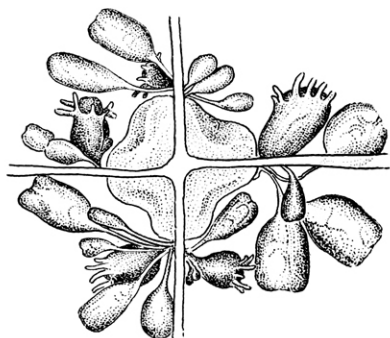


Fig. 86. *Bougainvillia platygaster*, aboral view of stomach with medusa-buds and polypoid buds (from KRAMP, redrawn by P. W.).

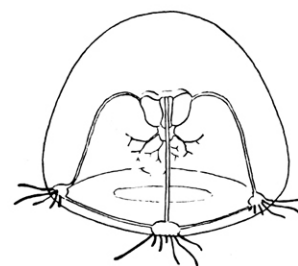


Fig. 87. *Bougainvillia ramosa* (from Pl. Sh.).

each with up to 60 tentacles, with ocelli. — Palao Islands in western Pacific; Chile. (UCHIDA 1947 a p. 301, fig. 4).

*Bougainvillia ramosa* (van BENEDEN 1844). 2–3.5 mm high and wide, semiglobular, jelly fairly thick; manubrium short, oral tentacles divided 1–2 times (rarely 3–6); four interradial gonads, in ♀ globular, in ♂ prolonged along the perradial sides of a low and broad peduncle; marginal bulbs small, with 3–5 (rarely 6–7) long tentacles; ocelli black, round. — East Australia (the hydroid in Australia, Amboina, China and Japan). North-western Europe, Mediterranean, Black Sea, West Africa, New England, Brazil. (RUSSELL 1953 p. 153, Pl. 8 fig. 1, Pl. 9 figs. 4, 5, textfigs. 74 A-C; VANNUCCI & REES 1961 p. 82).

#### *Doubtful species of Bougainvillia.*

*Bougainvillia bougainvillei* BRANDT 1835. 9 mm high, somewhat higher than wide, moderately thick walls; manubrium small, oral tentacles divided 4 times, without terminal knobs (!); gonads interradial; about 15 tentacles in each marginal bulb, with ocelli. — Bering Sea. (HARTLAUB 1911 p. 159, fig. 140).

*Bougainvillia prolifera* (VON LENDENFELD 1884). 3 mm high, 2.5 mm wide, dome-like; manubrium small, nearly cubical; oral tentacles simple, unbranched; medusa-buds on sides of the stomach; marginal bulbs large, “scrotum-shaped”, with 5 tentacles; ocelli? — New South Wales, Australia. (LENDENFELD 1884 p. 589, Pl. 23 figs. 38, 39; VANNUCCI & REES 1961 p. 80).

*Bougainvillia trinema* (VON LENDENFELD 1884). 3 mm wide, oval; manubrium small, oral arms end in three branches; gonads not developed; marginal bulbs small, with 3 tentacles. — Sydney harbour, Australia. (LENDENFELD 1884 p. 918, Pl. 41 fig. 13; KRAMP 1953 p. 264; VANNUCCI & REES 1961 p. 88).

*Nemopsis* L. AGASSIZ 1849. Bougainvilliidae with four clusters of marginal tentacles, in each cluster a median pair of club-shaped tentacles and on both sides a number of simple, filiform tentacles; with adaxial



ocelli; stomach with four radial lobes extending outwards along the radial canals; gonads on these lobes; oral tentacles dichotomously branched.

*Nemopsis dofleini* MAAS 1909. 13 mm high, 10 mm wide, jelly very thick; manubrium short and small, oral tentacles divided about 8 times; gonads along less than half of radial canal, ribbon-like and folded; about 40 tentacles in each marginal group. — Japan. (MAAS 1909 p. 11, Pl. 1 figs. 4, 5; UCHIDA 1925 p. 85 fig. 11). Synonym *Favonia nipponica* KISHINOUE 1910.

*Köllikerina* KRAMP 1939. Bougainvilliidae with eight groups of marginal tentacles, all alike in structure; with four oral tentacles dichotomously branched; marginal tentacles with or without adaxial ocelli. — Synonym *Köllikeria* L. AGASSIZ 1862, preoccupied. Most of the specific characters are variable. Discussion, see KRAMP, 1965 p. 20.

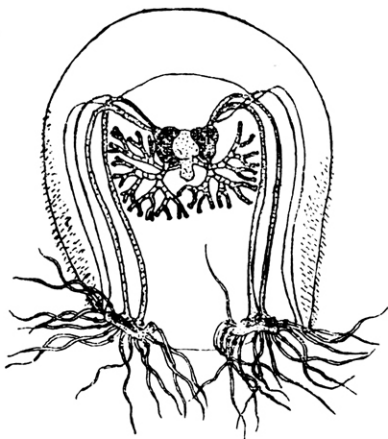


Fig. 88. *Bougainvillia bougainvillei* (from HARTLAUB).

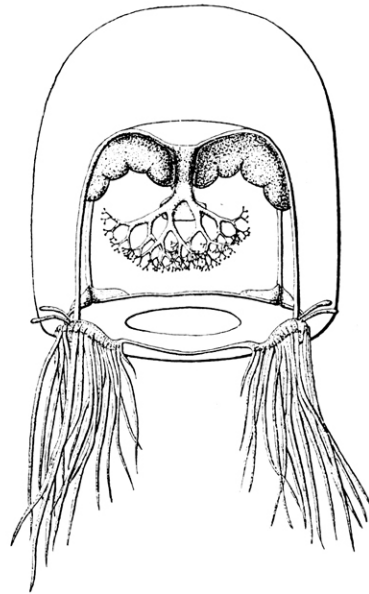


Fig. 89. *Nemopsis dofleini* (from UCHIDA).

#### Key to the species of *Köllikerina*.

1. Stomach elongate, narrow, on a distinct, slender peduncle ..... 2  
Stomach broad, more or less flat; peduncle, if present, low and wide<sup>1</sup> ..... 3
2. Gonads interradial, smooth; marginal bulbs each with 3–4 tentacles; umbrella dome-shaped ..... *elegans*  
Gonads perradial, horse-shoe-shaped, transversally folded; marginal bulbs with 11–13 tentacles; umbrella with a large, conical, pointed apical projection carrying a large, orange patch at utmost tip ..... *ornata*
3. Gonads interradial, smooth, with median incurvation ..... 4  
Gonads perradial, horse-shoe-shaped with concavity upwards, folded ..... 5
4. Marginal bulbs small, triangular, with ocelli ..... *octonemalis*  
Marginal bulbs linear; no ocelli ..... *maasi*
5. Gonads each with one median and 6–7 pairs of lateral folds; marginal bulbs kidney-shaped, each with 10–13 tentacles (in Mediterranean and Atlantic waters only) ..... *fasciculata*  
Gonads each with one median and no more than 3 lateral folds ..... 6
6. Marginal bulbs triangular, half as broad as interspaces, each with 7–8 tentacles ..... *constricta*  
Marginal bulbs linear, broader than interspaces, in younger specimens confluent, each with 12–16 tentacles *multicirrata*

*Köllikerina elegans* (MAYER 1900). 3–7 mm high, dome-shaped, sides almost vertical, walls moderately thick; stomach pear-shaped, small, on a distinct, slender, conical peduncle; gonads interradial, smooth; oral tentacles divided three times, each tip with three small branches with nematocysts; marginal tentacles stiff, curved upwards, 4 in the perradial, 3 in the interradial groups; ocelli dark brown. — India. Florida on the east coast of North America. (MAYER 1910 p. 181, Pl. 38 fig. 127, as *Rathkea elegans*; NAIR 1951 p. 55).

<sup>1</sup> In badly preserved specimens a gelatinous string, resembling a peduncle, may be artificially produced.



*Köllikerina ornata* KRAMP 1959. 8 mm high, with large, conical, apical projection, pointed, with a large orange patch at utmost tip; stomach on a slender peduncle, completely covered by the gonads, which are perradial, elongated horse-shoe-shaped, with one median and 4–5 lateral folds; mouth tube long and slender, no distinct lips; oral tentacles divided 5–6 times; marginal bulbs linear, separated by spaces half as wide,

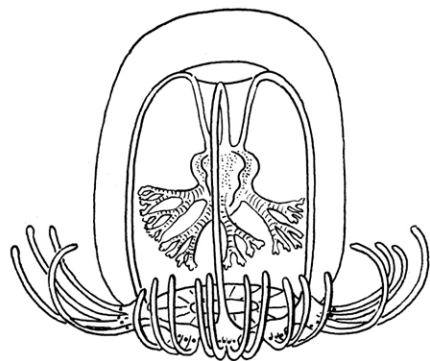


Fig. 90. *Köllikerina elegans* (from MAYER, redrawn by P. W.).

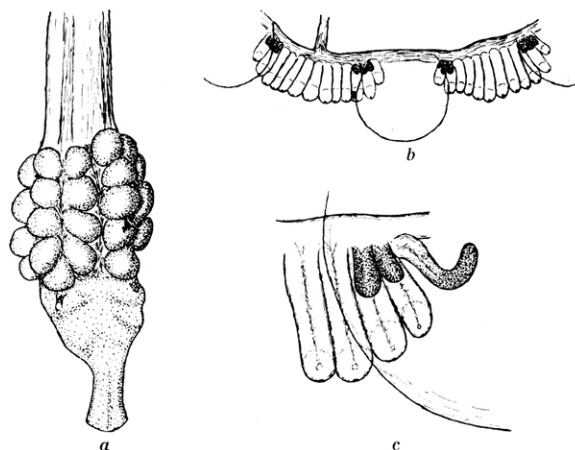


Fig. 91. *Köllikerina ornata*, manubrium and groups of tentacles (from KRAMP).

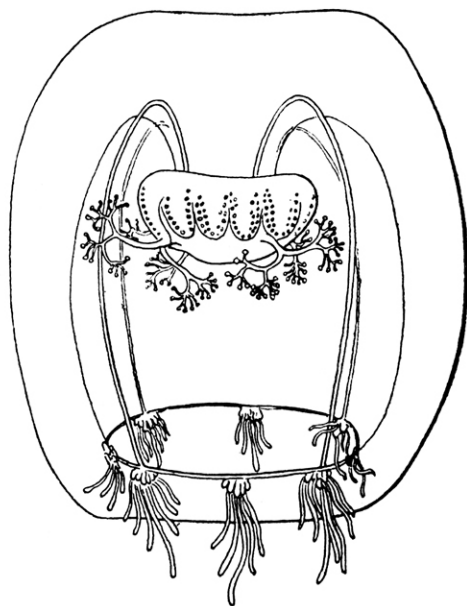


Fig. 92. *Köllikerina octonemalis* (from MAYER).

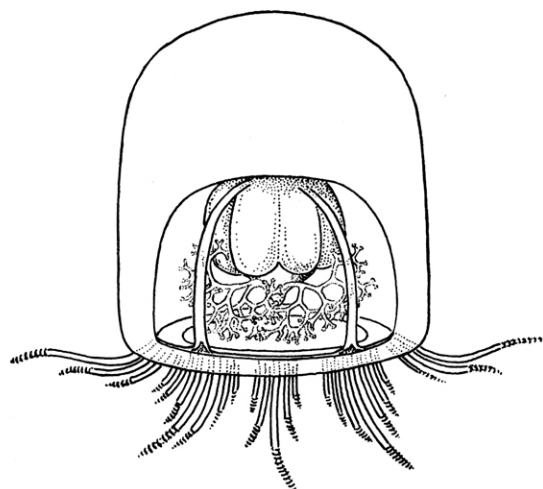


Fig. 93. *Köllikerina maasi* (from BROWNE, redrawn by P. W.).

with 11–13 tentacles, each with a round, dark-red ocellus, each bulb with two bright orange abaxial spots. — Ceylon. (KRAMP 1959 *b* p. 229, fig. 6 *a-c*).

*Köllikerina octonemalis* (MAAS 1905). 5–6 mm high, 4–5 mm wide, dome-shaped, with thick walls, bulging sides and flat top; stomach upon a short, wide, conical peduncle; gonads interrarial, doubly cleft, smooth; oral tentacles divided 4–5 times, basal trunk very short; marginal bulbs small, triangular, with 7–9 tentacles in perradial, 5–7 in interrarial groups; ocelli black. — Malayan Archipelago. (MAAS 1905 p. 12, Pl. 2 figs. 11–12; MAYER 1910 p. 180, fig. 95, as *Rathkea octonemalis*).

*Köllikerina maasi* (BROWNE 1910). 10 mm high, 9 mm wide, walls very thick; no peduncle; stomach large, cross-shaped; gonads four masses covering nearly whole interrarial walls of the stomach, separated perra-

dially, smooth; oral tentacles with short, thick trunk, divided 7–8 times; marginal bulbs triangular, with 5–7 tentacles decreasing in length from the median one towards both sides; no ocelli. — Antarctic; Madagascar. (BROWNE 1910 p. 22, Pl. 4 figs. 1–5; VANHÖFFEN 1912 p. 361, Pl. 25 fig. 2; KRAMP 1965 pp. 20, 21).

*Köllikerina constricta* (MENON 1932). 4 mm high, pyriform, with a solid, gelatinous apex; manubrium low, on a short peduncle; gonads V-shaped, with one median and three pairs of lateral folds; oral tentacles slender, divided 6–7 times; marginal bulbs triangular, half as broad as interspaces, with 7–8 tentacles; ocelli large, round, reddish-brown. — Madras in India; Ceylon; Banda Sea. (MENON 1932 p. 11, Pl. 2 fig. 11; KRAMP 1965 pp. 20, 22).

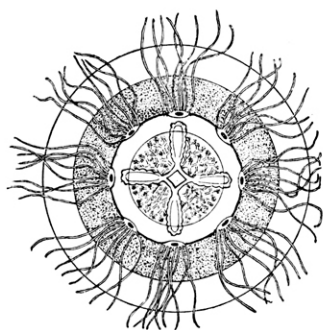


Fig. 94. *Köllikerina constricta*  
(from MENON).

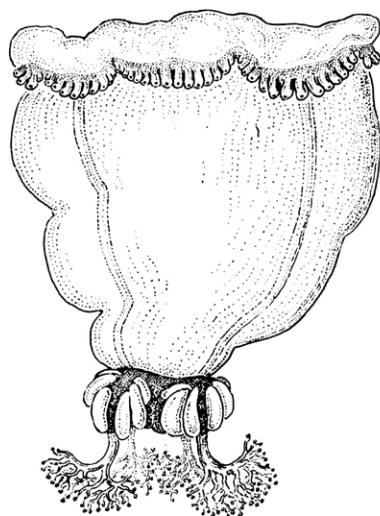


Fig. 95. *Köllikerina multicirrata* (from  
KRAMP, redrawn by P. W.).

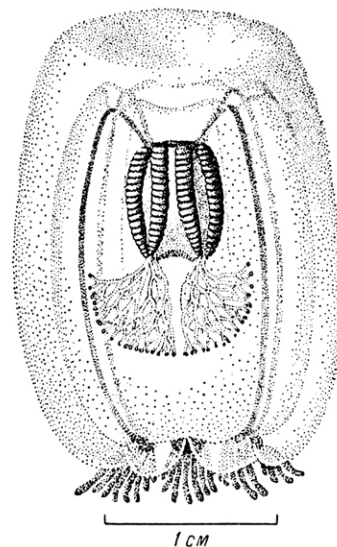


Fig. 96. *Chiarella centripetalis*  
(from NAUMOV).

*Köllikerina multicirrata* (KRAMP 1928). 5–6 mm high and wide, with fairly thin walls; no peduncle; stomach short; gonads perradial, V-shaped, each with one median and 2–3 pairs of lateral folds; oral tentacles divided 6–7 times, or more; marginal bulbs linear, broader than interspaces, in young specimens confluent, with 12–16 tentacles; ocelli large, round, reddish-brown. — Tropical Indian Ocean from East-Africa to New Guinea. (KRAMP 1928 p. 51, fig. 24; KRAMP 1965 pp. 20, 22).

*Chiarella* MAAS 1897. Bougainvilliidae with eight cleft tentacle clusters, so that the tentacles arise from 16 epaulet-shaped marginal swellings; oral tentacles dichotomously branched.

*Chiarella centripetalis* MAAS 1897. 15–25 mm high, 10–15 mm wide, dome-like, fairly thick at apex, but thin at margin; eight adradial, lappet-like emarginations which alternate with the radial and interradian clusters of tentacles; stomach barrel-shaped, shorter than half of bell cavity; four oral tentacles divided 5–6 times; marginal tentacles very short, up to 40 or more tentacles on each double-epaulet; with adaxial ocelli. — Gulf of California; Pacific coast of Mexico; Bering Sea and Ochotian Sea. (MAAS 1897 p. 15, Pl. 2 figs. 1–4; BIGELOW 1940 p. 294, figs. 11, 12; NAUMOV 1956 p. 36 and 1960 p. 196, Pl. 29 fig. 3, textfig. 82, as *Rathkea jasnovi*).

## Family Pandeidae.

Anthomedusae with umbrella with or without an apical projection; large stomach usually without a peduncle; mouth with four simple or crenulated lips; with four (rarely eight) radial canals, rarely with centripetal canals; with simple or folded gonads situated adradially or interradianly on stomach walls, sometimes extending along radial canals; with hollow marginal tentacles with tapering, conical basal bulbs, often laterally compressed; tentacles without terminal nematocyst knob; with or without rudimentary tentacles, warts or tentaculæ; with or without abaxial ocelli.

**Key to the genera of Pandeidae represented in Indo-Pacific waters.**

1. With 8 simple radial canals..... *Oclotiar*  
     With 4 primary radial canals ..... 2
2. With two simple and two bifurcated radial canals; tentacle bulbs develop into medusae ..... *Niobia*  
     With four undivided radial canals ..... 3
3. Tentacles with stalked nematocyst knobs in greater part of their length..... 4  
     Tentacles without stalked nematocyst knobs..... 5
4. Radial canals with long lateral diverticula; with numerous tentacles ..... *Zanclonia*  
     Radial canals without lateral diverticula; with only four tentacles; exumbrella with meridional lines of nematocysts ..... *Urashimea*
5. With a large, globular, adaxial protuberance containing nematocysts inside the base of each tentacle .. *Zanleopsis*  
     No such protuberances ..... 6
6. With only two well developed tentacles when adult ..... 7  
     With four or more well developed tentacles when adult ..... 10
7. With a well developed, broad gastric peduncle ..... *Stomotoca*  
     Without a peduncle ..... 8
8. Gonads on stomach walls only ..... *Amphinema*  
     Gonads extending from manubrium outwards along the radial canals ..... 9
9. Bell margin with several tentaculæ or rudimentary bulbs, each with an abaxial red ocellus .. *Amphinema turrida*  
     No marginal appendages between the four perradii (doubtful genus) ..... *Dissonema*
10. With oral armature of sessile nematocyst knobs ..... *Halimodusa*  
     Mouth rim without nematocyst knobs..... 11
11. With 4 or 8 large tentacles and several small, solid, cirrus-like marginal appendages ..... 12  
     Without marginal cirri ..... 13
12. Each cirrus placed beside a small marginal wart with an abaxial ocellus; four interradial gonads, horse-shoe-shaped, with diverging folds ..... *Cirrhitiara*  
     No marginal warts beside the cirri; gonads smooth, no ocelli ..... *Halitiara*
13. Gonads smooth; mouth with four simple lips ..... 14  
     Gonads folded or reticulate, or both; oral lips more or less folded or crenulated ..... 16
14. No mesenteries; 4 tentacles, no marginal rudiments ..... *Protiara*  
     Mesenteries well developed ..... 15
15. Stomach cross-shaped in section; gonads adradial..... *Merga*  
     Stomach broad, quadrangular, its entire upper surface attached to subumbrella; gonads interradial, flat, covering lateral sides of stomach ..... *Pandeopsis*
16. Gonads reticulate, with isolated interradial pits, with or without additional folds ..... 17  
     Gonads without isolated interradial pits, folds only ..... 19
17. Gonads altogether reticulate, without surrounding folds ..... *Pandea*  
     Gonads combined folds and pits ..... 18
18. Gonads in eight vertical, adradial series of transverse folds, interradial portion of stomach walls with isolated pits; no ocelli ..... *Neoturris*  
     Gonads mainly in irregular, more or less vertical folds, surrounding a reticulate area; ocelli present .... *Catablema*
19. Gonads interradial, horse-shoe-shaped, with diverging folds connected by an interradial, transverse bridge .. 20  
     Gonads more or less irregular folds, mainly vertical, without a transverse bridge; stomach very broad, cruciform, with perradial lobes closely connected with radial canals; large and small tentacles alternating ... *Annatiara*
20. With well developed mesenteries ..... *Leuckartiara*  
     Without mesenteries ..... *Halitholus*

*Halimodusa* BIGELOW 1916. Pandeidae with oral armature of sessile nematocyst knobs; stomach with four radial extensions over a gelatinous gastric peduncle. (Systematic position uncertain).

*Halimodusa typus* BIGELOW 1916. 16 mm high, 13 mm wide, walls thick, especially at apex; manubrium on a broad, low peduncle, gastric part cruciform, its four radial folds clasp the peduncle; oral part also cruciform, mouth rim studded with nematocyst knobs; gonads cover gastric part of manubrium; 4 perradial tentacles and four interradial groups of 10–11 tentacles each, all with ocelli. — Vancouver Island. (BIGELOW 1916 p. 91, Pl. 1 figs. 1–9).

*Protiara* HAECKEL 1879. Pandeidae with four well developed tentacles with hollow basal bulbs; with four or eight longitudinal gonads on the interradial sides of the stomach, smooth; four simple lips not folded nor crenulated; no mesenteries.

*Protiara tropica* BIGELOW 1912. 9 mm high and wide, globular, thick walls; manubrium about half as long as bell cavity, mouth quadratic, no lips, margin smooth; eight completely separated gonads along whole length of perradial corners of the stomach, smooth; four cylindrical tentacles; no ocelli. — Philippines; Kei Islands. (BIGELOW 1919 p. 281, Pl. 39 figs. 1–4; KRAMP 1928 p. 54, figs. 25, 26).

*Zancleopsis* HARTLAUB 1907. Pandeidae with a globular nematocyst knob inside the base of each tentacle; with four radial canals and four perradial, hollow tentacles with or without lateral branches, each branch as well as the tentacle itself with a terminal knob of nematocysts; tentacle bulbs with abaxial ocelli; gonads adradial, simple or with vertical folds. — The genus has formerly been referred to the Zancleidae. Discussion KRAMP 1965 pp. 25 ff. The two Indo-Pacific species may prove to be identical with the Atlantic *Z. dichotoma* (MAYER 1900).

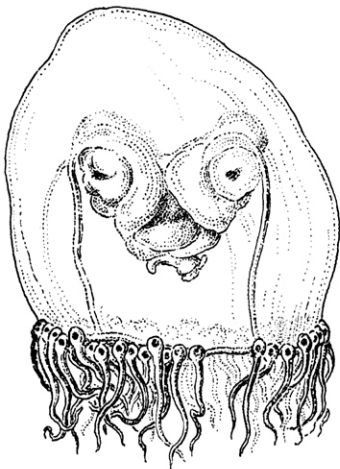


Fig. 97. *Halimedusa typus* (from BIGELOW, redrawn by P. W.).

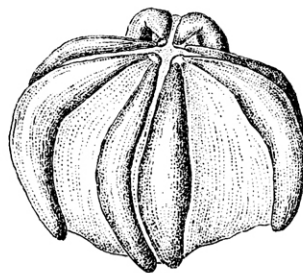


Fig. 98. *Protiara tropica* (from KRAMP, redrawn by P. W.).

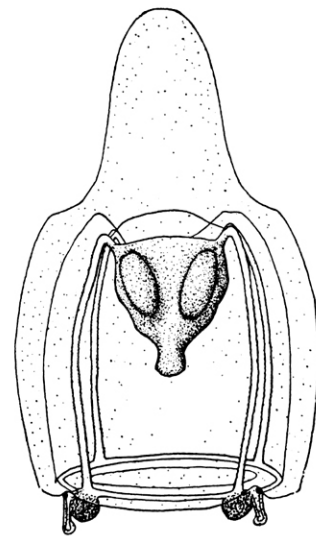


Fig. 99. *Zancleopsis gotoi* (from UCHIDA).

*Zancleopsis gotoi* UCHIDA 1927. 8 mm high, 4 mm wide, thick, rigid, with a solid apical projection; manubrium broadly flask-shaped, gonads simple, smooth, mouth without lips; tentacles short, two of them smaller than the others, with a small but distinct terminal knob, but without lateral knobs or branches. — Japan; East Australia; Nicobars; Madagascar. (UCHIDA 1927 a p. 204, fig. 33, as *Cnidotiarra gotoi* n. sp.; KRAMP 1965 p. 26).

*Zancleopsis tentaculata* KRAMP 1928. Up to 25 mm high and 14 mm wide, with a large apical projection; stomach cross-shaped, about half as long as bell cavity; gonads in vertical folds, mouth with four faintly indicated lips; two long tentacles, opposite each other, each with 2–3 knob-shaped protuberances or short branches, and two small tentacles terminating in a slight swelling. — Kei Islands; Samoa Islands. (KRAMP 1928 p. 40, figs. 14–18; KRAMP 1965 p. 27).

*Cirrhitiara* HARTLAUB 1913. Pandeidae with four or eight large tentacles and a number of rudimentary marginal bulbs each of which carries a lateral cirrus; all marginal bulbs with ocelli; gonads interradial, horse-shoe-shaped with folds directed perradially; long mesenteries.

*Cirrhitiara superba* (MAYER 1900). 5–7 mm high, with a well-developed apical projection; manubrium wide, four recurved, folded lips; gonads interradial, horse-shoe-shaped with diverging folds; four broad, flat, smooth-edged radial canals entering stomach by four wide, funnel-like openings; four long, hollow, perradial tentacles laterally compressed; 12 small rudimentary bulbs, each with a small, solid cirrus on one side; occasionally 8 tentacles and 8 rudimentary bulbs; all marginal bulbs with an abaxial ocellus. — North-East Australia. Florida; Bahamas; Brazil. (MAYER 1910 p. 126, Pl. 27 fig. 8, Pl. 28 figs. 3, 4; KRAMP 1953 p. 267).

*Halitiara* FEWKES 1882. Pandeidae with four radial canals; with four large, hollow perradial tentacles and several intermediate small solid tentacles or tentaculæ; no ocelli; gonads interradiar, not folded; mouth a simple cruciform opening.

*Halitiara formosa* FEWKES 1882. About 3 mm high, pear-shaped, with solid apical projection; manubrium pyriform, about half as long as bell cavity; four long, hollow and 24–35 short, solid tentacles, tightly coiled, cirrus-like; no ocelli; gonads interradiar; no mesenteries. — Tropical parts of the Indo-Pacific region; N. E. Pacific. Tortugas and the Bahamas. (MAYER 1910 p. 107, Pl. 6 figs. 4–6, Pl. 13 figs. 1, 2 as *Protiara formosa*; MENON 1932 p. 7, Pl. 1 fig. 4; KRAMP 1965 p. 27).

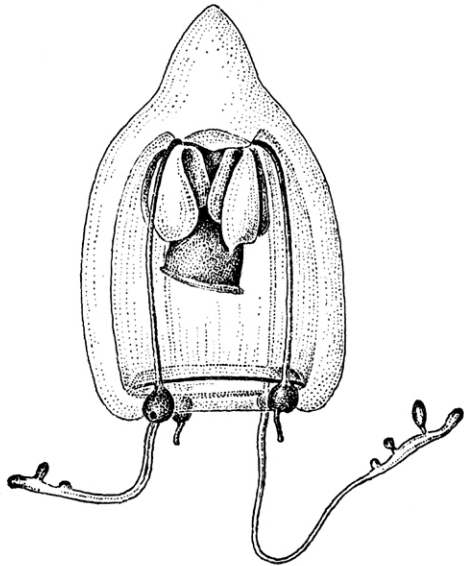


Fig. 100. *Zancleopsis tentaculata*  
(from KRAMP, redrawn by P. W.).

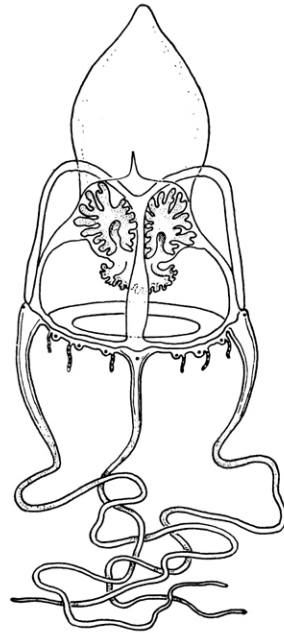


Fig. 101. *Cirrhitiara superba*  
(from MAYER, redrawn by P. W.).

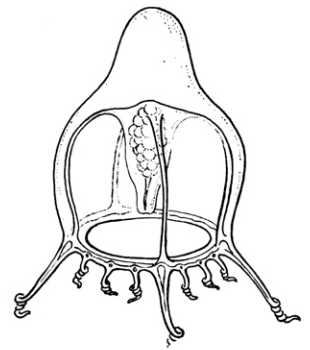


Fig. 102. *Halitiara formosa*  
(from MAYER, redrawn by P. W.).

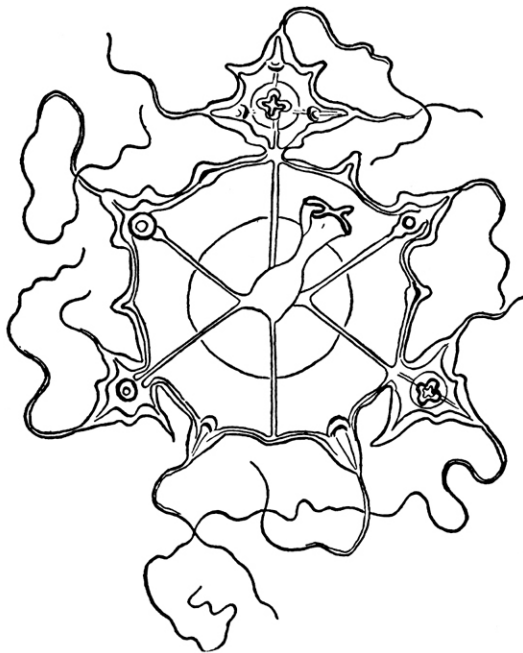


Fig. 103. *Niobia dendrotentaculata* (after MAYER, from BERRILL).

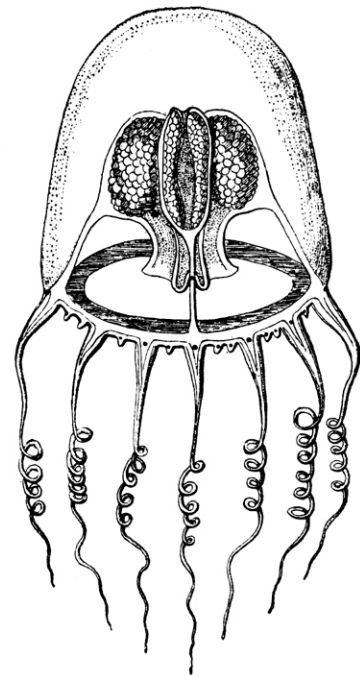


Fig. 104. *Merga violacea* (from MAYER, redrawn by P. W.).

*Niobia* MAYER 1900. Pandeidae with four main radial canals, two of which bifurcate, so that six canals reach the ring canal; gonads interradiar, no mesenteries; mouth with four simple lips; the marginal tentacles develop into medusae by a peculiar process.

*Niobia dendrotentaculata* MAYER 1900. 4 mm wide, flatter than a hemisphere; 12 tentacles; each bulb successively developed into a small medusa. — Trivandrum Coast, India; Vietnam. Mediterranean; Tortugas, Florida and the New England coast. (MAYER 1910 p. 187, Pl. 19 figs. 1–5).

*Merga* HARTLAUB 1913. Pandeidae with perradial edges of stomach connected with radial canals by mesenteries, usually long; with smooth gonads; with simple or faintly crenulated oral lips; with 4–8 or more long tentacles and as many or more rudimentary bulbs or tentaculæ; with or without ocelli.

*Merga violacea* (AGASSIZ & MAYER 1899). Up to 11 mm high and 7 mm wide, with thick walls and dome-like apex; manubrium about half as long as bell cavity, cross-shaped in transverse section; mesenteries very long; gonads adradial, smooth; four slightly crenulated oral lips; 8–12 long tentacles and 24–36 rudimentary tentacles, all with ocelli. — India; Nicobars; Vietnam; Sunda Strait; N. E. Australia; Fiji Islands; Mexico Pacific; Chile. Mediterranean; Florida and the Bahamas. (MAYER 1910 pp. 119, 490, Pl. 11 fig. 7, Pl. 12 fig. 1, as *Pandea violacea*; HARTLAUB 1913 p. 249, fig. 209, as *Merga violacea*).

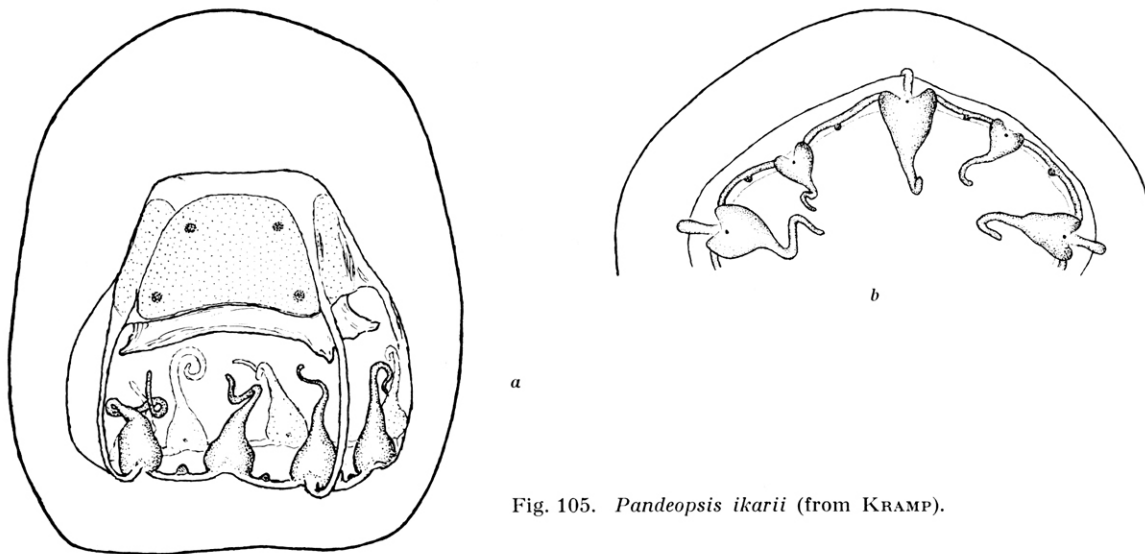


Fig. 105. *Pandeopsis ikarii* (from KRAMP).

*Pandeopsis* KRAMP 1959. Pandeidae with large stomach with broad base, perradial edges of stomach closely connected with the radial canals by long mesenteries; with smooth interradiar gonads; mouth with simple lips; several marginal tentacles and an about equal number of small rudimentary bulbs; no cirri or tentaculæ; all marginal bulbs with abaxial ocelli.

*Pandeopsis ikarii* (UCHIDA 1927). Up to 4.5 mm wide, almost globular, jelly very thick; stomach short and very broad, quadrangular, its entire upper surface attached to subumbrella; manubrium about half as long as bell cavity; four simple oral lips; four interradiar gonads, each like a flat sheet, trapezoid, smooth; 8–16 tentacles, the bulbs with a broad, heart-shaped base, no abaxial spurs; 8–12 small rudimentary bulbs; in living specimens each gonad with 3–4 small dark-red spots. — Japan; Gulf of Siam; Java Sea; Philippines; Kermadec Islands north of New Zealand. (UCHIDA 1927 a p. 208, fig. 35, as *Tiaranna ikarii*; KRAMP 1959 a p. 232, fig. 7 a, b, as *Pandeopsis scutigera*; KRAMP 1965 p. 39).

*Amphinema* HAECKEL 1879. Pandeidae never with more than two opposite, perradial tentacles; with marginal warts or tentaculæ; without a gastric peduncle; stomach with broad base, sessile; with or without mesenteries; mouth with four simple lips; gonads adradial or interradiar or extending along radial canals; with or without ocelli.



**Key to the Indo-Pacific species of *Amphinema*.**

1. Gonads folded, extending from adradial sides of stomach outwards along the radial canals; umbrella margin with tentaculæ ..... *turrida*  
     Gonads on stomach only ..... 2
2. Margin between tentacles with rudimentary warts ..... 3  
     Margin between tentacles with small, solid tentaculæ; gonads adradial, folded ..... 4
3. Tentacles and marginal warts with orange-red ocelli; gonads interradial ..... *australis*  
     Without ocelli; gonads adradial ..... *dinema*
4. With a transparent, jelly-like accessory bulb inside base of the large tentacles ..... *physophorum*  
     Without such accessory bulb ..... *rugosum*

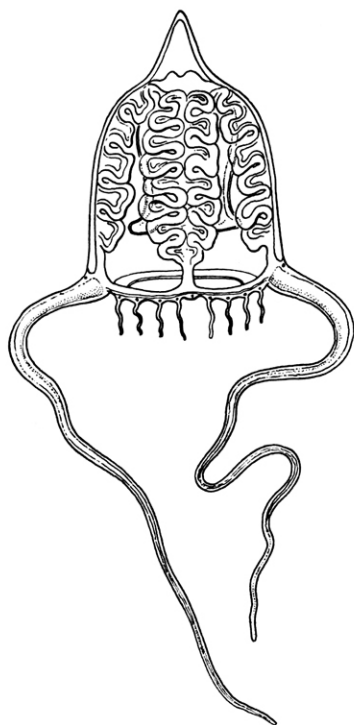


Fig. 106. *Amphinema turrida*  
(from MAYER, redrawn by P. W.).

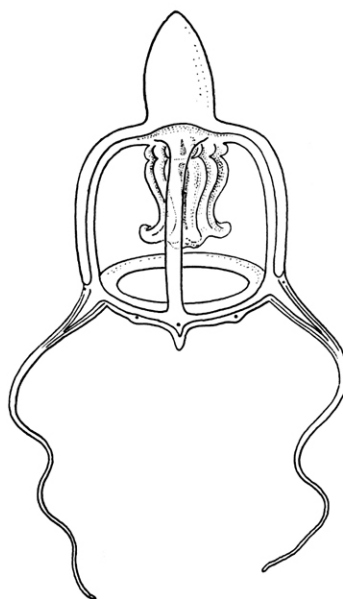


Fig. 107. *Amphinema australis*  
(from MAYER, redrawn by P. W.).

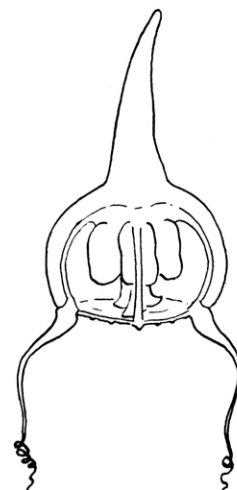


Fig. 108. *Amphinema dinema*  
(from Pl. Sh.).

*Amphinema turrida* (MAYER 1900). 4–7 mm high, somewhat higher than wide, with a conical, hollow apical projection; stomach pyriform, almost as long as bell cavity; four large, recurved, crinkled oral lips; gonads sac-like, folded, extending from adradial sides of stomach outwards along 3/4 length of the radial canals; two long tentacles with elongated conical basal bulbs and 14 small, solid tentaculæ, all with a red ocellus. — Mexico Pacific; Chile; Torres Strait; Japan. Florida and Bahamas. (BIGELOW 1909 p. 200, Pl. 7 fig. 2, Pl. 40 fig. 6, Pl. 43 fig. 3, Pl. 44 figs. 3, 4; MAYER 1910 pp. 116, 490, Pl. 10 fig. 1, Pl. 22 fig. 1, as *Dissonema turrida*).

*Amphinema australis* (MAYER 1900). 3 mm high, 2.5 mm wide, with a well-developed, sharp-pointed, solid apical projection; manubrium urn-shaped, wide, four recurved lips; gonads interradial, complexly folded; two opposite tentacles with an orange, abaxial ocellus; 4–6 rudimentary bulbs, one or two in each quadrant. — Pacific coast of Mexico. Florida and the Bahamas. (BIGELOW 1909 p. 199, Pl. 7 fig. 5, Pl. 38 figs. 10, 11; MAYER 1910 p. 111, Pl. 11 figs. 5, 6, as *Stomotoca octaedra*).

*Amphinema dinema* (PÉRON & LESUEUR 1809). Up to 6 mm high and 4 mm wide, with large, conical, solid apical projection; stomach cross-like in section, flask-shaped, almost as long as bell cavity; four prominent, recurved lips; gonads simple, adradial; two long tentacles with large, elongated conical basal bulbs; 14–24 small marginal warts; no ocelli. — N. E. Australia; Vietnam; India. Mediterranean; Gulf of Guinea;



N. W. Europe; North America from Florida to Cape Cod. (MAYER 1910 p. 109, Pl. 9 figs. 8–10, Pl. 10 figs. 1–4, as *Stomotoca dinema*; RUSSELL 1953 p. 180, Pl. 10 figs. 1, 2, 4, Pl. 11 figs. 1, 3, textfig. 89).

*Amphinema physophorum* (UCHIDA 1927). 2 mm high, 1.8 mm wide, with broad, pointed, solid apical projection; manubrium large, flask-shaped, cruciform; four recurved lips; gonads eight, adradial, transversely folded; radial canals and ring canal broad and jagged; two large tentacles and 14 very short, solid tentaculæ;

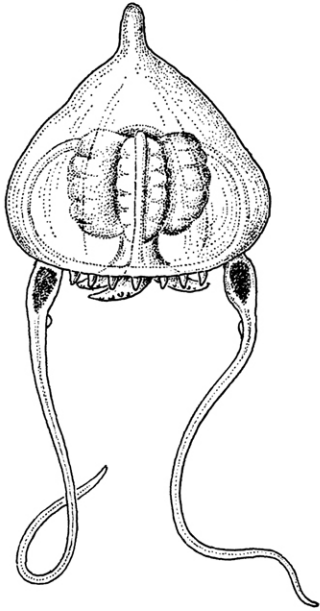


Fig. 109. *Amphinema physophorum* (from UCHIDA, redrawn by P. W.).

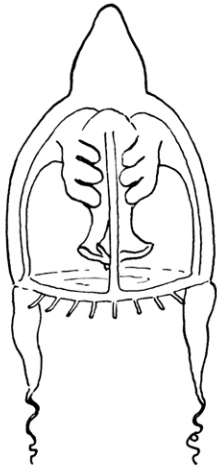


Fig. 110. *Amphinema rugosum* (from Pl. Sh.).

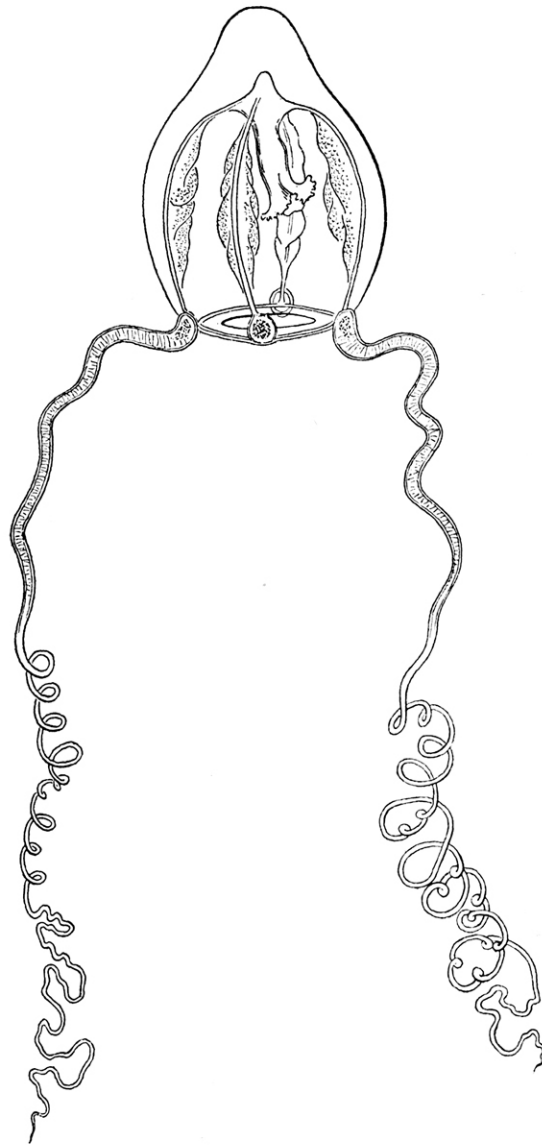


Fig. 111. *Dissonema saphenella* (from MAYER).

no ocelli; inside base of each large tentacle a transparent, jelly-like accessory bulb. — China and southern Japan. (UCHIDA 1927 a p. 202, Pl. 10 fig. 6, as *Stomotoca physophora*; LING 1937 p. 352, fig. 1, as *Stomotoca physophora*).

*Amphinema rugosum* (MAYER 1900). 5 mm high, 3 mm wide, with solid, elongated-conical or hemispherical apical projection; stomach cross-shaped in section, flask-shaped, almost as long as bell cavity; four prominent, recurved lips; gonads adradial, with 3–4 oblique folds; two long tentacles with large, elongated conical basal bulbs; 16–24 small, solid tentaculæ; no ocelli. — Japan; Chefoo, China; South China Sea; Sumatra; east and north of New Zealand; Madagascar. Adriatic Sea; N. W. Europe; Caribbean Sea; North American coast from Florida to Cape Cod. (MAYER 1910 p. 112, Pl. 10 figs. 5, 6, Pl. 11 figs. 1, 2; as *Stomotoca rugosa*; RUSSELL 1953 p. 183, Pl. 10 fig. 3, Pl. 11 figs. 2, 4, textfig. 90 A, B.; KRAMP 1965 p. 29).

*Amphinema* sp. BROWNE 1916. 2 mm high and wide; small apical projection (?); manubrium  $1\frac{1}{2}$  bell cavity; four small lips; gonads eight adradial, folded bands in upper half of manubrium, with few large eggs; two large, opposite tentacles; 10 small rudimentary bulbs; no ocelli. — Amirante Islands, Indian Ocean. (BROWNE 1916 p. 181). Systematic position uncertain.

*Dissonema* HAECKEL 1879. Pandeidae with two opposite tentacles; without marginal clubs; with abaxial ocelli; gonads extend from manubrium outwards along the radial canals.

*Dissonema saphenella* HAECKEL 1879. 6 mm high, 4 mm wide, pyriform; thick, solid apex; manubrium cylindrical, half as long as bell cavity; four short, crinkled lips; gonads extended almost to ring canal; two very long, opposite tentacles with large, swollen, conical basal bulbs; two rudimentary bulbs; no clubs or cirri. Doubtful species. — Australia. (HAECKEL 1879 p. 126, Pl. 8 fig. 3; MAYER 1910 p. 115, fig. 62).

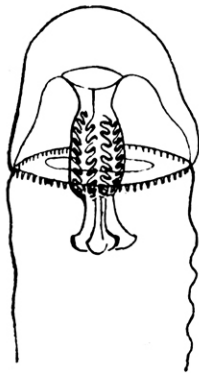


Fig. 112. *Stomatoca atra*  
(from HARTLAUB).

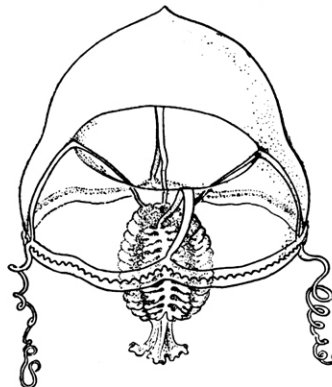


Fig. 113. *Stomatoca pterophylla*  
(from UCHIDA).

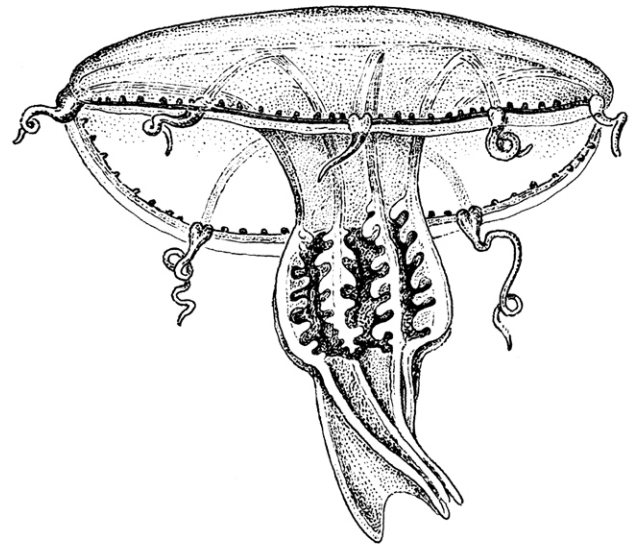


Fig. 114. *Octotiaru russelli* (from KRAMP, redrawn by P. W.).

*Stomatoca* L. AGASSIZ 1862. Pandeidae with two opposite, perradial tentacles and numerous marginal warts; stomach on a broad peduncle, extending beyond bell cavity; gonads in eight adradial rows, well separated.

*Stomatoca atra* L. AGASSIZ 1862. 20–25 mm high, 22–23 mm wide, bell-shaped; mouth-rim smooth, not crenulated; gonads simple, transverse folds; about 80 small rudimentary tentacles. — Vancouver Island region, west coast of America. (A. AGASSIZ 1865 p. 168, figs. 271–273; BIGELOW 1918 p. 370).

*Stomatoca pterophylla* HAECKEL 1879. Umbrella 10–12 mm high, 20–30 mm wide, somewhat conical, very thick at aboral pole, usually with a sharply pointed apex; stomach large, swollen; mouth with four prominent, complexly crenulated lips; gonads complexly transversally folded; two very long opposite tentacles and 60–80 rudimentary marginal warts; no ocelli. — Pacific coasts of Panama, Colombia and Peru; Japan. West-Indies; American coast from Florida to Gulf of Maine; Bahamas; Sargasso Sea; Gulf of Guinea, West Africa. (MAAS 1897 p. 11, Pl. 1 figs. 1–9, as *St. divisa* n. sp.; MAYER 1910 p. 113, Pl. 29 figs. 3–5, Pl. 30 fig. 7).

*Octotiaru* KRAMP 1953. Pandeidae with eight simple radial canals; with or without a gastric peduncle; with transversally folded gonads; without mesenteries.

*Octotiaru russelli* KRAMP 1953. Umbrella flatter than a hemisphere, 7–11 mm wide, sometimes with a large and broad gastric peduncle; manubrium in its entire length with eight deep longitudinal furrows; mouth tube long, with eight sharp edges terminating in eight pointed lips; gonads along each of the eight perradial edges of the stomach, deeply transversally folded, each with 7–10 furrows; usually 8 large tentacles, but occasionally up to 32, and about 64 small rudimentary tentacles. In living specimens the walls of the stomach

between the gonads have a dark, almost black violet colour. — N. E. Australia; Malayan Archipelago; Ceylon; S. E. Africa. (KRAMP 1953 p. 266, Pl. 1 figs. 1–3; KRAMP 1959 *b* p. 234, fig. 8 *a-c*, as *O. violacea*; KRAMP 1965 p. 38, the two species united).

*Halitholus* HARTLAUB 1913. Pandeidae with large, dome-like apical projection; manubrium cubical; gonads more or less horse-shoe-shaped, folded; mouth rim faintly crenulated; radial canals comparatively narrow, not or very faintly jagged; no mesenteries; 4 or more tentacles.

**Key to the species of *Halitholus*.**

1. About 40 tentacles; no ocelli ..... *cirratus*
- 4–8 tentacles, with ocelli ..... 2
2. Gonads with conspicuous horse-shoe-fold; ocelli small ..... *pauper*
- Horse-shoe-fold of gonads faintly developed; ocelli large ..... *intermedius*

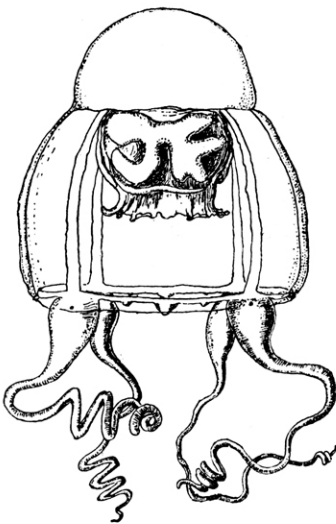


Fig. 115. *Halitholus pauper*  
(from HARTLAUB).

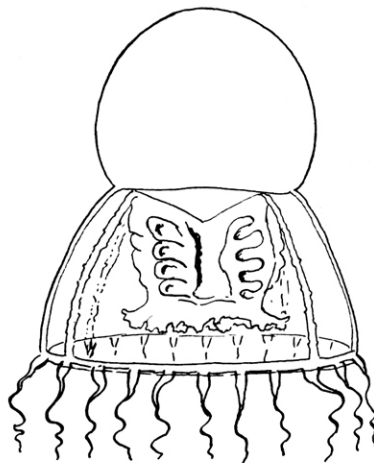


Fig. 116. *Halitholus cirratus*  
(from Pl. Sh.).

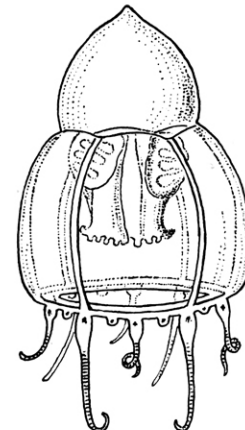


Fig. 117. *Halitholus intermedius*  
(after BROWNE & KRAMP, redrawn by P. W.).

*Halitholus pauper* HARTLAUB 1913. 10 mm high, 9 mm wide, with a low, rounded apical projection; manubrium half as long as bell cavity; gonads with conspicuous horse-shoe-fold; 4 large perradial and 4 small interradial tentacles, with small ocelli, and a few very small rudimentary bulbs. — Japan; S. W. Kamchatka; Vancouver Island. Iceland, Greenland and arctic Canada. (HARTLAUB 1913 p. 272, figs. 223, 224; KRAMP 1926 p. 71, Pl. 2 figs. 1–3).

*Halitholus cirratus* HARTLAUB 1913. 16 mm high, 14 mm wide, with large, globular apical projection; manubrium almost to velar level; about 40 tentacles; no ocelli. — Bering Sea; arctic circumpolar. Baltic and Kattegat. (HARTLAUB 1913 p. 274, figs. 225–234; KRAMP 1926 p. 74, Pl. 2 fig. 4).

*Halitholus intermedius* (BROWNE 1902). 9–10 mm high, 7 mm wide, with large, conical apical projection; manubrium  $1\frac{1}{2}$ – $\frac{2}{3}$  as long as bell cavity; interradial horse-shoe fold merely indicated; 4 large perradial and 4 smaller interradial tentacles, 8 adradial bulbs, all with conspicuous ocelli; also a variable number of minute bulbs. — Falkland Islands; South Africa. (BROWNE & KRAMP 1939 p. 288, Pl. 14 fig. 7, Pl. 16 figs. 1, 2).

*Leuckartiara* HARTLAUB 1913. Pandeidae usually with an apical projection of varying shape; with large stomach attached to radial canals by mesenteries; mouth with much folded or crenulated lips; gonads interradial, horse-shoe-shaped, with folds directed perradially; radial canals broad and ribbon-like, often with jagged edges; with numerous tentacles with elongated, laterally compressed basal bulbs; with or without ocelli; often with rudimentary tentacles.

**Key to the Indo-Pacific species of *Leuckartiara*.**

1. Exumbrella with narrow, longitudinal canals extending from abaxial side of the tentacle bulbs far upwards towards apex ..... 2  
    No longitudinal canals in exumbrella ..... 3
2. With four large perradial and 8–12 smaller tentacles of varying size; no distinct apical projection; horse-shoe fold in uppermost part of gonads ..... *zacae*  
    With only four, perradial tentacles and some minute tentaculæ; with conical apical projection; transverse bridge in middle part of gonads ..... *gardineri*
3. With 8 large tentacles and 8 small adradial, filiform tentacles, their proximal part adnate to umbrella margin and continued upwards on exumbrella; no apical projection ..... *annexa*  
    All tentacles issue from umbrella margin; apical projection well developed ..... 4
4. With tentacular rudiments between the large tentacles ..... 5  
    All tentacles of equal structure ..... 6
5. Rudimentary tentacles club-shaped ..... *octona*  
    Rudimentary tentacles cirrus-like ..... *hoepplii*
6. About 40 tentacles of varying size, with abaxial spurs; with ocelli ..... *nobilis*  
    100 or more densely crowded tentacles without abaxial spurs; without ocelli ..... *breviconis*

*Leuckartiara zacae* BIGELOW 1940. 21 mm high, 18 mm wide; exumbrella with longitudinal ribs above the tentacles, each containing a narrow canal; manubrium large, more than 2/3 as long as bell cavity, mouth rim complexly folded; gonads complexly folded, the two adradial parts connected in uppermost part; 4 large perradial tentacles and in each quadrant 2–3 other well-developed tentacles; 1–3 rudimentary knobs between successive tentacles; all with ocelli. — Gulf of Panama; Chile; Sumatra; Mozambique Channel. BIGELOW 1940 p. 284, figs. 3–5; KRAMP 1965 p. 33).

*Leuckartiara gardineri* BROWNE 1916. 6 mm high, 3.5 mm wide, with thin walls and a conical apex; exum-

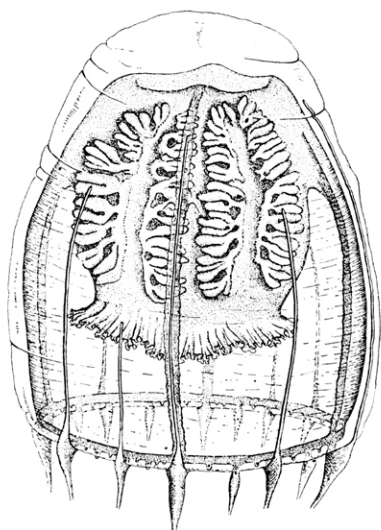


Fig. 118. *Leuckartiara zacae*  
(from BIGELOW).

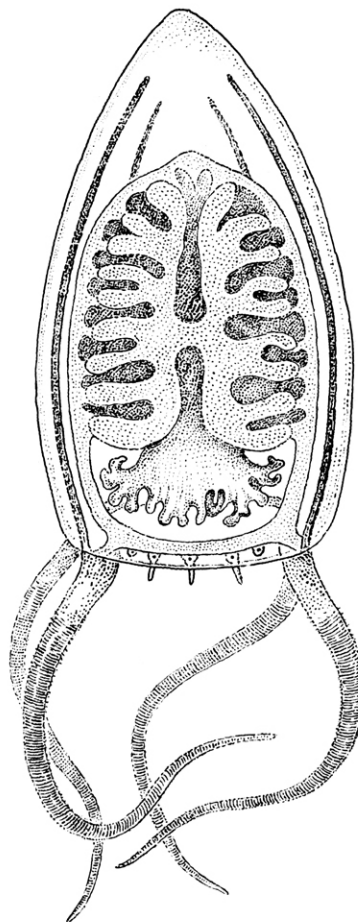


Fig. 119. *Leuckartiara gardineri*  
(from BROWNE, redrawn by P. W.).

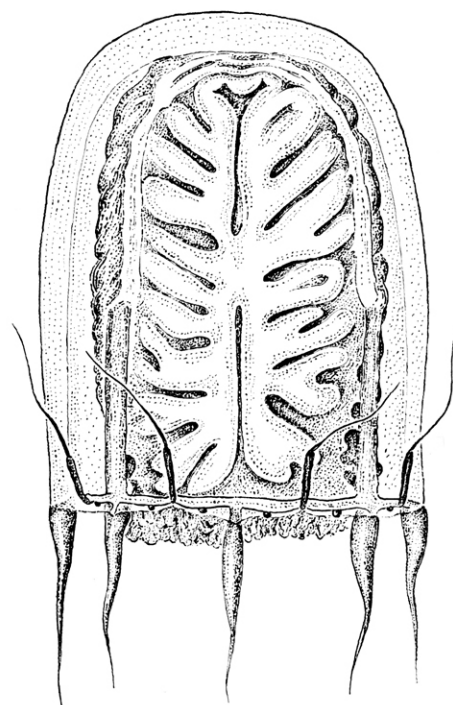


Fig. 120. *Leuckartiara annexa*  
(from KRAMP, redrawn by P. W.).

brella with four perradial, longitudinal canals extending from tentacle bulbs nearly to apex; manubrium nearly to velar level, mouth large, folded; gonads adradial, folded, connected by bridge in middle part; 4 long perradial tentacles and minute, thin inter- and adradial tentaculæ, with ocelli. — East-Africa; South China Sea; N. E. Australia; central North Pacific. (BROWNE 1916 p. 181, Pl. 39 fig. 4; KRSMP 1965 p. 32).

*Leuckartiara annexa* KRAMP 1957. 11 mm high and 9 mm wide, dome-shaped, without an apical projection, walls fairly thin; stomach very large, in upper half connected with radial canals; gonads typical, on whole surface of stomach, the transverse bridge in middle part of stomach wall; 8 large tentacles with large, elongated basal bulbs, each with a short abaxial spur; also 8 small adradial tentacles without basal swelling, their proximal part narrow, adnate to umbrella margin and continued upwards on exumbrella, from where a

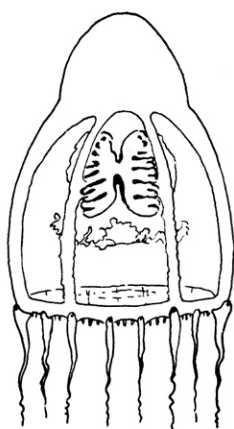


Fig. 121. *Leuckartiara octona*  
(from Pl. Sh.).

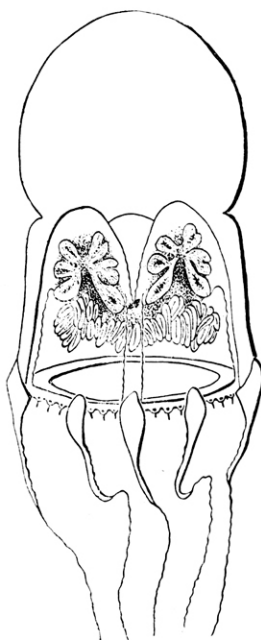


Fig. 122. *Leuckartiara hoepplii*  
(from Hsu).

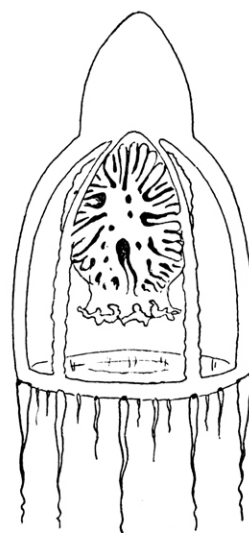


Fig. 123. *Leuckartiara nobilis*  
(from Pl. Sh.).

short filiform tentacle projects upwards and outwards; moreover 16 minute rudimentary marginal bulbs. — East-Africa; Sumatra; off southern Japan; east of Australia; Rarotonga in Polynesia. (KRAMP 1957 pp. 16, 96, 105, Pl. 2 figs. 5, 6; KRAMP 1965 p. 31).

*Leuckartiara octona* (FLEMING 1823). Up to 20 mm high, higher than wide, with conical or spherical apical projection, lateral walls thin; manubrium broad, of varying length; gonads typical, on whole surface of stomach; radial canals with smooth or slightly jagged edges; mesenteries along about half the length of the stomach; tentacles 12–24, usually 16, each with a pronounced abaxial spur, and 16 or more rudiments, which are club-shaped; tentacle bulbs and rudiments with red ocelli. — Almost cosmopolitan in temperate, and tropical coastal waters. (HARTLAUB 1913 p. 285, figs. 239–253; RUSSELL 1953 p. 188, Pl. 11 figs. 5, 6, Pl. 12 fig. 3, Pl. 31, textfigs. 91–96; KRAMP 1965 p. 30).

*Leuckartiara hoepplii* HSU 1928. 14–15 mm high, 7–8 mm wide, with a large, globular apical projection 7–8 mm high and wide; stomach wide, lips complexly folded, crenated and recurved; 8 well developed tentacles with abaxial spurs, without ocelli; about 24 very short rudimentary tentacles with ocelli, each with a small median cirrus. — Nicobars; Vietnam; Philippines; China and southern Japan. (BIGELOW 1919 p. 282, Pl. 39 figs. 5, 6, as *Leuckartiara octona*; HSU 1928 pp. 1–7, figs. 1–4; KRAMP 1965 p. 32).

*Leuckartiara nobilis* HARTLAUB 1913. Up to 27 mm high and 20 mm wide, apical projection well developed; manubrium large; lips complexly folded; mesenteries along half length of stomach; gonads typical, covering whole walls of stomach; radial canals broad, with short lateral diverticula; ring canal narrow, smooth; about 40 tentacles of different size, none permanently rudimentary; spurs faintly developed; no club-shaped

marginal rudiments; ocelli dark red. — Off southern Japan; Vancouver Island; north of Alaska. Northern Atlantic; Mediterranean. (HARTLAUB 1913 p. 308, figs. 257–260; RUSSELL 1953 p. 195, Pl. 12 fig. 4, textfig. 97; KRAMP 1965 p. 31).

*Leuckartiara brevicornis* (MURBACH & SHEARER 1902). Up to 45 mm high and 35 mm wide; apical projection low and rounded; manubrium broad, more than half as long as bell cavity; lips crenulated; gonads horse-shoe-shaped with horizontal folds, usually only in upper half of manubrium; radial canals jagged, ring canal broad, smooth; 100 or more tentacles, densely crowded, fully developed alternating with smaller ones; bulbs laterally compressed, grasping margin, but without true abaxial spur; no ocelli. — Japan; Ochotian Sea and Bering Sea; Vancouver Island; north of Alaska. North-western Europe; Iceland; West Greenland; Hudson Strait. (MURBACH & SHEARER 1902 p. 73, as *Turris brevicornis*; HARTLAUB 1913 p. 304, figs. 254–256, as *Leuckartiara brevicornis*; RUSSELL 1953 p. 198, Pl. 12 fig. 2, textfigs. 99, 100). The name has frequently been misinterpreted as *brevicornis*.

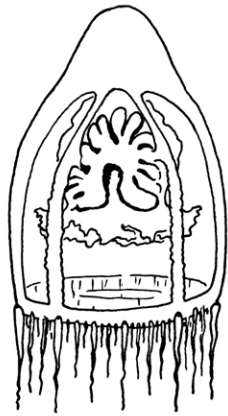


Fig. 124. *Leuckartiara brevicornis* (from Pl. Sh.).



Fig. 125. *Annatiara affinis* (from Pl. Sh.).

*Annatiara* RUSSELL 1940. Pandeidae without apical projection; exumbrella with nematocyst tracks; manubrium broad, cruciform, the four large lobes closely connected with the proximal half or more of the four radial canals; gonads interradial, with several folds; mouth very broad, cruciform, with folded margin; with several tentacles of two sizes, regularly alternating.

*Annatiara affinis* (HARTLAUB 1913). Up to 23 mm high and wide, bell-shaped, jelly thick, no apical projection, exumbrella with numerous meridional nematocyst tracks; manubrium very broad, cruciform, its four perradial lobes all over closely connected with the radial canals; mouth very wide, cruciform, with folded margin; gonads in irregular vertical folds on whole walls of stomach; up to 44 (usually 32) large tentacles with laterally compressed basal bulbs clasping umbrella margin, but without true abaxial spurs, alternating with as many very small tentacles, all with an abaxial ocellus. (The nematocyst tracks and the ocelli may be difficult to see). — East of Australia and north of New Zealand; central Indian Ocean; S. E. of Ceylon. Atlantic Ocean between 60° N. and the equator; S. W. Africa. In deep water. (HARTLAUB 1913 p. 269, figs. 220, 221, as *Tiaranna affinis*; RUSSELL 1953 p. 200, textfigs. 101–103, as *Annatiara affinis*; KRAMP 1965 p. 34).

*Neoturris* HARTLAUB 1913. Pandeidae with apical projection varying much in shape and size, sometimes much reduced; manubrium large and wide, with well developed mesenteries; gonads in eight adradial series of transverse folds directed interradially; interradial portion of stomach with isolated pits of gonads; with eight or more hollow tentacles with laterally compressed basal bulbs; without rudimentary tentacles or marginal warts.

#### Key to the species of *Neoturris*.

1. With an apical canal in a pointed apical projection; with only 8 or 12 tentacles; exumbrella with 8–12 narrow, light-coloured meridional lines ..... *papua*
- Without an apical canal; without light-coloured lines on exumbrella ..... 2



2. Transverse folds of gonads irregular, usually with numerous papillae; about 32 short tentacles without distinct abaxial spurs; edges of radial canals almost smooth; lips and stomach walls between gonads pink in newly preserved specimens ..... *pelagica*  
 Adradial series of gonads regularly transversally folded ..... 3
3. With about 16 large and 5 intermediate tentacles with laterally compressed bulbs, each with an abaxial pore, and about 40 very small tentacles with scattered granules of pigment; radial canals with glandular diverticula *fontata*  
 All tentacles of equal structure, basal bulbs without abaxial pores ..... 4
4. With 38 tentacles of varying size; radial canals almost smooth ..... *crockeri*  
 With numerous tentacles, more than 60 when adult ..... 5
5. Apical projection slender and pointed; gonadal pits faintly developed; edges of radial canals almost smooth; up to 120 tentacles ..... *bigelowi*  
 Apical projection, if present, rounded; interradii gonadal pits numerous and well developed; radial canals broad, with lateral diverticula; 60–80 tentacles ..... *pileata*

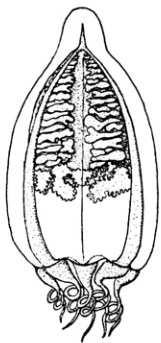


Fig. 126. *Neoturris papua*  
(from UCHIDA).

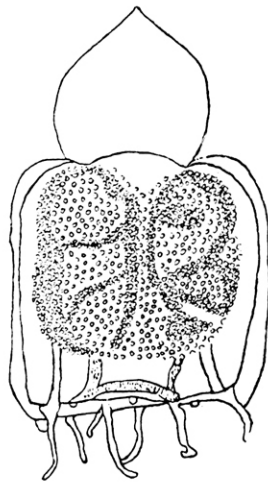


Fig. 127. *Neoturris pelagica*  
(from FOERSTER).

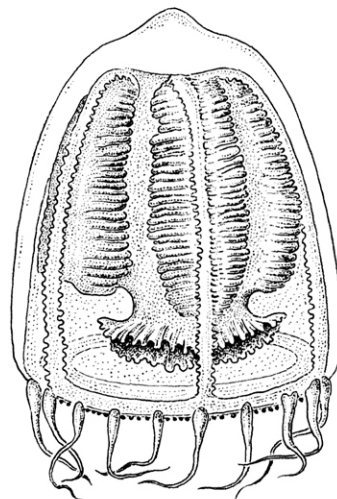


Fig. 128. *Neoturris fontata*  
(from BIGELOW, redrawn by P. W.).

*Neoturris papua* (LESSON 1843). 11 mm high, 6.2 mm wide (or larger), thin walls; a small, conical apical projection with an apical canal; 8–12 narrow, light lines on exumbrella; manubrium wide, lips considerably frilled; gonads in series of transverse folds separated in the interradii; radial canals wide, with smooth edges. ring canal stout; 8–12 tentacles, the perradial larger than the others; oral lips pink in preserved specimens, — Widely distributed in the coastal waters of the tropical parts of the Indo-West-Pacific Region from East Africa and Arabia to southern Japan and the Polynesian Islands; East Australia. (UCHIDA 1927 a p. 210, fig. 36; RANSON 1929 pp. 209–215, one fig.; KRAMP 1965 p. 36).

*Neoturris pelagica* (AGASSIZ & MAYER 1902). Up to 25 mm high and 17 mm wide, distinctly higher than wide; Manubrium large, lips complexly folded; gonads irregularly transversally folded, usually with numerous papillae; interradii areas with numerous pits; radial canals broad, their margin smooth or somewhat jagged; about 32 short tentacles with large, conical bulbs slightly laterally compressed, but without a distinct abaxial spur; lips and stomach walls between gonads pink in fresh or newly preserved specimens. — Vancouver Island; off California; east of Japan; S. E. Australia. (AGASSIZ & MAYER 1902 p. 142, Pl. 1 fig. 2, as *Turris pelagica*; FOERSTER 1923 p. 243, Pl. 2 fig. 4; KRAMP 1965 p. 34).

*Neoturris fontata* (BIGELOW 1909). 22 mm high, higher than wide, a low dome-like apical projection; manubrium long, lips complexly folded; radial canals wide, with glandular diverticula throughout their length; ring canal somewhat jagged; 16 large, 5 intermediate and about 40 small tentacles; large tentacles with compressed basal bulbs with abaxial spurs; small tentacles with scattered granules of pigment; each large bulb with an abaxial pore. Observed only once. — California. (BIGELOW 1909 p. 209, Pl. 39 fig. 8, Pl. 42 figs. 5–11, as *Turris fontata*).



*Neoturris crockeri* BIGELOW 1940. 28 mm high, 32 mm wide, walls thin, no apical projection; manubrium almost as long as bell cavity, mesenteries in upper half; radial canals broad, with nearly smooth edges; 38 tentacles of various sizes, no additional bulbs, basal bulbs compressed, clasping the umbrella margin; manubrium with a dense reddish-chocolate hue. Probably bathypelagic. Description based on a single, fragmentary specimen. — Gulf of Panama. (BIGELOW 1940 p. 287, figs. 6–10).

*Neoturris bigelowi* KRAMP 1959. Umbrella higher than wide, up to 21 mm wide; similar to *N. pileata*, but apical projection slender and pointed, the round pits in the interradial walls of stomach faintly developed, edges of radial canals almost smooth even in large specimens; the number of tentacles amounts to 120. — Madagascar; Ceylon; Sumatra; Philippines; Fiji Islands. (BIGELOW 1919 p. 285, as *N. pileata*; KRAMP 1965 p. 35).

*Neoturris pileata* (FORSKÅL 1775). Up to 25 mm wide and 40 mm high, when the apical projection is well developed, but it is sometimes much reduced; manubrium large and broad, mouth with complexly folded

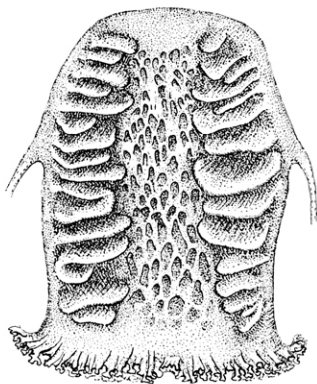


Fig. 129. *Neoturris crockeri*  
(from BIGELOW).

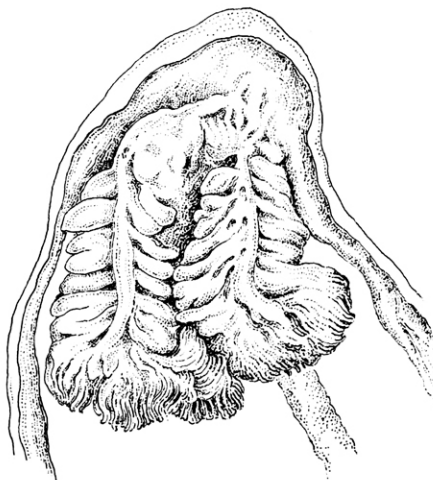


Fig. 130. *Neoturris bigelowi*  
(from BIGELOW, redrawn by P. W.).

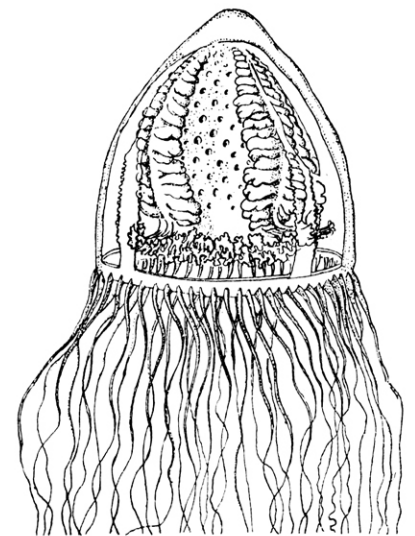


Fig. 131. *Neoturris pileata* (from HARTLAUB).

and crenulated lips; gonads in numerous round pits on interradial sides of stomach between adradial series of transverse folds; mesenteries along proximal half of the perradial edges of stomach; radial canals broad, with short, sometimes branches lateral diverticula; ring canal smooth; up to 90, usually 60–80 tentacles, densely crowded, with laterally compressed basal bulbs without conspicuous abaxial spurs; no ocelli. — Eastern Atlantic from Iceland to S. W. Africa; Mediterranean. A doubtful record from Vancouver Island, Pacific coast of North America. (HARTLAUB 1913 p. 326, figs. 270–281; RUSSELL 1953 p. 203, Pl. 12 fig. 1, textfigs. 104–106).

*Catablema* HAECKEL 1879. Pandeidae with large apical projection; with numerous tentacles; no gastric peduncle; stomach large, with broad base, with four short mesenteries; mouth-rim with four large, crenulated lips; radial canals broad, denticulated; gonads broadly separated in perradials, reticular, with irregular folds issuing from the perradial sides; with ocelli.

*Catablema vesicarium* (A. AGASSIZ 1862). Up to about 25 mm wide, 30 mm high including the large, globular apical projection; gonads in irregular folds, oblique in lateral parts, almost perpendicular in middle part of each gonad, with densely reticulate surfaces; free portion of radial canals comparatively long; about 32 tentacles. — Arctic waters; in the Pacific penetrating southwards to Vancouver and the Kurile Islands, in the Atlantic to northern Norway and to Cape Cod on the American coast. (HARTLAUB 1913 p. 321, figs. 263–267).

*Catablema multicirratum* KISHINOUE 1910. Up to 30 mm high and 35 mm wide; with large apical projection; gonads predominantly in vertical folds, faintly reticulate; free portions of radial canals very broad and short; 100–155 tentacles. — Northern Japan to Alaska, West coast of Greenland. (BIGELOW 1913 p. 19, Pl. 1 figs. 4–7).

*Pandea* LESSON 1843. Pandeidae with or without apical projection; gonads reticulate, at first in the adradial and eventually encircling the stomach, forming complex network; lips wide and folded; radial canals ribbon-like; with long mesenteries; with more than 8 tentacles.

*Pandea conica* (QUOY & GAIMARD 1827). Up to 21 mm high and 10 mm wide; with a conical apex at the end of which there is a peculiar thickening of the ectoderm; exumbrella with longitudinal ribs and ridges; manubrium about half as long as bell cavity, with short mouth tube and folded lips; radial canals fairly narrow, smooth, mesenteries long; 16–24 tentacles with laterally compressed basal bulbs, each with an ab-axial ocellus. — East Africa; Ceylon; Philippines; East Australia and New Zealand; Roratonga in Polynesia; Vietnam to Japan; central North Pacific; California. Atlantic Ocean from Bermuda to Patagonia and from the

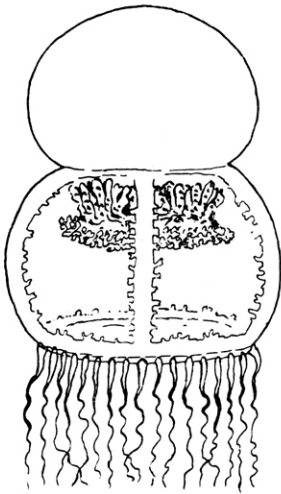


Fig. 132. *Catablema vesicarium*  
(from Pl. Sh.).



Fig. 133. *Catablema multicirrata*  
(after BIGELOW, from HARTLAUB).

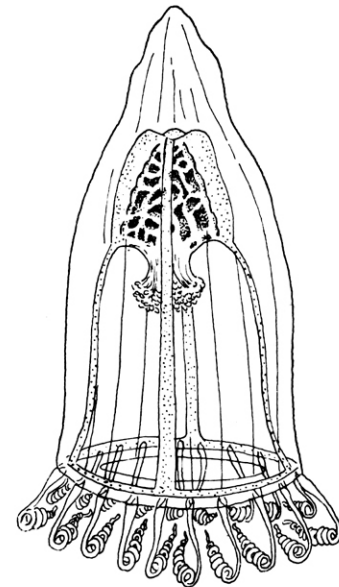


Fig. 134. *Pandea conica* (from Pl. Sh.).

Azores to South Africa; Mediterranean. (MAYER 1910 p. 118, fig. 63; HARTLAUB 1913 p. 338, figs. 286, 287; RUSSELL 1953 p. 207, figs. 107–110; KRAMP 1965 p. 40).

*Pandea rubra* BIGELOW 1913. Up to 75 mm high and wide, with fairly thin and soft walls, no apical projection; manubrium wide, half as long as bell cavity, attached to radial canals for 4/5 of the length of the radial canals; mouth-rim cruciform, very complexly folded; gonads close network on entire interradial areas; radial canals jagged; up to 25 tentacles with large, conical bulbs, not compressed. Subumbrella, manubrium, velum and tentacles deep brownish-red. — Sea of Okhotsk and Kamchatka; North-East Pacific and central North Pacific; Indian Ocean near Ceylon; Indian and Atlantic portions of antarctic seas. North Atlantic west of British Isles; Bermuda. Mainly in deep water. (BIGELOW 1913 p. 14, Pl. 2 figs. 1–7; RUSSELL 1953 p. 211, figs. 111, 112; KRAMP 1965 p. 41).

*Pandea minima* VON LENDENFELD 1884. 3 mm high, 2 mm wide; exumbrella with 8 adradial lines of nematocysts; manubrium slender, half as long as bell cavity, four small lips; four longitudinal gonads, narrow and smooth; 8 tentacles. Doubtful species. — New South Wales, Australia. (LENDENFELD 1884 p. 916, Pl. 42 figs. 10–12).

*Pandea* sp. BROWNE 1916. Young stage; exumbrella with conspicuous longitudinal ridges of nematocysts above all tentacles and bulbs, the perradial ridges extending to summit; gonads not yet developed; 4 perradial and 4 interradial tentacles and 8 adradial bulbs in state of development; ocelli present. — Chagos Archipelago, Indian Ocean. (BROWNE 1916 p. 182).

*Zanclonia* HARTLAUB 1913. Pandeidae with long transversal diverticula on both sides of the four radial canals; with several tentacles provided with numerous stalked nematocyst knobs on their adaxial side.

*Zanclonia weldoni* (BROWNE 1910). Up to 36 mm high, bell-shaped, with thick walls and a rounded summit; stomach large and globular, half as long as bell cavity; mouth large with folded lips; gonads in eight longitudinal rows of transverse folds; four broad radial canals with about 20 pairs of long diverticula at right angles to the radial canals; 24–32 long tentacles, each with an adaxial series of filaments with nematocysts. — Antarctic, circumpolar. (BROWNE 1910 p. 13, Pl. 1 figs. 1–5, as *Catablema weldoni*; HARTLAUB 1913 pp. 313, 348, figs. 261, 262; KRAMP 1957 p. 18).

*Urashimea* KISHINOUE 1910. Pandeidae with four radial canals, with four hollow tentacles with numerous stalked nematocyst knobs on their whole surface; exumbrella with several meridional nematocyst tracts; oral lips with nematocysts.

*Urashimea globosa* KISHINOUE 1910. Up to 16 mm high, slightly higher than wide, bell-shaped or globular; exumbrella with numerous (up to about 36) meridional lines of nematocysts; manubrium short, four-sided,

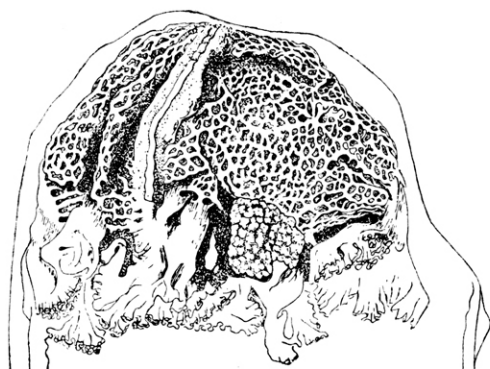


Fig. 135. *Pandeia rubra*, manubrium (after BIGELOW, from HARTLAUB).

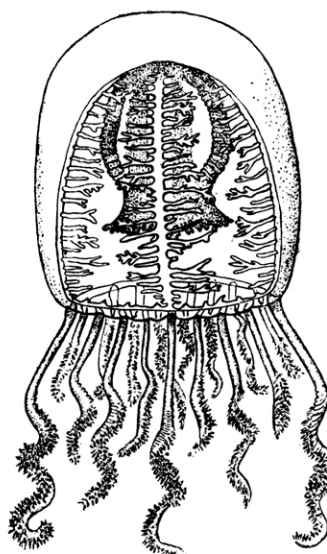


Fig. 136. *Zanclonia weldoni* (after BROWNE, from HARTLAUB).

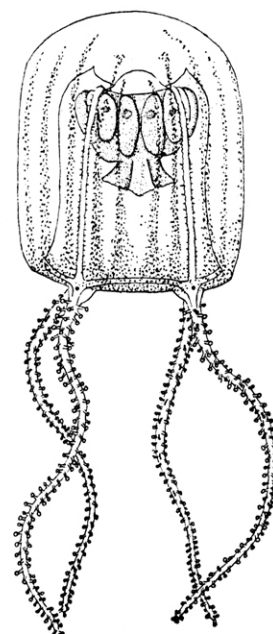


Fig. 137. *Urashimea globosa* (from UCHIDA).

four frilled lips with nematocysts; gonads 8–16 sac-like protuberances in walls of stomach; four long tentacles with numerous stalked nematocyst knobs in their entire length; with abaxial ocelli. — Japan and Saghalin; Amoy in China. (KISHINOUE 1910 p. 27, Pl. 5 figs. 27–29; UCHIDA 1927 *a* p. 218, Pl. 10 fig. 8, textfig. 34; UCHIDA & NAGAO 1961 pp. 200–204, figs. 1–7).

## Family Calycopsidae.

Anthomedusae without apical projection; without gastric peduncle; mouth with four simple or crenulated lips; with simple or folded gonads on stomach walls; with four or eight simple or branched radial canals; with or without centripetal canals; with eight or more hollow marginal tentacles without basal swellings and each terminating in a large nematocyst cluster; with or without rudimentary or dwarf tentacles; without (rarely with) ocelli.

### Key to the genera of Calycopsidae.

- |  |   |
|--|---|
| 1. With centripetal canals, blind or joining base of stomach ..... | 2 |
| Without centripetal canals .....                                   | 3 |

2. All tentacles hollow, nematocysts only in the terminal knob ..... *Calycopsis*  
Two kinds of tentacles: large, hollow, with rings of nematocysts and a terminal knob, and small, solid, without terminal knob ..... *Eumedusa*
3. Radial canals simple, unbranched, gonads smooth ..... 4  
Radial canals branched, gonads folded ..... 5
4. With eight radial canals; tentacles with abaxial, basal ocelli ..... *Bythocellata*  
With four radial canals; no ocelli ..... *Heterotiara*
5. Radial canals bifurcated (some few additional branches may occur as abnormalities) ..... *Bythotiara*  
Radial canals branching repeatedly at various levels ..... *Sibogita*

*Heterotiara* MAAS 1905. Calycopsidae with four simple radial canals; without centripetal canals; gonads purely interradial, without transverse folds; without secondary tentacles.

*Heterotiara anonyma* MAAS 1905. Up to 22 mm high and 20 mm wide, with thick walls; 8–12 tentacles. — Near the Seychelles in Indian Ocean; Malayan Archipelago; North Pacific north of 50° N.; coast of Peru.

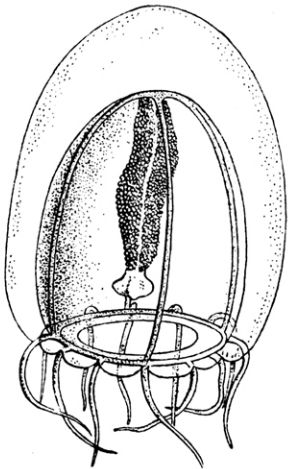


Fig. 138. *Heterotiara anonyma* (after BIGELOW, from HARTLAUB).

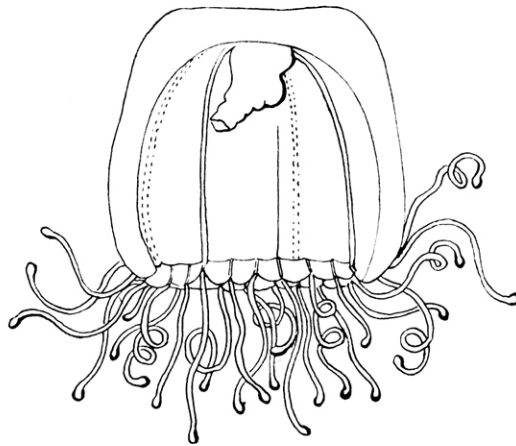


Fig. 139. *Heterotiara minor* (from VANHÖFFEN).

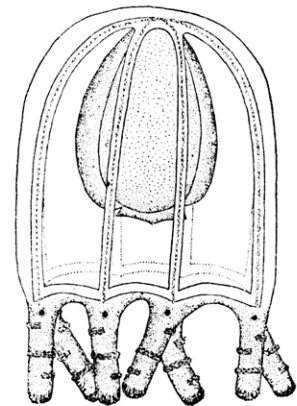


Fig. 140. *Bythocellata cruciformis* (from NAIR).

S. E. Africa. Warm central part of the Atlantic Ocean. (BIGELOW 1909 p. 216, Pl. 41 figs. 12, 13; KRAMP 1965 p. 41).

*Heterotiara minor* VANHÖFFEN 1911. Up to 12 mm high and 10 mm wide, with thick walls; 16–24 tentacles. — Generally distributed in coastal waters from East Africa to the Malayan Archipelago and to the Philippines and Formosa, New Guinea and N. E. Australia. (VANHÖFFEN 1911 p. 212, Pl. 22 fig. 5, textfig. 8; BIGELOW 1919 p. 287, Pl. 39 fig. 9, Pl. 40 figs. 2–4; KRAMP 1965 p. 42).

*Bythocellata* NAIR 1951. Calycopsidae with eight separate unbranched radial canals; without centripetal canals; with rows of nematocysts on exumbrella; gonads interradial; tentacle bases with abaxial ocelli; without secondary tentacles.

*Bythocellata cruciformis* NAIR 1951. 4 mm high, 3.5 mm wide, with thin walls; exumbrella with eight meridional rows of nematocysts; eight straight, flat radial canals with smooth edges; manubrium half as long as bell cavity, mouth cruciform; four interradial gonads, probably smooth; eight stiff, hollow tentacles with incomplete rings of nematocysts, without basal bulbs, but each with an abaxial, red ocellus. — Trivandrum Coast, India. (NAIR 1951 p. 56, Pl. 1 figs. 4, 5).

*Eumedusa* BIGELOW 1920. Calycopsidae with primarily four unbranched radial canals and with four (or more?) centripetal canals arising from the ring canal; gonads folded; with two kinds of tentacles, large hollow tentacles with rings of nematocysts and a terminal knob, and small solid tentacles without a terminal knob.

*Eumedusa birulai* (LINKO 1913). Up to 13 mm high and 10 mm wide; gonads irregularly folded; four interradial centripetal canals, blind in young specimens, joining base of stomach in adult; 8 or 16 long tentacles,

hollow, with a terminal knob of nematocysts; numerous small; solid tentacles without terminal knob. — Arctic, from Barents Sea to Alaska. (LINKO 1913 p. 8, Pl. 1 figs. 5, 6, as *Sibogita birulai*; BIGELOW 1920 p. 7, Pl. 1 figs. 4, 5, Pl. 2 figs. 1, 2, as *Eumedusa similis*; KRAMP 1961 p. 122, bibliography).

*Bythotiara* GÜNTHER 1903. Calycopsidae with four narrow, simple or bifurcate radial canals; without centripetal canals; gonads with transverse furrows, with or without secondary tentacles.

**Key to the species of *Bythotiara*.**

1. With bifurcate radial canals; with secondary tentacles ..... *murrayi*
- With four simple radial canals; without secondary tentacles ..... 2
2. With 4 tentacles ..... *drygalskii*
- With 8 tentacles ..... *depressa*

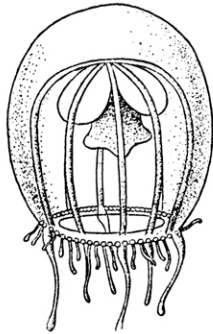


Fig. 141. *Eumedusa birulai*  
(after LINKO, from JASCHNOW).

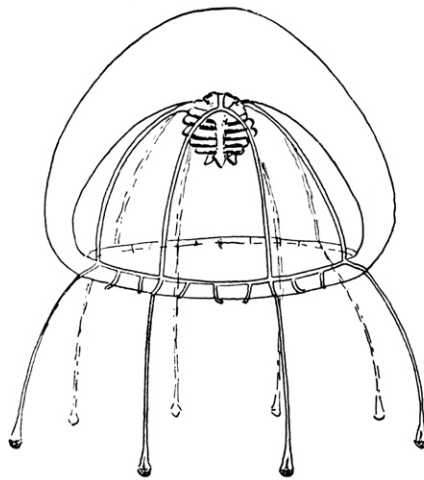


Fig. 142. *Bythotiara murrayi*  
(from Pl. Sh.).

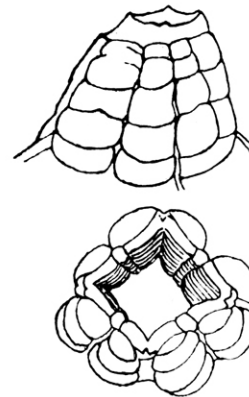


Fig. 143. *Bythotiara drygalskii*  
(from HARTLAUB).

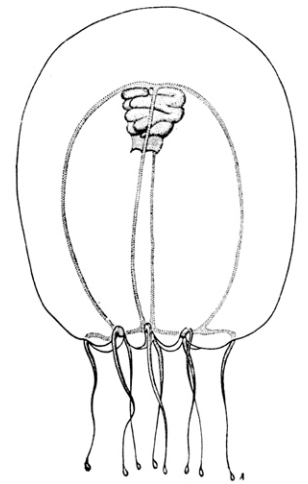


Fig. 144. *Bythotiara depressa*  
(from NAUMOV).

*Bythotiara murrayi* GÜNTHER 1903. Up to about 20 mm high and wide, with thick walls; stomach small, with four interradial gonads with transverse furrows; radial canals generally four, bifurcate (but additional branching may occur); long tentacles as many as ends of radial canals; some small secondary tentacles and minute dwarf-tentacles. — Tropical part of the Indian Ocean; Kermadec Trench north of New Zealand. Oceanic in the eastern part of the Atlantic Ocean from Norway to South Africa; Mediterranean. Mainly bathypelagic. (MAYER 1910 p. 185, figs. 97, 98; RUSSELL 1953 p. 215, Pl. 13 fig. 1, textfigs. 113–116; KRAMP 1965 p. 45).

*Bythotiara drygalskii* VANHÖFFEN 1912. 11 mm high; stomach large; gonads eight, adradial, with transverse furrows; four unbranched radial canals; four perradial tentacles. — N. W. of Gauss Station, Antarctic. (VANHÖFFEN 1912 p. 363, fig. 1; HARTLAUB 1913 p. 358, fig. 302).

*Bythotiara depressa* NAUMOV 1960. 20 mm high, with thick walls, especially in apical part; bell laterally compressed; manubrium very short, in nearly whole length covered with folded gonads; mouth simple, square or round; four unbranched radial canals with smooth edges; eight tentacles each with a terminal knob; no secondary tentacles. — Sea of Okhotsk, Kurile Islands, Bering Sea. (NAUMOV 1960 p. 191, fig. 77).

*Calycopsis* FEWKES 1882. Calycopsidae with primarily four unbranched radial canals and with four or more centripetal canals arising from the ring canal, blind or joining the cruciform base of the stomach; gonads transversely folded, frequently forming eight adradial rows of deep transverse furrows; basal portion of tentacles adnate to umbrella margin; all tentacles hollow, nematocysts only in the terminal knob.

**Key to the Indo-Pacific species of *Calycopsis*.**

1. Oral lips complexly folded, their margin with numerous nematocyst knobs; two kinds of tentacles ... *nematophora*
- Oral lips simple or faintly crenulated, without nematocyst knobs ..... 2



2. Gonads in pockets; one centripetal canal in each quadrant; 8–16 tentacles all alike ..... *borchgrevinki*  
     Gonads in exterior folds ..... 3
3. Marginal lobes between tentacles with well-marked exumbrel papillae; two centripetal canals in each quadrant;  
     8–12 tentacles all alike ..... *papillata*  
     Marginal lobes without well-marked papillae ..... 4
4. Numerous centripetal canals, 7 or more in each quadrant, most of them joining base of stomach or upper part of  
     neighbouring canals; 16–32 tentacles ..... *chuni*  
     Only one or two centripetal canals in each quadrant ..... 5
5. With four interradial centripetal canals, blind; eight long and many small tentacles ..... *bigelowi*  
     With eight adradial centripetal canals, blind or joining base of stomach; 12 large and occasionally some small  
     tentacles ..... *simulans*

*Calycopsis nematophora* BIGELOW 1913. Up to 30 mm high, almost as wide as high; mouth complexly folded, with labial nematocyst knobs; about 16 canals, all (or nearly all) joining the cruciform base of the stomach;

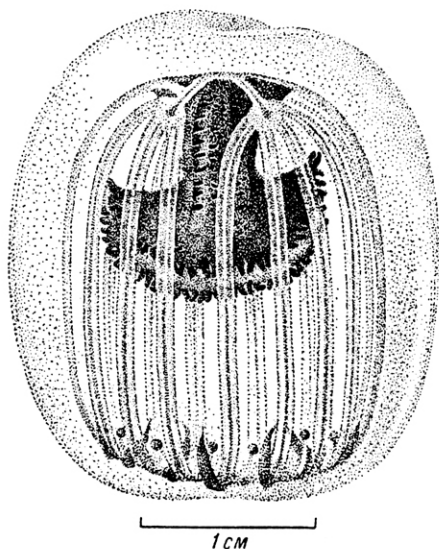


Fig. 145. *Calycopsis nematophora* (from NAUMOV).

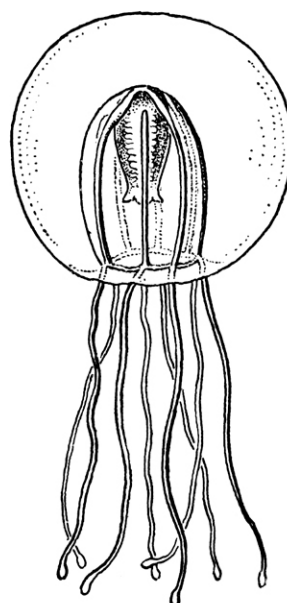


Fig. 146. *Calycopsis borchgrevinki*  
 (after VANHÖFFEN, redrawn by P. W.).

usually a large tentacle to each canal, and moreover several small tentacles. — Bering Sea; Sea of Okhotsk. (BIGELOW 1913 p. 23, Pl. 2 fig. 8, Pl. 3 figs. 1–3; NAUMOV 1960 p. 194, Pl. 29 fig. 2, textfig. 79).

*Calycopsis borchgrevinki* (BROWNE 1910). 20 mm high, 15–18 mm wide; gonads in pockets, embedded in the walls of the stomach, not in exterior folds; four interradial centripetal canals, blind or joining base of stomach; 8–16 tentacles. — Antarctic and subantarctic, circumpolar. (BROWNE 1910 p. 17, Pl. 2 figs. 1–5, as *Sibogita borchgrevinki*; VANHÖFFEN 1911 p. 215, Pl. 22 fig. 7, textfig. 10).

*Calycopsis papillata* BIGELOW 1918. 27–33 mm high, 26 mm wide, jelly very thick and rigid; each of the marginal lobes between the tentacles with a group of prominent gelatinous papillae; eight centripetal canals, usually adradial in position, blind or joining base of stomach; 8–12 tentacles, all alike. — Near Madagascar. Atlantic Ocean west of Africa; West-Indies; Florida. (BIGELOW 1918 p. 378, Pl. 2 figs. 1–7, Pl. 3 fig. 10; KRAMP 1955 p. 252, Pl. 1 figs. 2, 3; KRAMP 1965 p. 47).

*Calycopsis chuni* VANHÖFFEN 1911. Up to 40 mm high and 30 mm wide, jelly thick and rigid; manubrium about half as long as bell cavity, lips fairly short, crenulated; gonads with 19–32 transverse folds in each of the eight rows; 28–56 centripetal canals, most of them communicating either directly with the base of the stomach or with neighbouring canals close by the stomach; 16–32 tentacles. — Indian Ocean from East Africa to the Malayan Archipelago; East Australia; Gulf of Panama. Atlantic west of Africa; West-Indies.

(VANHÖFFEN 1911 p. 217, Pl. 22 fig. 8, as *Calycopsis chuni*; ibid. p. 214, Pl. 22 fig. 6, as *C. typa* Fewkes; HARTLAUB 1913, p. 360, as *Calycopsis valdiviae*; KRAMP 1965 p. 48).

*Calycopsis bigelowi* VANHÖFFEN 1911. 16 mm high and wide, jelly thick; gonads with about 10 transverse folds in each of the adradial rows; four interradii centripetal canals, blind; 8 long and numerous, up to

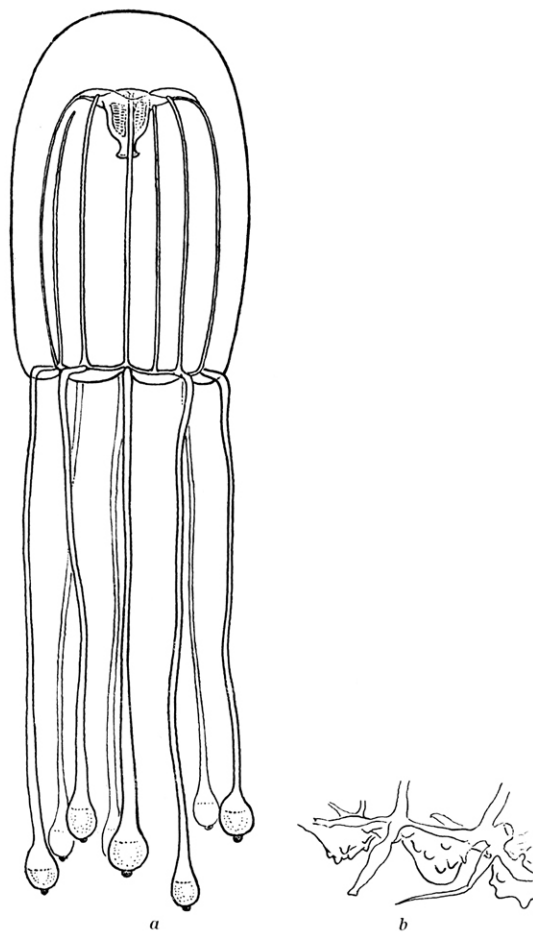


Fig. 147. *Calycopsis papillata*; a, medusa (after KRAMP, redrawn by P. W.); b, part of bell margin showing gelatinous warts (after BIGELOW, redrawn by P. W.).

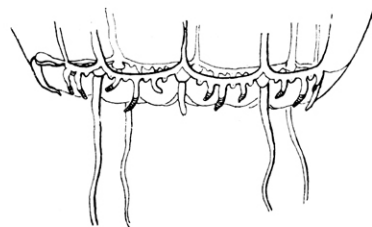


Fig. 149. *Calycopsis bigelowi*, bell margin (after VANHÖFFEN, from HARTLAUB).

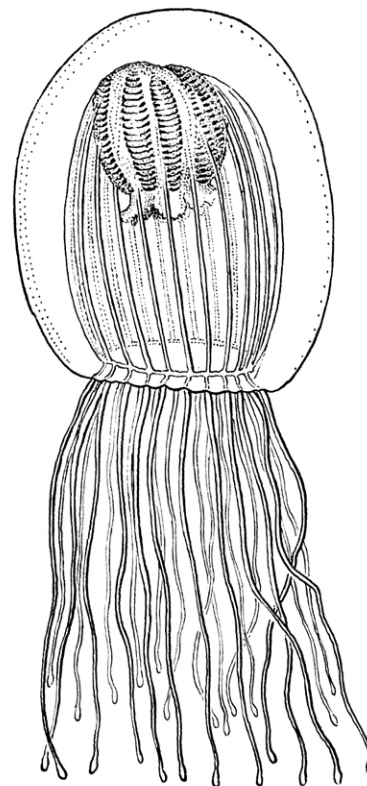


Fig. 148. *Calycopsis chuni* (from VANHÖFFEN, redrawn by P. W.).

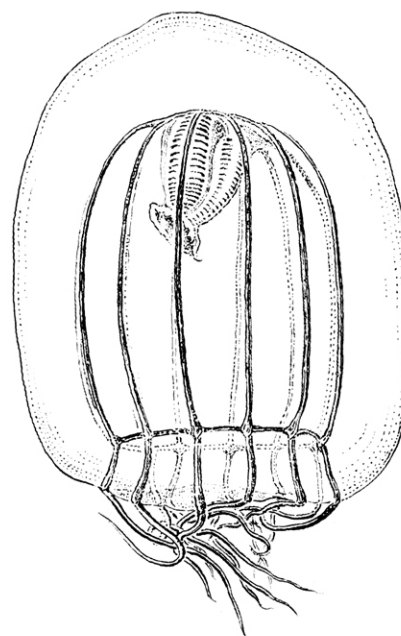


Fig. 150. *Calycopsis simulans* (from BIGELOW, redrawn by P. W.).



40, small tentacles, all tentacles structurally alike. — Malayan Archipelago; Gulf of Aden; near Cape of Good Hope. (VANHÖFFEN 1911 p. 218, fig. 12; KRAMP 1965 p. 46).

*Calycopsis simulans* (BIGELOW 1909). 30 mm high and 22 mm wide; eight centripetal canals, adradial, blind or joining base of stomach; 12 large tentacles opposite to the canals and occasionally some small tentacles between the canals. — Gulf of Panama; Philippines; Indian Ocean near the Cocos Islands and off Mombasa in East Africa. (BIGELOW 1909 p. 213, Pl. 5 figs. 4, 5, Pl. 41 figs. 8, 9, Pl. 43 figs. 1, 2, as *Sibogita simulans*; KRAMP 1965 p. 47).

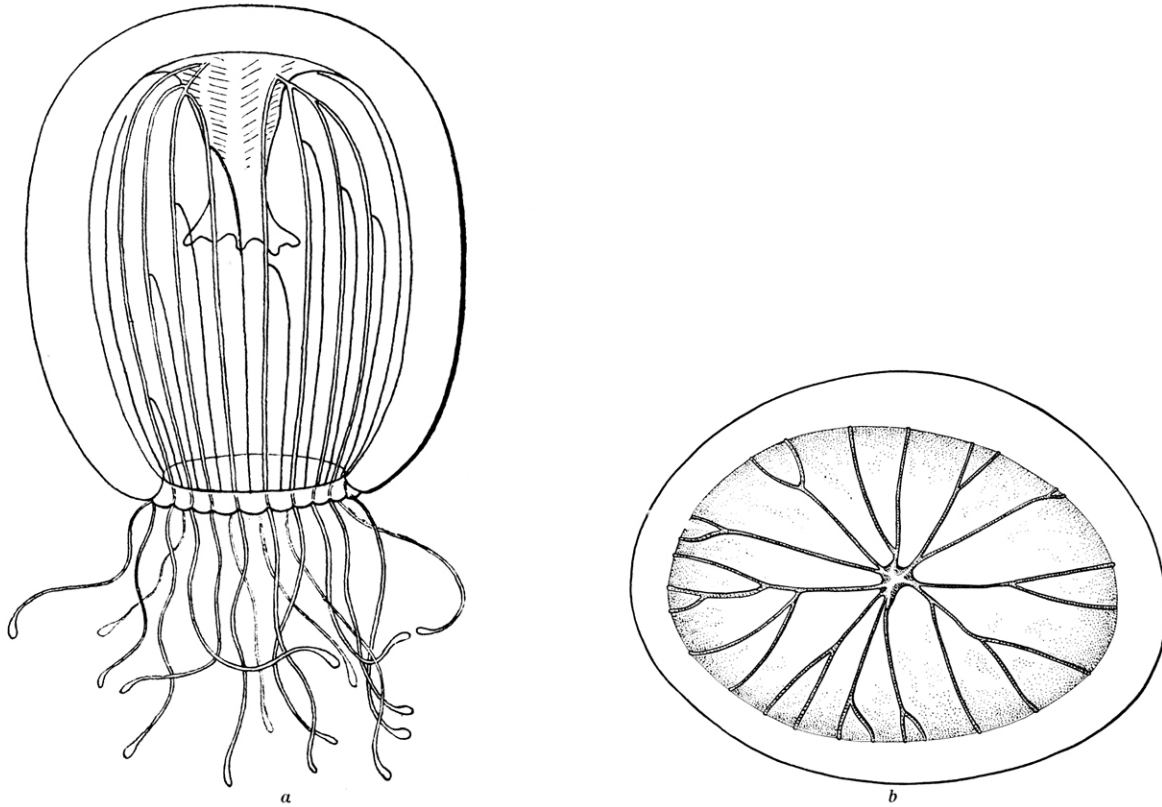


Fig. 151. *Sibogita geometrica* (a from MAYER, b from KRAMP, redrawn by P. W.).

*Sibogita* MAAS 1905. Calycopsidae with primarily four radial canals which branch repeatedly at various levels; without centripetal canals; gonads transversely folded.

*Sibogita geometrica* MAAS 1905. Up to 38 mm high and about 20 mm wide; the four primary radial canals give rise to alternating lateral branches, from which lateral branches of second and third order arise at various levels, up to about 40 canals joining the ring canal; gonads in about 13 transverse folds in each of the eight adradial rows; tentacles in same number as, or half as many as the canals. — Malayan Archipelago and tropical Indian Ocean. Atlantic Ocean near the Azores and in the Bay of Biscay. (MAAS 1905 p. 17, Pl. 3 figs. 16–18; BIGELOW 1919 p. 290, Pl. 40 figs. 5–7, Pl. 41 fig. 2; KRAMP 1959 a p. 28, Pl. 1 figs. 11, 12, textfigs. 4, 5, as *S. geometrica occidentalis*; KRAMP 1965 p. 49).

#### *Species with uncertain affinity.*

*Meator rubatra* BIGELOW 1913. 17 mm high, 18 mm wide, jelly very thick, globular; four simple radial canals, no centripetal canals; stomach cruciform, connected with the radial canals in entire length, with eight smooth adradial gonads; four large, perradial and numerous small tentacles, without a terminal knob. — Sea of Okhotsk, Kurile Islands. (BIGELOW 1913 p. 12, Pl. 1 figs. 1–3; NAUMOV 1960 p. 190, Pl. 29 fig. 1, textfig. 76).

*Kanaka pelagica* UCHIDA 1947. 1.8 mm high, 1.5 mm wide, with thick apex; four radial canals, narrow, curved concave in middle portion, distal half slightly widened and ragged; no centripetal canals; manubrium small; gonads seem to develop on the lower half of the radial canals (?) eight long, hollow tentacles, each with a terminal knob of nematocysts. — Central Pacific. (UCHIDA 1947 *a* p. 303, fig. 5).

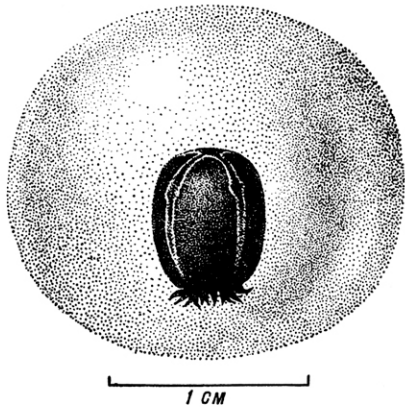


Fig. 152. *Meator rubatra* (from NAUMOV).

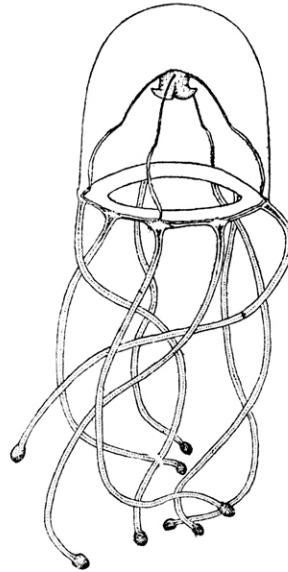


Fig. 153. *Kanaka pelagica* (from UCHIDA).

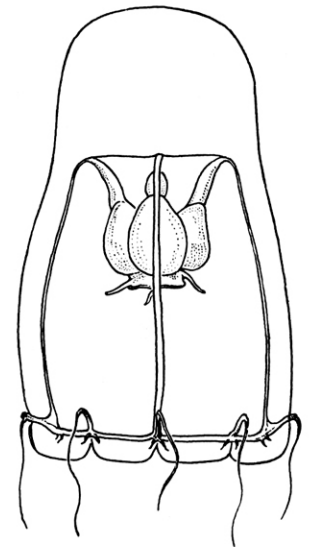


Fig. 154. *Russellia mirabilis* (from KRAMP, redrawn by P. W.).

## Family Russelliidae.

Anthomedusae with unbranched oral tentacles without terminal clusters of nematocysts, situated above the mouth opening, mouth with simple perradial lips; with groups of hollow, marginal tentacles without basal swellings, partly sunk into narrow fissures of the umbrella margin; with adaxial ocelli.

*Russellia* KRAMP 1957. Russelliidae with an apical projection; with cruciform stomach mounted upon a peduncle; with four pointed oral tentacles; with eight smooth, adradial gonads; with four simple radial canals; with eight groups of marginal tentacles, each group with one large and two small tentacles, the basal part of the large tentacle sunk into a deep furrow of the umbrella margin; with an adaxial ocellus at the base of the free portion of the tentacles.

*Russellia mirabilis* KRAMP 1957. 15 mm high, 9 mm wide, with a large apical projection; stomach about half as long as bell cavity; adradial gonads occupying entire length of stomach; mouth quadrangular, with very short perradial lips; four perradial oral tentacles inserted above the mouth, finger-shaped, pointed, with scattered nematocysts along entire length; four perradial and four interrarial tentacles, their basal part deeply sunk into a narrow fissure between two prominent lobes of the umbrella margin, and each flanked by a pair of small tentacles. — Antarctic, west of Graham Land and near South Georgia; West-Indies. (KRAMP 1957 p. 27, Pl. 4 figs. 1–6; KRAMP 1959 *a* pp. 30, 129, fig. 142).

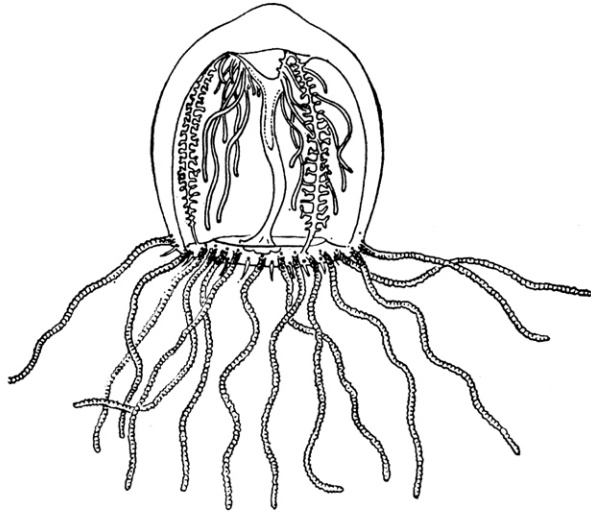
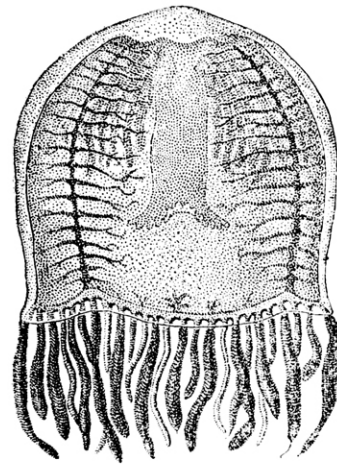
## Family Polyorchidae.

Anthomedusae with a more or less pronounced gastric peduncle; with four oral lips densely set with nematocysts forming a distinct marginal band; with four radial canals with tendency to develop blind lateral branches; gonads sausage-shaped or spiral.

## Key to the genera of Polyorchidae.

1. Tentacles in eight marginal clusters; gonads spirally twisted ..... *Spirocodon*  
 Tentacles not in clusters; gonads sausage-shaped, pendent ..... 2
2. Radial canals with lateral branches ..... *Polyorchis*  
 Radial canals without lateral branches ..... *Scrippsia*

*Polyorchis* A. AGASSIZ 1862. Polyorchidae with four radial canals giving rise to many blind lateral branches; with or without centripetal canals issuing from the ring canal; tentacles along the whole bell margin, not in clusters, with abaxial ocelli; gonads sausage-shaped, hanging down from the junction points of the radial canals with the manubrium. — The species (revised by SKOGSBERG, 1948) are distinguished from each other merely by numerical characters, which are variable.

Fig. 155. *Polyorchis penicillatus* (from MAYER).Fig. 156. *Polyorchis karafutoensis* (from NAUMOV).

*Polyorchis penicillatus* (ESCHSCHOLTZ 1829). 50–60 mm high, 30–40 mm wide; radial canals with 15–25 pairs of lateral branches which may be dilatated or faintly branched in their distal ends; ring canal simple or with a few knob-like centripetal diverticula; peduncle short; manubrium prismatic, about as long as bell cavity; 4–11 sausage-shaped gonads hanging down from the peduncular part of each radial canal; up to 160 tentacles. — Gulf of California to Vancouver Island; Hawaii. (MAYER 1910 p. 218, fig. 111; LITTLE 1914 pp. 307–328, Pl. 13–15; SKOGSBERG 1948 p. 118).

*Polyorchis karafutoensis* KISHINOUE 1910. 60 mm high, 50 mm wide, radial canals with 16–22 pairs of lateral diverticula, long and profusely branched; ring canal with branched centripetal canals; manubrium prismatic; about 10×4 sausage-like gonads, irregularly branched, longer than the manubrium; 80–120 tentacles. — Japan; Saghalin. (KISHINOUE 1910 p. 30, Pl. 5 fig. 31; UCHIDA 1925 p. 88, fig. 13; UCHIDA 1927 b p. 227; NAUMOV 1960 p. 549, fig. 438).

*Polyorchis montereyensis* SKOGSBERG 1948. 40 mm high; radial canals with about 25–30 lateral diverticula on either side, occasionally with 1–4 short secondary branches; ring canal with or without short centripetal canals, sometimes faintly branched; gonads more or less branched, 45 or more on each peduncular canal; up to about 80 tentacles. — California. (SKOGSBERG 1948 p. 114, fig. 2, diagram).

*Polyorchis haplus* SKOGSBERG 1948. 15–20 mm high; radial canals simple in small specimens, in large specimens with closely set knob-like diverticula; ring canal with or without knob-like diverticula; gonads about 20–25 on each canal, in fully developed specimens along entire length of peduncle; up to 24 tentacles. — California. (SKOGSBERG 1948 p. 121, no figure).

*Scrippsia* TORREY 1909. Polyorchidae with a large, gelatinous stomachal peduncle, from which numerous sausage-shaped gonads are hanging down; with four narrow radial canals without lateral diverticula.

*Scrippsia pacifica* TORREY 1909. 75 mm high, deep bell-shaped, with slight apical prominence; peduncle broadly conical, more than half as long as bell cavity, with numerous gonads, long and narrow, 30–60 hanging down from each radial canal; about 256 tentacles in seven cycles, the longest projecting from the sides of the exumbrella, the smallest with abaxial ocelli. — California. (TORREY 1909, p. 15, fig. 3; MAYER 1910 p. 493, fig. 327).

*Spirocodon* HAECKEL 1880. Polyorchidae with tentacles in eight marginal clusters; radial canals and ring canal with branched diverticula; four perradial gonads attached to stomachal peduncle, hanging down as spirally twisted loops.

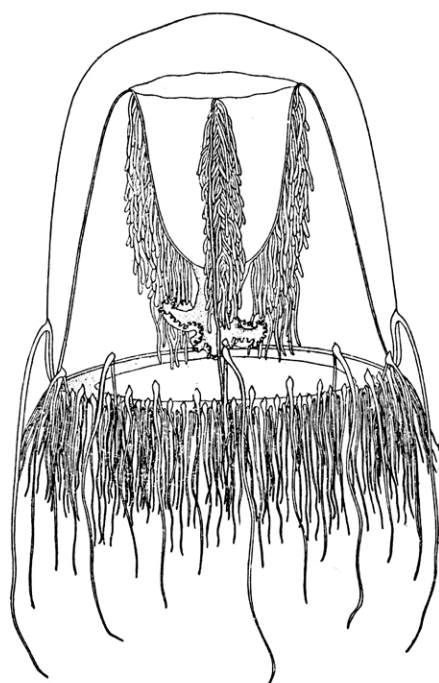


Fig. 157. *Scrippsia pacifica* (from MAYER).

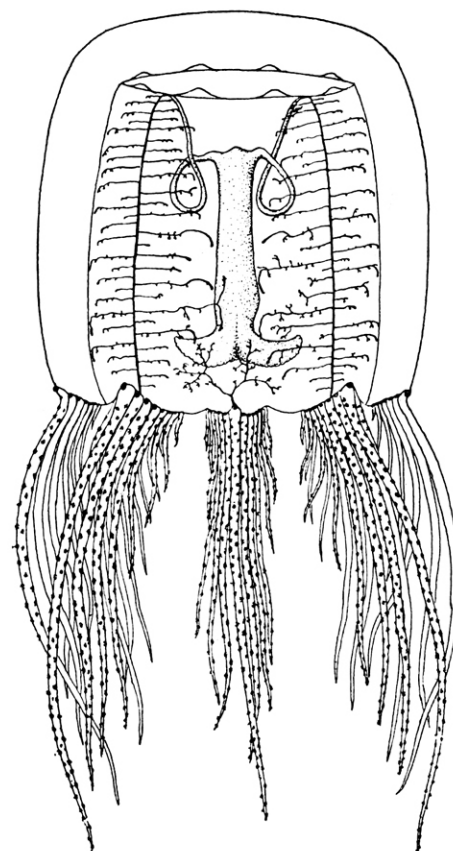


Fig. 158. *Spirocodon saltator* (from UCHIDA).

*Spirocodon saltator* (TILESUS 1818). Up to 75 mm high and 65 mm wide; radial canals very narrow, with numerous dendritic lateral branches; four interrarial dendritic centripetal canals from ring canal; numerous tentacles in eight curved groups, all with abaxial ocelli. — Japan. (MAAS 1909 p. 18, Pl. 2 figs. 10–13; UCHIDA 1927 a p. 230, Pl. 10 fig. 9, Pl. 11, textfigs. 1–12, 16–19, 43–46).

## Family Tiarannidae.

Anthomedusae without apical projection and without gastric peduncle; with large, cruciform stomach; mouth with simple or folded lips; with four radial canals; with folded gonads on the walls of the stomach and its perradial lobes; with numerous hollow marginal tentacles with conical basal bulbs; with hollow marginal spindle-shaped cordylus-like structures with nematocysts at distal end; without ocelli.

### Key to the genera of Tiarannidae.

Gonads lateral folds .....	<i>Tiaranna</i>
Gonads sac-like invaginations .....	<i>Chromatonema</i>

*Tiaranna* HARTLAUB 1913. Tiarannidae in which the gonads are lateral folds on both sides of the perradial stomachal lobes and connected in the interradii.

*Tiaranna rotunda* (QUOY & GAIMARD 1827). 20 mm wide, somewhat less in height, apex evenly rounded, jelly thick; manubrium broad, cruciform, perradial edges of stomach in their entire length connected with subumbrella; mouth with four large, slightly crenulated lips; gonads in regular transverse folds on interradiial walls of stomach extending outwards along the perradii; 16–28 tentacles with conical bulbs; between successive tentacles 2–3 minute spindle-shaped cordylus-like appendages with distal bundle of nematocysts. — Deep and intermediate strata in the Atlantic Ocean and the western Mediterranean; antarctic waters south of Australia. (KRAMP 1920 p. 6, Pl. 1 figs. 2–4; RUSSELL 1953 p. 219, figs. 117–119).

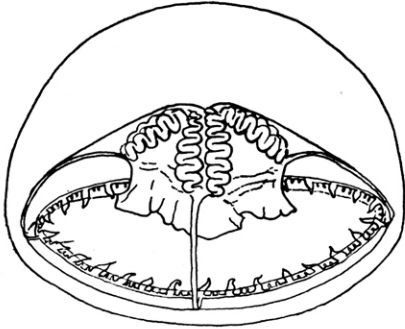


Fig. 159. *Tiaranna rotunda* (from Pl. Sh.).

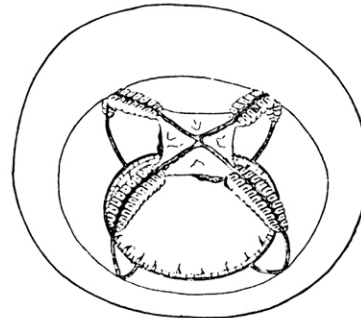


Fig. 160. *Chromatonema rubrum* (from Pl. Sh.).

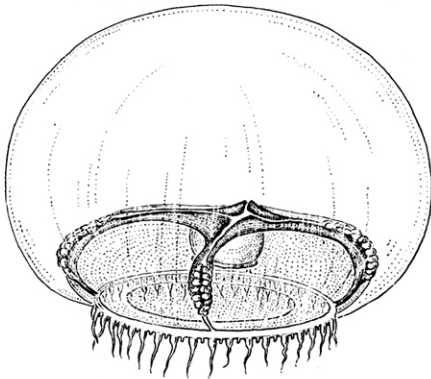


Fig. 161. *Chromatonema erythrogonon* (from BIGELOW, redrawn by P. W.).

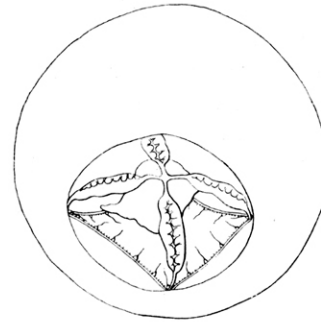


Fig. 162. *Chromatonema hertwigi* (from VANHÖFFEN).

*Tiaranna sagamina* UCHIDA 1947. Size unknown; jelly very thick; seems to lack ring canal; 12 tentacles; gonads not yet developed; otherwise like *T. rotunda*. — Japan. (UCHIDA 1947 b p. 334, fig. 2).

*Chromatonema* FEWKES 1882. Tiarannidae in which the gonads constitute eight series of sac-like invaginations from the surface of the perradial stomachal lobes, separated in the interradii.

*Chromatonema rubrum* FEWKES 1882. Up to 27 mm wide and 22 mm high, jelly thick, apex evenly rounded; Manubrium broad, quadrangular, with four perradial lobes extending for half or two-thirds the distance towards bell margin; mouth with four short, slightly crenulated lips; 10–16 sac-like gonads on each side of each stomach lobe; 20–24 tentacles with conical bulbs; between successive tentacles two, rarely only one, minute cordylus-like appendages with distal bundle of nematocysts. — Bathypelagic, widely distributed in the deep parts of the Atlantic Ocean and off the Atlantic and Indian sectors of the Antarctic Continent; (KRAMP 1919 p. 7, Pl. 1 figs. 1–8, textfigs. 3, 4 a; RUSSELL 1953 p. 223, figs. 120, 121).

*Chromatonema erythrogonon* (BIGELOW 1909). Up to 44 mm wide, with up to 64 tentacles, 1–2 cordyli between successive tentacles. — Eastern Pacific, Peru to California. (BIGELOW 1909 p. 150, Pl. 5 fig. 1, Pl. 38 figs. 8, 9, Pl. 39 figs. 1–7; BIGELOW 1940 p. 297, fig. 13; KRAMP 1965 p. 50).

*Chromatonema hertwigi* (VANHÖFFEN 1911). 50 mm wide, with 20 tentacles; 5 cordyli between successive tentacles. — Bay of Bengal (VANHÖFFEN 1911 p. 220, Pl. 22 fig. 9, textfig. 13 a, b).

## II. Order LEPTOMEDUSAE

Hydromedusae with umbrella usually hemispherical or flattened; with gonads on radial canals; marginal sense organs, when present, in form of cordyli or marginal vesicles of ectodermal origin; occasionally with ocelli.

### Key to the families of Leptomedusae.

1. With no marginal sense organs..... 2  
     With marginal sense organs ..... 4
2. Stomach upon a gelatinous peduncle; ring canal with blindly ending centripetal canals ..... Timoididae  
     Without a gastric peduncle ..... 3
3. Base of stomach broad, attached over its whole surface; with 8 or more radial canals ..... Melicertidae  
     Base of stomach narrow; radial canals either branched or, if simple, irregularly arranged ..... Dipleurosomatidae
4. With marginal cordyli ..... Laodiceidae  
     With marginal vesicles; without cordyli ..... 5
5. Marginal vesicles open ..... Mitrocomidae  
     Marginal vesicles closed ..... 6
6. With a distinct gastric peduncle ..... 7  
     Without a distinct gastric peduncle..... 8
7. With numerous marginal vesicles; gonads restricted to umbrellar portion of radial canals; tentacle bulbs usually with excretory pores ..... Eirenidae  
     Marginal vesicles usually eight; if more, the gonads extend from bell margin down along the peduncle almost to the stomach; no excretory pores ..... Eutimidae
8. Stomach very broad; with many radial canals; tentacle bulbs with excretory pores ..... Aequoreidae  
     Stomach narrow; with (normally) 4 or 8 radial canals ..... 9
9. Tentacle bulbs with excretory pores; 4–8 radial canals ..... Phialuciidae  
     Without excretory pores; 4 radial canals ..... 10
10. Tentacle bulbs with lateral cirri or marginal cirri between tentacles ..... Lovenellidae  
     Without cirri ..... 11
11. Gonads divided into two lateral parts by a median groove; 8 marginal vesicles ..... Phialellidae  
     Gonads completely surrounding radial canals; 8 or more marginal vesicles ..... Campanulariidae

## Family Dipleurosomatidae.

Leptomedusae without any kind of marginal sense organs; with stomach with narrow base; with three, four or more radial canals either branched or, if simple, irregularly arranged; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal or lateral cirri.

*Dipleurosoma* BOECK 1866. Dipleurosomatidae with three or more main radial canals, some or all of which branch irregularly and join the circular canal; tentacles numerous.

*Dipleurosoma pacificum* AGASSIZ & MAYER 1902. 23 mm wide; exumbrella reticulated by hexagonal elevations; manubrium very short, mouth with six small lips; six radial canals in groups of three, two of which bifurcate; gonads in the middle regions of the eight canals; about 100 tentacles; with adaxial ocelli; slender club-shaped bodies scattered between tentacles. — Pacific Ocean north of Tahiti. (AGASSIZ & MAYER 1902, p. 148, Pl. 3 figs. 13, 14; MAYER 1910 p. 225, fig. 118).



## Family Melicertidae.

Leptomedusae without any kind of marginal sense organs; with base of stomach attached over its entire surface; with eight simple or bifurcate radial canals; with hollow marginal tentacles; without marginal or lateral cirri; with or without ocelli.

### Key to the genera of Melicertidae.

1. Radial canals bifurcated ..... *Nelocertoides*  
    Radial canals simple ..... 2
2. Eight radial canals, four of which are developed centripetally from the ring canal ..... *Melicertoides*  
    All radial canals arise from the stomach ..... 3
3. With 8 large tentacles and a few rudimentary bulbs ..... *Orchistomella*  
    With numerous tentacles ..... *Melicertum*

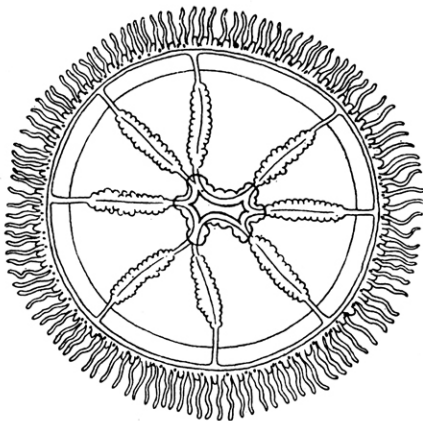


Fig. 163. *Dipleurosoma pacificum* (from MAYER).

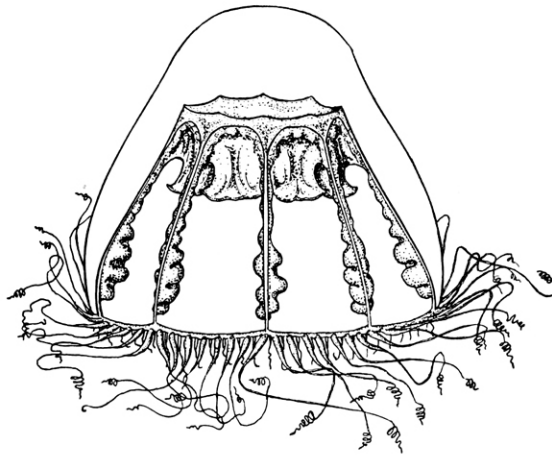


Fig. 164. *Melicertum octocostatum* (from KRAMP).

*Melicertum* L. AGASSIZ 1862. Melicertidae with eight simple radial canals, four primary and four secondary, all of which arise from the stomach; with gonads on the radial canals separated from stomach; usually (? always) without ocelli.

*Melicertum octocostatum* (M. SARS 1835). 11–14 mm high and wide, conical to pyriform; thick, solid apex and thinner sides; in each octant 5–7 fine lines of nematocysts upon subumbrella; velum narrow; stomach short and broad, octagonal, eight small lips; eight sinuous, linear gonads almost to bell margin; about 64–72 large tentacles alternating with as many small ones; no ocelli. — Bering Sea; Sea of Okhotsk; northern Japan; ? Vancouver. North-western Europe from English Channel to Barents Sea; Iceland; West Greenland; North America from Woods Hole to Halifax. (MAYER 1910 p. 207, Pl. 23 figs. 4, 5, Pl. 24 fig. 5, as *M. campanula*; RUSSELL 1953 p. 245, Pl. 13 figs. 2–4, textfigs. 138–142; NAUMOV 1960 p. 324, fig. 216).

*Melicertum georgicum* A. AGASSIZ 1862. 20 mm high and wide; stomach wide, flat and octagonal, mouth with four (?) lips; eight gonads covering nearly entire length of the eight radial canals, but not touching ring canal; about 30–40 tentacles with large basal bulbs; ocelli ?. — Washington on the Pacific coast of North America. (A. AGASSIZ 1865 p. 135, figs. 215, 216; MAYER 1910 p. 209).

*Melicertoides* KRAMP 1959. Melicertidae with eight simple radial canals, four primary and four secondary, the latter developed centripetally from the ring canal; with gonads adjacent to stomach.

*Melicertoides centripetalis* KRAMP 1959. 1 mm high, higher than wide, jelly thin; stomach broad and swollen, mouth opening simple; eight radial canals, all alike in the adult and fairly broad, with funnel-shaped openings into the middle zone of the stomach; gonads (immature) small, adjacent to stomach; four periradial tentacles opposite to the four primary radial canals; 12 other tentacles irregularly scattered. — Philippines. (KRAMP 1959 b p. 239, figs. 10, 11).



*Netocertoides* MAYER 1900. Melicertidae with eight main radial canals bifurcating once; gonads on main radial canals adjacent to stomach; without ocelli.

*Netocertoides brachiatus* MAYER 1900. 4–5 mm high, higher than wide; stomach broad and disk-like, mouth with four simple lips; 8 main radial canals bifurcated once; 16 long, hollow tentacles opposite to the 16 canals, 16–25 small tentacles. — Philippines and around Madagascar. Bahamas and Florida. (MAYER 1910 p. 229, Pl. 27 figs. 4–6; KRAMP 1965 p. 51).

*Orchistomella* KRAMP 1959. Melicertidae with eight or more simple radial canals, all of which arise from the stomach; tentacle bulbs with adaxial ocelli. (Two species, formerly referred to the same genus, are probably young specimens of *Aequorea*; see KRAMP 1961 p. 444).



Fig. 165. *Melicertum georgicum* (from AGASSIZ).

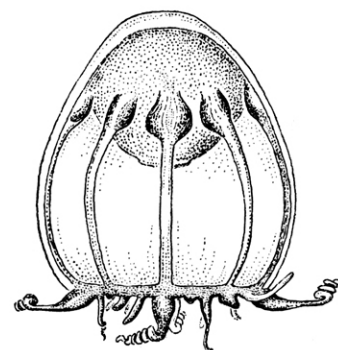


Fig. 166. *Melicertoides centripetalis* (from KRAMP, redrawn by P. W.).

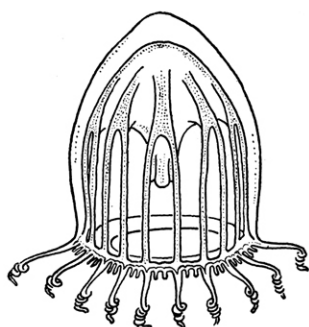


Fig. 167. *Netocertoides brachiatus* (from MAYER, redrawn by P. W.).

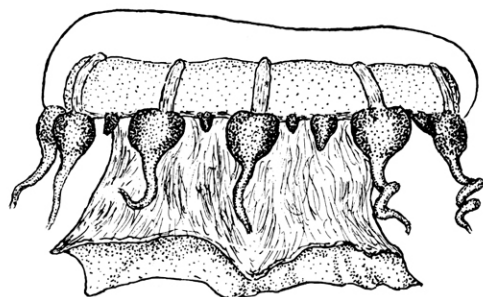


Fig. 168. *Orchistomella applanata* (from KRAMP).



Fig. 169. *Timoides agassizi* (from MAYER).

*Orchistomella applanata* KRAMP 1959. 1.5 mm wide, flat-topped, jelly fairly thick, a gelatinous plug extending downwards into the centre of the very broad stomach; mouth broad, with four broad lips; eight simple radial canals; gonads not observed; eight large tentacles with very large, almost globular bulbs, each with an adaxial, black ocellus; one or two rudimentary bulbs between successive tentacles. — Philippines. (KRAMP 1959 b p. 242, fig. 12; KRAMP 1965 p. 52).

## Family Timoididae.

Leptomedusae without any kind of marginal sense organs; ring canal with blindly ending centripetal canals; with stomach upon a peduncle.

*Timoides* BIGELOW 1904. Timoididae with four radial canals; with numerous tentacles and marginal cirri.

*Timoides agassizi* BIGELOW 1904. 20 mm wide, 14 mm high, apex very thick; stomach very long; four long, lancet-shaped, complexly folded lips; peduncle twice as long as the bell cavity, with flaring base; gonads on lower half of peduncle, above stomach, forming four ridges of papilliform processes; 12 interradial and adradial centripetal canals; 32 tentacles; numerous marginal cirri, no lateral cirri. — Maldives Islands in the Indian Ocean (BIGELOW 1904 p. 254, Pl. 3 figs. 10, 11; MAYER 1910 p. 212, fig. 108).

## Family Laodiceidae.

Leptomedusae with marginal cordyli; with 4–8 or more simple or branched radial canals; with hollow marginal tentacles; with or without marginal cirri; without marginal vesicles; with or without ocelli.

### Key to the genera of Laodiceidae represented in Indo-Pacific waters.

1. With 6 or more radial canals ..... 2  
     With 4 radial canals ..... 3
2. Some or all of the radial canals dichotomously branched, all branches joining ring canal ..... *Toxorchis*  
     With eight simple, unbranched radial canals ..... *Melicertissa*
3. Radial canals open grooves forming large cruciform mouth ..... *Staurophora*  
     Radial canals closed ..... 4
4. Radial canals with one or a few pairs of lateral branches ..... *Staurodiscus*  
     Radial canals simple or with short lateral diverticula ..... 5
5. Some or all tentacle bulbs with adaxial ocelli ..... *Laodicea*  
     No ocelli ..... *Ptychogena*

*Laodicea* LESSON 1843. Laodiceidae with four simple radial canals; with simple wavy gonads; with or without marginal cirri; with adaxial ocelli. — The limitation of the species was discussed by the present author, KRAMP 1953 pp. 268–270.

### Key to the Indo-Pacific species of *Laodicea*.

1. Stomach with large perradial lobes ..... *pulchra*  
     Stomach with short perradial lobes ..... 2
2. With 8 tentacles and 8 very large marginal clubs; 2 mm wide ..... *fertilis*  
     With numerous tentacles ..... 3
3. Gonads in short, complexly folded lateral diverticula; no marginal cirri ..... *fijiana*  
     Gonads sinuous on radial canals, contiguous with stomach; with marginal cirri ..... 4
4. One cordylus between successive tentacles; ocelli on about every second tentacle ..... *indica*  
     With 2–3 cordyli between successive tentacles; ocelli on nearly all tentacles ..... *marama*

*Laodicea pulchra* BROWNE 1902. 15 mm high, 25 mm wide; stomach very large, with four large, perradial lobes extending more than half-way to bell margin; four large, slightly folded lips; gonads from near centre of stomach nearly to ring canal, with numerous lateral folds; about 50 tentacles without basal spur; no cirri; 3–4 cordyli between successive tentacles, with nematocysts; adaxial ocelli on each tentacle bulb and cordylus. — Kerguelen Island. Falkland Islands and southern Patagonia. (BROWNE & KRAMP 1939 p. 291, Pl. 16 figs. 3–5).

*Laodicea fertilis* (LENDENFELD 1884). 2 mm wide, 2.5 mm high; stomach a four-sided pyramid, four simple lips; gonads complexly folded, over entire length of the four radial canals, fused on sides of the sto-

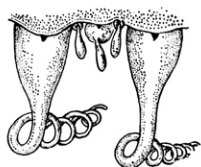


Fig. 170. *Laodicea pulchra*, part of bell margin with tentacles and cordyli (from BROWNE & KRAMP, redrawn by P. W.)

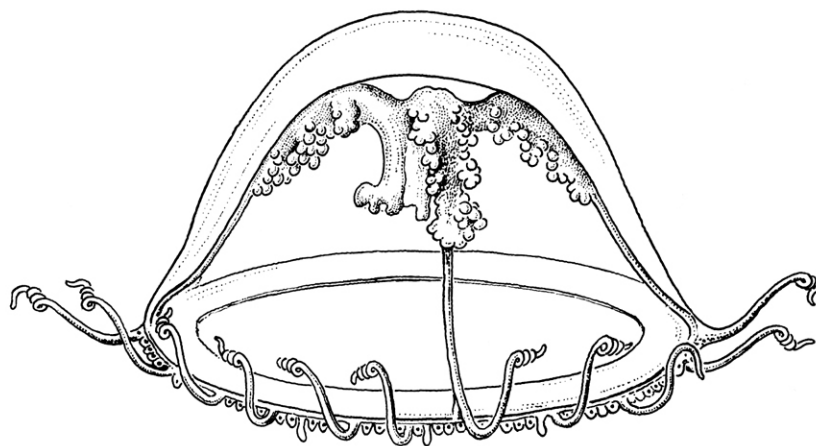


Fig. 171. *Laodicea fijiana* (from AGASSIZ & MAYER, redrawn by P. W.).

mach; eight tentacles; eight very large adradial clubs. — Sydney, Australia. The present author has examined the type-specimen in the British Museum, London, and found that LENDENFELD's short description is adequate, but his figures misleading. (KRAMP 1953 p. 310).

*Laodicea fijiana* AGASSIZ & MAYER 1899 (*non*. MAAS 1906). 6 mm high and wide; gonads upon short, complex lateral diverticula in proximal half of the radial canals; about 70 tentacles without basal spur; very few cordyli; no cirri. — Fiji Islands. (BROWNE 1907 p. 467; KRAMP 1919 p. 22; KRAMP 1953 p. 269).

*Laodicea indica* BROWNE 1905. 20–25 mm wide, two to four times as wide as high; walls moderately thick; stomach cross-shaped, fairly large, oral lips short, slightly folded; gonads from corners of stomach along half part of radial canals or almost to bell margin, sinuous, may be well developed even in small specimens; up to 180 tentacles, small basal spurs on young tentacles; ocelli on about every second tentacle; one cordylus

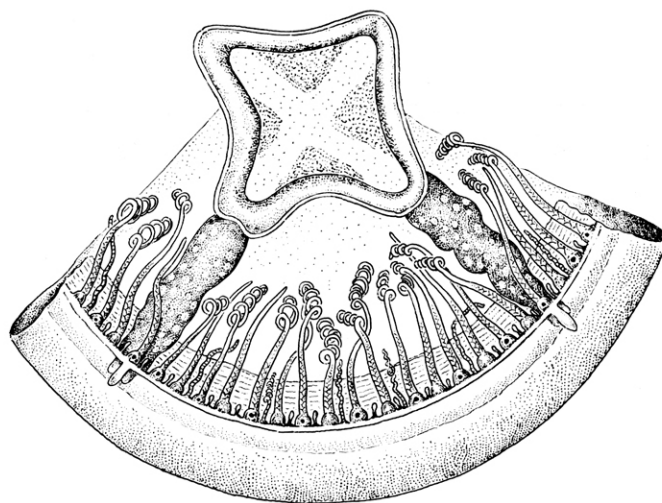


Fig. 172. *Laodicea indica* (from BROWNE, redrawn by P. W.).

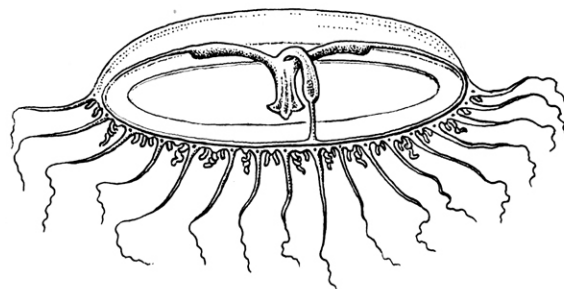


Fig. 173. *Laodicea marama* (from AGASSIZ & MAYER, redrawn by P. W.).

between successive pairs of tentacles; cirri present, but readily lost by preservation. — Widely distributed in coastal waters from South and East Africa to Tahiti. (BROWNE 1905 p. 136, Pl. 1 fig. 5, Pl. 4 figs. 7–11; MAAS 1905 p. 25, Pl. 2 figs. 14, 15, Pl. 5 figs. 32–35, as *L. fijiana* var. *indica*; BROWNE 1907 p. 266 as *L. maasi*, nov. nom for *L. fijiana* var. *indica* MAAS; KRAMP 1953 p. 269; KRAMP 1965 p. 52). Closely related to the Atlantic *L. undulata* (FORBES & GOODSIR).

*Laodicea marama* AGASSIZ & MAYER 1899. 5.5 mm wide (young medusa); resembling *L. indica*, but distinguished by the presence of 2–3 cordyli between successive tentacles; cirri are present, but the tentacles are said to be without basal spur. — Fiji Islands. (AGASSIZ & MAYER 1899 p. 162, Pl. 3 figs. 7, 8; BROWNE 1907 p. 466; KRAMP 1953 p. 269, discussion).

*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 cirri; without ocelli.

#### Key to the Indo-Pacific species of *Ptychogena*.

1. Umbrella almost as high as wide, dome-shaped; gonadal diverticula short and simple; about 50 tentacles *californica*  
 Umbrella almost flat, jelly very thick with a thin margin; gonadal diverticula lamellar, compressed; numerous tentacles ..... 2
2. Gonadal lamellae in their entire length attached to subumbrella ..... *lactea*  
 Gonadal lamellae not attached to subumbrella ..... *antarctica*

*Ptychogena californica* TORREY 1909. 10 mm wide, more than half as high as wide; manubrium shallow, broad, mouth large; gonads with 12–14 short lateral folds on either side of the proximal half of the radial canals; about 48 tentacles; 1–5 cordyli between tentacles. — San Diego, California. (TORREY 1909 p. 13, figs. 1, 2).

*Ptychogena lactea* A. AGASSIZ 1865. Up to 90 mm wide and 30 mm high, very thick; stomach short, quadratic, mouth rim slightly crenulated, four short lips; radial canals with 20–30 lamelliform diverticula on either side, at right angles to the canals, in their entire length attached to subumbrella, their free margin with papilliform appendages; 300–500 tentacles and as many club-shaped cordyli without nematocysts. — Arctic, circumpolar;

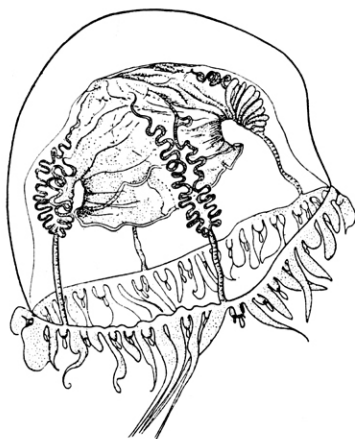


Fig. 174. *Ptychogena californica* (from TORREY).

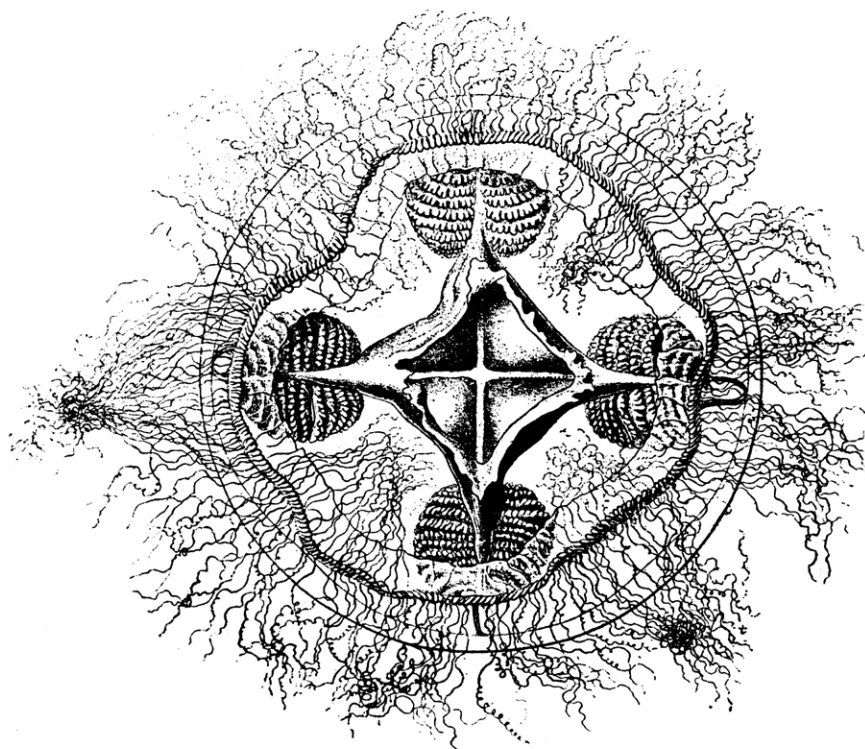


Fig. 175. *Ptychogena lactea* (after HAECKEL, from MAYER).

Bering Sea, Sea of Okhotsk, northern Japan. (KRAMP 1910 p. 31, Pl. 3 figs. 1–6, textfig. 5; YASHNOV 1948 p. 71, Pl. 20 fig. 1; NAUMOV 1960 p. 297, fig. 190).

*Ptychogena antarctica* BROWNE 1907. 60–100 mm wide, slightly convex, jelly very thick; stomach wide, with funnel-shaped perradial lobes almost to terminal portions of the gonads; gonads on nearly whole length of radial canals, in 10–15 lateral folds on either side, each of them further divided into 2–5 lamellar folds, not attached to subumbrella; about 300 tentacles and as many cordyli with few nematocysts. — Antarctic: Gauss Station. South Orkney Islands; Cape Adare and McMurdo Sound. (BROWNE 1910 p. 29, Pl. 2 figs. 6–9; KRAMP 1957 p. 28, Pl. 5 fig. 8).

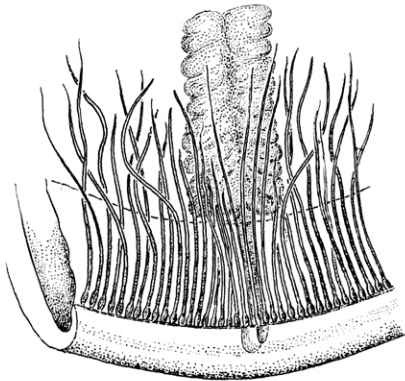


Fig. 176. *Ptychogena antarctica*  
(from BROWNE, redrawn by P. W.).

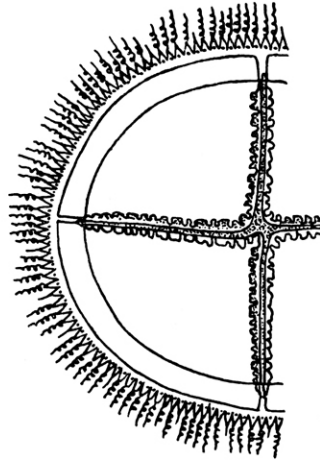


Fig. 177. *Staurophora mertensi*  
(from MAYER).

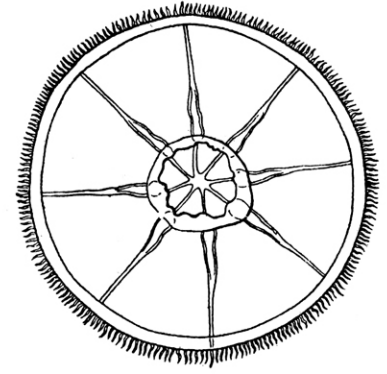


Fig. 178. *Melicertissa malayica*  
(from MAYER).

*Staurophora* BRANDT 1838. Laodiceidae with four radial canals which for the greater part of their length are open grooves forming a large, cruciform mouth; gonads in branched diverticula from the lateral walls of the cruciform mouth; with adaxial ocelli; no cirri.

*Staurophora mertensi* BRANDT 1838. 100–200 mm wide, flatter than a hemisphere; up to 4400 short tentacles, all with adaxial ocellus, alternating with club-shaped cordyli without nematocysts. — Northern Pacific from Alaska to northern Japan. Arctic circumpolar; northern Atlantic as far south as the North Sea and Cape Cod on the American coast. Falkland Islands and South Orkney Islands in southern Atlantic. (MAYER 1910 p. 291, Pl. 26 figs. 4–9; RUSSELL 1953 p. 239, textfigs. 132–137; NAUMOV 1960 p. 300, figs. 28, 31, 50 B,b, 191, 192).

*Staurophora purpurea* FOERSTER 1923. Position doubtful. — Vancouver. (FOERSTER 1923 p. 250, Pl. 4 figs. 2–5).

*Melicertissa* HAECKEL 1879. Laodiceidae with eight simple, narrow radial canals. — The distinction between the species is provisional (discussed in KRAMP 1961 pp. 198 ff).

#### Key to the Indo-Pacific species of *Melicertissa*.

1. With about 100–150 tentacles ..... *malayica*  
With no more than 17 tentacles ..... 2
2. With eight long, lanceolate lips; 8 tentacles ..... *platygastra*  
Oral lips very short ..... 3
3. Eight tentacles, 24 cordyli ..... *clavigera*  
About 16 tentacles, about 32 cordyli ..... *orientalis*

*Melicertissa malayica* (MAAS 1905). 32 mm wide; stomach flat, eight simple lips; gonads linear, upon proximal 1/3 length of radial canals; about 150 tentacles, every fourth with an ocellus; cordyli irregularly

scattered; a few coiled cirri. — Malayan Archipelago. (MAAS 1905 p. 28, Pl. 5 figs. 29–31, as *Melicertidium adriaticum*; MAYER 1910 p. 211, fig. 107; KRAMP 1961 p. 198).

*Melicertissa platygastra* NAIR 1951. 7 mm wide, almost watch-glass-shaped, very thick in the centre, thin towards margin; stomach flat, wide, mouth with eight long, lanceolate lips; gonads short, in middle of radial canals; 8 short, stumpy tentacles with large, conical bulbs; in each octant 4–6 cordyli and 12–14 dark ocelli. — Trivandrum Coast, India. (NAIR 1951 p. 60, Pl. 1 figs. 6, 7; KRAMP 1961 *b* p. 198; KRAMP 1965 p. 55).

*Melicertissa clavigera* HAECKEL 1879. 10 mm wide, flatter than a hemisphere, moderately thin; stomach flat, with eight short lips; gonads somewhat sinuous, upon middle half of radial canals; 8 tentacles, 32 cordyli, 32 ocelli; no cirri. — Trivandrum Coast, India. Originally described from Canary Islands. (HAECKEL 1879

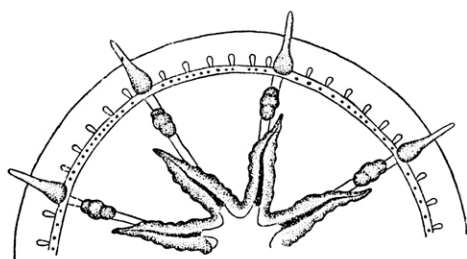


Fig. 179. *Melicertissa platygastra* (from NAIR).



Fig. 180. *Melicertissa clavigera* (after HAECKEL, from MAYER).

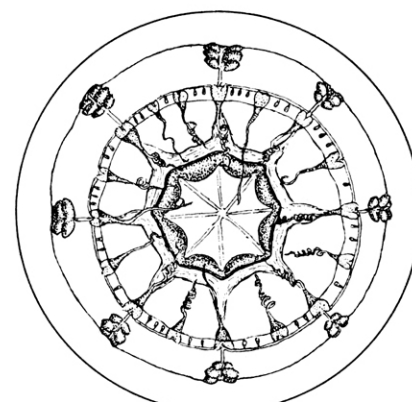


Fig. 181. *Melicertissa orientalis* (from KRAMP).

p. 135, Pl. 8 figs. 8–12; MAYER 1910 p. 210, textfig. 106 (*non* Pl. 24 figs. 2, 3); NAIR 1951 p. 59; KRAMP 1959 p. 139; KRAMP 1961 pp. 198 ff.; KRAMP 1965 p. 55).

*Melicertissa orientalis* KRAMP 1961. 11 mm wide, flatter than a hemisphere, jelly fairly thick; stomach broad and rather flat, the eight radial canals continued inwards as narrow grooves meeting in the centre of the dorsal wall of the stomach; eight faintly indicated oral lips; gonads along about two-fifths of radial canals, as wavy, lateral bands with about five extensions, almost lamelliform, to each side; 17 tentacles, all alike, with broadly conical bulbs; between successive tentacles 2–3 cordyli, club-shaped, with a small distal cap of nematocysts; an adaxial ocellus at the base of each tentacle and cordylus. — N. E. Australia. (KRAMP 1961 *b* p. 198, figs. 1–3; KRAMP 1965 p. 55).

*Melicertissa* sp. KRAMP 1965. Young medusa, 2 mm wide and high; stomach broadly attached to subumbrella, without a central stars-shaped figure; oral lips faintly indicated; gonads small, oval, in proximal part of the eight radial canals; 7 fully developed tentacles and 5 young bulbs, all with a black ocellus; 10 club-shaped cordyli, each with a distal cluster of nematocysts. — Malacca Strait. (KRAMP 1965 p. 54).

*Staurodiscus* HAECKEL 1879. Laodiceidae with four radial canals, each giving rise to one or more pairs of lateral branches which may or may not communicate with the ring canal; primary radial canals proceeding straight to the ring canal; gonads on main canals and branches; with adaxial ocelli; without marginal cirri. (Discussion in KRAMP 1962 pp. 320–324).

#### Key to the Indo-Pacific species of *Staurodiscus*.

- |   |                     |
|---|---------------------|
| 1. Lateral branches of radial canals blind.....   | 2                   |
| Lateral branches joining ring canal.....          | 3                   |
| 2. Lateral branches one pair.....                 | <i>tetrastaurus</i> |
| Lateral branches 3–4 pairs.....                   | <i>gotoi</i>        |
| 3. Lateral branches one pair.....                 | <i>nigricans</i>    |
| Lateral branches 2 pairs, somewhat irregular..... | <i>vietnamensis</i> |



*Staurodiscus tetrastaurus* HAECKEL 1879. Up to 6 mm wide, half as high; stomach small, cruciform, mouth with four prominent lips; radial canals each with two opposite blind lateral branches; gonads on side branches and distal parts of radial canals; 8–16 long tentacles; up to 48 cordyli with nematocysts; 32 ocelli. — Coasts of India; Singapore. Canary Islands; Florida. (MAYER 1910 p. 214, Pl. 9 figs. 7, 8; Pl. 25 fig. 5, Pl. 26 figs. 10, 11; MENON 1932 p. 14, Pl. 2 figs. 14, 19; KRAMP 1965 p. 55).

*Staurodiscus gotoi* (UCHIDA 1927). 15 mm wide, 20 mm high; manubrium short, four-sided, with folded lips; radial canals with 3–4 pairs of lateral branches, not quite opposite each other, the proximal longer than the distal, canals and branches with secondary diverticula; the branches do not quite reach to the ring canal;

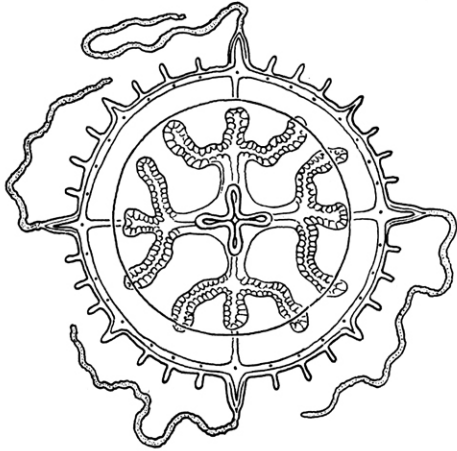


Fig. 182. *Staurodiscus tetrastaurus*  
(from MAYER, redrawn by P. W.).

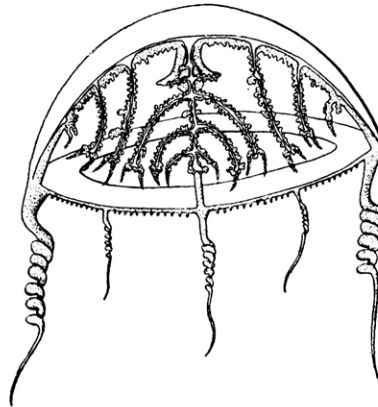


Fig. 183. *Staurodiscus gotoi*  
(from UCHIDA).

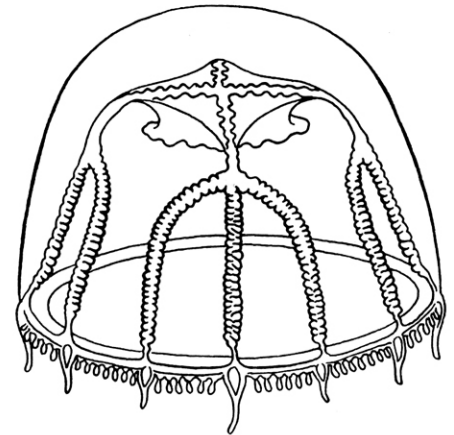


Fig. 184. *Staurodiscus nigricans*  
(from MAYER).

gonads along canals and branches; 4 long and 4 smaller tentacles; 88 cordyli; ocelli on base of cordyli. — Shimizu Bay in Japan; Sunda Strait. (UCHIDA 1927 c p. 165, figs. 1, 2, as *Staurodiscoides gotoi*; KRAMP 1965 p. 56).

*Staurodiscus nigricans* AGASSIZ & MAYER 1899. 14 mm wide, dome-shaped, thin and flexible; manubrium short, mouth wide; from each of the radial canals two opposed lateral branches reaching ring canal; gonads along the twelve terminal canals; 12 short tentacles; about 84 cordyli. — Fiji Islands. (AGASSIZ & MAYER 1899 p. 164, Pl. 4 figs. 11, 12; MAYER 1910 p. 221, fig. 113, erroneously as synonym of *Cannota dodecantha* HCKL.; KRAMP 1955 p. 307).

*Staurodiscus vietnamensis* KRAMP 1962. 13 mm wide, 5 mm high, fairly thick; stomach quadrangular, mouth with four large, folded lips; four radial canals proceeding straight to the perradial points of the bell

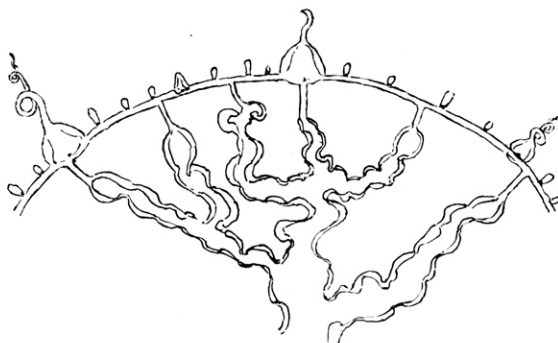


Fig. 185. *Staurodiscus vietnamensis* (from KRAMP).

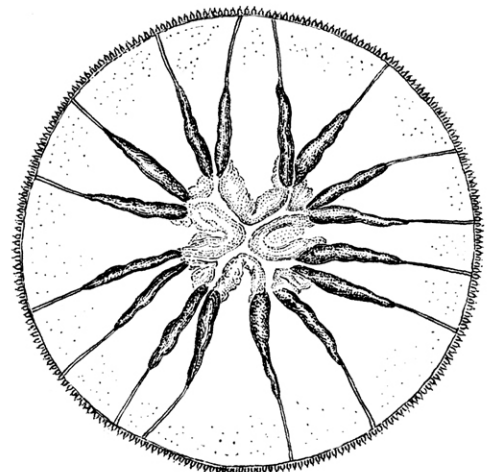


Fig. 186. *Toxorchis polynema* (from KRAMP, redrawn by P.W.).



margin, each giving rise to two pairs of lateral branches more or less opposite each other, some of the proximal branches with a secondary lateral branch; gonads continuous, irregularly folded bands along the main radial canals and their branches from their points of origin almost to the umbrella margin, the distal ends free of gonads and communicating with the ring canal; 12 tentacles and 4 young bulbs; about 48 cordyli with a distal cap of nematocysts; ocelli at the base of each tentacle and cordylus. — Coast of Vietnam. (KRAMP 1962 p. 319, fig. 6; KRAMP 1965 p. 56).

*Toxorchis* HAECKEL 1879. Laodiceidae with four, six or more main radial canals, some or all branching dichotomously one or more times, all branches reaching ring canal; primary radial canals not proceeding to ring canal; gonads upon outermost branches; numerous tentacles and cordyli; cirri may be present. (Discussion in KRAMP 1962 pp. 320–324).

*Toxorchis thalassinus* (PÉRON & LESUEUR 1809). About 50 mm wide, dome-shaped; stomach shallow, with six wide lips; 6 wide radial canals, branching dichotomously 3–4 times, about 100 branches reaching ring canal; sac-like, folded gonads on outermost branches; 100 or more long tentacles with cordyli and cirri between them. — New Guinea and North Australia. (MAYER 1910 p. 228; KRAMP 1953 p. 306).

*Toxorchis polynema* KRAMP 1959. 17 mm wide, flat; stomach broad and flat, mouth with broad and crenulated lips; four groups of radial canals, each bifurcating twice inside the cruciform base of the stomach, 16 (4×4) canals leaving the stomach, all running to the ring canal; gonads along proximal 2/3 to 3/4 of the length of the radial canals; about 300 tentacles and as many cordyli. — Around Madagascar; Maldives Islands to Ceylon; Malayan Archipelago; New Zealand; Society Islands and Samoa. Angola in West Africa. (KRAMP 1959 a pp. 34, 141, Pl. 1 fig. 13, Pl. 2 fig. 4; KRAMP 1965 p. 56).

## Family Mitrocomidae.

Leptomedusae with open marginal vesicles; with base of stomach attached to subumbrella along edges of radial furrows; with gonads on radial canals separated from stomach; with hollow marginal tentacles; with or without marginal cirri; with or without ocelli. (Revision of genera and species in KRAMP 1932).

### Key to the genera of Mitrocomidae represented in Indo-Pacific waters.

- |   |                     |
|---|---------------------|
| 1. Without ocelli .....   | 2                   |
| With a large black ocellus at the base of each marginal vesicle .....           | 5                   |
| 2. With marginal cirri, spiral and with a terminal cluster of nematocysts ..... | 3                   |
| Without marginal cirri .....  | 4                   |
| 3. With 8–16 marginal vesicles .....  | <i>Mitrocomella</i> |
| With numerous marginal vesicles .....   | <i>Mitrocoma</i>    |
| 4. With 8 marginal vesicles .....   | <i>Cosmetirella</i> |
| With numerous marginal vesicles .....   | <i>Halistaura</i>   |
| 5. With only one kind of tentacles; 8 marginal vesicles .....                   | <i>Tiaropsis</i>    |
| With two kinds of tentacles .....   | <i>Tiaropsidium</i> |

*Mitrocomella* HAECKEL 1879. Mitrocomidae with four radial canals; with 8, 12 or 16 marginal vesicles without ocelli; with marginal cirri which coil spirally.

*Mitrocomella frigida* (BROWNE 1910). 13–17 mm wide, almost hemispherical, with thin walls; stomach short and broad; gonads along greater part of radial canals, leaving both ends free, hanging down in large vertical folds; 32–72 tentacles; about 8 cirri between successive tentacles; 8 marginal vesicles. — Antarctic: McMurdo Sound; Gauss Station; South Georgia. West of Cape of Good Hope. (KRAMP 1932 p. 345, Pl. 10 figs. 5, 6, textfig. 23).

*Mitrocomella sinuosa* (FOERSTER 1923). 4 mm wide, almost hemispherical; stomach small, mouth large, wide, with four recurved lips; radial canals narrow; gonads sinuous, along distal half of radial canals, distinctly longitudinally divided; about 50 tentacles with thick, conical bulbs, fairly short; 3–5 cirri between successive tentacles; 12 marginal vesicles. — Vancouver, Pacific coast of North America. (FOERSTER 1923 p. 35, Pl. 4 fig. 6, as *Mitrocoma sinuosa*; KRAMP 1932 p. 343, fig. 38).

*Mitrocomella grandis* KRAMP 1965. 50 mm wide, watch-glass-shaped, thin in peripheral part, but central part very thick; stomach cruciform, mouth with four large, pointed, crenulated lips; gonads linear, along greater part of radial canals; about 220 tentacles, all alike, with long, tapering bulbs; 5–8 cirri between successive tentacles; 16 marginal vesicles. — South Africa. (KRAMP 1965 p. 57, fig. 2).

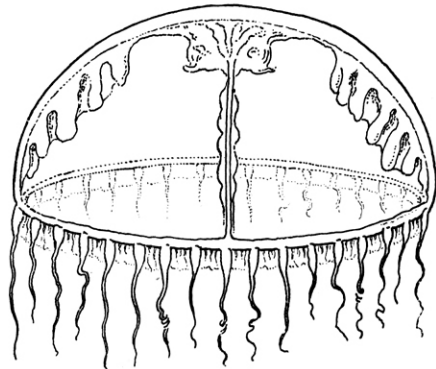


Fig. 187. *Mitrocomella frigida*  
(from KRAMP, redrawn by P. W.).

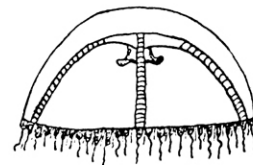


Fig. 188. *Mitrocomella sinuosa*  
(from FOERSTER).

*Mitrocoma* HAECKEL 1879. Mitrocomidae with four radial canals; with numerous marginal vesicles without ocelli; with marginal cirri which coil spirally.

*Mitrocoma discoidea* TORREY 1909. 45 mm wide, flatter than a hemisphere, jelly moderately thick; stomach short and narrow, mouth with four long and pointed lips; gonads narrow, along almost whole length of radial canals; 180–240 short tentacles with conical bulbs; one cirrus between every two tentacles; 20–60 marginal vesicles with numerous concretions. — Coast of California; Vancouver. (TORREY 1909 p. 17, fig. 4; KRAMP 1932 p. 349, figs. 22, 33, 41).

*Cosmetirella* BROWNE 1910. Mitrocomidae with four radial canals; with 8 marginal vesicles without ocelli; without marginal cirri.

*Cosmetirella davis* (BROWNE 1902). Up to 60 mm wide, larger in subantarctic than in antarctic waters; almost hemispherical; stomach small, lips somewhat folded; gonads linear, sinuous, along  $1\frac{1}{2}$ – $\frac{2}{3}$  of radial canals; number of tentacles very variable, up to 180; normally 8 marginal vesicles with several concretions. — Antarctic and subantarctic, circumpolar; coast of Chile; South Africa. (BROWNE 1902 p. 281, as *Tiaropsis davis*; BROWNE 1910 p. 34, Pl. 1 figs. 6–8, as *Cosmetirella simplex*; Kramp 1932 p. 359, figs. 4, 34, 46; BROWNE & KRAMP 1939 p. 293, Pl. 17 fig. 1.)

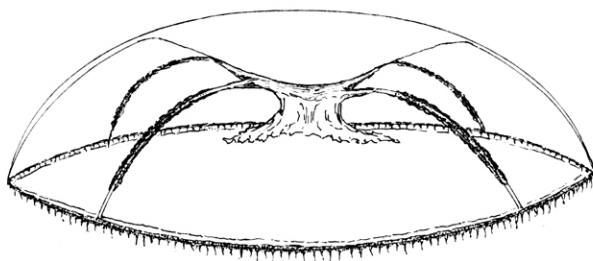


Fig. 189. *Mitrocomella grandis* (from KRAMP).

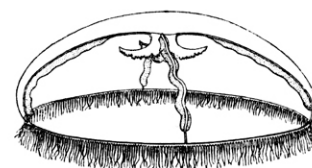


Fig. 190. *Mitrocoma discoidea* (from KRAMP).

*Halistaura* BIGELOW 1913. Mitrocomidae with four radial canals; with numerous marginal vesicles without ocelli; without marginal cirri.

*Halistaura cellularia* (A. AGASSIZ). 50–90 mm wide, almost hemispherical, thick, especially at apex; stomach very small, with four long, slender, crenulated lips; gonads narrow, along nearly whole length of radial canals; 250–340 tentacles with swollen, cylindrical bulbs; 16–24 marginal vesicles. — Vancouver Island region; southern Alaska; Point Barrow on the north coast of Alaska. (MURBACH & SHEARER 1903 p. 172, Pl. 17 fig. 2, 2 b; as *Thaumantias cellularia*; KRAMP 1932 p. 362, fig. 47; MCGINITIE 1955 pp. 95, 119).

*Tiaropsis* L. AGASSIZ 1849. Mitrocomidae with four radial canals; with 8 marginal vesicles each with a basal ocellus; with only one kind of tentacles; without marginal cirri.

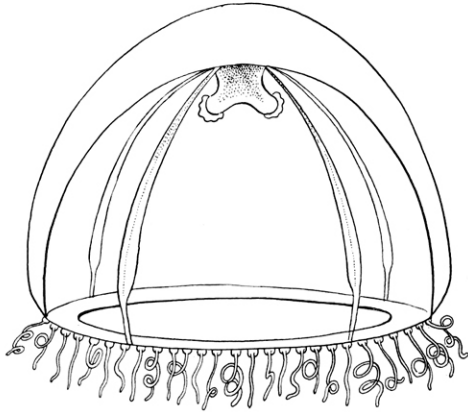


Fig. 191. *Cosmetirella davisi* (from BROWNE & KRAMP, redrawn by P. W.).

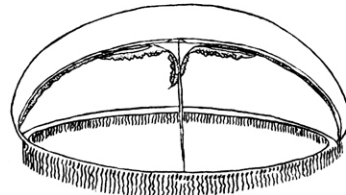


Fig. 192. *Halistaura cellularia* (from KRAMP).

*Tiaropsis multicirrata* (M. SARS 1835). About 20 mm wide, flatter than a hemisphere, a broad, flat stomachal peduncle; mouth with four lips, fairly long and broad, margin much folded and crenulated; gonads along middle 1/2–2/3 of the radial canals, somewhat sinuous, from base of peduncle outwards; about 300 fairly short tentacles with broad, swollen bulbs; 8 marginal vesicles, each with about 12 concretions and with a black ocellus at the base. — Sea of Okhotsk; Bering Sea; Chukotski Sea north of Bering Strait. Northwestern Europe from the Barents Sea to the English Channel; Mauretania; Iceland; west coast of Greenland; New Foundland to Woods Hole on the American coast. (MAYER 1910 p. 258, Pl. 31 fig. 11, Pl. 32 figs. 8, 9; KRAMP 1919 p. 77, Pl. 4 figs. 6–10, textfigs. 11–14; KRAMP 1932 p. 364, figs. 14, 15, 20, 35, 48; RUSSELL 1953 p. 278, Pl. 17 fig. 1, textfigs. 167–171).

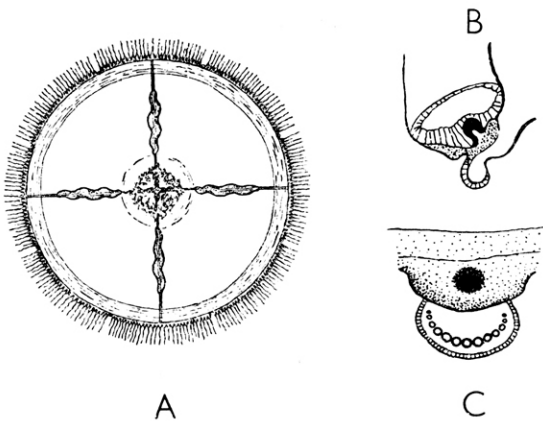


Fig. 193. *Tiaropsis multicirrata*; A, oral view of medusa, B and C, marginal vesicle with ocellus (from KRAMP).

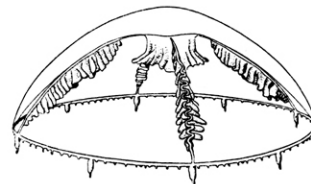


Fig. 194. *Tiaropsidium kelsey* (from KRAMP).

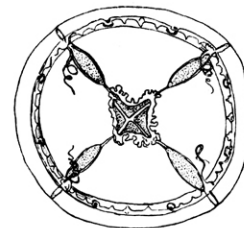


Fig. 195. *Tiaropsidium roseum* (from KRAMP).

*Tiaropsidium* TORREY 1909. Mitrocomidae with four or more (up to 16) radial canals; with 8 or 16 (rarely 48) marginal vesicles, each with a basal ocellus; with two kinds of tentacles; without marginal cirri.

**Key to the Indo-Pacific species of *Tiaropsidium*.**

1. With about 16 radial canals ..... *polyradiatum*  
     With 4 radial canals ..... 2
2. With 8 marginal vesicles ..... 3  
     With 16 marginal vesicles ..... *japonicum*
3. With 4 large tentacles; gonads oval ..... *roseum*  
     With 8 large tentacles; gonads curtain-like ..... *kelseyi*

*Tiaropsidium kelseyi* TORREY 1909. About 50 mm wide, three times as broad as high, somewhat conical; stomach short, fairly broad, slightly frilled lips; gonads curtain-like, much folded, along almost entire length

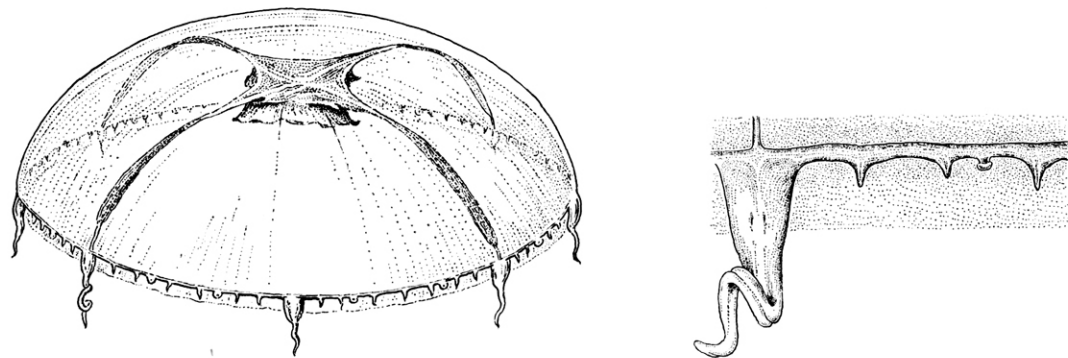


Fig. 196. *Tiaropsidium japonicum* (from KRAMP, redrawn by P. W.).

of the four radial canals; 8 tentacles, fairly short, with elongated bulbs, all of equal size; about 5–8 small rudimentary tentacles between every two of the large tentacles; 8 marginal vesicles, each with a basal ocellus. — Coast of California between San Diego and Monterey; Vancouver Island region. (TORREY 1909 p. 19, fig. 5; FOERSTER 1923 p. 37, Pl. 4 fig. 7; KRAMP 1932 p. 369, fig. 51).

*Tiaropsidium roseum* (MAAS 1905). Up to 15 mm wide, flattened, stomach broad and flat, four very short, crenulated lips; gonads elongated oval, along somewhat more than 1/3 of the length of the four radial canals; 4 perradial, fairly long tentacles with broad bulbs; 7 rudimentary tentacles in each quadrant, each with a broad base and a small, pointed tip; 8 marginal vesicles, each with about 15 concretions and with a basal ocellus. — Mauritius east of Madagascar; Nicobars; Damar in the Malayan Archipelago; off Sydney in East Australia; Fiji Islands. (MAAS 1905 p. 30, Pl. 7 figs. 45–47, as *Tiaropsis rosea*; KRAMP 1932 p. 368, figs. 2, 50; KRAMP 1965 p. 59).

*Tiaropsidium japonicum* KRAMP 1932. 18–34 mm wide, watch-glass-shaped, thin; stomach small, flattened, lips very short, slightly folded; gonads linear, along almost entire length of the four radial canals; 8 large tentacles with large, swollen bulbs; 6–7 small, pointed rudimentary tentacles between two large tentacles; 16 marginal vesicles, each with a basal ocellus; number of concretions unknown. — Misaki in southern Japan; east of Cook Strait, New Zealand. (KRAMP 1932 p. 370, Pl. 10 figs. 1, 2, textfigs. 1, 24, 36; KRAMP 1965 p. 58).

*Tiaropsidium polyradiatum* KRAMP 1965. About 30 mm wide, thin and flat; stomach fairly broad, mouth with folded and crenulated lips; about 16 radial canals; gonads along entire length of radial canals; about 24–32 large tentacles; between the tentacles several small, tenon-like rudimentary tentacles; more than 8 marginal vesicles, each with a basal ocellus. — Nicobars. (KRAMP 1965 p. 59, fig. 4).

## Family Campanulariidae.

Leptomedusae with normal or reduced velum; with small stomach, without a peduncle; with normally four simple radial canals; with gonads completely surrounding radial canals, separated from stomach; with hollow, rarely solid, marginal tentacles; without excretory pores; without marginal or lateral cirri; with closed marginal vesicles; without ocelli.

### Key to the genera of Campanulariidae represented in Indo-Pacific waters.

1. Without manubrium, without tentacles; exumbrella with meridional ridges; abortive medusa ..... *Eucopeila*  
     With normal manubrium and tentacles ..... 2
2. With more than one manubrium ..... *Gastroblasta*  
     With normally only one manubrium ..... 3
3. With solid tentacles; with reduced velum ..... *Obelia*  
     With hollow tentacles; with normal velum; ..... *Phialidium*

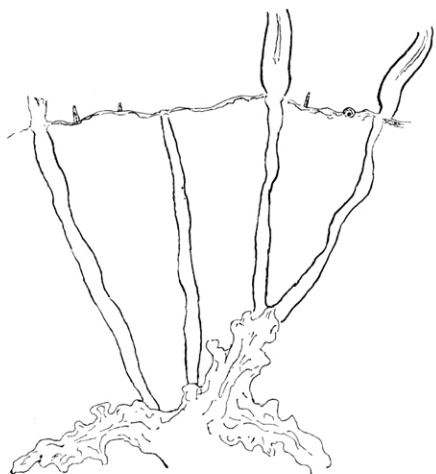


Fig. 197. *Tiaropsidium polyradiatum* (from KRAMP).

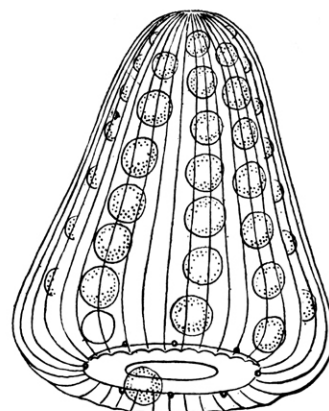


Fig. 198. *Eucopeila bilabiata* (from MAYER).

*Eucopeila* VON LENDENFELD 1883. Campanulariidae without manubrium and without tentacles. Exumbrella with longitudinal ridges. With four radial canals which give rise to blindly ending side branches. Gonads developed between branches of radial canals. With eight adradial lithocysts.

*Eucopeila bilabiata* (COUGHTREY 1875). 1.5 mm high, pyriform, thin walls; 30–40 meridional ridges on exumbrella; radial canals closed and obliterated near apex, with numerous side branches; bell cavity almost filled with genital organs. No trace of tentacles. Eight marginal vesicles with one concretion. Lives but a few hours. — New Zealand and Australia. (COUGHTREY 1875, p. 293, Pl. 20, fig. 45; MAYER 1910, p. 233, fig. 120).

*Eucopeila crenata* HARTLAUB 1901. Hydroid with medusae in gonotheca; the medusae contain the sex-cells before liberation. — New Zealand. (HARTLAUB 1901, p. 364, Pl. 22, figs. 27–31, 33–35).

*Gastroblasta* KELLER 1883. Campanulariidae with four or more radial canals and more than one manubrium. Numerous marginal vesicles alternating with tentacles. Centripetal canals from ring canal.

*Gastroblasta timida* KELLER 1883. 3–4 mm wide, 1–1.5 mm high; bell circular in outline. 1–4 manubria; 4–17 radial canals, 17 centripetal canals; 17 oval gonads. 68 tentacles and as many marginal vesicles, each with one concretion. (Retained as only species of *Gastroblasta*; all other species are abnormal specimens of *Phialidium*). — Red Sea.

*Obelia* PÉRON & LESUEUR 1809. Campanulariidae with reduced velum; with solid marginal tentacles; with eight lithocysts.

*Obelia* spp. Up to 6 mm wide, flat, jelly thin; velum rudimentary; stomach short, with quadrangular base, mouth with four short, simple lips; gonads round, sac-like, on middle of radial canals; numerous short, solid tentacles, somewhat stiff, with axial core of single row of endoderm cells; each tentacle with small basal bulb and a short prolongation of endoderm into mesogloea of umbrella margin; eight adradial lithocysts, each situated on underside of basal bulb of marginal tentacle, each with one concretion. — The numerous species, reared from different hydroids, can not be distinguished from each other. — The genus almost cosmopolitan.

*Phialidium* LEUCKART 1856. Campanulariidae with normal velum; with hollow marginal tentacles; with numerous marginal vesicles.

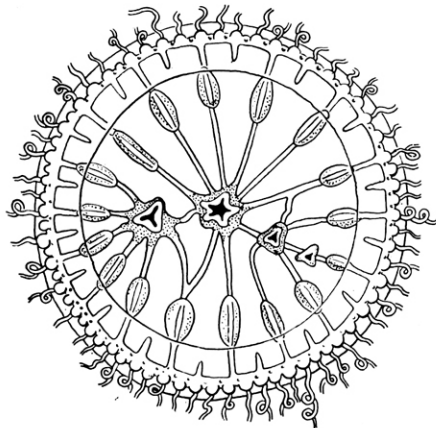


Fig. 199. *Gastroblasta timida* (from MAYER).

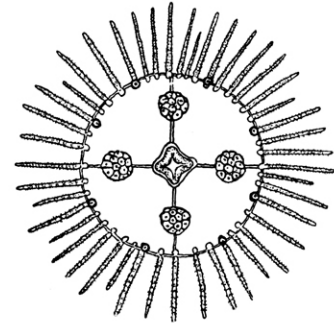


Fig. 200. *Obelia* sp. (from KRAMP).

#### Key to the Indo-Pacific species of *Phialidium*.

1. Subumbrella iridescent ..... *iridescens*  
    Subumbrella not iridescent ..... 2
2. A prominent, brown pigment spot at base of each tentacle; about 30 short, thick tentacles ..... *brunescens*  
    No brown pigment spot at base of tentacles ..... 3
3. Stomach large, globular; 4 prominent lips ..... *malayense*  
    Stomach fairly narrow ..... 4
4. Marginal vesicles in about same number as tentacles + young bulbs ..... 5  
    Marginal vesicles about twice as numerous as tentacles ..... 7
5. Gonads small, oval, near margin, ♀ with few, very large eggs; 16–26 tentacles ..... *rangiroae*  
    Gonads elongated ..... 6
6. Gonads on less than half the distal part of radial canals; about 32 tentacles ..... *lomae*  
    Gonads along distal 1/2–3/4 of radial canals; 60–85 tentacles ..... *simplex*
7. With very long, fringed lips; about 60 tentacles ..... *gregarium*  
    Lips short, simple ..... 8
8. Tentacle bulbs globular ..... *hemisphaericum*  
    Tentacle bulbs remarkably small ..... *uchidai*

Immature medusae: *P. ambiguum* (AGASSIZ & MAYER 1899); *P. pacificum* (AGASSIZ & MAYER 1899, non MAAS 1906 = *P. malayense* KRAMP 1961).

Abnormal medusae: *P. chengshanense* (LING 1937), *P. gardineri* (BROWNE 1905).

*Phialidium hemisphaericum* (L.). Up to 20 mm wide, nearly hemispherical, jelly fairly thin. Stomach small, four short, simple lips. Gonads oval or linear, 1/2 to 3/4 of the length of radial canals, somewhat nearer to



margin than to stomach. 16 or 30–58 tentacles with globular bulbs; 1–3, usually 2, statocysts between tentacles, each with one concretion. — The Indo-West-Pacific region from East Africa to New Zealand. Coastal waters in the eastern Atlantic from Iceland and northern Norway to the Cape of Good Hope; Mediterranean. (KRAMP 1919, p. 91, Pl. 4, fig. 14, Pl. 5, fig. 3, text-figs. 16, 17; RUSSELL 1953, p. 285, Pl. 16, fig. 1, Pl. 17, fig. 6, text-figs. 172–179).

*Phialidium simplex* BROWNE 1902. Up to 22 mm wide, 10 mm high, watch-glass-shaped. Stomach short, with four large fimbriated lips. Gonads along distal 1/2 to 3/4 of radial canals, linear, slightly folded. 60–85 tentacles with globular bulbs, and a few young bulbs. One statocyst between tentacles, each with one concretion. Specimens seen with three and six radial canals. — Tropical parts of Indo-West-Pacific Region; coast

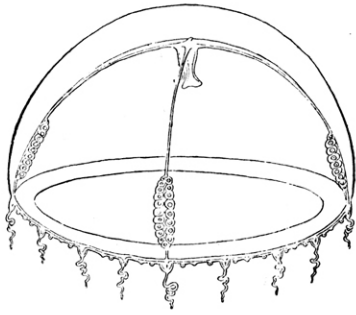


Fig. 201. *Phialidium hemisphaericum* (from MAYER).

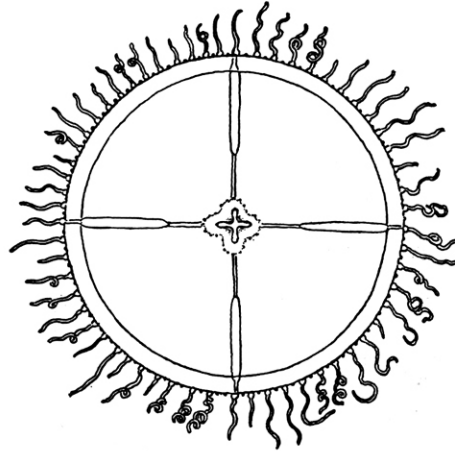


Fig. 202. *Phialidium simplex* (after BROWNE & KRAMP, redrawn by P. W.).

of Chile; South Africa. Brazil. The subantarctic islands Campbell Island in the Pacific and Falkland Islands in the Atlantic. (KRAMP 1965 p. 63).

*Phialidium rangiroae* (AGASSIZ & MAYER 1902). 7 mm wide, flatter than a hemisphere; stomach very short, quadratic, not cruciform, four slightly recurved lips; gonads small, oval, near margin; 16–26 well developed tentacles with large, conical bulbs; statocysts in same number as tentacles, each with one concretion. — Philippines; New Guinea; N. E. Australia; Polynesian Islands. (AGASSIZ & MAYER 1902 p. 145, Pl. 1, fig. 4; KRAMP 1965 p. 61).

*Phialidium malayense* KRAMP 1961. 5 mm wide; stomach large, globular; mouth with four prominent lips; four large, oval gonads on middle 1/3 of radial canals; 32 or more equally spaced tentacles; 0–2 stato-

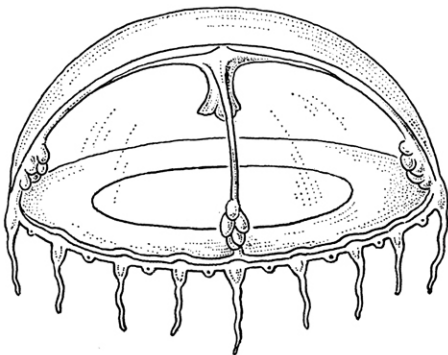


Fig. 203. *Phialidium rangiroae* (from AGASSIZ & MAYER, redrawn by P. W.).

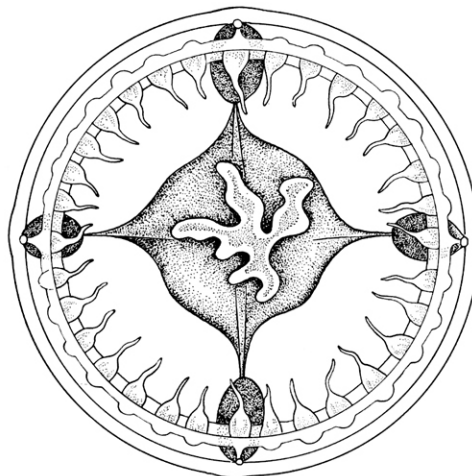


Fig. 204. *Phialidium malayense* (from MAAS, redrawn by E. L.).

cysts between tentacles. — North Australia; Amboina; Vietnam; China. (MAAS 1906 *a* p. 91, Pl. 2, fig. 7, as *Phialidium pacificum* (AGASSIZ & MAYER)).

*Phialidium lomae* TORREY 1909. 9–12, rarely 14 mm wide, about four times broader than high, thin; manubrium short, cruciform, with four slightly frilled lips; gonads narrow, on less than half the distal part of radial canals; 28–37 tentacles and some young bulbs; one, rarely two, statocysts between adjoining tentacles, each with one concretion. — California. (TORREY 1909 p. 22, fig. 8).

*Phialidium gregarium* (L. AGASSIZ 1862). 12 mm wide, hemispherical; stomach small, four very long, curved, fringed lips; gonads linear, along distal half of radial canals; 60 tentacles with large, spherical bulbs; 1–2 statocysts between tentacles, each with one concretion. — Pacific coast of North America. (MURBACH & SHEARER 1903 p. 179, Pl. 20, figs. 1, 1 *a*; KRAMP 1962 p. 25; ROOSEN-RUNGE 1962 p. 15, figs. 1–5).

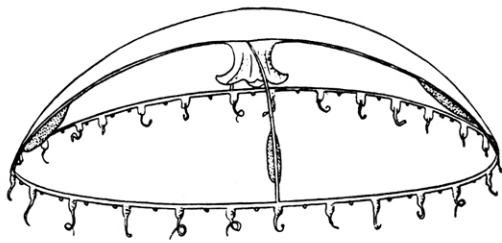


Fig. 205. *Phialidium lomae* (from TORREY).

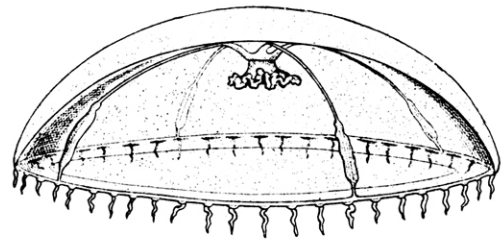


Fig. 206. *Phialidium gregarium* (from MURBACH & SHEARER).

*Phialidium iridescens* MAAS 1906. 4–5 mm wide, somewhat globular, jelly fairly thick, subumbrella iridescent; stomach wide, quadrangular, mouth with four small, complexly folded lips; gonads spindle-shaped, along middle portion of radial canals; 16 well developed tentacles with broad, conical bases, and 16 small tentacles, large and small ones not regularly alternating; number and structure of statocysts unknown. — Antarctic Ocean. (MAAS 1906 *b* p. 13, Pl. 1, fig. 6).

*Phialidium brunescens* (BIGELOW 1904). 2 mm wide, 0.7 mm high; manubrium very short and broad, four lips; gonads large, thick and prominent, proximal; about 30 short, thick tentacles; a prominent, brown pigment spot at base of each tentacles; 32–40 small statocysts with 1–2 concretions. — Maldive Islands. (BIGELOW 1904 p. 253, Pl. 1, fig. 2, as *Oceania brunescens*).

*Phialidium uchidai* KRAMP 1961. 10 mm wide, low-dome-like; manubrium four-sided; gonads near, but not reaching circular vessel, oval to oblong; 16–28 short tentacles, tentacle bulbs less prominent than in other species; 24–42 statocysts, irregularly placed. — Palao Islands, Pacific Ocean. (UCHIDA 1947 *a* p. 305, fig. 7, as *Phialidium simplex*; KRAMP 1961 *a* p. 172, as *P. uchidai* nov. nom.).

*Phialidium ambiguum* (AGASSIZ & MAYER 1899). 4 mm wide, jelly very thick; immature gonads near manubrium, which is flask-shaped, with four simple lips; 16 short tentacles with large bulbs; 1–2 statocysts between tentacles, with one concretion. — Fiji Islands. (AGASSIZ & MAYER 1899 p. 167, Pl. 6, figs. 18, 19).

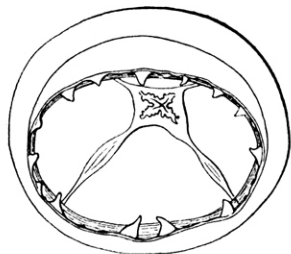


Fig. 207. *Phialidium iridescens* (after MAAS, from MAYER).

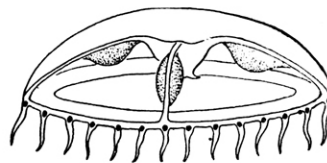


Fig. 208. *Phialidium brunescens* (after BIGELOW, from MAYER).

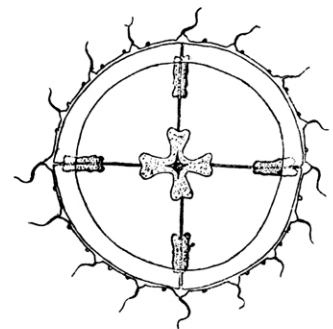


Fig. 209. *Phialidium uchidai* (from UCHIDA).

*Phialidium gardineri* (BROWNE 1905). 5 mm wide, jelly thin; stomach small, four or five short lips; a small gonad on middle of each radial canal; five radial canals, four of them about 90° apart, the fifth between two of the others; about 13–14 tentacles and somewhat more rudimentary bulbs, irregularly spaced; about 32 statocysts. Probably an abnormal specimen of a four-radiated form. — Maldive Islands. (BROWNE 1905 a p. 731, Pl. 55, figs. 1–3, as *Pseudoclytia gardineri*).

*Phialidium chengshanense* (LING 1937). 5–6×3.5–4 mm wide, flat, oval (young specimens circular); up to six manubria; usually four radial canals to each fully developed stomach, reaching ring canal; to each young stomach 2–3 canals, partly incomplete; no centripetal canals observed; gonads ovoid, distal, 2–6 in number; numerous well developed tentacles, alternating with rudimentary ones; statocysts numerous. An abnormal *Phialidium*. — Japan and China. (LING 1937 p. 356, figs. 6–8; KOMAI & YAMAZI 1944 pp. 105–08, figs. 1–3).

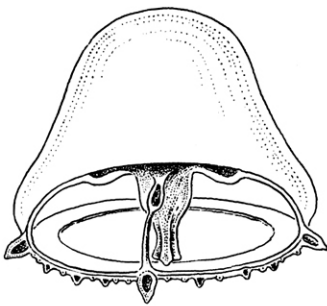


Fig. 210. *Phialidium ambiguum*  
(from AGASSIZ & MAYER).

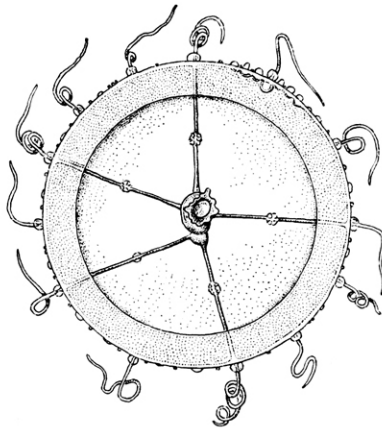


Fig. 211. *Phialidium gardineri*  
(from BROWNE, redrawn by P. W.).

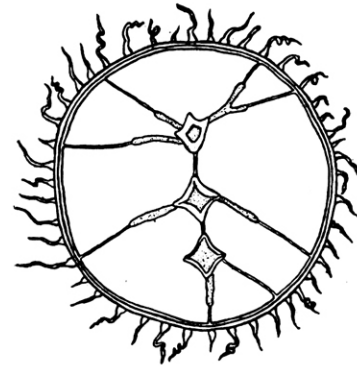


Fig. 212. *Phialidium chengshanense*  
(from CHIU).

## Family Lovenellidae.

Leptomedusae with small stomach; without peduncle; with four simple radial canals; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without excretory pores; with lateral or marginal cirri; with closed marginal vesicles; without ocelli. Hydroids, where known, *Lovenella*-like, hydrotheca with operculum.

### Key to the genera of Lovenellidae represented in Indo-Pacific waters.

- |   |                      |
|---|----------------------|
| 1. With marginal cirri; without lateral cirri .....                 | <i>Cirrholovenia</i> |
| With lateral cirri; without marginal cirri .....                    | 2                    |
| 2. Marginal vesicles usually 8, occasionally 4 or 12 .....          | <i>Eucheilota</i>    |
| Number of marginal vesicles indefinite, 16 or more when adult ..... | <i>Lovenella</i>     |

*Cirrholovenia* KRAMP 1959. Lovenellidae with marginal cirri, without lateral cirri.

### Key to the Indo-Pacific species of *Cirrholovenia*.

- |                                |                  |
|--------------------------------|------------------|
| 4 tentacles .....              | <i>tetranema</i> |
| About 32 (–40) tentacles ..... | <i>polynema</i>  |

*Cirrholovenia polynema* KRAMP 1959. Up to 12 mm wide, about hemispherical, jelly fairly thick; velum very broad; stomach square, mouth with four slightly crenulated lips; gonads linear, along middle half of

radial canals; about 32–40 tentacles; up to eight marginal cirri between successive tentacles, long, spirally coiled; twice as many marginal vesicles as tentacles, each with one concretion. — East Africa to Tahiti; Japan; New Zealand. (KRAMP 1959 *b* p. 251, fig. 16 *a-c*).

*Cirrholovenia tetranema* KRAMP 1959. Up to 1.5 mm high and wide, jelly thin, velum narrow; stomach small, cruciform, mouth with very short, simple lips; gonads thick, cylindrical, along almost whole length of radial canals; four long perradial tentacles with broad basal bulbs; no rudimentary bulbs; 7–8 marginal cirri in each quadrant; four interradial or eight adradial marginal vesicles. — Strait of Malacca; Gulf of Siam; Philippines; Bali; Solomon Islands. Mediterranean. (KRAMP 1959 *b* p. 253, fig. 17 *a, b*).

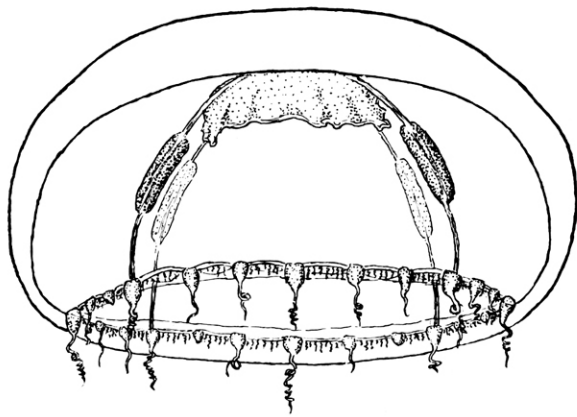


Fig. 213. *Cirrholovenia polynema* (from KRAMP).

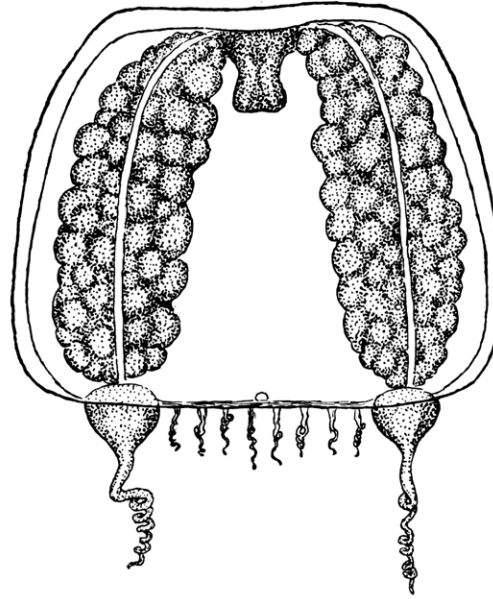
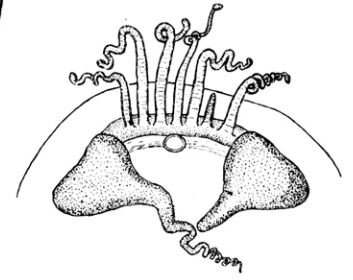


Fig. 214. *Cirrholovenia tetranema* (from KRAMP).



*Lovenella* HINCKS 1868. Lovenellidae with lateral cirri, without marginal cirri; with indefinite number of marginal vesicles, 16 or more when adult. Hydroid: *Lovenella*.

#### Key to the Indo-Pacific species of *Lovenella*.

- 4 tentacles; gonads large, oval sacs ..... *assimilis*  
8–16 tentacles; gonads spindle-shaped, distal ..... *cirrata*

*Lovenella cirrata* (HAECKEL 1879). 16 mm wide, nearly hemispherical; stomach short, urn-shaped, four lips; four spindle-shaped gonads on distal half of radial canals. 8–16 tentacles with large bulbs flanked by 5–7 pairs of spiral cirri; 3–5 rudimentary marginal warts between successive tentacles; about 16 marginal vesicles, each with about three concretions. — Malayan Archipelago. Mediterranean; west coast of Africa; Brazil. (HAECKEL 1879 p. 182, Pl. 11, figs. 9–11, as *Mitrocomium cirratum*).

*Lovenella assimilis* (BROWNE 1905). 2.5 mm wide, a little broader than high, jelly fairly thick; stomach short, with a quadrangular base; gonads large oval sacs, longitudinally divided, close by ring canal; four tentacles with large basal bulbs, each flanked by 3–4 pairs of lateral cirri; in each quadrant about five rudimentary bulbs, the median one the largest, and about five marginal vesicles with two concretions. — Ceylon; Chefoo in China. (BROWNE 1905 *b* p. 137, Pl. 1, fig. 3, as *Mitrocomium simile*; CHOW & HUANG 1958 pp. 182, 191, Pl. 4, figs. 31, 32).

*Eucheilota* MCCRADY 1857. Lovenellidae with lateral cirri; without marginal cirri; with fixed number of marginal vesicles, usually eight, occasionally four or twelve. A revision of the species is needed.

**Key to the Indo-Pacific species of *Eucheilota*.**

1. With medusa-buds on gonads; 4 large tentacles and 4 or more rudimentary bulbs, all with 1-3 pairs of cirri; 8 marginal vesicles ..... *paradoxa*  
     No medusa-buds ..... 2
2. 16 or more well-developed tentacles ..... 3  
     No more than 2-8 well-developed tentacles ..... 4
3. Tentacles and small bulbs with 1-3 pairs of cirri; about 16 tentacles and 24 young bulbs; 7-14 marginal vesicles; stomach on low peduncle ..... *comata*  
     With 16 tentacles and 16 rudimentary bulbs with one pair of cirri, about 24 minute knobs without cirri; 8 marginal vesicles ..... *ventricularis*
4. With 12 marginal vesicles; 4 tentacles with one pair of cirri; no rudimentary bulbs ..... *duodecimalis*  
     With 8 marginal vesicles ..... 5

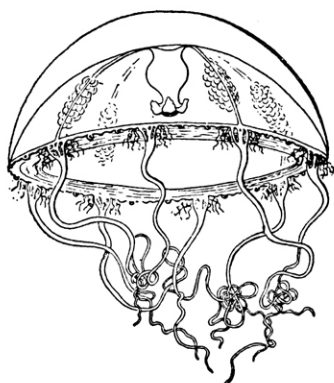


Fig. 215. *Lovenella cirrata* (after HARTLAUB, from MAYER).

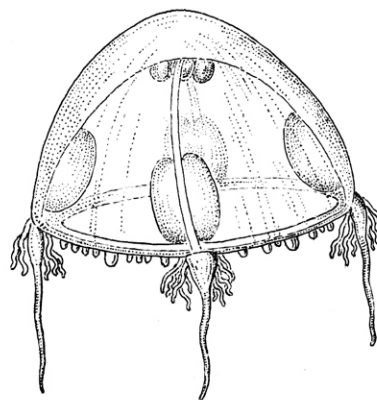


Fig. 216. *Lovenella assimilis* (from BROWNE).

5. With two well-developed tentacles (young stages) ..... 6  
     With 4-8 well-developed tentacles ..... 7
6. With 2 large and 2 rudimentary tentacles; 4 marginal vesicles ..... *bakeri*  
     With 2 tentacles and about 32 small bulbs, each with black pigment in tip; 8 marginal vesicles ..... *diademata*
7. Gonads globular; 4 perradial tentacles with 2-3 pairs of cirri, 4 interradial tentacles without cirri; tentacles and rudimentary bulbs with black pigment ..... *menoni*  
     Gonads elongated; 4 perradial tentacles and 12-20 rudimentary bulbs with one pair of cirri; no black pigment on marginal bulbs ..... *tropica*

*Eucheilota ventricularis* McCrady 1857. 10 mm wide, hemispherical; manubrium short, four prominent lips; gonads linear, along middle 1/3 of radial canals; 16 tentacles and 16 rudimentary bulbs, all with a pair of lateral cirri; also about 24 minute knobs without cirri; 8 statocysts, each with about eight concretions.

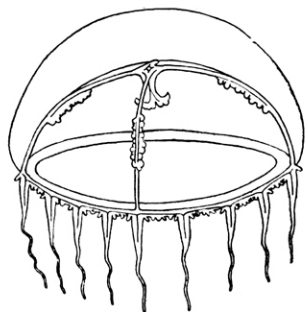


Fig. 217. *Eucheilota ventricularis* (after MAYER, from KRAMP).

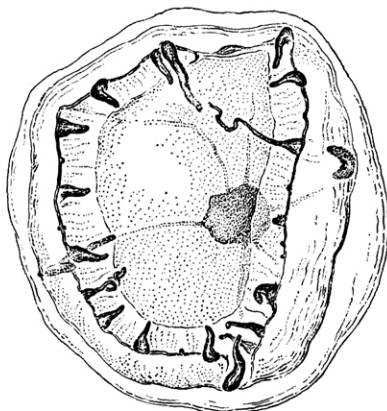


Fig. 218. *Eucheilota comata* (from BIGELOW, redrawn by P. W.).



Fig. 219. *Eucheilota paradoxa* (from MAYER, redrawn by P. W.).

— Red Sea; Chagos Islands, Indian Ocean; Malayan Archipelago; Solomon Islands, Melanesia. Coastal waters in southern parts of east coast of North America; Brazil; west coast of Africa. (McCRADY 1857 p. 85, Pl. 11, figs. 1, 2, Pl. 12, figs. 1–3; MAYER 1910 p. 282, Pl. 37, fig. 5, Pl. 38, fig. 1).

*Eucheilota comata* (BIGELOW 1909). 6–12 mm wide, somewhat higher than a hemisphere, thick; manubrium short, flask-shaped, four slightly crenulated lips, low peduncle; gonads linear from middle 1/3 to near distal end of radial canals; 17 tentacles and 23 rudimentary bulbs (in Pacific specimens) or 19 tentacles and 62 rudimentary bulbs (in West-Indian specimens), each flanked by 1–3 pairs of lateral cirri; 7–14 large statocysts. — Mexico Pacific; Chile. West-Indies. (BIGELOW 1909 p. 158, Pl. 5, figs. 6, 7, Pl. 6, fig. 9, Pl. 37, figs. 9, 10, 12, as *Phialucium comata*).

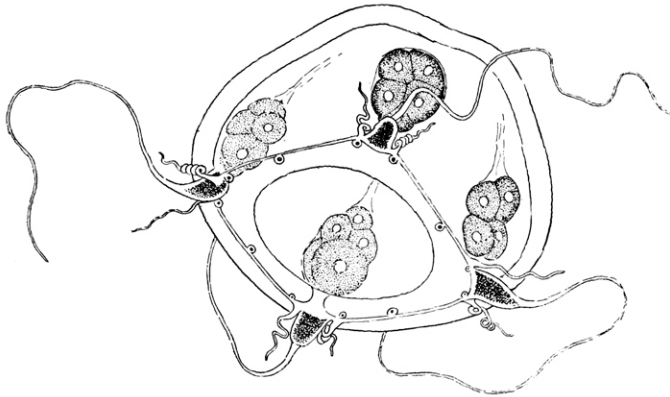


Fig. 220. *Eucheilota duodecimalis* (from MAYER).

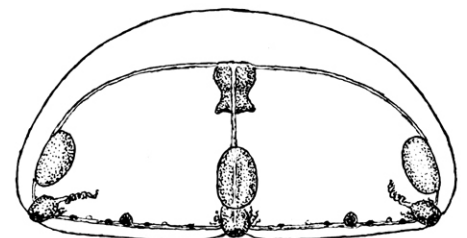


Fig. 221. *Eucheilota menoni* (from KRAMP).

*Eucheilota paradoxia* MAYER 1900. 4 mm wide, higher than a hemisphere; manubrium small, flask-shaped; gonads along middle portion of radial canals, medusa-buds on gonads; four large tentacles with a pair of lateral cirri; four or more rudimentary bulbs flanked by cirri; eight marginal vesicles with one concretion. — Malayan Archipelago; Japan. Florida and the Bahamas. (MAYER 1900 b p. 56, Pl. 40, figs. 134–36; MAYER 1910 p. 285, Pl. 37, figs. 3–3").

*Eucheilota duodecimalis* A. AGASSIZ 1862. 2.5 mm wide, higher than a hemisphere; manubrium very short; gonads along distal half of radial canals; 12 marginal vesicles, each with one concretion; four tentacles with one pair of lateral cirri. — Mexico Pacific. New England; South Carolina; Florida. (MAYER 1910 p. 283, Pl. 36, fig. 6, Pl. 37, figs. 1, 2, textfig. 151).

*Eucheilota menoni* KRAMP 1959. 2.5 mm wide, hemispherical, jelly fairly thick; velum very broad; globular

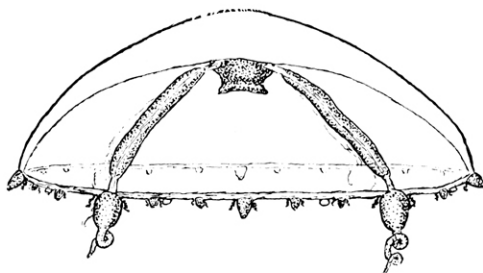


Fig. 222. *Eucheilota tropica* (from KRAMP).

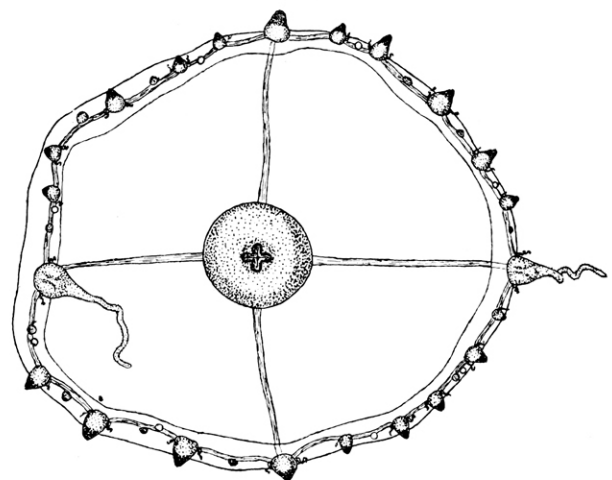


Fig. 223. *Eucheilota diademata* (from KRAMP).



gonads with large ova between middle and distal portion of radial canals; four large perradial tentacles with 2–3 pairs of lateral cirri, four large interradial and 16 very small rudimentary bulbs without cirri. Eight adradial marginal vesicles with one concretion; lateral walls of stomach with black pigment granules; perradial and interradial marginal bulbs with black pigment. — Madras, India; Java Sea; Nicobar Islands; Strait of Malacca; Philippines. (MENON 1932 p. 17, Pl. 1, fig. 9, as *Eucheilota* sp. II; KRAMP 1959 *b* p. 248, fig. 14 *a, b*, as *E. menoni*).

*Eucheilota tropica* KRAMP 1959. 4 mm wide, 1.5 mm high, apical jelly thick; velum narrow; manubrium short; gonads elongated, along almost entire length of radial canals; four large perradial tentacles and in each

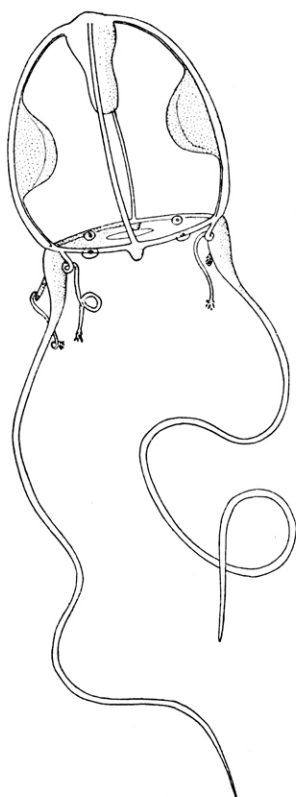


Fig. 224. *Eucheilota bakeri* (from TORREY).

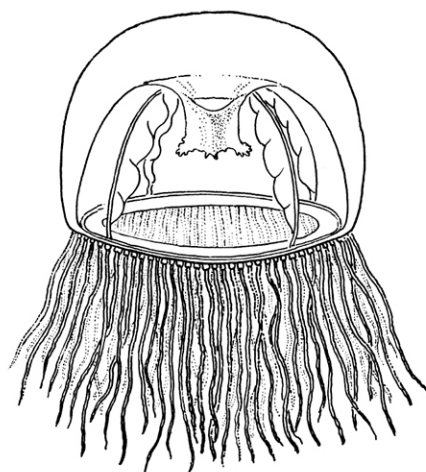


Fig. 225. *Phialella falklandica* (from BROWNE & KRAMP, redrawn by P. W.).

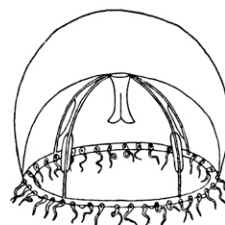


Fig. 226. *Phialella quadrata* (after BROWNE, from KRAMP).

quadrant up to five rudimentary bulbs, the interradial larger than the others and sometimes developed into tentacles; tentacles and marginal bulbs with one pair of lateral cirri and without black pigmentation; eight marginal vesicles with 1–3 concretions. — India; Malayan Archipelago; Philippines; Japan. (MENON 1932 p. 17, Pl. 1, fig. 6, as *Eucheilota* sp. I; KRAMP 1959 *b* p. 247, fig. 13, as *E. tropica*).

*Eucheilota diademata* KRAMP 1959. 3 mm wide (young medusa), watch-glass-shaped; velum narrow; manubrium bottle-shaped; no gonads; two opposite, perradial tentacles with conical bulbs, with one pair of lateral cirri and without pigmentation; 29 rudimentary marginal bulbs with one pair of cirri and each with a distinct black spot on the extreme tip; eight marginal vesicles with three concretions. — Philippines. (KRAMP 1959 *b* p. 249, fig. 15).

*Eucheilota bakeri* (TORREY 1909). Young medusa: four marginal vesicles; two gonads; two well developed and two small tentacles, the two large ones with a pair of lateral cirri. Hydroid a *Campanularia*. — California. (TORREY 1909 p. 21, fig. 7, as *Phialium bakeri*).

## Family Phialellidae.

Leptomedusae with small stomach; without peduncle; with four simple radial canals; with gonads with median groove, on radial canals separated from stomach; with hollow marginal tentacles; without excretory pores; without marginal or lateral cirri; with eight closed marginal vesicles usually with two or more concretions; without ocelli. Hydroids, where known, with hydranth without webs, hydrotheca with operculum.

*Phialella* BROWNE 1902. Phialellidae with the characters of the family.

### Key to the Indo-Pacific species of *Phialella*.

Gonads along almost entire length of radial canals, hanging down in wavy folds; about 60 tentacles ..... *falklandica*  
 Gonads elongated, oval, in distal 1/3 of radial canals; 16–32 tentacles ..... *quadrata*, incl. *fragilis*

Doubtful species; *P. annulata* (LENDENFELD), *P. hyalina* (LENDENFELD), *P. dissonema* (HAECKEL), *P. sp.* MENON.

*Phialella falklandica* BROWNE 1902. Up to 17 mm wide, semi-globular, thick walls; stomach short, quadrangular; four lips with fimbriated margin; gonads along greater part of radial canals, hanging down in wavy folds; about 60 tentacles with large bulbs; statocysts on broad, cushion-like bulbs, with two or more concretions. — Southern part of west coast of South America; Falkland Islands; Auckland and Campbell Islands south of New Zealand. (BROWNE & KRAMP 1939 p. 296, Pl. 17, figs. 2–4, Pl. 19, figs. 3–5, textfig. 1).

*Phialella quadrata* (FORBES 1848). 13 mm wide, hemispherical, thick walls; stomach short, quadratic, with small base; four short, slightly folded lips; gonads on distal 1/3 of radial canals, elongated oval; 16–32 tentacles with small, globular basal bulbs; no ocelli; statocysts on cushion-like swellings, with 2–4 or more concretions. — Malayan Archipelago; Philippines; Japan; New Zealand; Chile. North-western Europe; West-Africa. (RUSSELL 1953 p. 315, Pl. 16, figs. 4–6, Pl. 17, fig. 5, textfigs. 196–200).

*Phialella fragilis* (UCHIDA 1938). 5–6 mm wide, 9–12 mm high, dome-shaped, jelly thin and soft; manubrium small, four well developed lips; gonads linear, sac-like, along distal 1/3 of radial canals; 16 tentacles; statocysts mounted on warts. — Japan. (UCHIDA 1938 p. 51, fig. 4, as *Eucope fragilis*).

*Phialella hyalina* (VON LENDENFELD 1884). 6 mm wide, watch-glass-shaped, thick at centre; stomach half as long as bell cavity, wide; four large, oval gonads on distal 1/3 of radial canals; eight tentacles, bulbs nearly cylindrical; large marginal vesicles, each with three concretions. — Australia. (VON LENDENFELD 1884 p. 920, Pl. 42, figs. 16–18, as *Eucope hyalina*).

*Phialella dissonema* (HAECKEL 1879). 5 mm wide, 7 mm high, pyriform; exumbrella thickly besprinkled with nematocysts; manubrium spindle-shaped, half the length of bell cavity, four short recurved lips; gonads sac-like, along middle half of radial canals; short, conical apical canal; two opposite tentacles, with large, pyriform bulbs, very long; statocysts each with one concretion. Doubtful species. — Hawaiian Islands. (HAECKEL 1879 p. 169, Pl. 11, fig. 5, as *Saphenella dissonema*).

## Eucopida incertae sedis.

With closed marginal vesicles.

*Blackfordia* MAYER 1910. Eucopida with four radial canals; without gastric peduncle; with gonads completely surrounding radial canals; with numerous hollow marginal tentacles; the endodermal cores of the

tentacles extend inwards from the bell margin into the gelatinous substance of the bell; with numerous closed marginal vesicles; without permanently rudimentary tentacles; without marginal or lateral cirri.

*Blackfordia virginica* MAYER 1910. 14 mm wide, higher than a hemisphere, with rounded apex; stomach narrow, half as long as bell cavity, four long, recurved, fluted lips; gonads linear, from corners of stomach extending along somewhat more than half the length of radial canals; about 80 long tentacles with finger-shaped or broadly oval diverticula into bell margin; one (rarely two) marginal vesicles between successive tentacles, each with 2–3 concretions. According to the original description black pigment granules are present at base of marginal vesicles, but examination of specimens from all three localities has revealed no such pigment. — Ganges estuary, India. Atlantic coast of New England; Black Sea. (MAYER 1910 p. 277, Pl. 36, figs. 3–5, Pl. 37, fig. 6; KRAMP 1958 p. 343, fig. 1).

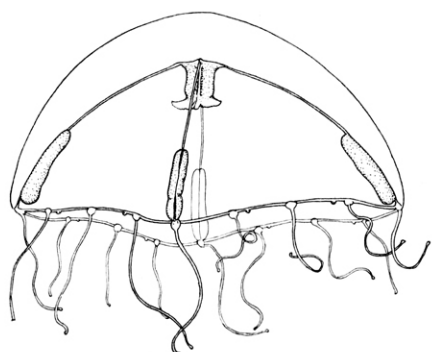


Fig. 227. *Phialella fragilis* (from UCHIDA).

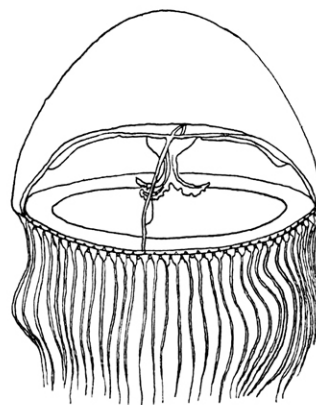


Fig. 228. *Blackfordia virginica* (after MAYER, from THIEL).

## Family Phialuciidae.

Leptomedusae with small stomach; with 4–8 simple radial canals; without peduncle; with gonads completely surrounding radial canals (except in *Octocannoides*) and separated from stomach; with excretory papillae on adaxial side of marginal bulbs; without marginal or lateral cirri; with closed marginal vesicles. Hydroids unknown.

### Key to the genera of Phialuciidae.

1. With normally 4 radial canals; no ocelli ..... *Phialucium*  
     With normally 8 or 16 radial canals ..... 2
2. With 8 tentacles with adaxial ocelli ..... *Octocannoides*  
     Without ocelli ..... *Octophialucium*

*Phialucium* MAAS 1905. Phialuciidae with normally four radials canals; with permanently rudimentary tentacle bulbs and marginal bulbs with adaxial excretory papillae; without ocelli.

### Key to the species of *Phialucium*.

1. Gonads along almost entire length of the four radial canals, which are ribbon-like and folded; 25–32 tentacles ..... *multitentaculata*  
     Gonads half as long as radial canals, or less ..... 2
2. Gonads situated very near corners of stomach ..... *condensum*  
     Gonads in distal part of radial canals ..... 3
3. Rudimentary marginal bulbs tenon-like, conical, all alike, permanently rudimentary, without excretory papillae ..... *mbenga*

- Rudimentary marginal bulbs knob-like, the median one between successive tentacles larger than the others and provided with an excretory papilla ..... 4
4. Gonads linear, simple, in distal half of radial canals; 16–36 tentacles ..... *carolinae*  
 Gonads wide ribbons, slightly twisted, near margin; 8 or more tentacles ..... *taeniogonia*

*Phialucium mbenga* (AGASSIZ & MAYER 1899). 9–12 mm wide, flatter than a hemisphere; stomach urn-shaped, wider than long; gonads linear, swollen, along distal half of radial canals; 16 tentacles and about 80 rudiments, tenon-like, triangular, all alike; 32 statocysts with 5–9 concretions. — Indo-West-Pacific tropical region from East Africa to the Melanesian Islands. (AGASSIZ & MAYER 1899 p. 168, Pl. 8, figs. 24, 25, as *Mitrocoma mbenga*; BIGELOW 1904 p. 252, Pl. 1, figs. 3, 4, as *Oceania virens*; MAAS 1905 p. 32, Pl. 6, figs. 36, 37, as *Phialucium virens*; KRAMP 1953 p. 275, fig. 1, synonyms).

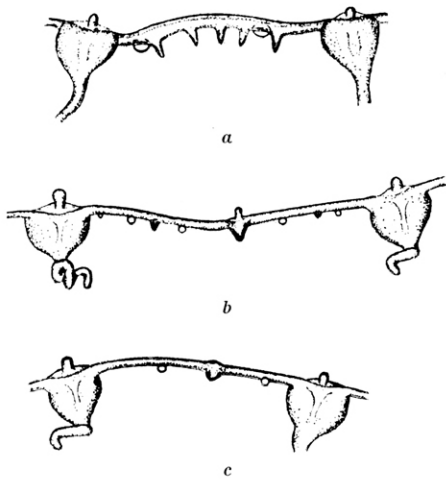


Fig. 229. Marginal organs: a *Phialucium mbenga*  
 b and c *Ph. carolinae* (from KRAMP).

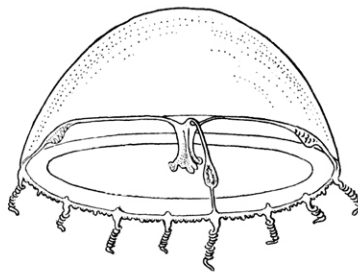


Fig. 230. *Phialucium carolinae*  
 (from MAYER, redrawn by P. W.).

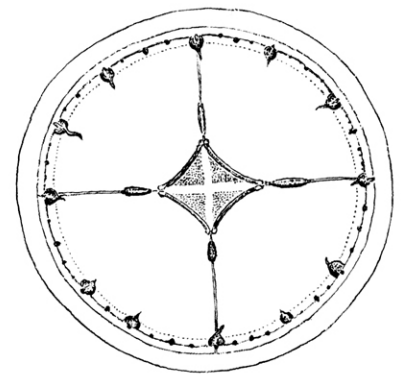


Fig. 231. *Phialucium condensum*  
 (from KRAMP).

*Phialucium carolinae* (MAYER 1900). 14–20 mm wide, not quite hemispherical, jelly fairly thick; stomach flask-shaped, simple lips, usually four but sometimes up to eight radial canals; gonads linear, along distal half of radial canals; 16–36 well developed tentacles; between successive tentacles usually three rudimentary bulbs, the middle one the largest, and four marginal vesicles, each with two concretions. — Indo-West-Pacific Region from East Africa to Australia and to Chefoo in China. (MAYER 1900 a, p. 7, Pl. 3, fig. 9, Pl. 4, figs. 10, 11, as *Oceania carolinae*; MAYER 1910 p. 275, Pl. 36, figs. 1', 1''; KRAMP 1953 p. 276, figs. 2, 3, variation and synonyms; KRAMP 1965 p. 70).

*Phialucium condensum* KRAMP 1953. Diameter 6–7 mm; similar to *P. carolinae*, but gonads very near the corners of the stomach, 1/4 to 1/3 of the length of radial canals. — North-eastern Australia; Kei Islands in the Banda Sea. (KRAMP 1953 p. 279, Pl. 1, fig. 4, textfig. 4).

*Phialucium multitentaculatum* MENON 1932. 11 mm high, 14 mm wide, very thick; stomach rectangular, small, with four fimbriated lips, rather long; four radial canals, ribbon-like and folded in adult; gonads along almost entire length of the radial canals; 25–32 tentacles, 3–4 rudiments between tentacles; about 150 statocysts, with 2 (–4) concretions. — Madras in India; Gulf of Tonkin. (MENON 1932, p. 16, Pl. 2, figs. 15, 16).

*Phialucium taeniogonia* CHOW & HUANG 1958. Up to 15 mm wide, higher than a hemisphere, jelly thick, thinning towards margin; stomach quadrate, mouth tube very short, four simple lips; four narrow radial canals; gonads slightly twisted wide ribbons near umbrella margin; generally eight or more marginal tentacles, at somewhat irregular distances from each other, with globular or broadly conical bulbs; between successive tentacles 3–8 small rudimentary bulbs, the median one larger than the others; statocysts alternating with tentacles and rudimentary bulbs. — Chefoo in China. (CHOW & HUANG 1958 pp. 180, 190, Pl. 3, figs. 24–26).

*Octocannoides* MENON 1932. Phialuciidae with eight simple radial canals which arise separately from periphery of stomach; eight tentacles with abaxial ocelli; "sense clubs" (?) on bell margin; statocysts without ocelli; no peduncle; eight lips; gonads consisting of two lateral halves.

*Octocannoides ocellata* MENON 1932, *non* KRAMP 1958. 5–7 mm wide, flatter than a hemisphere, not thick; eight large gonads on middle portion of radial canals, each consisting of two lateral halves; tentacles with large, conical bulbs with conspicuous abaxial ocelli (not cordyli); in each octant about five statocysts with 2–3 concretions. — India. (MENON 1932 p. 21, Pl. 3, figs. 27, 28).

*Octophialucium* KRAMP 1955. Phialuciidae with normally eight radial canals; without ocelli.

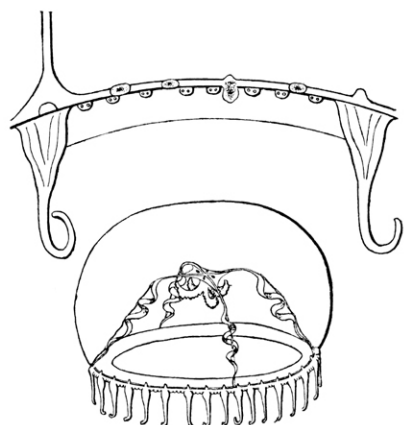


Fig. 232. *Phialucium multitentaculatum*  
(from MENON).

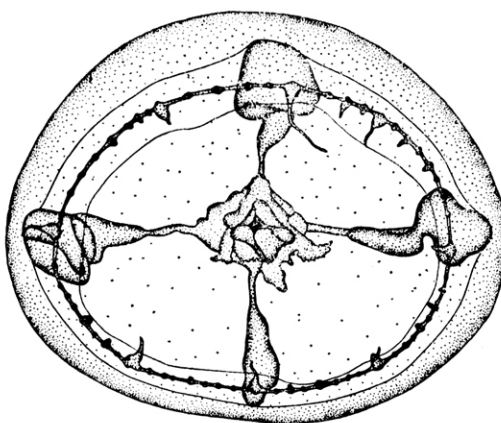


Fig. 233. *Phialucium taeniogonia*  
(from CHOW & HUANG).



Fig. 234. *Octocannoides ocellata* (from MENON).

#### Key to the Indo-Pacific species of *Octophialucium*.

- |   |                  |
|---|------------------|
| 1. Gonads along greater part of radial canals.....  | 2                |
| Gonads in distal 1/5 or less of radial canals .....   | 4                |
| 2. With 4 tentacles; about 10 rudimentary bulbs without excretory papillae per quadrant, marginal vesicles as many as tentacles plus rudiments .....  | <i>solidum</i>   |
| With 8–16 tentacles; with excretory papillae.....   | 3                |
| 3. Gelatinous substance very thick, umbrella almost spherical; with 8 radial canals; gonads swollen, along almost whole length of radial canals; with 8 tentacles; 1–3 rudimentary bulbs between successive tentacles ..... | <i>bigelowi</i>  |
| Umbrella evenly vaulted, not very thick; with 6–11, usually 8 radial canals; gonads linear, along distal 2/3–3/4 part of radial canals; with about 16 tentacles, 3–5 rudimentary bulbs between successive tentacles .....   | <i>medium</i>    |
| 4. Tentacles very numerous, closely crowded, no rudimentary bulbs between tentacles; marginal vesicles more numerous than tentacles .....   | <i>aphrodite</i> |
| 19–28 tentacles; 3–5 rudimentary bulbs between successive tentacles; marginal vesicles in same number as tentacles plus rudiments .....   | <i>indicum</i>   |

*Octophialucium indicum* KRAMP 1958. Up to 25 mm wide, disk-like or lenticular, thick; stomach short, 1/6 as wide as umbrella; eight pointed crenulated lips; 6–11 radial canals (usually 8) continued inwards almost to centre of stomach; gonads along distal 1/5 or less of radial canals; 19–28 tentacles with broadly conical bulbs with long excretory papillae; no abaxial exumbrellar clasps; between tentacles 3–5 small triangular bulbs with excretory papillae; one statocyst between successive marginal bulbs. — Indo-West-Pacific tropical region from Madagascar to Tahiti. (MENON 1932 p. 23, Pl. 3, fig. 25, as *Octocanna polynema*; KRAMP 1958 p. 347, textfig. 2 a, b, as *Octophialucium indicum*).

*Octophialucium medium* KRAMP 1955. 15–30 mm wide, evenly vaulted, not lenticular; stomach 1/7 as wide as umbrella, with broad, star-shaped figure; 8 pointed, crenulated lips; gonads linear, along distal 2/3–3/4 part of radial canals; about 16 tentacles; 3–5 rudimentary bulbs between successive tentacles, one

marginal vesicle between successive marginal bulbs; number of radial canals usually 8, varying from 6 to 11. — Gulf of Guinea; Philippines; Ceylon. (KRAMP 1955 p. 257, Pl. 2 fig. 1, textfigs. 4, 5).<sup>1</sup>

*Octophialucium bigelowi* KRAMP 1955. 10 mm high, 8 mm wide, with very thick jelly; mouth with eight pointed lips; gonads swollen, along almost entire length of radial canals; eight large tentacles; 1–3 triangular bulbs with excretory papillae between tentacles; 3–5 statocysts between tentacles. — Mexico Pacific; Panama. (BIGELOW 1909, p. 169, Pl. 6, figs. 6, 10, Pl. 38, figs. 1–3, as *Octocanna polynema*).

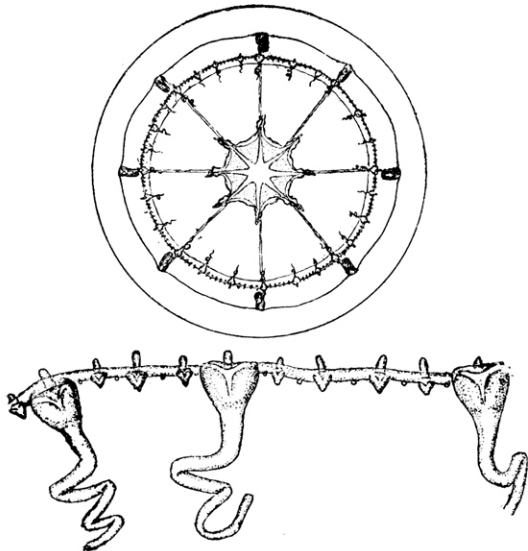


Fig. 235. *Octophialucium indicum* (from KRAMP).

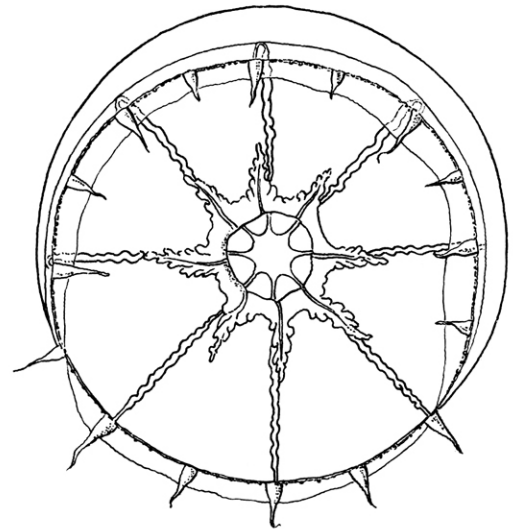


Fig. 236. *Octophialucium medium* (from KRAMP, redrawn by P. W.).

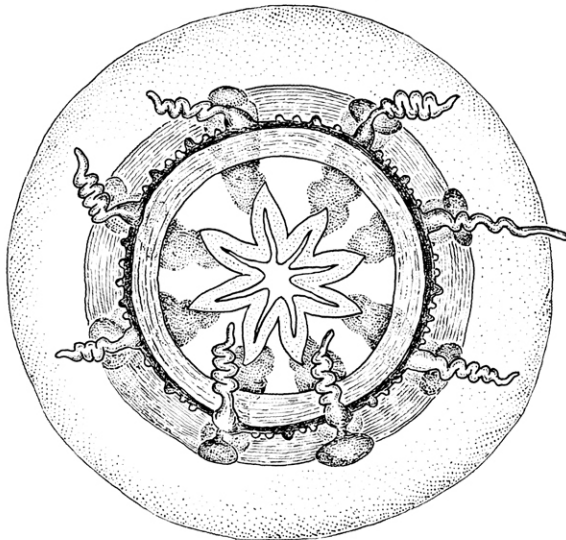


Fig. 237. *Octophialucium bigelowi* (from BIGELOW, redrawn by P. W.).

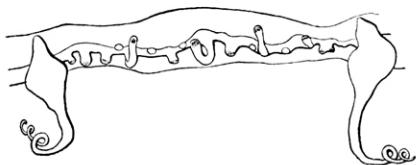


Fig. 238. *Octophialucium solidum* (from MENON).

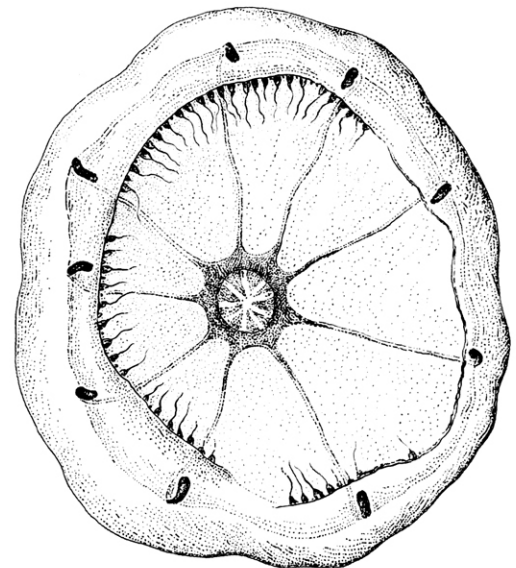


Fig. 239. *Octophialucium aphrodite* (from BIGELOW, redrawn by P. W.).

<sup>1</sup> After the above was written a specimen of *O. medium* was found in the collection of the Zoological Museum, Copenhagen; it was taken near Jolo between Mindanao and Borneo by Dr. TH. MORTENSEN in 1914; the specimen agrees exactly with the type specimen from the Gulf of Guinea, West Africa, as described by me in 1955, and I have ascertained that the medusa from Ceylon, described by BROWNE (1905) as *Octocanna polynema*, belongs to the same species, as then presumed by me.



*Octophialucium solidum* (MENON 1932). About 10 mm, hemispherical; stomach broad, eight short lips; eight radial canals; gonads along almost entire length of radial canals; four tentacles with large bulbs with excretory papillae and exumbrellar clasps, several small "tentacle-like structures" without papillae or clasps; about one statocyst between each pair of these. — Madras in India; Mergui Archipelago; Sunda Strait. (MENON p. 305, as *Octocanna polynema*; KRAMP 1965 p. 73).

*Octophialucium aphrodite* (BIGELOW 1919). 15–25 mm wide, 7–9 radial canals; gonads spindle-shaped, along distal 1/5–1/2 of radial canals; tentacles very numerous, closely crowded, well developed excretory papillae; no permanently rudimentary bulbs; statocysts more numerous than tentacles. — Malayan Archipelago; Philippines; Mozambique Channel. (MAAS 1906 a p. 95, Pl. 3, fig. 10, as *Octocanna polynema*; BIGELOW 1919 p. 307, Pl. 42, figs. 1, 2, as *Octocanna aphrodite*).

## Family Eirenidae.

Leptomedusae with small stomach; with a gastric peduncle; with four or six simple radial canals; with gonads on radial canals restricted to subumbrella; with hollow marginal tentacles; with or without excretory pores; with or without lateral or marginal cirri; with a large and indefinite number of closed marginal vesicles; without ocelli. Hydroids, where known, hydranth with web between tentacles, hydrotheca with operculum.

### Key to the genera of Eirenidae.

1. Without cirri ..... *Eirene*
- With cirri ..... 2
2. With lateral cirri ..... *Helgicirra*
- With marginal cirri ..... *Phialopsis*

*Eirene* ESCHSCHOLTZ 1829. Eirenidae with a distinct peduncle; without lateral or marginal cirri.

### Key to the Indo-Pacific species of *Eirene*.

1. Peduncle wide ..... 2
- Peduncle slender ..... 5
2. With (normally) 6 radial canals (30–50 tentacles; gonads distal, less than half as long as radial canals) .. *hexanemalis*
- With 4 radial canals ..... 3
3. With 150–180 tentacles, closely set, all alike; peduncle very short, conical ..... *mollis*
- With up to 32 tentacles ..... 4
4. Gonads short and oval, distal ..... *kambara*
- Gonads elongated, somewhat nearer to margin than to peduncle ..... *tenuis*
5. Gonads short and oval, in middle portion of radial canals; no excretory papillae ..... *brevigona*
- Gonads elongated ..... 6
6. Gonads only half as long as radial canals, almost distal; 4 large perradial and 12 small tentacles and about 40 rudimentary bulbs ..... *elliceana*
- Gonads almost from base of peduncle to margin ..... 7
7. About 3 rudimentary bulbs (and 2–4 marginal vesicles) between successive tentacles; about 50 tentacles; excretory papillae conspicuous ..... *palkensis*
- None or very few rudimentary bulbs between tentacles ..... 8
8. Without excretory papillae; 32–48 tentacles all alike ..... *menoni*
- Excretory papillae distinct ..... 9
9. Base of peduncle pyramidal; 60 or more tentacles of different sizes ..... *viridula*
- Base of peduncle narrow; 100 or more tentacles of equal size ..... *ceylonensis*

*Eirene ceylonensis* BROWNE 1905. 15–25 mm wide; peduncle long, narrow, cylindrical; gonads extending from base of peduncle to near bell margin; 100 or more tentacles, short, with excretory pores; no or very

few young bulbs; about 100 statocysts. — Coastal waters in the Indo-West-Pacific Region from East Africa to New Zealand and to Chefoo in China. (BROWNE 1905 *b* p. 140, Pl. 3, figs. 9–11).

*Eirene palkensis* BROWNE 1905. Up to 20 mm wide; peduncle long, narrow, cylindrical; gonads extending from base of peduncle to near margin; about 50 short tentacles and about three times as many rudimentary bulbs, three between each successive pair of tentacles, the middle one a little larger than the others; tentacle bulbs and rudiments with conspicuous excretory papillae. — Coastal waters in the Indo-West-Pacific Region from East Africa to North-East Australia. (BROWNE 1905 *b* p. 141, Pl. 3, figs. 12–16; KRAMP 1965 p. 75).

*Eirene menoni* KRAMP 1953. 7–12 mm wide; peduncle not particularly broad at the base, narrows towards the tip; four prominent lips with folded margin; gonads highly variable in length; about 48 tentacles, no

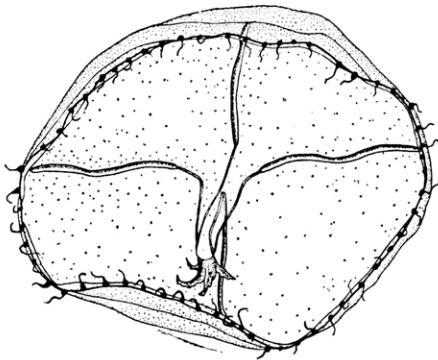


Fig. 240. *Eirene ceylonensis*  
(from CHOW & HUANG).

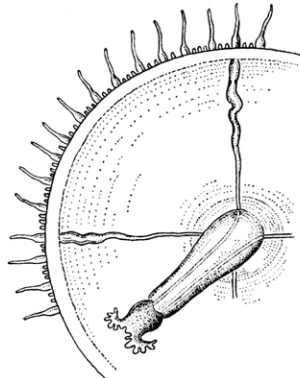


Fig. 241. *Eirene palkensis*  
(from BROWNE, redrawn by P. W.)

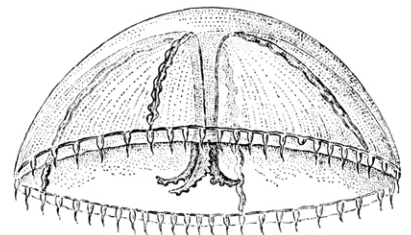


Fig. 242. *Eirene menoni*  
(from KRAMP, redrawn by P. W.).

excretory papillae; one, sometimes 2–3, statocysts between tentacles, with one concretion. — Coastal waters in the Indo-West-Pacific Region from East Africa to Polynesia. (ANNANDALE 1907 p. 79, Pl. 2, fig. 5, as *Irene ceylonensis*; KRAMP 1953 p. 286, Pl. 2, fig. 6, *Eirene menoni*; KRAMP 1965 p. 76).

*Eirene viridula* (PÉRON & LESUEUR 1809). 20–30 mm wide, umbrella hemispherical, middle portion fairly thick; peduncle slender, with pyramidal base, stomach fairly small but with four long, pointed lips with crenulated margins; gonads linear, extending from somewhat beyond base of peduncle almost to bell margin; about 60 or more tentacles of different sizes, large and small frequently alternating; bulbs conical, with distinct adaxial excretory papillae; 40 or more marginal vesicles, each with 1–4 concretions. — East Africa;

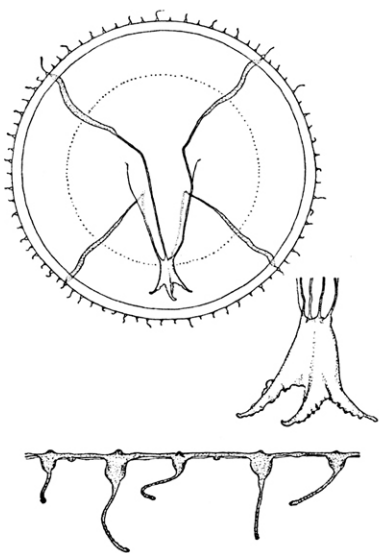


Fig. 244. *Eirene mollis* (from TORREY).

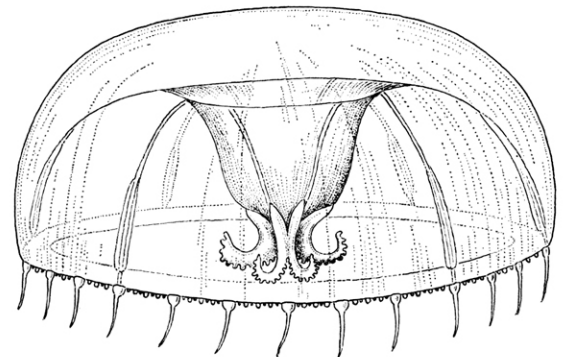
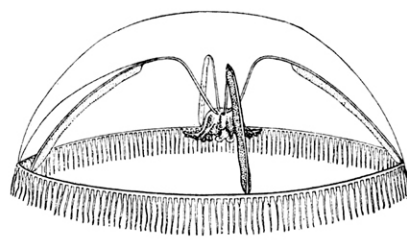


Fig. 245. *Eirene hexanemalis* (from BROWNE,  
redrawn by P. W.).

Fig. 243. *Eirene viridula*, with stomach and bell margin (from KÜNNE).

Ceylon. Mediterranean; West Africa; north-western Europe. (ESCHSCHOLTZ 1829 p. 94: *Eirene viridula*; WILL 1844 p. 70, Pl. 2, figs. 8–12, as *Geryonia pellucida*; KÜNNE 1934 p. 30, fig. 2 a-c; RUSSELL 1953 p. 321, Pl. 20, figs. 3, 4, textfigs. 201–05: *E. pellucida* = *viridula*; KRAMP 1959 a p. 158, fig. 215).

*Eirene mollis* TORREY 1909. 15–20 mm wide; peduncle very short, conical; 150–180 closely set tentacles, all alike; lithocysts even more numerous. — Pacific coast of North America from San Diego to Vancouver Island. (TORREY 1909 p. 26, fig. 11; KRAMP 1965 p. 77).

*Eirene hexanemalis* (GOETTE 1886). Up to 18 mm wide; peduncle thick, conical, stomach very small; gonads along less than the distal half of the normally six radial canals, in young stages four radial canals; 30–50 short, slender, tapering tentacles with large, swollen bulbs, with excretory papillae; three or more

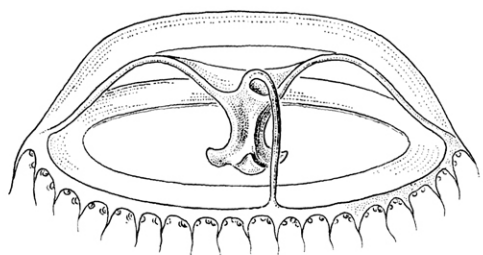


Fig. 246. *Eirene kambara* (from AGASSIZ & MAYER, redrawn by P. W.).

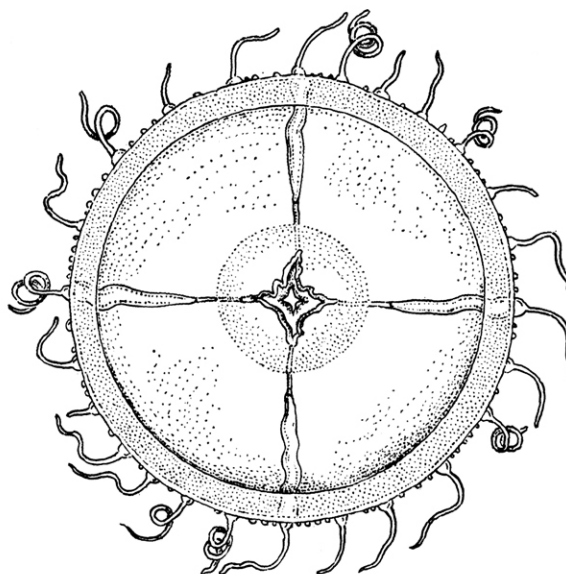


Fig. 247. *Eirene tenuis* (from BROWNE, redrawn by P. W.).

rudimentary bulbs and about four statocysts between every two tentacles. — Coastal waters in the Indo-West-Pacific Region from South and East Africa to Australia and Melanesia; southern China and Japan. (MAYER 1910 p. 310, fig. 171, as *Irenopsis hexanemalis*; VANHÖFFEN 1911 p. 229, fig. 19; KRAMP 1965 p. 77, fig. 5, development).

*Eirene kambara* AGASSIZ & MAYER 1899. 8 mm wide; peduncle distinct, short and broad; gonads on distal portions of radial canals, short and oval; 16–32 very small, slender tentacles; 64 statocysts. — Fiji Islands; North-East Australia; Vietnam. (AGASSIZ & MAYER 1899 p. 169, Pl. 8, fig. 29; KRAMP 1953 p. 283, Pl. 2, fig. 5, textfig. 6).

*Eirene tenuis* (BROWNE 1905). 10–15 mm wide; peduncle short and broad; gonads nearer to the margin than to the peduncle; 25–32 tentacles, bulbs long, broad, with a small excretory papilla; between tentacles 1–3 small, rudimentary bulbs and 2–4 statocysts. — Maldivé and Nicobar Islands. (BROWNE 1905 a p. 730, Pl. 54, fig. 4, Pl. 57, fig. 16, as *Phialidium tenue*; KRAMP 1958 p. 351: *E. tenuis* a valid species, referred to genus *Eirene*).

*Eirene brevigona* KRAMP 1959. 6 mm wide, peduncle slender, hardly as long as bell radius; mouth large, with four short lips; gonads short and oval, in middle portion of radial canals; 24 tentacles and seven young bulbs, no excretory papillae; one marginal vesicle between successive tentacles. — East coast of Malaya. (KRAMP 1959 b p. 255, fig. 18).

*Eirene elliceana* (AGASSIZ & MAYER 1902). About 16 mm wide; peduncle about as long as bell diameter, slender, with broad, pyramidal base; about 56 tentacles bulbs: four large perradial, 12 of medium size (three in each quadrant) and 40 very small, rudimentary bulbs; about 56 statocysts. — Ellis Islands in tropical

Pacific; Philippines. (AGASSIZ & MAYER 1902 p. 146, Pl. 2, figs. 5–7, as *Phortis elliceana*; BIGELOW 1919 p. 305, Pl. 41, figs. 3–7).

*Helgicirra* HARTLAUB 1909. Eirenidae with a distinct stomachal peduncle; with lateral cirri at the base of some or all of the tentacle bulbs; with excretory pores.

**Key to the Indo-Pacific species of *Helgicirra*.**

1. With clusters of medusa-buds on gonads; gonads in distal 1/3 of radial canals ..... *medusifera*  
Without medusa-buds ..... 2
2. Stomach very elongated; gonads in distal 1/3 of radial canals; 32 tentacles and about 70 rudimentary bulbs *danduensis*  
Stomach short; gonads from margin to base of peduncle or somewhat down the peduncle; 30–141 tentacles *malayensis*

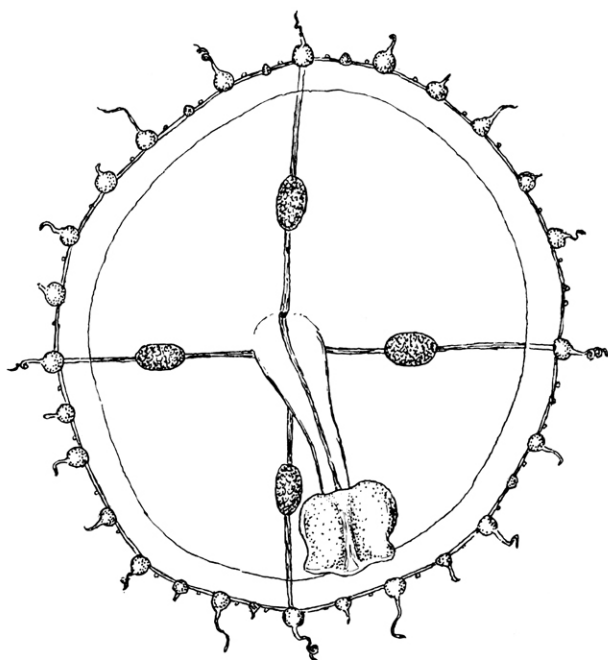


Fig. 248. *Eirene brevigona* (from KRAMP).



Fig. 249. *Eirene elliceana* (from MAYER).

*Helgicirra malayensis* (STIASNY 1928). About 20 mm wide, jelly thin; peduncle conical, about half as long as broad, stomach short; gonads as a rule long, extending from margin inwards, sometimes continuing along upper part of peduncle; 30–141 tentacles, with fairly thick, conical bulbs, with lateral cirri; rudimentary tentacles without cirri, varying number; about 1–2 statocysts between every two tentacles. — Indo-West-Pacific Region from Arabia to North-East Australia and Chefoo in China. (STIASNY 1928 p. 210, fig. 1, as *Eirene malayensis*; MENON 1932 p. 20, Pl. 3, fig. 23, as *E. malayensis*, Pl. 3, fig. 24, as *E. madrasensis*; KRAMP 1965 p. 81, figs. 6, 7).

*Helgicirra danduensis* (BIGELOW 1904). Up to 25 mm wide; peduncle long and conical, stomach very elongated; spindle-shaped gonads along distal 2/3 of radial canals; 32 tentacles, the perradial a little longer, with lateral cirri; about 70 rudimentary bulbs without cirri; 32 statocysts. — Maldives and Nicobar Islands; North Australia. (BIGELOW 1904 p. 254, Pl. 1, fig. 5, Pl. 2, fig. 6, as *Eirene danduensis*).

*Helgicirra medusifera* (BIGELOW 1909). Up to 13 mm wide; peduncle slender; gonads along distal 1/3 of radial canals, not quite reaching margin; clusters of medusa-buds on gonads; 16–21 tentacles with swollen, conical bases; also a few marginal knobs, probably young tentacles; all with one or two pairs of lateral cirri; statocysts alternating with tentacles. — Pacific coast of Mexico and Panama. (BIGELOW 1909 p. 161, Pl. 37, figs. 1–8, as *Eirene medusifera*; KRAMP 1965 p. 80).

*Phialopsis* TORREY 1909. Eirenidae with four radial canals; without excretory pores; with marginal cirri; gastric peduncle feebly developed.

*Phialopsis diegensis* TORREY 1909. 20–30 mm wide, 3–4 times as wide as high, jelly moderately thick in middle portion; peduncle very short, conical; stomach very short, mouth with very short, crenulated lips; gonads linear, extending from basal part of peduncle almost to bell margin; 16–28 tentacles with elongated conical bulbs; between successive tentacles 3–9 triangular rudimentary bulbs, 3–9 scattered marginal cirri, and 2–5 marginal vesicles, each with 2–6 concretions; no lateral cirri. — Eastern Pacific; western part of Indian Ocean. Atlantic Ocean from about 35° S. to 60° N.; partly oceanic. (TORREY 1909 p. 23, fig. 9; RUSSELL 1953 p. 333, Pl. 20, fig. 5, textfigs. 213, 214).

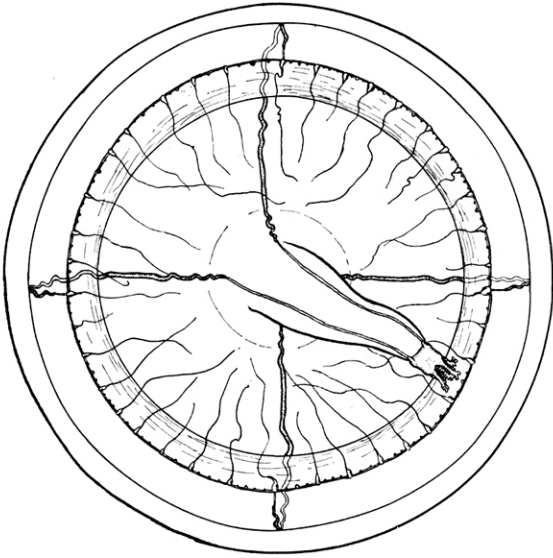


Fig. 250. *Helgicirrho malayensis* (from KRAMP).

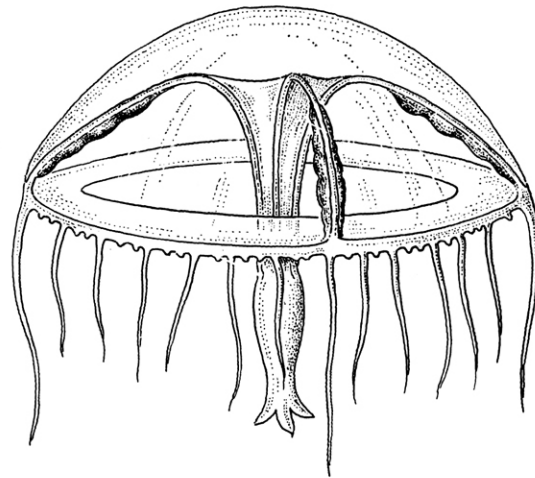


Fig. 251. *Helgicirrho danduensis* (from BIGELOW, redrawn by P. W.).

## Family Eutimidae.

Leptomedusae with small stomach; with distinct peduncle; with four simple radial canals; with gonads on radial canals separated from stomach either on peduncle or subumbrella only, or on both; with hollow marginal tentacles; without excretory pores; without marginal cirri; with or without lateral cirri; with closed marginal vesicles, usually eight; without ocelli. Hydroids, where known, *Campanopsis*-like.

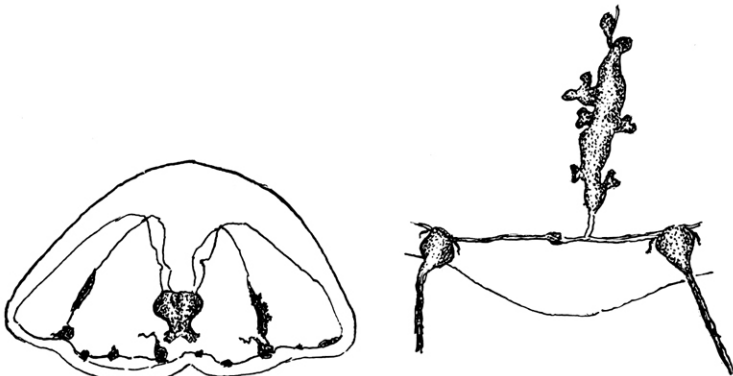


Fig. 252. *Helgicirrho meducifera* (from BIGELOW, redrawn).

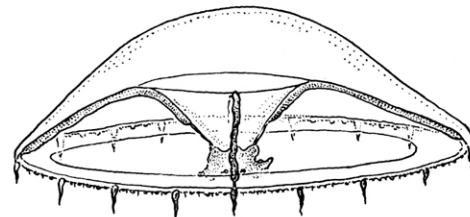


Fig. 253. *Phialopsis diegensis* (from RUSSELL, redrawn by P. W.).

**Key to the Indo-Pacific genera of Eutimidae.**

1. With 8 (rarely 12) marginal vesicles; with or without marginal warts ..... 2  
     With numerous marginal vesicles and marginal warts ..... *Tima*
2. Without cirri and without marginal warts ..... *Eutonina*  
     With cirri ..... 3
3. With marginal cirri between tentacles ..... *Eutimalphes*  
     With lateral cirri on marginal warts, usually also at base of tentacles ..... *Eutima*

*Tima* ESCHSCHOLTZ 1829. Eutimidae with numerous marginal vesicles; without cirri; with marginal warts; with gonads upon entire length of radial canals.

*Tima saghalinensis* BIGELOW 1913. 100 mm wide; peduncle very short, lips much folded; about 300 tentacles; statocysts about half as numerous as tentacles, each with 8–10 concretions. — Ochotian Sea. (BIGELOW 1913 p. 35; PETERSEN 1962 p. 102, figs. 1, 2).

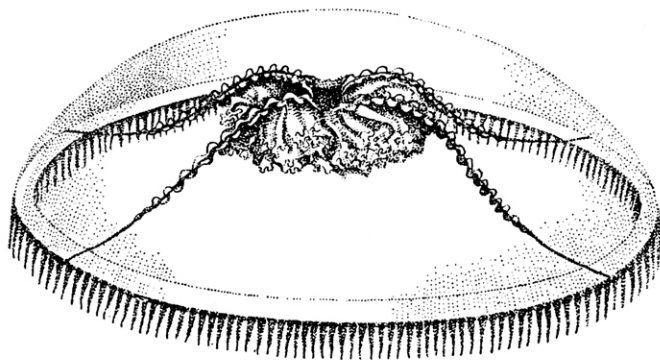


Fig. 254. *Tima saghalinensis* (from NAUMOV).

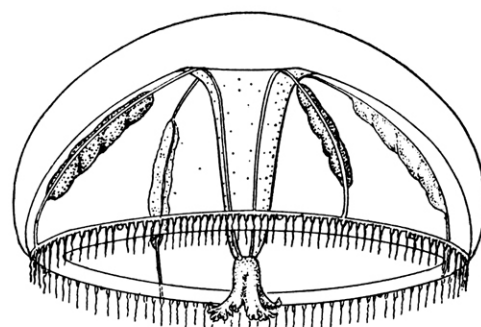


Fig. 255. *Eutonina indicans* (from KRAMP).

*Eutonina* HARTLAUB 1897. Eutimidae with eight marginal vesicles; without cirri; without marginal warts; with gonads restricted to subumbrella.

**Key to the species of Eutonina.**

- Gonads linear, sinuous, along nearly whole length of subumbrellar portion of radial canals; about 200 tentacles ..... *indicans*
- Gonads in distal 1/4–1/3 of radial canals; about 16 tentacles ..... *scintillans*

*Eutonina indicans* (ROMANES 1876). 25–35 mm wide, slightly flatter than a hemisphere; jelly rather thick; peduncle thick, conical; stomach short, four folded lips; gonads linear, sinuous, along nearly whole subumbrellar portion of radial canals; about 200 short tentacles; marginal vesicles with about 12 concretions. — Japan; Kamchatka; Aleutian Islands; Vancouver Island. North-western Europe; Iceland. (HARTLAUB 1897 p. 506, Pl. 22, figs. 1, 3, 4, 6, 7, Pl. 20, figs. 19, 20, as *Eutonina socialis*; RUSSELL 1953 p. 374, Pl. 22, fig. 2, textfigs. 240–45).

*Eutonina scintillans* (BIGELOW 1909). 10 mm wide, 5 mm high, jelly thick; peduncle short; stomach globular; four simple or slightly crenulated lips; gonads extending along distal 1/4–1/3 of radial canals; marginal vesicles with 2–5 concretions. — Pacific coast of Mexico; Djibouti in East Africa. Adriatic Sea.

*Eutima* MCCRADY 1857. Eutimidae with eight (rarely 12) marginal vesicles; with lateral cirri and with marginal warts; with 2–32 tentacles.

Subgenus *Eutima* MCCRADY 1857. With marginal swellings without adaxial papillae.

Subgenus *Octorchis* HAECKEL 1879. With marginal swellings with adaxial papillae.



Key to the Indo-Pacific species of *Eutima*.

1. With 8 gonads, 4 on subumbrella and 4 on peduncle ..... 2  
     With 4 gonads, either on subumbrella or on peduncle ..... 4
2. With 12–14 tentacles without cirri; about 32 marginal warts with lateral cirri ..... *hartlaubi*  
     Tentacles with lateral cirri ..... 3
3. With 4 tentacles and 60–80 marginal warts ..... *orientalis*  
     With 8 tentacles and up to 100 marginal warts ..... *levuka*
4. Gonads on peduncle only; 4 tentacles with abaxial hook-like process; 120–140 marginal warts ..... *curva*  
     Gonads on subumbrellar portion of radial canals ..... 5
5. Without marginal warts; up to 30 tentacles, each with 1–3 pairs of cirri ..... *brownei*  
     With marginal warts ..... 6

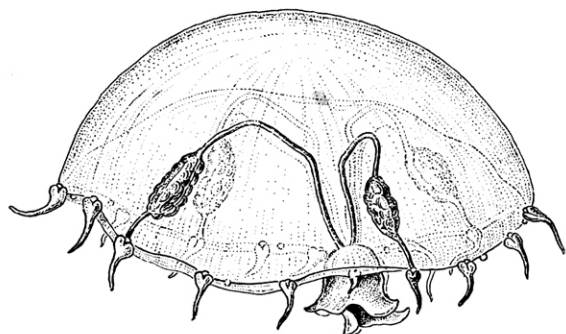


Fig. 256. *Eutonina scintillans* (from NEPPI & STIASNY, redrawn by P. W.).

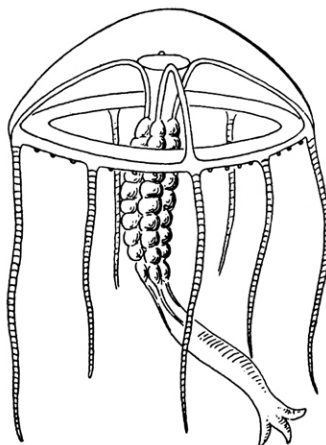


Fig. 257. *Eutima levuka* (from MAYER).

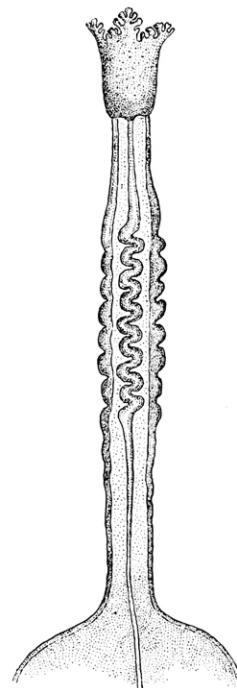


Fig. 258. *Eutima orientalis* (from BROWNE, redrawn by P. W.).

6. With 16 tentacles with swollen bulbs, with lateral cirri; gonads in middle portion of radial canals ..... *modesta*  
     With 8 tentacles ..... 7
7. Tentacles without cirri; gonads with lateral swellings, not reaching to peduncle ..... *neucaledonia*  
     Tentacles with lateral cirri; gonads extending from bell margin to short way down the peduncle ..... *japonica*

*Eutima levuka* (AGASSIZ & MAYER 1899). Up to 15 mm wide, flatter than a hemisphere, jelly fairly thin; peduncle slender,  $1\frac{1}{2}$  times as long as diameter of bell; eight gonads, four on middle portion of peduncle and four on subumbrella; usually eight tentacles, sometimes more, with lateral cirri; up to 100 marginal warts with cirri. — Coastal waters in the Indo-West-Pacific Region from East Africa to the Fiji Islands, northwards to Formosa; east coast of Australia. (AGASSIZ & MAYER 1899 p. 163, Pl. 9, figs. 30, 31; KRAMP 1965 p. 83).

*Eutima orientalis* (BROWNE 1905). 5–6 mm wide; peduncle twice as long as bell diameter, with dome-like base and elongate, prismatic central part; eight gonads, four on peduncle and four on subumbrella; four tentacles, with lateral cirri; 60–80 marginal warts, with lateral cirri. — Coastal waters in the Indo-West-Pacific Region from Africa to New Zealand, northwards to Formosa. (BROWNE 1905 *b* p. 139, Pl. 3, fig. 4, as *Octorchis orientalis*; KRAMP 1965 p. 84).

*Eutima curva* BROWNE 1905. 10 mm wide, jelly quite thick; peduncle about as long as bell diameter, pyramidal above, prismatic below; four gonads on prismatic portion of peduncle only; four tentacles with

lateral cirri; tentacle bulbs curve upwards over margin of bell, with black pigment; 120–140 marginal warts with cirri. — Coastal waters in the Indo-West-Pacific Region from the Seychelles to North-East Australia. (BROWNE 1905 *b* p. 138, Pl. 3, figs. 1–3; KRAMP 1965 p. 84).

*Eutima japonica* UCHIDA 1925. 4.5 mm wide, jelly thick; peduncle short; four gonads extending from bell margin to short way down the peduncle; eight tentacles, the perradial longer than the interradial, with lateral cirri; in each octant four marginal warts, the two middle ones larger and with lateral cirri. — Japan; central North Pacific. (UCHIDA 1925 p. 93, fig. 17; KRAMP 1965 p. 85).

*Eutima hartlaubi* KRAMP 1958. 15 mm wide, flatter than a hemisphere, jelly fairly thick; peduncle slender, tapering, about half as long as diameter of bell; eight gonads, four on subumbrella extending almost from

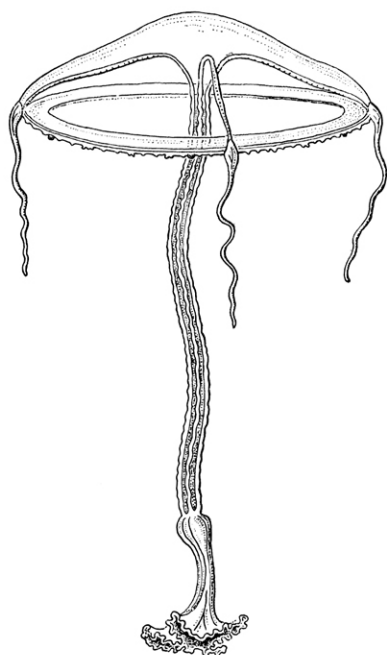


Fig. 259. *Eutima curva*  
(from MAYER, redrawn by P. W.).

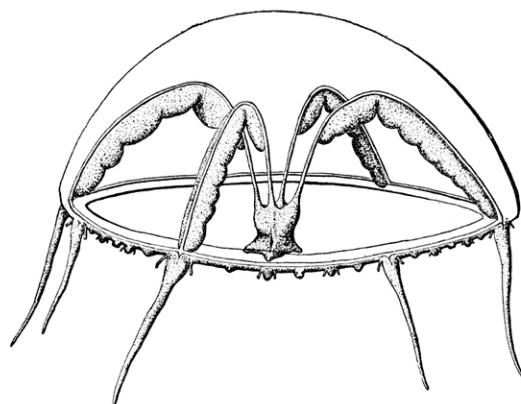


Fig. 260. *Eutima japonica* (from UCHIDA).



Fig. 261. *Eutima hartlaubi* (from  
HARTLAUB, redrawn by P. W.).

base of peduncle to bell margin, and four short on middle portion of peduncle; 12–14 large tentacles without cirri; about 32 marginal warts with lateral cirri; a large, spherical, gelatinous protuberance above the base of each tentacle. — Djibouti in East Africa; Nicobars. (HARTLAUB 1909 *a* p. 456, Pl. 20, figs. 11–15, as *Octorchandra orientalis* n. sp.; KRAMP 1958 p. 358, fig. 4, as *Eutima hartlaubi* nov. nom.).

*Eutima modesta* (HARTLAUB 1909). 8 mm wide, flat, with thin walls; peduncle about half as long as diameter of bell, slender, tapering; four gonads, on subumbrella only, a little nearer to peduncle than to margin; 16 tentacles with swollen bulbs, with lateral cirri; 16 or more marginal warts, with lateral cirri. — Djibouti in East Africa. (HARTLAUB 1909 *b* p. 454, Pl. 19, figs. 6, 7, as *Eutimalphes modesta*).

*Eutima brownei* (TORREY 1909). 15 mm wide, hemispherical, jelly thick; peduncle wide, conical, short; mouth with four wide, frilled lips; gonads on subumbrellar portions of radial canals only; about 130 short tentacles with bulbous bases flanked by one to three pairs of long, slender cirri; no marginal warts. — San Diego, California. (TORREY 1909 p. 25, fig. 10, as *Eutimalphes brownei*).

*Eutima neucaledonia* UCHIDA 1964. 9 mm wide, very flat; peduncle slender, nearly as long as diameter of bell, stomach short with four slightly crenulated lips; four gonads, on subumbrella only, from near bell margin, not reaching to base of peduncle, linear with many lateral swellings; eight tentacles, the perradial longer than the interradial, without cirri; in each octant 6–7 small marginal warts, some of which have cirri. — New Caledonia. (UCHIDA 1964 p. 110, figs. 2, 3).

*Eutimalphes* HAECKEL 1879. Eutimidae with eight adradial statocysts; with numerous tentacles and marginal cirri. Only one species, which was observed only once.

*Eutimalphes pretiosa* HAECKEL 1879. 40 mm wide, 20 mm high; jelly thick; peduncle broad, conical, about half as long as bell diameter; stomach large; very large lips, complexly folded; gonads continuous, extending along almost entire length of radial canals; 60–80 very short tentacles and a few marginal warts; numerous marginal cirri. — Australia. (HAECKEL 1879 p. 195, Pl. 11, fig. 8).

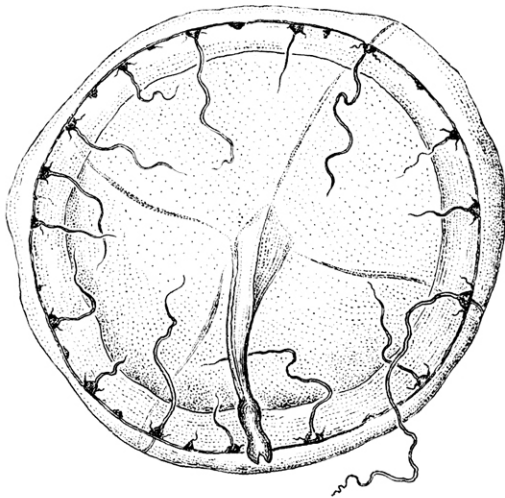


Fig. 262. *Eutima modesta* (from HARTLAUB, redrawn by P. W.).

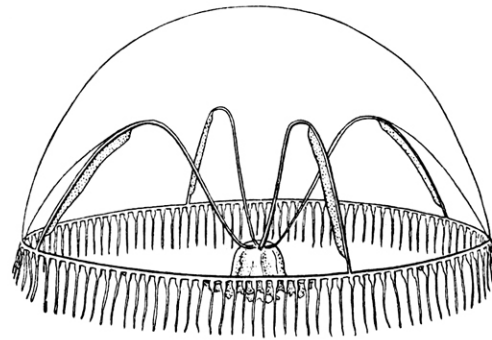


Fig. 263. *Eutima brownei* (from TORREY).

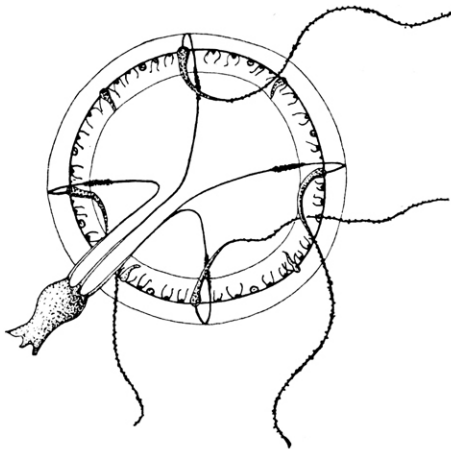


Fig. 264. *Eutima neucaledonia* (from UCHIDA).

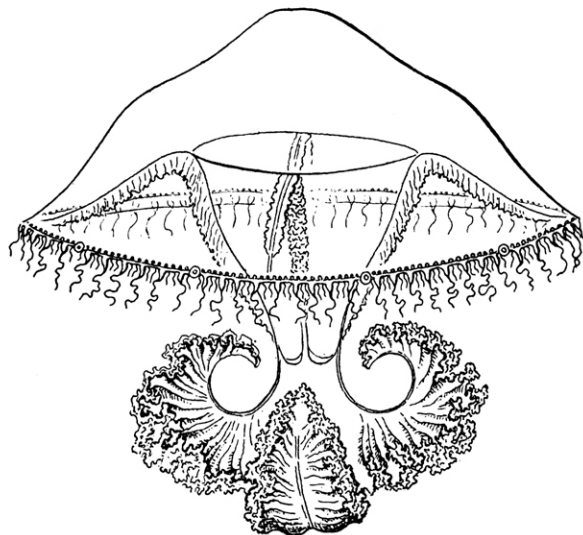


Fig. 265. *Eutimalphes pretiosa* (from MAYER).

## Family Aequoreidae.

Leptomedusae with very broad stomach; usually without peduncle; with many simple or branched radial canals; with gonads on radial canals separated from stomach; with hollow marginal tentacles; with excretory pores; without marginal or lateral cirri; with closed marginal vesicles; with or without ocelli. Hydroids, where known, tentacles with webs, hydrotheca with operculum.

### Key to the Indo-Pacific genera of Aequoreidae.

Radial canals simple, undivided ..... *Aequorea*  
 Radial canals bifurcated or branched ..... *Zygocanna*

*Aequorea* PÉRON & LESUEUR 1809. Aequoreidae with numerous simple radial canals. Subumbrella without rows of papillae. The species are more or less doubtful.

**Key to the Indo-Pacific species of *Aequorea*.**

- |  |                     |
|--|---------------------|
| 1. Gonads no more than half as long as radial canals .....   | 2                   |
| Gonads along almost whole length of radial canals .....  | 3                   |
| 2. About 16 radial canals and twice as many tentacles; umbrella high, conical, 9 mm wide; mouth with long and slender lips; gonads laterally compressed, in proximal half of radial canals ..... | <i>conica</i>       |
| With 16–32 (40) radial canals and as many tentacles with excretory papillae; umbrella low, up to 45 mm wide; gonads in distal half of radial canals .....  | <i>australis</i>    |
| 3. More than 3 times as many tentacles as radial canals; about 100 radial canals; tentacle bulbs laterally compressed .....  | <i>coerulescens</i> |
| Less, usually much less, than 3 times as many tentacles as radial canals .....   | 4                   |

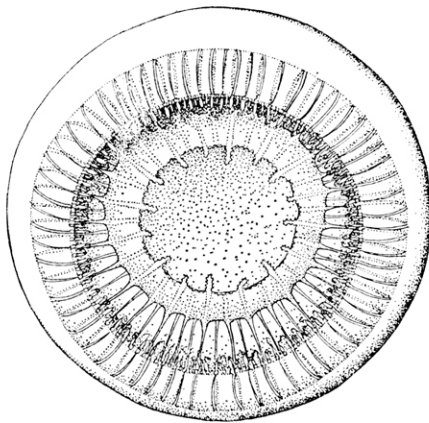


Fig. 266. *Aequorea coerulescens* (from UCHIDA).

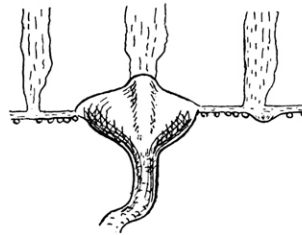


Fig. 267. *Aequorea macrodactyla*, tentacle bulb (from RUSSELL).



Fig. 268. *Aequorea pensilis*, tentacle bulb (from MAAS, redrawn by the author).

- |  |                     |
|--|---------------------|
| 4. With about 4–10 or more times as many radial canals as tentacles .....  | 5                   |
| With at least half as many tentacles as radial canals .....  | 7                   |
| 5. Umbrella flat, thick, up to 27 mm wide; with up to 32 radial canals and 4–8 tentacles .....   | <i>parva</i>        |
| Umbrella large, more or less biconvex; with numerous (60–250) radial canals .....  | 6                   |
| 6. Tentacle bulbs broad, with an abaxial keel and prominent excretory papillae .....   | <i>macrodactyla</i> |
| Tentacle bulbs with long lateral extensions and without excretory papillae .....   | <i>pensilis</i>     |
| 7. Umbrella hemispherical, very thick, 20–40 mm wide; 30–50 radial canals and as many tentacles; no excretory papillae .....   | <i>globosa</i>      |
| Umbrella up to 175 mm wide, saucer-shaped, gradually thinner towards margin; tentacle bulbs elongated, conical, with excretory pores on short papillae; half to twice as many tentacles as radial canals ..... | <i>aequorea</i>     |

*Aequorea coerulescens* (BRANDT 1838). Up to 145 mm wide, usually 60–80 mm, low and thick; stomach about half as wide as umbrella; about 100 radial canals; gonads extending along almost whole length of radial canals; 3–6 times as many tentacles as radial canals and numerous small bulbs; tentacle bulbs elongated, laterally compressed, with prominent excretory papillae; statocysts numerous, crowded. — Coastal waters in the warm parts of the eastern and western Pacific, the Indian Ocean and southern Atlantic. (BIGELOW 1909 p. 177, Pl. 4, fig. 4, Pl. 35, figs. 3–8; KRAMP 1965 p. 86).

*Aequorea macrodactyla* (BRANDT 1835). Up to 75 mm wide, central disk thick, lens-shaped, margin thin; stomach about half as wide as umbrella; 60–100, up to 150 radial canals; gonads extending along almost entire length of radial canals; 10–30 (rarely up to 40) tentacles and 6–8 times as many small bulbs; tentacle bulbs broad, each with a distinct abaxial keel and with a prominent excretory papilla; statocysts very numerous. — Eastern tropical Pacific; Melanesian Islands and the Tasman Sea; Indo-Malayan coastal waters, Formosa, Japan; western parts of the Indian Ocean from the Maldiv Islands to Madagascar and the east

coast of Africa; off south-eastern Africa. Within the Atlantic area the occurrence seems to be somewhat scattered: off the west coast of Africa; off the southern part of the east coast of South America; the Caribbean Sea; an isolated population occurs off the south-western coasts of the British Isles. (BIGELOW 1909 p. 174, Pl. 36; BIGELOW 1919 pp. 310, 313, Pl. 43, fig. 7; KRAMP 1959 *a* p. 38, fig. 235; KRAMP 1965 p. 87, fig. 8).

*Aequorea pensilis* (ESCHSCHOLTZ 1829). Up to 100 mm wide, central disk thick, lens-shaped, margin thin; stomach  $1/2$ – $2/3$  as wide as umbrella; 100–250 radial canals; gonads extending along almost entire length of radial canals; 10–16 tentacles and 8–16 times as many small bulbs; tentacle bulbs with long lateral extensions, no abaxial keel; no excretory papillae but excretory pores; statocysts very numerous. — Coastal waters of the Indo-West-Pacific Region from South and East Africa to the east coast of Australia. (BIGELOW 1919

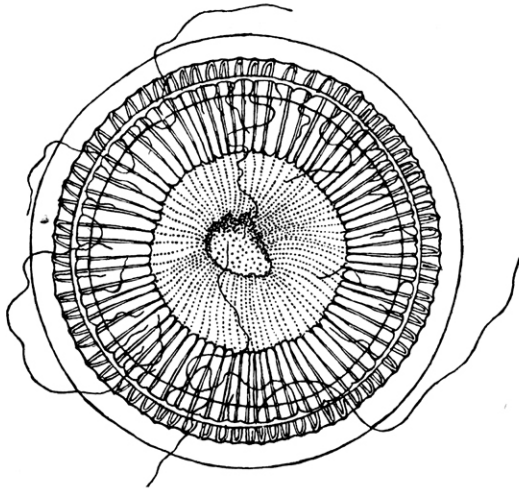


Fig. 269 a. *Aequorea aequorea* (from MAYER).

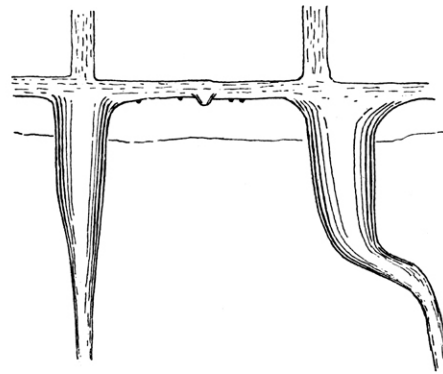


Fig. 269 b. *Aequorea aequorea*, bell margin (from RUSSELL).

p. 311, Pl. 42, fig. 3, 4; KRAMP 1953 p. 295: variation and comparison with *Ae. macrodactyla*; KRAMP 1959 *a* p. 167, fig. 236; KRAMP 1965 p. 92).

*Aequorea aequorea* (FORSKÅL 1775). Up to 175 mm wide, saucer-shaped, thick in centre, gradually thinning towards margin; stomach usually half as wide as umbrella; radial canals usually 60–80, sometimes fewer or up to 160; gonads extending along almost whole length of radial canals; tentacles usually less numerous than radial canals but varying from half to twice as many; small bulbs few, scattered; tentacle bulbs elongated conical, excretory pores on short papillae; 5–10 statocysts between successive radial canals. — South-East Africa and Madagascar; east coast of Australia and north of New Zealand; north-eastern Pacific. Western Atlantic from Cape Cod to Florida and in Patagonia; eastern Atlantic generally distributed from Norway to South Africa; Mediterranean. (FORSKÅL 1775 p. 110, as *Medusa aequorea*; PÉRON & LESUEUR 1809 p. 336, as *Aequorea forskalea*; RUSSELL 1953 p. 342, Pl. 21, fig. 3, Pl. 32, figs. 1, 2, textfigs. 220, 221, as *Ae. forskalea*; KRAMP 1965 p. 95).

*Aequorea australis* UCHIDA 1947. Up to 40 mm wide, lower than a hemisphere, jelly rather thin; diameter of stomach a little less than half of that of umbrella; 16–50 radial canals; gonads about half as long as radial canals, nearer to margin than to stomach; 16–40 tentacles and a varying number of small bulbs; statocysts about same number as tentacle bulbs with distinct excretory papillae. — Coastal waters in the Indo-West-Pacific Region, from East Africa to Tahiti, northwards to Chefoo in China, southwards to north-eastern Australia. (UCHIDA 1947 *a* p. 307, fig. 8; KRAMP 1953 p. 290, fig. 7, variation and comparison with *Ae. globosa*; KRAMP 1965 p. 96).

*Aequorea globosa* ESCHSCHOLTZ 1829. 20–40 mm wide, almost hemispherical, jelly very thick; stomach about half as wide as diameter of umbrella; gonads extending along almost entire length of radial canals; 30–40 radial canals, same number of tentacles and about twice as many small bulbs; about twice as many

statocysts as tentacles; no excretory papillae. — East Africa; Malayan Archipelago; Melanesian Islands; Chile. (MAAS 1905 p. 43, Pl. 8, figs. 48–50; KRAMP 1965 p. 98).

*Aequorea conica* BROWNE 1905. 9 mm wide, 10–12 mm high, conical, jelly very thick; stomach half as wide as diameter of umbrella, often broad and flat; lips long and slender, with an inward furrow which continues along inside of stomach to the radial canals; about 16 radial canals; gonads along proximal half portion of

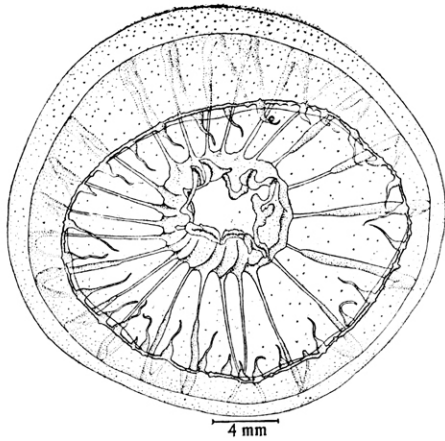


Fig. 270. *Aequorea australis* (from CHOW & HUANG).

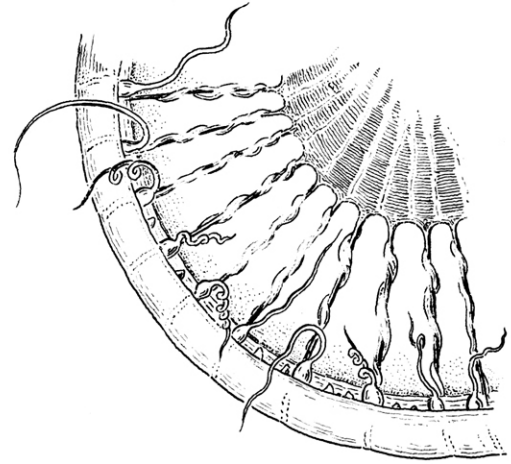


Fig. 271. *Aequorea globosa* (from MAAS, redrawn by P. W.).

radial canals; 26–30 tentacles and as many small bulbs; about twice as many statocysts as tentacles; no excretory papillae. — Mozambique Channel; coastal waters of India and the Malayan Archipelago; Amoy in China; North Australia. (BROWNE 1905 *b* p. 145, Pl. 1, fig. 2, Pl. 2, figs. 16–18; KRAMP 1953 p. 289; KRAMP 1965 p. 99).

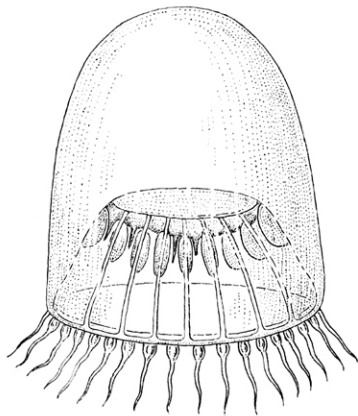


Fig. 272. *Aequorea conica* (from BROWNE, redrawn by P. W.).

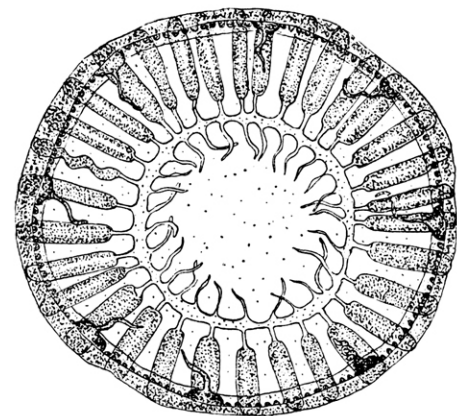


Fig. 273. *Aequorea parva* (from STIASNY).

*Aequorea parva* BROWNE 1905. 12–27 mm wide, flat, thick, with vaulted apex; stomach about half as wide as diameter of umbrella; 32 radial canals; gonads along almost entire length of radial canals; 4–8 tentacles; about 100 small bulbs; 1–2 statocysts between successive bulbs; excretory papillae present? — India; Singapore; Java Sea; Amoy in China. (BROWNE 1905 *b* p. 146, Pl. 2, figs. 5–7; STIASNY 1928 p. 215, figs. 3, 4, as *Ae. parva* var. *buitendijki*; MENON 1932 p. 24, Pl. 3, figs. 29–33).

Doubtful species; *Ae. victoria* (MURBACH & SHEARER).

*Zygocanna* HAECKEL 1879. Aequoreidae with numerous radial canals, bifurcated or branched; subumbrella sometimes with radial rows of gelatinous papillae.



Key to the Indo-Pacific species of *Zygocanna*.

1. Radial canals branched more than once..... 2  
    Radial canals bifurcated ..... 3
  2. Subumbrella with radial rows of gelatinous papillae; branching of radial canals inside the periphery of the stomach ..... *vagans*  
    Subumbrella without rows of papillae; radial canals divided into 3–6 branches outside stomach ..... *buitendijki*
  3. Stomach on large, conical peduncle ..... *diploconus*  
    No gastric peduncle ..... 4
  4. 16–20 radial canals, 10–16 tentacles ..... *pleuronota*  
    12 radial canals, tentacles very numerous ..... *purpurea*
- (The latter three species are uncertain).

*Zygocanna vagans* BIGELOW 1912. Up to 76 mm wide, flat, thin; subumbrella with radial rows of gelatinous papillae; stomach  $1\frac{1}{3}$ – $1\frac{1}{2}$  as wide as umbrella; about 30–45 radial canals from the periphery of the

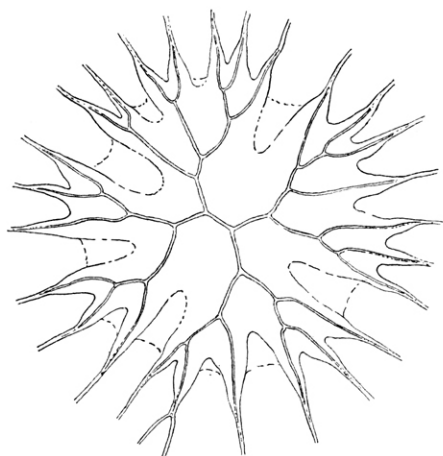


Fig. 274. *Zygocanna vagans*, aboral view of stomach (from BIGELOW).

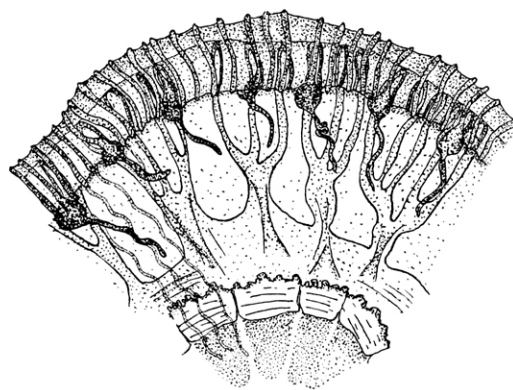


Fig. 275. *Zygocanna buitendijki* (from STIASNY).

stomach without branching, but from a cruciform figure in centre of stomach branching grooves pass to the points of origin of the free canals; gonads extending along greater portion of radial canals; 28–70 tentacles and several small bulbs, with long excretory papillae; statocysts very numerous. — Warm parts of the Pacific and Indian oceans, from Central America to East Africa, northwards to Formosa, southwards to Sydney in East Australia. Atlantic west of the Cape of Good Hope and near the Azores. (BIGELOW 1919 p. 315, Pl. 42, figs. 5–7, Pl. 43, fig. 6; BIGELOW 1940 p. 299, fig. 14; KRAMP 1959 a p. 39, figs. 7, 238; KRAMP 1965 p. 100).

*Zygocanna buitendijki* STIASNY 1928. Up to 65 mm wide, exumbrella with 70–100 radial ribs containing hollow tubes; no subumbrellar papillae between radial canals; stomach about half as broad as diameter of umbrella; radial canals divided into 3–6 branches, 80–100 reaching ring canal; 16–18 large tentacles and as many small ones or bulbs; about 200 statocysts; excretory papillae present. — Indo-Malayan coastal waters. (STIASNY 1928 p. 218, figs. 5 a-e, 6, 7; MENON 1932 p. 25, Pl. 3, figs. 34, 35; KRAMP 1965 p. 101).

*Zygocanna diploconus* (HAECKEL 1879). 60–100 mm wide, higher than a hemisphere, exumbrella with numerous radial ridges; stomach on large, conical, gelatinous peduncle; 25–35 radial canals, bifurcated; 50–70 long tentacles; 200–300 statocysts; excretory papillae? Colour rose red. — Sunda Strait. (HAECKEL 1879 p. 216, Pl. 15, fig. 6).

*Zygocanna pleuronota* (PÉRON & LESUEUR 1809). 20–30 mm wide, 8–10 mm high, disk-shaped; exumbrella with 40–50 radial ribs; stomach cylindrical; 16–20 radial canals, bifurcated; 10–16 tentacles; statocysts? — North Australia and New Guinea. (HAECKEL 1879 p. 214: as *Zygocanna pleuronota*; p. 215, Pl. 15, figs. 7, 8: as *Z. costata*).

*Zygocanna purpurea* (PÉRON & LESUEUR 1809). 80–100 mm wide, 10–16 mm high; stomach  $\frac{1}{4}$  as broad

as diameter of umbrella, cylindrical; 12 radial canals, bifurcated; gonads each forming a cluster of five parallel, serrated lamellae; tentacles very numerous; statocysts? Colour violet-purple. — Australia. (MAYER 1910 p. 338).

### III. Order LIMNOMEDUSAE

Hydromedusae with alternating generations. The sexual generation is a velar medusa with hollow tentacles; the gonads either on the stomach wall with or without perradial lobes extending along the radial canals, or on the radial canals only; if statocysts are present, they are internal and provided with an endodermal axis. The asexual generation is a sessile polyp with power of vegetative propagation, with or without tentacles; the endoderm of the tentacles in direct connection with that of the gastral cavity.

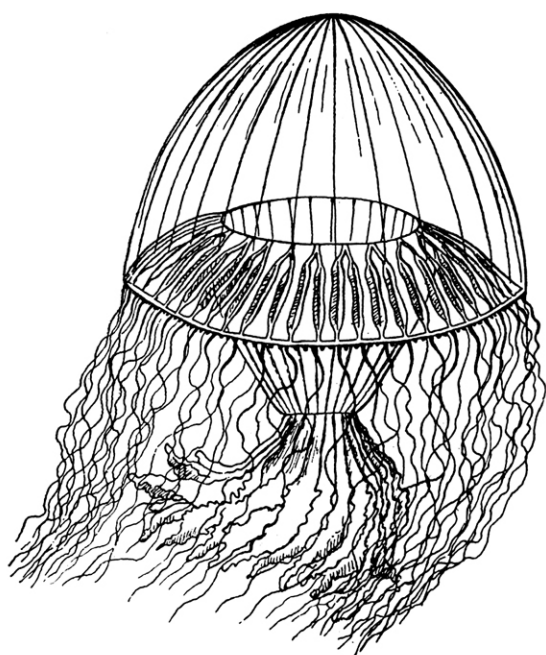


Fig. 276. *Zygocanna diploconus* (after HAECKEL, from MAYER).

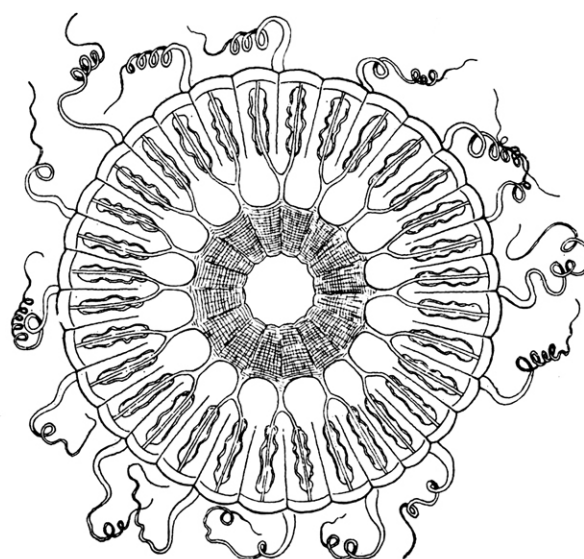


Fig. 277. *Zygocanna pleuronota* (after HAECKEL, from MAYER).

#### Key to the families of Limnomedusae.

1. With gonads on radial canals only; with internal statocysts; without ocelli ..... Olindiadidae
- With gonads on stomach walls, usually extending along radial lobes of stomach; usually without statocysts ... 2
2. With 4 simple radial canals; tentacle bulbs with abaxial ocelli ..... Moerisiidae
- With 4 or 6 or more radial canals generally branched; without ocelli ..... Proboscidae

### Family Moerisiidae.

Limnomedusae usually without marginal vesicles; with gonads on the stomach wall and in radial lobes of stomach extending outwards along the radial canals; with four simple, unbranched radial canals; tentacle bulbs with abaxial ocelli. Hydroids, where known, small, with hollow tentacles.

#### Key to the genera of Moerisiidae represented in Indo-Pacific waters.

1. Stomach on a short gelatinous peduncle; mouth with four well-developed, crenulated lips ..... *Tiaricodon*
- No peduncle; mouth without distinct lips ..... 2
2. Tentacle bulbs globular, not clasping over exumbrella; without statocysts ..... *Moerisia*
- Basal part of tentacles adnate to exumbrella; with internal statocysts (almost invisible) ..... *Ostroumovia*

*Moerisia* BOULENGER 1908. Moerisiidae with four or more tentacles with rings of nematocysts throughout their length; bulbs globular, not clasping exumbrellar margin; stomach cruciform, without a peduncle; mouth without distinct lips; gonads on radial canals continuous with those on the stomach walls, smooth; without statocysts.

Polyp with filiform tentacles in one more or less distinct whorl; with a thin perisarc.

*Moerisia gangetica* KRAMP 1958. 3 mm wide, 2 mm high, globular, jelly very thick; stomach very small, mouth-opening cross-shaped without lips, radial lobes nearly extending to ring-canal, distal parts sac-like, pendent; 19 tentacles of equal size, with semi-globular basal bulbs, each with an abaxial red ocellus; nematocysts in rings along whole length of tentacle. Polyp unknown. — Near Calcutta, India. (KRAMP 1958 p. 363, figs. 5 a, b).

*Tiaricodon* BROWNE 1902. Moerisiidae with four perradial tentacles; stomach with four perradial lobes extending along a broad, gelatinous peduncle; mouth with four distinct lips.

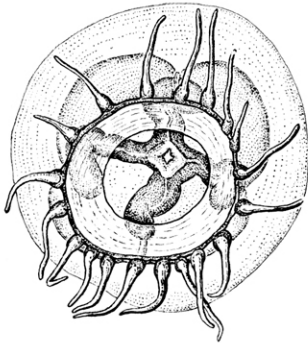


Fig. 278. *Moerisia gangetica*  
(from KRAMP, redrawn by P. W.).

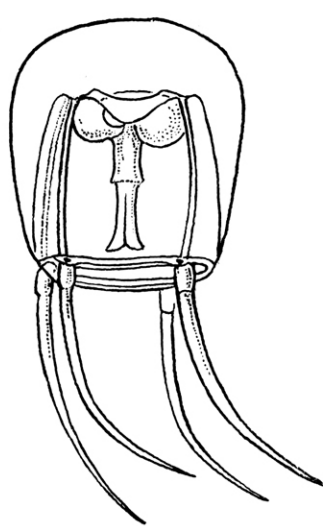


Fig. 279. *Tiaricodon coeruleus*  
(from BROWNE & KRAMP, redrawn  
by P. W.).

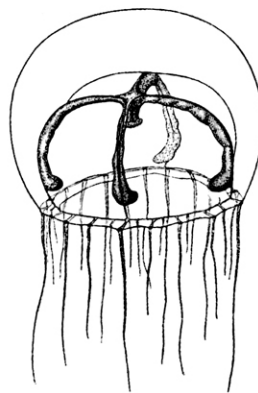


Fig. 280. *Ostroumovia*  
*inkermanica* (from KRAMP).

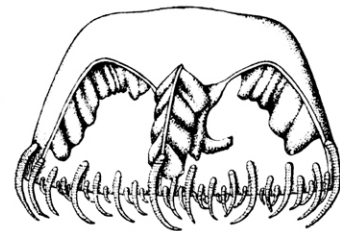


Fig. 281. *Eperetmus typus*  
(from UCHIDA).

*Tiaricodon coeruleus* BROWNE 1902. 24 mm wide, 25 mm high, jelly thick, bell-shaped; stomach nearly to velar level, four lips distinct, crenulated; radial lobes sac-like, on peduncle only; four perradial tentacles, stout, tapering, nematocysts in proximal part in small, rounded warts, in middle part forming transversal clasps, in distal part rings; an abaxial ocellus. Polyp unknown. — Chile and Peru. Weddell Sea; Falkland Islands; coast of Argentina. (VANHÖFFEN 1913 p. 6, Pl. 1, fig. 2, Pl. 2, figs. 2–6; BROWNE & KRAMP 1939 p. 311, Pl. 18, figs. 1–6, Pl. 19, figs. 8–11).

*Ostroumovia* HADŽI 1928. Moerisiidae with small internal statocysts; stomach without a peduncle, cruciform with long perradial lobes; mouth cruciform without distinct lips; with gonads on radial lobes continuous with those in the stomach walls; with tentacles with rings of nematocysts throughout their length, basal part of tentacles adnate to exumbrella. Polyp sessile, with scattered moniliform tentacles.

*Ostroumovia inkermanica* (PALTSCHIKOWA-OSTROUMOVA 1925). Up to 8 mm wide and 6 mm high, dome-shaped, jelly very thick; stomach very small, prismatic, with radial lobes extending nearly to bell margin; gonads on radial lobes with distal portions sac-like, pendent; up to 32 tentacles of different length, proximal part of tentacle narrow, adnate to exumbrella, with an ocellus at the point of issue of the free part of the tentacles; internal statocysts very small, almost invisible except in microtome sections. — Vizagapatam

Channel, east coast of India; Black Sea. (PALTSCHIKOWA-OSTROUMOVA 1925 pp. 273–84, figs. 1–3: as *Moerisia inkermanica*; VALKANOV 1936 pp. 292–301, figs. 20–27; KRAMP 1938 pp. 45–60, Pl. figs. 1–6, textfigs. 1–5; PASPALEFF 1938 pp. 29–40, figs. 1–15; KRAMP 1958 p. 364; India).

## 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.

### Key to the genera of Olindiadidae represented in Indo-Pacific waters.

1. With centripetal canals ..... 2  
 Without centripetal canals ..... 3
2. Tentacles all of one kind, situated on exumbrella at different height above bell margin; without adhesive pads  
*Eperetmus*  
 With primary tentacles projecting above bell margin and with terminal adhesive pads; secondary tentacles on bell margin, without adhesive pads ..... *Olindias*
3. Tentacles in groups (8 perradial and interradianal nematocyst pads, each with one large and one minute tentacle; moreover several tentacles singly placed; no adhesive pads) ..... *Gossea*  
 Tentacles not in groups ..... 4
4. With 6 radial canals; no adhesive pads ..... *Nuarchus*  
 With 4 radial canals; some or all tentacles with adhesive pads ..... 5
5. Some tentacles with terminal adhesive pads ..... *Vallentinia*  
 All tentacles with an adhesive pad at some distance from outer end ..... 6
6. With numerous statocysts ..... *Gonionemus*  
 With no more than 16 statocysts ..... *Scolionema*

*Eperetmus* BIGELOW 1915. Olindiadidae with four radial canals and several centripetal, blind canals; oral lips with nematocysts knobs; with numerous tentacles of one kind, not in groups, situated on exumbrella at different height above bell margin, with rings of nematocysts, without adhesive pads; with numerous statocysts.

*Eperetmus typus* BIGELOW 1915. 23 mm wide, 15 mm high; four well developed, crenulated lips with one row of nematocyst knobs; centripetal canals up to about 16 in each quadrant, tapering upwards; tentacles more numerous than centripetal canals, of different size; statocysts nearly alternating with tentacles. — Alaska; Pacific coast of Canada; Japan. (BIGELOW 1915 p. 401, Pl. 59, figs. 1–8; UCHIDA 1929 p. 364, Pl. 1, fig. 5, textfig. 8).

*Olindias* F. MÜLLER 1861. Olindiadidae with four radial canals and with numerous centripetal canals; gonads with papilliform processes; numerous tentacles of two kinds: primary tentacles issuing above bell margin, with distal adhesive pads and with nematocysts in transverse clasps; secondary tentacles on bell margin, without adhesive pads and with nematocysts in rings; also numerous marginal clubs which may develop into tentacles; statocysts usually in pairs at base of primary tentacles.

### Key to the Indo-Pacific species of *Olindias*.

1. With 6 radial canals; some of the primary tentacles very high up on exumbrella ..... *formosa*  
 With 4 radial canals ..... 2
2. Usually 2 statocysts at base of each primary tentacle ..... *malayensis*  
 Usually only one statocyst at base of each primary tentacle ..... *singularis*

*Olindias formosa* (GOTO 1903). 75 mm wide, height about half of diameter; gonads along nearly whole length of radial canals; 264 primary tentacles; 18–23 centripetal canals in each quadrant; 10–15 long secondary tentacles; about 300 clubs; statocysts twice as many as primary tentacles. — Japan. (GOTO 1903 p. 3, Pl. 1, figs. 1–9, Pl. 2, figs. 14–16, Pl. 3, figs. 17–20, as *Olindioides formosa*; UCHIDA 1929 p. 368, Pl. 1, figs. 6–10, textfigs. 9, 10, as *Olindias formosa*).

*Olindias malayensis* MAAS 1905. 25–35 mm wide, height greater than half diameter; jelly thick; 7–9 centripetal canals in each quadrant; gonads along nearly whole length of radial canals, gonadal papillae thickly

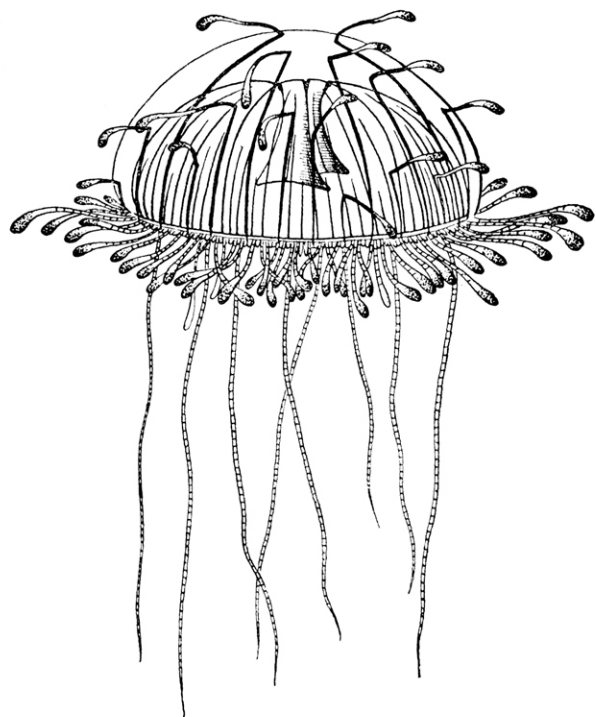


Fig. 282. *Olindias formosa* (from MAYER).

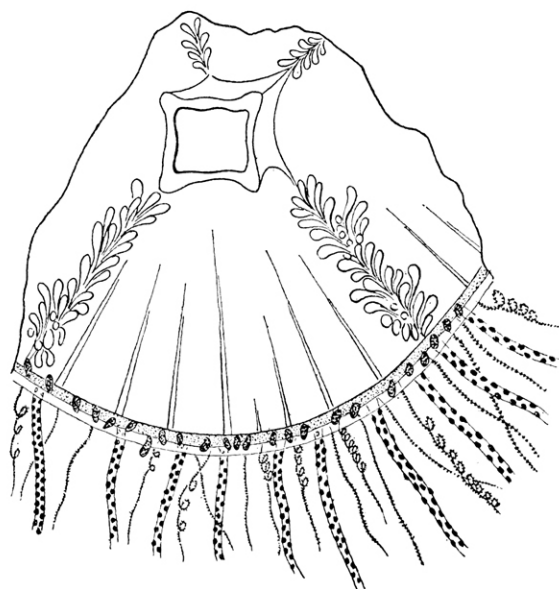


Fig. 283. *Olindias malayensis* (from MAYER).

crowded, very elongated, club-shaped; 20–30 primary tentacles, thick; 30–40 secondary tentacles, thin; 120 clubs. — Malayan Archipelago. (MAAS 1905 p. 47, Pl. 9, figs. 60, 61).

*Olindias singularis* BROWNE 1905. 13–36 mm wide, height half of diameter; 4–12 centripetal canals in each quadrant; gonads along distal half of radial canals or slightly longer; 28–86 primary tentacles, adhesive pads rudimentary; 16–50 secondary tentacles; 32 to more than 100 clubs; usually only one statocyst at base of each primary tentacle. — Tropical coasts of the Indo-West-Pacific Region, from Gulf of Iran to the Philippines; east and south coast of Australia; Low Archipelago in central Pacific. (BROWNE 1905 a p. 737, Pl. 56, fig. 2, Pl. 57, fig. 1; BIGELOW 1909 p. 109, Pl. 4, fig. 1, Pl. 31, figs. 1–10, Pl. 32, fig. 8; KRAMP 1965 p. 102, fig. 10 (young stage)).

*Gossea* L. AGASSIZ 1862. Olindiadidae with four radial canals; without centripetal canals; with one kind of tentacles arranged in groups, without adhesive pads.

*Gossea brachymera* BIGELOW 1909. Up to 20 mm wide, dome-shaped, jelly thick and rigid; stomach small, on a short, broad peduncle; four short lips with nematocysts; gonads extending from base of peduncle almost to ring canal, wavy, distal ends sac-like, pendent; four perradial and four interradial marginal nematocyst pads, each with one large and one minute tentacle; in addition several isolated tentacles at very different stages of development, without adjacent dwarf-tentacle; eight statocysts enclosed in the perradial and interradial nematocyst pads. — Pacific coast of Mexico. Gulf of Mexico; Strait of Magellan; mouth of Rio Colorado,

Argentina. (BIGELOW 1909 p. 103, Pl. 30, figs. 1–10; RUSSELL 1938 pp. 707–10, Pl. 1, figs. 1–3; KRAMP 1957 pp. 42, 124, Pl. 5, figs. 2, 3, textfig. 8).

*Nuarchus* BIGELOW 1912. Olindiadidae with six radial canals, without centripetal canals; tentacles of one kind, without adhesive pads, not in groups; mouth simple, circular; gonads leaf-like; statocysts at base of tentacles.

*Nuarchus halius* BIGELOW 1912. 12 mm wide, thick centrally, thinner near margin; stomach hexagonal, flat, mouth with simple, circular, thickened margin; gonads flat and leaf-like, on greater portion of the six

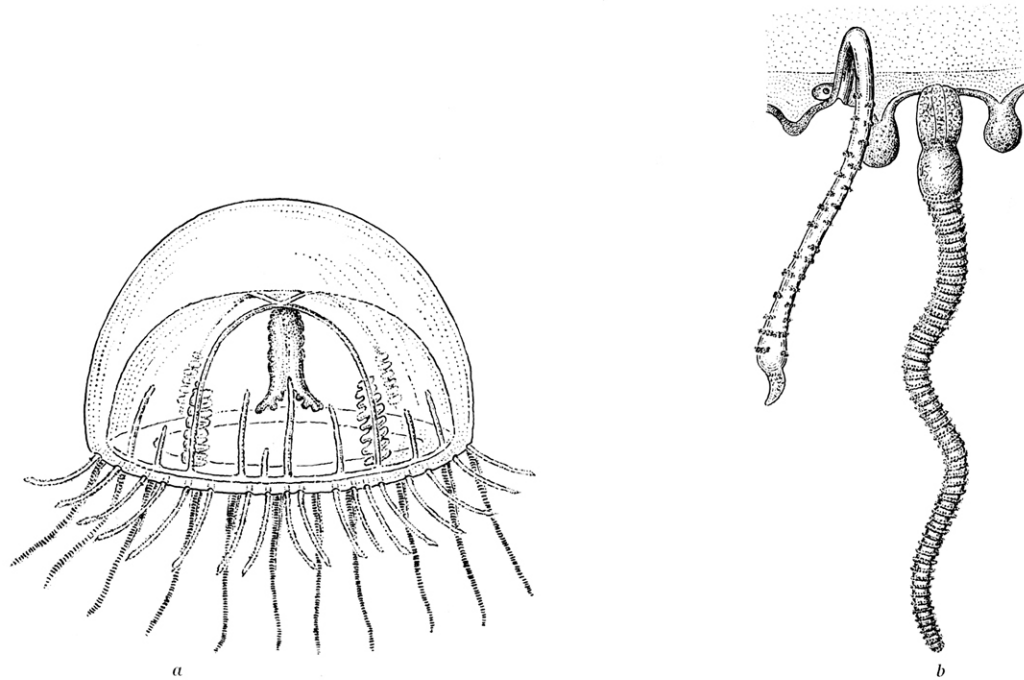


Fig. 284. *Olindias singularis*, a, whole medusa, b, one primary and one secondary tentacle (from BROWNE, redrawn by P. W.).

radial canals; 12 equidistant tentacles with rings of nematocysts distally, issuing from above margin; a statocyst close beside each tentacle. — Philippines. (BIGELOW 1919 p. 320, Pl. 43, figs. 1–5).

*Vallentinia* BROWNE 1902. Olindiadidae with four radial canals; without centripetal canals; with 4–8 large, hollow tentacles with a terminal adhesive pad, and numerous tentacles without adhesive pads but with numerous rings of nematocysts; with 16 or more statocysts.

*Vallentinia adherens* HYMAN 1947. Size? Bowl-shaped; stomach short, quadrangular; gonads extending as a ruffled fold under the radial canals; four long tentacles with terminal adhesive disks, not perradially placed; 40 or more tentacles with rings of nematocysts; small cirrus-like tentacles with rings of nematocysts, approximately alternating with the other tentacles; statocysts one or two between successive tentacles. — California. (HYMAN 1947 p. 264, figs. 6, 7).

*Gonionemus* A. AGASSIZ 1862. Olindiadidae with four radial canals; without centripetal canals; with numerous uniform tentacles, all with an abaxial pad near outer end, and with rings of nematocysts; with a large and indefinite number of statocysts.

*Gonionemus vertens* A. AGASSIZ 1862. 15–20 mm wide, hemi-spherical or somewhat flatter; stomach somewhat shorter than bell cavity, mouth with four short, crenulated lips; gonads along greater portion of radial canals, folded; 60–80 long, rather stiff tentacles, each with an adhesive pad near distal end which is sharply bent; statocysts about as numerous as tentacles. — Strictly littoral: Vancouver Island on west coast of North America; Aleutian Islands; Asian coasts from Sachalin to Vietnam. Mediterranean; north-west Europe;



New England coast. (A. AGASSIZ 1862 p. 350; MAYER 1901 p. 5, as *G. murbachi*; GOTO 1903 p. 12, Pl. 2, figs. 10–13, Pl. 3, figs. 21, 22, as *Gonionema depressum*; MURBACH & SHEARER 1903 p. 185, Pl. 21, figs. 1–3, Pl. 22, fig. 3, as *G. agassizi*; MAYER 1910 p. 343, as *G. vertens*; Pl. 45, figs. 1–4, Pl. 46, figs. 1–3, textfig. 197, as *G. murbachi*; UCHIDA 1929 p. 359, Pl. 1, fig. 1, as *G. oshoro*; RUSSELL 1953 p. 398, Pl. 23, fig. 2, textfig. 263, Pl. 35).

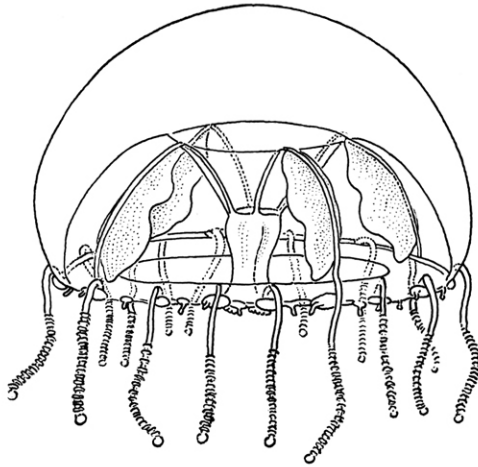


Fig. 285. *Gossea brachymera* (from RUSSELL, redrawn by P. W.).

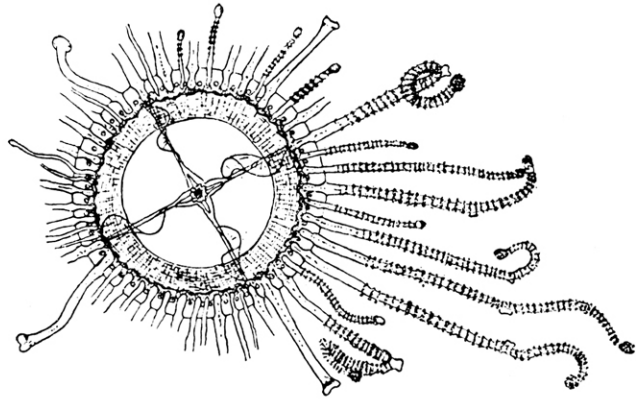


Fig. 286. *Vallentinia adherens* (from HYMAN).

*Scolionema* KISHINOUE 1910<sup>1</sup>. Similar to *Gonionemus*, but with number of statocysts not exceeding 16.

*Scolionema suvaense* (AGASSIZ & MAYER 1899). 9 mm wide, about 6 mm high, jelly thick; gastric peduncle indicated; stomach cruciform, about half as long as bell cavity, mouth with four small lips; gonads extending along

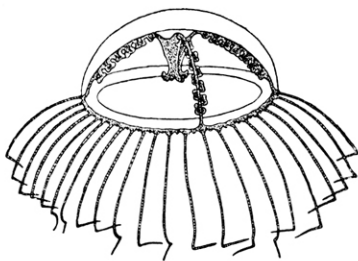


Fig. 287. *Gonionemus vertens* (after MAYER, from KRAMP).

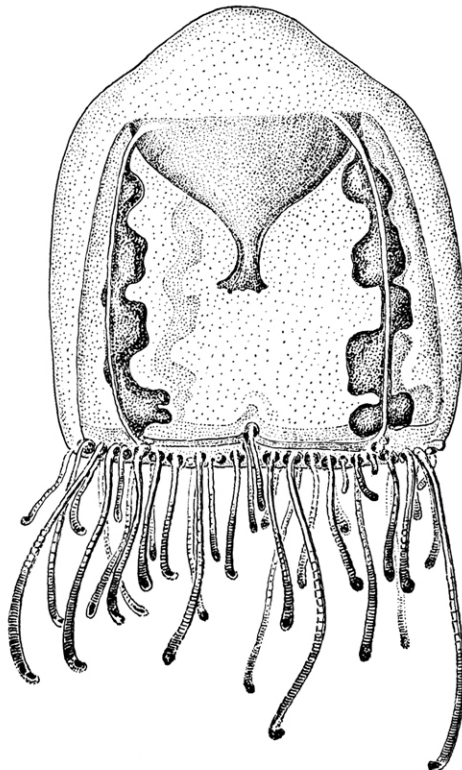


Fig. 288. *Gonionemus hamatus* (from KRAMP, redrawn by P. W.).

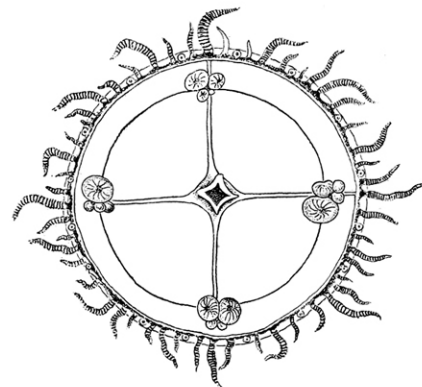


Fig. 289. *Scolionema suvaense* (from UCHIDA, redrawn by P. W.).

<sup>1</sup> In a paper, recently published in Australia (1965), I have replaced *Scolionema* in the genus *Gonionemus*, and described a new species of this genus: *G. hamatus*. Higher than wide, diam. 7 mm; stomach with broad base; four short oral lips with warts of nematocysts; gonads laterally compressed, wavy bands along almost entire length of the four radial canals; about 48 tentacles of unequal length, with prominent rings of nematocysts, the terminal end hook-like with an adhesive pad; no ocelli. — South Africa.

distal 1/3–1/2 of radial canals, ribbon-shaped, much folded; 40–70 tentacles of different lengths, globular bulbs with brownish pigment spots; nematocyst rings throughout whole length of tentacles; distal end sharply bent, but adhesive pads rudimentary; 16 statocysts. — Coasts of India; Maldives and Nicobar Islands; Fiji Islands and Low Archipelago in tropical Pacific; Japan. Lion Gulf in the Mediterranean; Bermuda in western Atlantic. (AGASSIZ & MAYER 1899 p. 164, Pl. 5, figs. 14–16; BROWNE 1905 b p. 149, Pl. 1, fig. 6, Pl. 2, fig. 4, as *G. hornelli*; BIGELOW 1909 p. 106, as *G. hornelli*; p. 107, Pl. 3, figs. 4, 5, Pl. 32, figs. 1–7, as *G. suvaensis*; KISHINOUE 1910 p. 31, Pl. 5, figs. 32, 33, as *Scolionema* n. g. *gemmifera*).

## Family Proboscidae.

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 on to basal lobes, rarely interrational on stomach wall alone; radial canals generally branched; tentacle bulbs without ocelli. Polyps, where known, *Lar*-like.

### Key to the genera of Proboscidae.

- With exumbrellar clusters of nematocysts; gonads on radial lobes of stomach; radial canals branched ..... *Proboscidae*  
 Without exumbrellar clusters of nematocysts; gonads on stomach wall alone; radial canals generally unbranched ..... *Pochella*

*Proboscidae* BRANDT 1835. Proboscidae with clusters of nematocysts on the exumbrella between the tentacles; with gonads extending on to radial lobes of stomach; with 4–6 or more branched radial canals; usually without a ring canal.

### Key to the Indo-Pacific species of *Proboscidae*.

1. With 20 radial canals, some bifurcated ..... *abyssicola*  
 With 4–8 primary radial canals more or less branched ..... 2
2. With (normally) 6 primary radial canals, up to 24 terminal branches and as many tentacles ..... *stellata*  
 With (normally) 4 primary radial canals ..... 3
3. Radial canals with 54–70 or more terminal branches, and as many tentacles; no medusa-buds ..... *flavicirrata*  
 Radial canals with 16–20 terminal branches, and same number of tentacles; medusae may arise from corners of stomach or forkings of radial canals ..... *ornata*

*Proboscidae ornata* (McCRADY 1857). 5 mm wide, slightly higher than a hemisphere, jelly thick and rigid; stomach normally with four radial lobes, mouth with four recurved crenulated lips; normally four primary radial canals, 16–20 (rarely more) terminal branches and as many tentacles; no ring canal; medusa-buds may arise from corners of stomach or forkings of radial canals. — Circumglobal in warm coastal waters. (MAAS 1905 p. 21, Pl. 4, figs. 24–28; MAYER 1910 p. 189, Pl. 20, figs. 1–10, textfig. 100; p. 191, fig. 101; p. 192, Pl. 21, figs. 1–3, textfig. 101 a; p. 194; KRAMP 1957 p. 13, Pl. 3, fig. 7: asexual reproduction; KRAMP 1962 p. 342: development of polyps on stomach wall; KRAMP 1965 p. 103). Synonyms: *Proboscidae gemmifera* (FEWKES), *P. tropica* BROWNE, *P. varians* BROWNE, *P. typica* UCHIDA, *P. conica* MENON.

*Proboscidae flavicirrata* BRANDT 1835. 12 mm wide, 10 mm high; four primary radial canals, 54–70 or more terminal branches and same number of short tentacles; no ring canal. — Pacific coast of North America from Vancouver to California; Asiatic coasts from Kamchatka to Vietnam. (HARTLAUB 1917 p. 366, textfigs. 312–15; CHOW & HUANG 1958 pp. 185, 189, Pl. 5, fig. 40; NAUMOV 1960 p. 504, figs. 391, 392).

*Proboscidae pacifica* (MAAS 1909). 5–7 mm wide, 2–3 mm high, flattened; six primary radial canals, 96–108 terminal branches; ring canal rudimentary; as many tentacles as terminal branches of radial canals; nematocyst tracks short. ? = *P. flavicirrata*. — Japan. (MAAS 1909 p. 17, Pl. 3, fig. 16, as *Willia pacifica*).

*Proboscidactyla occidentalis* (FEWKES 1889). Size? Pyriform, jelly thick; four primary radial canals, 20 terminal branches; 20 tentacles; nematocyst tracks with only one cluster of nematocysts. Probably = *P. flavicirrata* juv. — California. (FEWKES 1889 p. 109, Pl. 5, fig. 3, as *Willia occidentalis*; KRAMP 1959 a p. 177: probably = *P. flavicirrata*).

*Proboscidactyla stellata* (FORBES 1846). 9 mm wide, 8 mm high, jelly thick, evenly rounded; stomach normally with six radial lobes; mouth with six folded lips; six primary radial canals, up to 24 terminal bran-

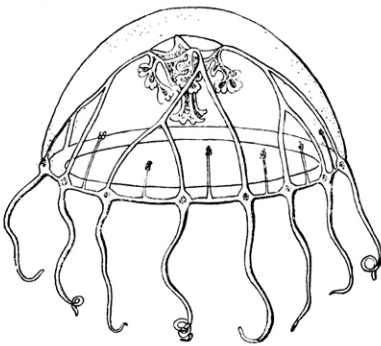


Fig. 290. *Proboscidactyla ornata*, with medusa-buds (after MAYER, from HARTLAUB).

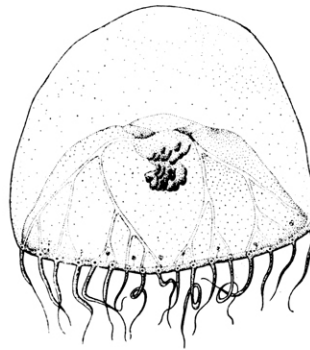


Fig. 291. *Proboscidactyla flavicirrata* (from CHOW & HUSANG).

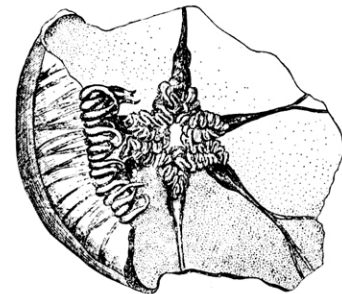


Fig. 292. *Proboscidactyla pacifica* (from HARTLAUB).

ches; no ring canal; up to 24 short tentacles with adaxial basal nematocyst cushions. — Japan; Chefoo in China; Vietnam. North-western Europe. (HARTLAUB 1917 p. 374, textfigs 324–28, as *Willia stellata*; RUSSELL 1953 p. 386, Pl. 23, figs. 3, 4, textfigs. 250–56; CHOW & HUANG 1958 pp. 186, 189, Pl. 5, fig. 39).

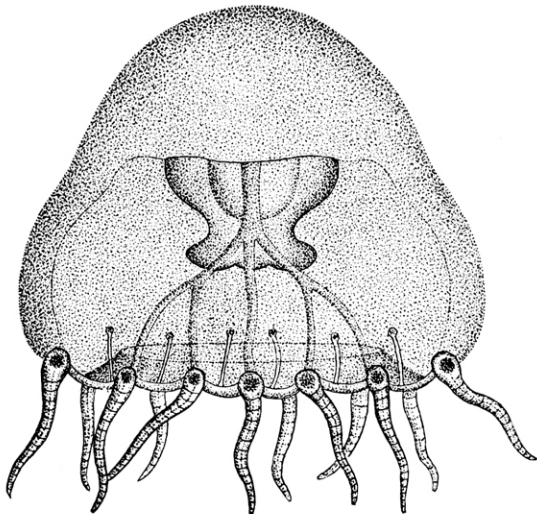


Fig. 293. *Proboscidactyla occidentalis* (from FEWKES).

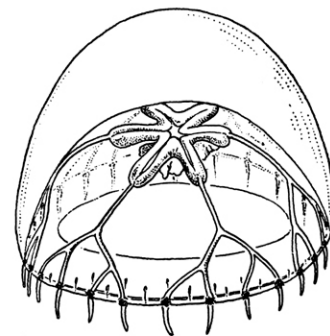


Fig. 294. *Proboscidactyla stellata* (from RUSSELL, redrawn by P. W.).

*Proboscidactyla abyssicola* UCHIDA 1947. 20 mm wide, 10 mm high; 20 radial canals, some bifurcated; ring canal present; gonads extending along proximal half of all radial canals; no tentacles. — Japan; Ceram Sea and Celebes Sea in the Malayan Archipelago. (UCHIDA 1947 b p. 335, fig. 3; KRAMP 1965 p. 104).

*Pochella* HARTLAUB 1917. Proboscidactylidae without exumbrellar nematocyst clusters; with four radial canals usually unbranched; with gonads on interradiar walls of stomach.

*Pochella polynema* HARTLAUB 1917. 2–3 mm wide, bell-shaped or hemispherical, jelly fairly thick; stomach large, about 2/3 as long as bell cavity; slightly wavy lips; radial canals often with exceedingly fine branches;

gonads cushion-like; 30–40 or more tentacles. — Vancouver on Pacific coast of North America. North-western Europe. (HARTLAUB 1917 p. 414, figs. 344–46; FOERSTER 1923 p. 248, Pl. 3, figs. 5–7, Pl. 4, fig. 1; RUSSELL 1953 p. 394, textfigs. 257–62).

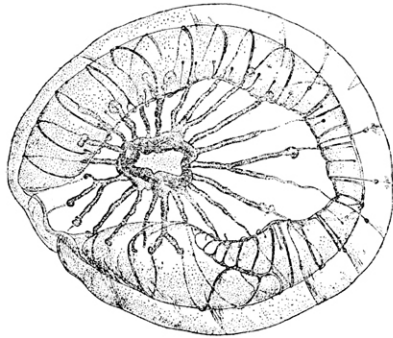


Fig. 295. *Proboscidactyla abyssicola* (from UCHIDA).

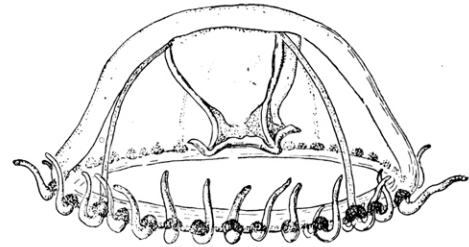


Fig. 296. *Pochella polynema* (from HARTLAUB).

#### IV. 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.

##### Key to the families of Trachymedusae.

1. Numerous tentacles arranged in groups, most of them with a terminal adhesive disk; stomach broad with eight radial lobes ..... *Ptychogastridae*  
Tentacles without adhesive disks ..... 2
2. With centripetal canals and with flattened, leaf-shaped gonads ..... *Geryoniidae*  
Without centripetal canals ..... 3
3. With 4 radial canals ..... *Petasidae*  
With 8, rarely more, radial canals..... 4
4. With broad, circular stomach and broad radial canals ..... *Halicreatidae*  
Stomach and radial canals narrow ..... *Rhopalonematidae*

#### Family Ptychogastridae.

Trachymedusae with marginal tentacles grouped into more or less well defined clusters; some tentacles with adhesive disks; with eight radial canals; stomach eight-lobed, with eight mesenterial partitions; gonads on the sides of the eight stomach lobes or on radial canals adjacent to stomach lobes; with free sensory clubs.

*Ptychogastria* ALLMAN 1878. With the characters of the family.

*Ptychogastria polaris* ALLMANN 1878. 18–22 mm wide, hemispherical or somewhat conical, exumbrella with 16 radiating ridges; velum very wide; stomach about half as long as bell cavity, eight-rayed above, mouth with four lips; 16 separated gonads along the sides of the eight stomach lobes; about 48 clusters of solid tentacles (in adult), each cluster with three filiform tentacles and numerous tentacles with adhesive organs; 16 statocysts. — South Shetland Islands and Graham Land in Antarctic; Aleutian Islands; circum-polar in arctic waters. (MAYER 1910 p. 372, textfig. 212; VANHÖFFEN 1912 p. 386, Pl. 25, fig. 6, textfig. 20, as *Ptychogastria opposita*; KRAMP 1947 p. 4, Pl. 1, figs. 1–4, Pl. 6, figs. 1, 2; KRAMP 1957 pp. 45, 98, 99).

*Ptychogastrina antarctica* (HAECKEL 1879). Doubtful species, probably not belonging to *Ptychogastrina*. — Kerguelen Island, Antarctic.

## Family Petasidae.

Trachymedusae with four radial canals; with well developed manubrium; marginal tentacles not in clusters, solid, with a terminal, club-shaped knob of nematocysts; with free sensory clubs.

*Petatus* HAECKEL 1879. Petasidae with marginal tentacles regularly arranged, at equal intervals.

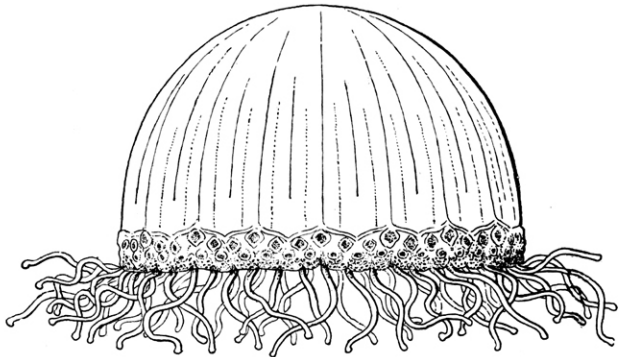


Fig. 297. *Ptychogastrina polaris* (after HAECKEL, from BROCH).

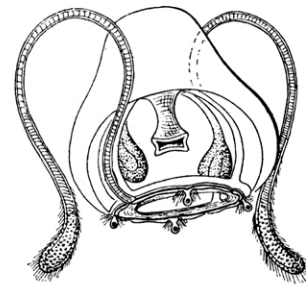


Fig. 298. *Petatus digonimus* (from MAYER).

*Petatus digonimus* (HAECKEL 1879). 1 mm high and wide; two gonads on middle 1/3 of two opposite radial canals; two tentacles; four statocysts. Doubtful species. — Kerguelen Island. (HAECKEL 1879 p. 249, Pl. 18, fig. 2).

*Petatus eucope* (HAECKEL 1879). 10 mm wide, 5 mm high; gonads spherical or spindle-shaped; eight tentacles; eight statocysts. Doubtful species. — Red Sea; south of Madagascar. (HAECKEL 1879 p. 249, Pl. 18, fig. 3).

*Petatus tiaropsis* (HAECKEL 1879). 10 mm wide, 3 mm high; gonads extending along 2/3 of the radial canals; more than 100 tentacles densely crowded; eight statocysts. Doubtful species. — South China Sea. (HAECKEL 1879 p. 250).

*Petasiella* UCHIDA 1947. Petasidae with marginal tentacles arising asymmetrically, at unequal intervals.

*Petasiella asymmetrica* UCHIDA 1947. Up to 1 mm wide, bell-shaped, jelly moderately thick; stomach small, flask-shaped; gonads small, globular, at distal points of the four radial canals; up to 28 tentacles, irregularly placed, with terminal cluster of nematocysts; four statocysts. — Palao Islands; Philippines; Malayan Archipelago (UCHIDA 1947 b p. 311, textfigs. 10, 11; KRAMP 1959 b, p. 256).

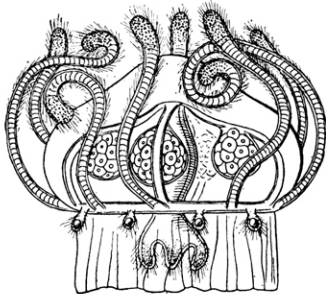


Fig. 299. *Petatus eucope* (from MAYER).

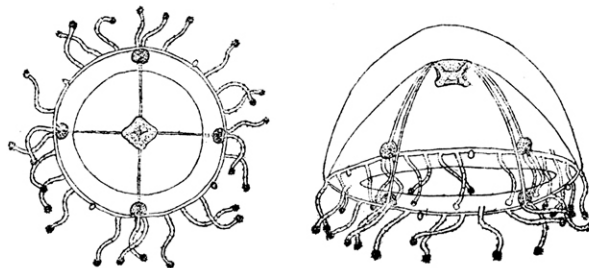


Fig. 300. *Petasiella asymmetrica* (from UCHIDA).

## Family Halicreatidae.

Trachymedusae with wide, circular stomach; with broad radial canals; with numerous marginal tentacles of different sizes, but all structurally alike and arranged in a single series; each tentacle divisible into a soft, flexible proximal and a stiff, spine-like distal region; with free sensory clubs; with neither peduncle nor proboscis.

### Key to the Indo-Pacific genera of Halicreatidae.

- |   |                    |
|---|--------------------|
| 1. With about 16 or more radial canals .....              | <i>Halitrephes</i> |
| With 8 radial canals .....                                | 2                  |
| 2. With tentacles arranged in 16 groups .....             | <i>Botrynema</i>   |
| With tentacles in a continuous row .....                  | 3                  |
| 3. With perradial gelatinous papillae on exumbrella ..... | <i>Halicreas</i>   |
| Without exumbrellar papillae .....                        | <i>Haliscera</i>   |

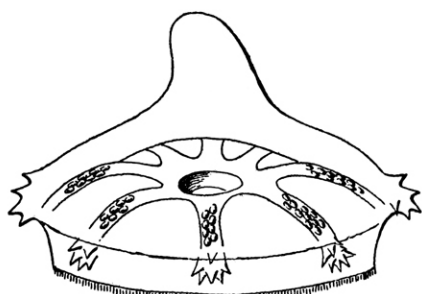


Fig. 301. *Halicreas minimum*  
(after VANHÖFFEN, from MAYER).



Fig. 302. *Haliscera conica*  
(after VANHÖFFEN, from MAYER).

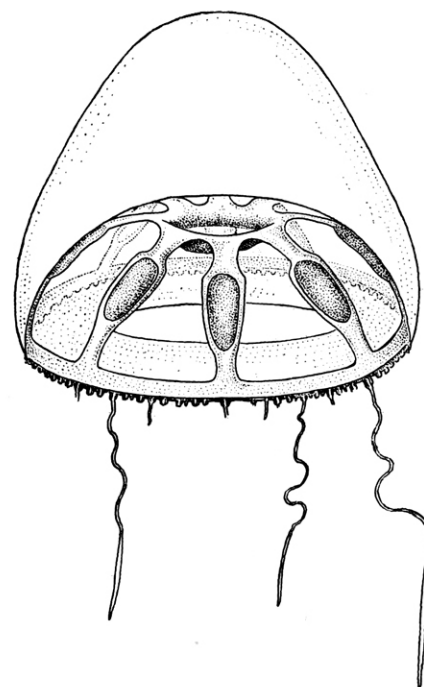


Fig. 303. *Haliscera bigelowi* (from RUSSELL, redrawn by P. W.).

*Halicreas* FEWKES 1882. Halicreatidae with eight radial canals; with a continuous row of tentacles; with perradial gelatinous papillae on the exumbrella.

*Halicreas minimum* FEWKES 1882. 30–40 mm wide, thick, disk-like, with a small, conical apical projection of varying size; eight clusters of gelatinous papillae above margin; mouth a wide, circular opening; eight broad, band-like radial canals and a broad ring canal; gonads flattened, extending along almost entire length of canals; tentacles very numerous, up to 640; 3–4 statocysts in each octant. — Mainly abyssal, cosmopolitan except in arctic waters and in the Mediterranean. (VANHÖFFEN 1902 p. 68, Pl. 9, figs. 7, 8, Pl. 11, fig. 30, as *H. papillosum*; BIGELOW 1909 p. 138, Pl. 3, fig. 3, Pl. 33, figs. 8, 9, Pl. 34, figs. 1–3, 5, 8, 10, 11, as *H. papillosum*; KRAMP 1947 p. 7, Pl. 6, fig. 3; RUSSELL 1953 p. 452, textfigs. 299–300; KRAMP 1965 p. 105).

*Haliscera* VANHÖFFEN 1902. Halicreatidae with eight radial canals; with a continuous row of tentacles; without papillae on exumbrella.



*Haliscera conica* VANHÖFFEN 1902. Up to 18 mm wide, with a thick, bluntly conical apical projection; gonads oval, on middle portion of the eight broad radial canals; 8–9 tentacles and two statocysts in each octant, the base of each tentacle surrounded by a broad thickening of the marginal nematocyst tissue. — Bathypelagic: off Chile and East Australia; circumpolar in antarctic waters. Eastern Atlantic; Mediterranean. (VANHÖFFEN 1902 p. 72, Pl. 9, fig. 6, Pl. 11, fig. 33; KRAMP 1957 pp. 46, 47, 48, 100, 110 ff., 126, textfig. 17).

*Haliscera bigelowi* KRAMP 1947. 15–17 mm wide, 9–10 mm high, almost hemispherical, with very thick hemispherical apex and thin jelly in marginal region; gonads broadly oval, about  $\frac{2}{5}$  of the length of radial canals, slightly nearer to stomach than to bell margin; about 12 tentacles and three statocysts in each octant; the thickenings of the nematocyst tissue around the bases of the tentacles are less pronounced than in *H. conica*. — Bathypelagic in the eastern tropical Pacific and north and west of New Zealand. Atlantic Ocean

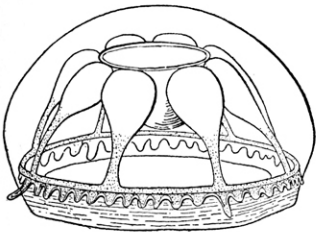


Fig. 304. *Haliscera racovitzae*  
(after MAAS, from MAYER).

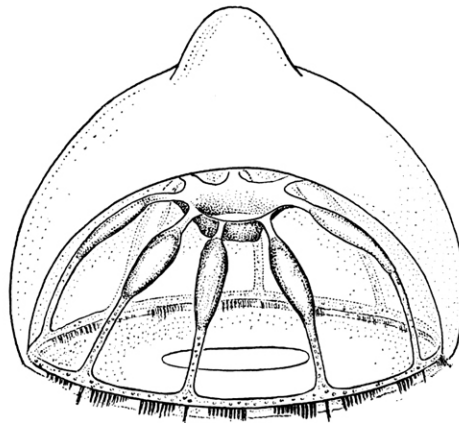


Fig. 305. *Botrynema brucei*  
(from RUSSELL, redrawn by P. W.).

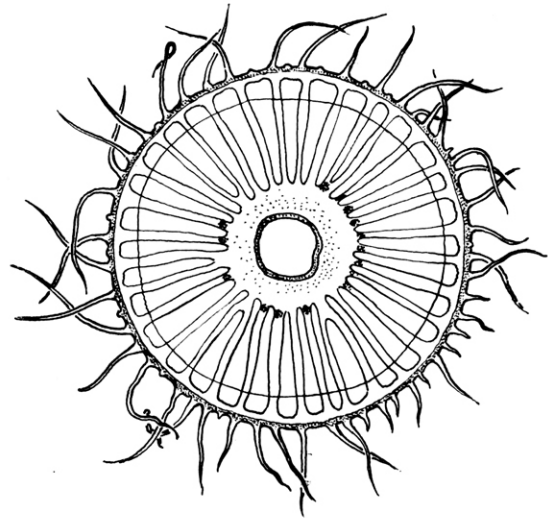


Fig. 306. *Halitrephes maasi*  
(from BIGELOW, redrawn by P. W.).

from West Africa to Iceland. (BIGELOW 1909 p. 142, Pl. 3, figs. 1, 2, Pl. 33, figs. 6, 11, Pl. 34, fig. 9, as *Homoeonema alba*; KRAMP 1947 p. 8, Pl. 1, figs. 5–8, Pl. 2, figs. 1, 2; RUSSELL 1953 p. 456, Pl. 24, fig. 2, textfigs. 301, 302; KRAMP 1965 p. 107).

*Haliscera racovitzae* (MAAS 1906). 8 mm wide, 4 mm high, almost hemispherical, moderately thick jelly, flaccid, apex evenly rounded; stomach a truncated cone; gonads along proximal  $\frac{1}{2}$  to  $\frac{2}{5}$  of the radial canals, close to the stomach; six tentacles and two statocysts in each octant. — Bathypelagic in antarctic and subantarctic waters; north and east of New Zealand. (MAAS 1906 b p. 10, Pl. 1, figs. 3, 4, Pl. 2, fig. 13, as *Homoeonema racovitzae*; KRAMP 1965 p. 108).

*Botrynema* BROWNE 1908. Halicreatidae with eight radial canals; with 16 groups of tentacles (two groups containing many tentacles in a single row in each octant) and eight solitary perradial tentacles.

*Botrynema brucei* BROWNE 1908. Up to about 25 mm wide; the apical jelly is very thick and terminates in a distinct and sharply defined knob; stomach wide, circular and short; gonads oval, on proximal or central halves of radial canals; 11–12 tentacles in each of the 16 groups; usually three statocysts in each interradial space and 1–2 on either side of the solitary perradial tentacles. — Bathypelagic in the oceans: northern Pacific and the surroundings of Australia and New Zealand; widely distributed in the Indian and Atlantic Oceans. (BROWNE 1908 p. 239, Pl. 1, figs. 8, 9, Pl. 2, fig. 1; KRAMP 1947 p. 11, Pl. 1, fig. 9, Pl. 2, fig. 3, Pl. 6, fig. 4; RUSSELL 1953 p. 459, Pl. 27, fig. 1, textfigs. 303, 304; KRAMP 1965 p. 108).

*Halitrephes* BIGELOW 1909. Halicreatidae with several (16 or more) radial canals; with a continuous row of tentacles; without papillae on exumbrella.

*Halitrephes maasi* BIGELOW 1909. Up to about 100 mm wide, low, rounded, jelly fairly thin, soft and flaccid; stomach circular; 16–30 broad, ribbon-like radial canals, some of which may be bifurcated; shape of gonads unknown; 100–300 tentacles; number of statocysts unknown. — Mainly abyssal: circumglobal in the warm and temperate parts of the oceans. (BIGELOW 1909 p. 146, Pl. 33, figs. 1–5, 7, 10, Pl. 45, fig. 13; VANHÖFFEN 1912 p. 384, as *H. valdiviae*; KRAMP 1948 a p. 7, textfig. 1, as *H. medius*; KRAMP 1965 p. 109).

## Family Rhopalonematidae.

Trachymedusae with narrow stomach with or without peduncle; usually with eight, rarely more, radial canals; without centripetal canals; 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.

### Key to the genera of Rhopalonematidae represented in Indo-Pacific waters.

1. Without a gastric peduncle (one species of *Crossota* has a short peduncle) ..... 2  
     With a gastric peduncle ..... 8
2. With only 4 gonads, pendent; 8 radial canals; 4 large and about 24 small tentacles ..... *Tetrorchis*  
     With 8 (rarely more) gonads ..... 3
3. With 8 long, club-shaped and up to 24 small, cirrus-like tentacles; gonads elongated, along radial canals *Rhopalonema*  
     With tentacles all of one kind ..... 4
4. With gonads adjacent to stomach (sometimes also eight small gonads free of stomach); very numerous tentacles ..... *Arctapodema*  
     Gonads separated from stomach ..... 5
5. Exumbrella with numerous meridional furrows; gonads sausage-shaped, pendent; very numerous tentacles ..... *Crossota*  
     Exumbrella smooth; gonads not pendent ..... 6
6. With only 8 tentacles; gonads globular, distal ..... *Sminthea*  
     Gonads linear ..... 7
7. With up to 32 tentacles successively developed ..... *Colobonema*  
     With 48 or more tentacles of equal size ..... *Pantachogon*
8. Peduncle short, conical (in young specimens almost invisible) ..... 9  
     Peduncle long, slender; gonads sausage-shaped, pendent ..... 10
9. With only two, pendent gonads ..... *Persa*  
     With 8 globular or oval gonads ..... *Amphogona*
10. Gonads attached to peduncle ..... *Aglaura*  
     Gonads attached to subumbrellar portion of radial canals ..... *Aglantha*

*Rhopalonema* GEGENBAUR 1856. Rhopalonematidae without a gastric peduncle; with gonads along the eight radial canals separated from stomach; with tentacles of two kinds: radial clubs, and inter- and adradial cirri; with enclosed marginal statocysts.

### Key to the species of *Rhopalonema*.

- Umbrella with a distinct apical knob; gonads oval, along middle 1/3 of radial canals; statocysts close beside tentacles and cirri ..... *velatum*
- Umbrella without an apical knob; gonads along distal 2/3 of radial canals; statocysts in middle of the spaces between tentacles and cirri ..... *furnerarium*

*Rhopalonema velatum* GEGENBAUR 1856. 8–10 mm wide, somewhat flatter than a hemisphere, with a conical apical thickening; stomach narrow, elongated, reaching almost to velar opening; four short, simple lips; gonads linear or oval, extending along middle 1/3 of radial canals; eight radial club-shaped tentacles; a

statocyst close beside each of the radial tentacles and the interradial cirri; velum very broad. — Mainly in upper and intermediate water layers; generally distributed in warm and temperate parts of the oceans and in the Mediterranean. (MAYER 1910 p. 378, textfigs. 213–19; RUSSELL 1953 p. 430, textfigs. 283, 284; KRAMP 1965 p. 110).

*Rhopalonema funerarium* VANHÖFFEN 1902. Up to 17 mm wide and 14 mm high, somewhat conical, without an apical projection; stomach narrow, elongated, hardly reaching velar opening; gonads linear, extending along distal 2/3 of radial canals; eight radial tentacles; eight interradial and 16 adradial cirrus-like, very small tentacles each with a globular terminal knob; 32 statocysts in middle of the spaces between tentacles and cirri; velum very broad. — In deep and intermediate water: eastern tropical Pacific; east of New Zealand; Malayan Archipelago; Indian Ocean. Widely distributed in the Atlantic Ocean, mainly in the eastern parts.

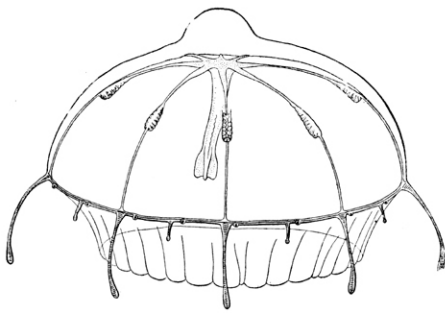


Fig. 307. *Rhopalonema velatum* (from MAYER).

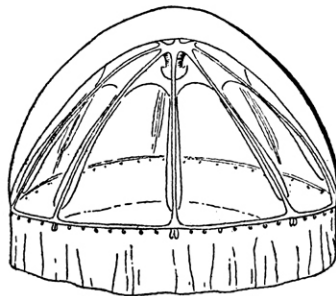


Fig. 308. *Rhopalonema funerarium* (after VANHÖFFEN, from MAYER).

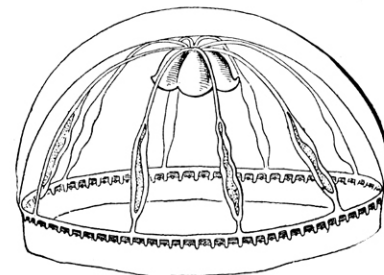


Fig. 309. *Pantachogon haeckeli* (after VANHÖFFEN, from MAYER).

(VANHÖFFEN 1902 p. 61, Pl. 9, fig. 2, Pl. 10, fig. 17, Pl. 11, fig. 31; MAYER 1910 p. 380, textfig. 223, as *R. coerulum*; KRAMP 1947 p. 14, Pl. 2, figs. 4, 5; RUSSELL 1953 p. 434, textfigs. 285, 286; KRAMP 1965 p. 116).

*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.

#### Key to the Indo-Pacific species of *Pantachogon*.

With 64 tentacles ..... *haeckeli*  
With about 120 tentacles ..... *scotti*

*Pantachogon haeckeli* MAAS 1893. About 12 mm high and wide, bell-shaped, with thin jelly and without an apical projection; with very strong and conspicuous musculature; stomach short; four small, simple lips; gonads extending along greater portion of the eight radial canals; 64 tentacles all alike; 64 club-shaped statocysts; velum very broad. — Bathypelagic in the oceans: in western Pacific from Australia to the Bering Sea and in the Gulf of Alaska; entire Indian Ocean to the slope of the Antarctic Continent. Atlantic from Antarctic to Iceland and Davis Strait. (MAAS 1893 p. 17, Pl. 1, fig. 2, as *Pantachogon haeckelii*; VANHÖFFEN 1902 p. 63 Pl. 9, fig. 9, Pl. 10, figs. 19, 20, Pl. 11, fig. 25, as *P. rubrum*; BIGELOW 1938 p. 115; KRAMP 1947 p. 19, Pl. 2, figs. 7, 8; RUSSELL 1953 p. 440, Pl. 25, fig. 2, textfigs. 290–92; NAUMOV 1960 p. 561, Pl. 30, fig. 4, textfig. 452; KRAMP 1965 p. 117).

*Pantachogon scotti* BROWNE 1910. About 4 mm wide, a little broader than high, with thin jelly and without an apical projection; with strong musculature; stomach very small; four short lips; gonads linear, extending along proximal 2/3 of the eight radial canals; about 120 tentacles all alike; number of statocysts unknown. — Epipelagic in Indian and Atlantic sectors of Antarctic. (BROWNE 1910 p. 36, Pl. 3, figs. 5, 6; VANHÖFFEN 1912 p. 378, textfig. 16; KRAMP 1959 a pp. 186, 242, 252, fig. 274).

*Colobonema* VANHÖFFEN 1902. Rhopalonematidae without a gastric peduncle; with the apical outlines of the subumbrellar muscular fields forming a star-shaped figure; with elongated gonads extending along the eight radial canals; with tentacles all of one kind, developing in succession; with free, club-shaped marginal statocysts.

**Key to the species of *Colobonema*.**

At least twice as high as wide, up to 14 mm high; gonads in middle half part of radial canals ..... *igneum*<sup>1</sup>  
 About as high as wide, up to 45 mm; gonads along greater part of radial canals; 32 tentacles ..... *sericeum*  
 (Doubtful species, with 40 tentacles) ..... *typicum*

<sup>1</sup> Formerly named *Aglantha ignea*.

*Colobonema sericeum* VANHÖFFEN 1902. Up to 45 mm wide and 35 mm high; bell-shaped, slightly conical, with fairly thin jelly and without an apical projection; stomach more or less elongated, tubular; four small

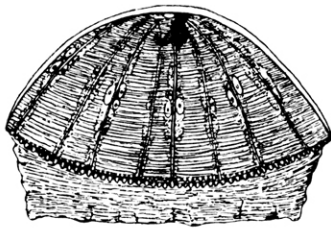


Fig. 310. *Pantachogon scotti*  
(from VANHÖFFEN).

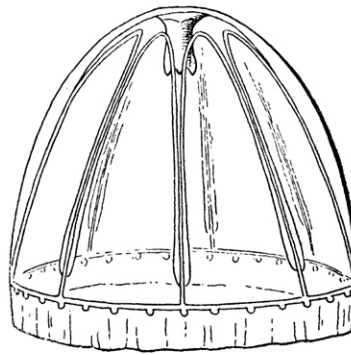


Fig. 311. *Colobonema sericeum*  
(after VANHÖFFEN, from MAYER).

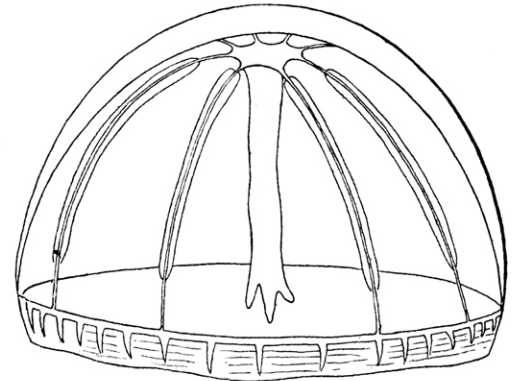


Fig. 312. *Colobonema typicum* (from MAYER).

lips; gonads linear, straight, extending along greater part of radial canals; 32 tentacles, the adradial tentacles developed before the interrarial; statocysts probably alternating with the tentacles; velum broad. — Bathypelagic in the deep parts of the oceans, except in the Mediterranean and the arctic and antarctic seas, in the Pacific as far north as off Japan. (VANHÖFFEN 1902 p. 57, Pl. 9, fig. 1, Pl. 12, figs. 39–42; MAAS 1905 p. 53, Pl. 10, figs. 62–65, as *C. typicum*; RANSON 1936 b p. 152, Pl. 2, figs. 14, 15; RUSSELL 1953 pp. 436, 440, Pl. 25, fig. 1, textfigs. 287–289; KRAMP 1965 p. 118).

*Colobonema typicum* (MAAS 1897, non 1905). 20 mm wide, 12 mm high, jelly thin but rigid; stomach short, urn-shaped, four small lips; gonads along distal half of radial canals; about 40 tentacles; statocysts? (The description incomplete, partly based on figure). — Pacific coast of Central America. (MAAS 1897 p. 22, Pl. 3, figs. 1–3, as *Homoeonema typicum*).

*Colobonema igneum* (VANHÖFFEN 1902). 14 mm high, 7 mm wide; stomach short, less than half as long as bell cavity, four simple lips; gonads along middle part of the eight radial canals; eight large and 24 small tentacles; eight free sensory clubs. — Off East Africa; near Galapagos Islands in eastern Pacific; in deep water. (VANHÖFFEN 1902 p. 76, Pl. 9, fig. 10, as *Aglicra ignea*; MAYER 1910 p. 405, textfig. 256, as *Aglantha ignea*; KRAMP 1965 p. 121, fig. 11).

*Sminthea* GEGENBAUR 1856. Rhopalonematidae without a gastric peduncle; with globular gonads on the eight radial canals; with only eight radial tentacles; with enclosed marginal statocysts.

*Sminthea eurygaster* GEGENBAUR 1856. Up to 6 mm wide and about half as high, with a small apical gelatinous projection; stomach short; four very short lips; gonads close to the ring canal; eight marginal statocysts. — Off Gulf of Panama; the waters east of Australia; near Ceylon; the Chagos Islands; north of Madagascar.

Atlantic Ocean from about 45° S. to the Bay of Biscay. Deep and intermediate water layers. (MAYER 1910 p. 383, textfigs. 226, 227; KRAMP 1965 p. 122).

*Arctapodema* DALL 1907. Rhopalonematidae without a gastric peduncle; with gonads on radial canals adjacent to stomach; with eight narrow radial canals; with numerous tentacles, all alike, in a single row; with free club-shaped marginal statocysts.

**Key to the Indo-Pacific species of *Arctapodema*.**

1. With 4 interradial gonads encircling stomach but interrupted in the perradial corners..... *antarctica*
- With 8 gonads..... 2

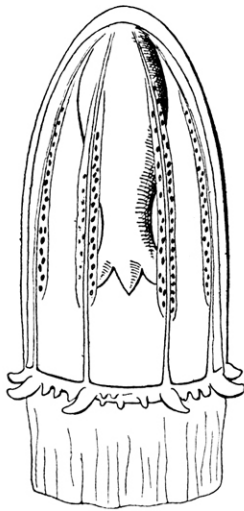


Fig. 313. *Colobonema igneum* (from MAYER).

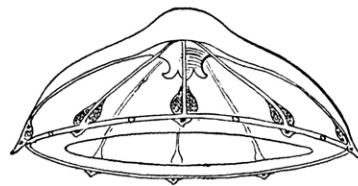


Fig. 314. *Sminthea eurygaster*  
(after HAECKEL, from MAYER).

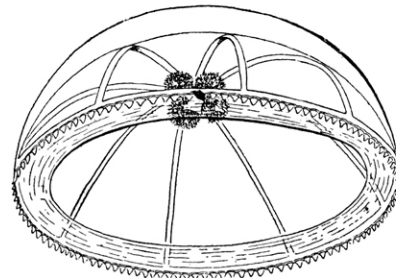


Fig. 315. *Arctapodema ampla*  
(after VANHÖFFEN, from MAYER).

2. Gonads extending from radial lobes of stomach outwards on proximal parts of radial canals, sometimes also eight pairs of small gonads on radial canals separated from stomach..... *ampla*
- Gonads on radial canals near base of stomach..... 3
3. Gonads pendent..... *australis*
- Gonads spherical..... *macrogaster*

*Arctapodema ampla* (VANHÖFFEN 1902). Up to 15 mm wide, somewhat flatter than a hemisphere, thin jelly, thicker at apex; stomach short, urn-shaped, with eight radial lobes; four simple lips; eight swollen gonads adjacent to the gastral lobes; the gonads may be of unequal size, and some of them may be radially divided into two halves; small additional gonads may also appear in pairs on the radial canals at a short distance from the gastral lobes; about 100 tentacles; 4–8 marginal statocysts. — Antarctic waters. West Africa; Mediterranean; intermediate and deep water. (VANHÖFFEN 1902 p. 65, Pl. 10, fig. 21, Pl. 11, figs. 24, 26, 27, as *Homoeonema amplum*; MAAS 1906 b p. 5, Pl. 1, figs. 1, 2, 7, Pl. 2, figs. 8, 12, Pl. 3, figs. 14, 20, as *Isonema amplum*; RANSON 1936 pp. 156, 157, Pl. 2, fig. 17; KRAMP 1957 pp. 55, 56, 99, 126, Pl. 5, fig. 4, textfig. 9).

*Arctapodema antarctica* (VANHÖFFEN 1912). Up to 16 mm wide, hemispherical, fairly thin jelly; stomach tubular; four interradial gonads encircling base of stomach but interrupted in the four perradial corners; no gonads on the radial canals; about 120 tentacles; statocysts unknown; stomach red in adult. — Antarctic waters; southern part of Indian Ocean; in deep water. (VANHÖFFEN 1912 p. 375, textfigs. 8, 9, as *Isonema antarcticum*; KRAMP 1957 pp. 55, 56, 58, 99, 100, 126, Pl. 5, figs. 5, 6, textfig. 9).

*Arctapodema australis* (VANHÖFFEN) 1912. Up to 23 mm wide and 14 mm high, thin jelly; stomach short and broad, with 16 radial folds; four lips; eight gonads globular or club-shaped, pendent, on the radial canals near base of stomach; about 112 tentacles; statocysts unknown; stomach violet, canals and tentacles wine-red, gonads yellow. — Southern Indian Ocean; Indian sector of Antarctic; intermediate and deep water.

(VANHÖFFEN 1912 p. 376, textfigs. 10, 11, as *Isonema australe*; KRAMP 1957 pp. 55, 56, 58, 99, 100, 126, Pl. 5, figs. 5, 6, textfig. 9).

*Arctapodema macrogaster* (VANHÖFFEN 1902). 7 mm wide; stomach fairly large, four lips; eight spherical gonads adjacent to stomach; 84 tentacles; 32 statocysts. Possibly = *A. australis*. — Southern Indian Ocean; intermediate depth. (VANHÖFFEN 1902 p. 66, Pl. 10, fig. 22, as *Homoeonema macrogaster*; MAYER 1910 p. 388, textfig. 238).

*Amphogona* BROWNE 1905. Rhopalonematidae with a short, conical gastric peduncle; exumbrella smooth; with ellipsoidal or sac-shaped, pendent gonads on the eight radial canals; gonads usually of unequal size; with tentacles all alike, not densely crowded; with free, club-shaped marginal statocysts.

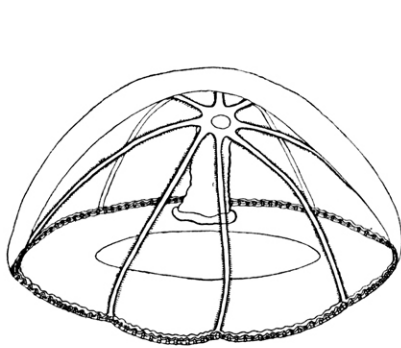


Fig. 316. *Arctapodema antarctica*  
(from VANHÖFFEN).

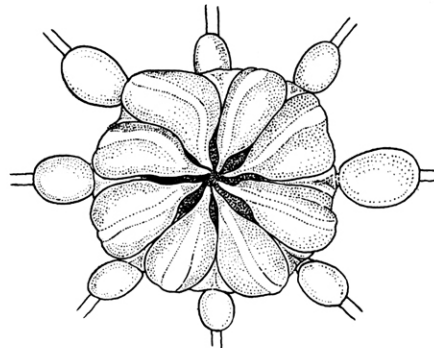


Fig. 317. *Arctapodema australis*, aboral view of stomach  
and gonads (from KRAMP, redrawn by P. W.).

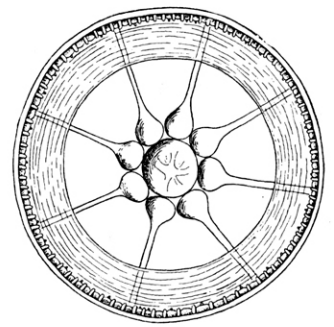


Fig. 318. *Arctapodema macrogaster*  
(from MAYER).

#### Key to the species of *Amphogona*.

1. With a bluntly conical apical projection; gonads pendent, in middle part of radial canals; about 64 tentacles *apicata*  
About hemispherical, without an apical projection; gonads spherical or ellipsoidal ..... 2
2. With 16 tentacles; gonads of equal size ..... *pusilla*  
With 50–80 tentacles; gonads ellipsoidal, distal, unequal, alternately four larger and four smaller ..... *apsteini*

*Amphogona apsteini* (VANHÖFFEN 1902). 4–6 mm wide, lower than a hemisphere, with thin jelly; stomach small; four short simple lips; gonads ellipsoidal, nearer to ring canal than to base of peduncle, of unequal size, alternately very small and somewhat larger; 50–80 tentacles; 16–24 statocysts. — Epipelagic: tropical parts of eastern and western Pacific; Malayan Archipelago; Indian Ocean from Sumatra to Madagascar. Gulf of Guinea on the Atlantic coast of Africa. (BROWNE 1905 a p. 740, Pl. 54, fig. 5, Pl. 56, fig. 1, Pl. 57, figs. 10–15; BIGELOW 1909 p. 126, Pl. 2, figs. 1, 2, Pl. 34, figs. 12–15, Pl. 45, fig. 10; KRAMP 1965 p. 123, figs. 12, 13).

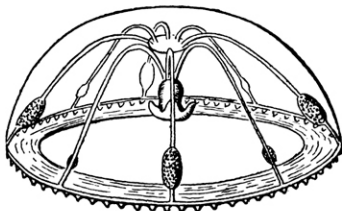


Fig. 319. *Amphogona apsteini*  
(after VANHÖFFEN, from MAYER).



Fig. 320. *Amphogona pusilla*  
(from HARTLAUB).

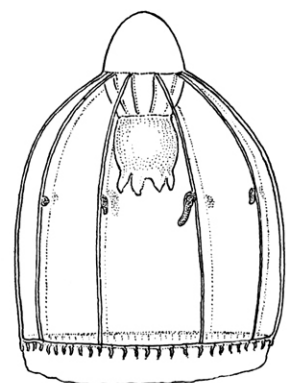


Fig. 321. *Amphogona apicata*  
(from KRAMP, redrawn by P. W.).



*Amphogona pusilla* HARTLAUB 1909. 1.5–2 mm wide, nearly hemispherical, with thin jelly; stomach small; four simple lips; gonads spherical on radial canals, leaving 1/4 of the length of radial canal near ring canal free; 16 tentacles; statocysts unknown. — Djibuti in East Africa; coast of Malacca. (HARTLAUB 1909 a p. 462, Pl. 21, fig. 27; KRAMP 1965 p. 124).

*Amphogona apicata* KRAMP 1957. Up to 7 mm wide and 8 mm high, with thin walls and a bluntly conical apical projection; stomach small, tubular; four short simple lips; gonads sac-shaped, pendent, near middle points of radial canals; about 64 tentacles; statocysts unknown. — New Zealand; Mozambique Channel. West Africa; south-western Atlantic in deep water. (KRAMP 1957 p. 59, Pl. 5, fig. 7; KRAMP 1965 p. 124).

*Tetrorchis* BIGELOW 1909. Rhopalonematidae without a gastric peduncle; with only four gonads attached to four of the eight radial canals; gonads sausage-shaped, pendent; with four large perradial and several small tentacles.

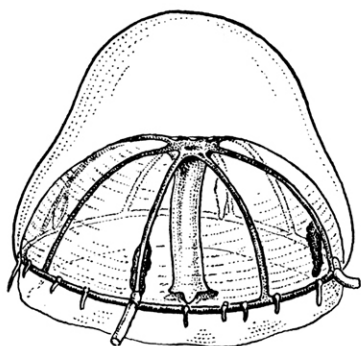


Fig. 322. *Tetrorchis erythrogaster*  
(from BIGELOW, redrawn by P. W.).

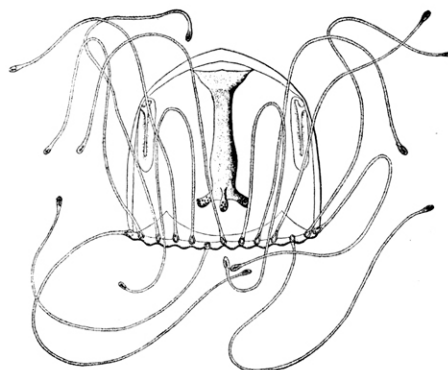


Fig. 323. *Persa incolorata* (from MAYER).

*Tetrorchis erythrogaster* BIGELOW 1909. 10–12 mm wide, 8 mm high, pyriform, apex very thick, lateral jelly thin; stomach tubular, reaching slightly beyond velar level; four small lips; gonads attached to four of the eight radial canals near their middle points; four large perradial tentacles opposite to the four gonad-bearing radial canals, and 16–24 small tentacles; statocysts unknown; stomach a brilliant carmine. — Eastern tropical Pacific; east of New Zealand. Eastern tropical Atlantic. In deep and intermediate water layers. (BIGELOW 1909 p. 124, Pl. 29, figs. 1–3; KRAMP 1957 p. 60).

*Persa* MCCRADY 1857. Rhopalonematidae with a short gastric peduncle; with only two gonads, pendent, on the subumbrellar portions of two opposite radial canals; eight radial canals; with numerous long tentacles, all alike, each with a terminal knob; statocysts free, club-shaped.

*Persa incolorata* MCCRADY 1857. 3 mm wide, 4 mm high; umbrella with or without a small apical knob; lateral jelly thin; stomach tubular, elongated; four small, broadly rounded lips; gastric peduncle very retractile; two oval or sausage-shaped, pendent gonads near middle points of two opposite radial canals; up to 48 long tentacles with a terminal knob; eight statocysts. — South-East Australia; Sunda Strait. Widely distributed in warm and temperate parts of the Atlantic Ocean; Mediterranean; epipelagic. (MCCRADY 1857 p. 206, Pl. 12, fig. 3; MAYER 1910 p. 408, textfigs. 261, 262; KRAMP 1959 a p. 189, fig. 283; KRAMP 1965 p. 125).

*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 pendent, sausage-shaped gonads on radial canals; with numerous densely crowded tentacles all alike; with free, club-shaped statocysts.

#### Key to the species of *Crossota* represented in Indo-Pacific waters.

1. With a short cylindrical peduncle; up to 640 tentacles; umbrella reddish brown ..... *pedunculata*
- No peduncle ..... 2

2. Gonads nearer ring canal than stomach; umbrella colourless ..... *alba*  
 Gonads near base of stomach ..... 3
3. With 200–250 tentacles in one row; umbrella deep reddish brown ..... *rufobrunnea*  
 With 600 or more tentacles, apparently in several rows; umbrella pale brown ..... *brunnea*

*Crossota brunnea* VANHÖFFEN 1902. Up to about 30 mm wide and 22 mm high; without a gastric peduncle; stomach bottle-shaped, short, with eight large, deep longitudinal fissures and above them eight similar small invaginations; mouth with four small lips; eight radial canals; gonads on the radial canals near base of stomach; 600 or more tentacles very densely crowded; number of statocysts unknown; colour of umbrella brown. — Bathypelagic in the oceans from the Antarctic Continent to slightly north of the Equator. (VAN-

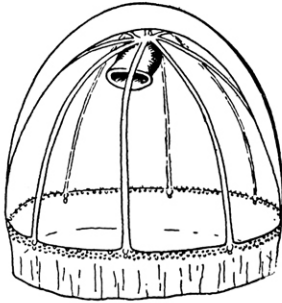


Fig. 324. *Crossota brunnea*  
 (after VANHÖFFEN, from MAYER).

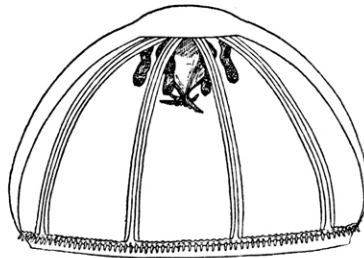


Fig. 325. *Crossota rufobrunnea*  
 (from KRAMP).

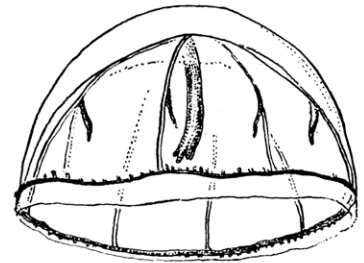


Fig. 326. *Crossota alba*  
 (from BIGELOW, redrawn by P. W.).

HÖFFEN 1902 p. 73, Pl. 9, figs. 11–13, Pl. 12, figs. 34–38, 43–47; BIGELOW 1909 p. 135, Pl. 2, fig. 7, Pl. 45, fig. 9; KRAMP 1965 p. 125).

*Crossota rufobrunnea* (KRAMP 1913). Up to 15 mm wide and 10 mm high; without a gastric peduncle; stomach bottle-shaped, short, with eight large, deep longitudinal fissures and above them eight similar small invaginations; mouth with four small, out-turned lips; eight radial canals; gonads on the radial canals near base of stomach; about 200–250 tentacles; number of statocysts unknown; umbrella, stomach and tentacles deep reddish-brown. — Bathypelagic in northern Pacific, as far south as Japan, and in northern Atlantic. (KRAMP 1913 p. 273, figs. 1, 2, as *Aglantha rufobrunnea*; KRAMP 1947 p. 22, Pl. 2, figs. 9, 10, Pl. 3, figs. 1–8, Pl. 4, figs. 1–4, Pl. 6, fig. 5, textfigs. 9 a-e, 10 a, b; NAUMOV 1960 p. 558, Pl. 30, fig. 2, textfig. 449).

*Crossota alba* BIGELOW 1913. Up to 42 mm wide and 28 mm high; no peduncle; stomach tubular, narrow, with eight sharp longitudinal ridges separated by eight broad, flat furrows; four small lips; gonads on the eight radial canals somewhat nearer to ring canal than to stomach; up to 190 tentacles; number of statocysts unknown; stomach dark chocolate-brown, almost black, oral lips white, umbrella colourless. — Bathypelagic in the western Pacific and the eastern Atlantic. (BIGELOW 1913 p. 149, Pl. 3, figs. 9–12; NAUMOV 1960 p. 559, fig. 450; KRAMP 1965 p. 126).

*Crossota pedunculata* BIGELOW 1913. 25 mm wide; stomach flask-shaped, on a short cylindrical peduncle; eight radial canals; gonads during growth gradually displaced from 1/3 to 2/3 meridional distance from base of stomach; up to 640 or more tentacles; statocysts unknown; colour of umbrella reddish-brown. — Off Columbia River, west coast of North America; epipelagic. (BIGELOW 1913 p. 51, Pl. 3, fig. 13).

*Aglantha* HAECKEL 1879. Rhopalonematidae with a long and slender gastric peduncle; with eight pendent, sausage-shaped gonads on the subumbrellar portions of the eight radial canals; with numerous tentacles all alike; with free, club-shaped marginal statocysts.

#### Key to the species of *Aglantha*.

1. Gonads close to base of peduncle ..... 2  
 Gonads about midway between peduncle and bell margin ..... *elata*

2. Radial canals on the peduncle S-shaped, arranged in four pairs ..... *intermedia*  
 Radial canal on peduncle straight and equidistant ..... *digitale*

*Aglantha digitale* (O. F. MÜLLER 1775). 10–40 mm high, about half as wide as high, thimble-shaped, with a small conical apical projection, lateral walls thin, subumbrellar muscles strong; peduncle slender, almost as long as bell cavity; stomach small; mouth with four small, simple lips; gonads long, close to base of peduncle; 80 or more tentacles; eight statocysts; local varieties differ in size and colour. — Northern Pacific from Bering Strait to Vancouver Island and southern Japan; generally distributed in all arctic and subarctic waters, mainly in the uppermost 200 metres. (MAYER 1910 p. 402, Pl. 49, figs. 2, 2'; RUSSELL 1953 p. 447, Pl. 26, figs. 1–10, textfigs. 297, 298; KRAMP 1965 p. 126).



Fig. 327. *Crossota pedunculata*.

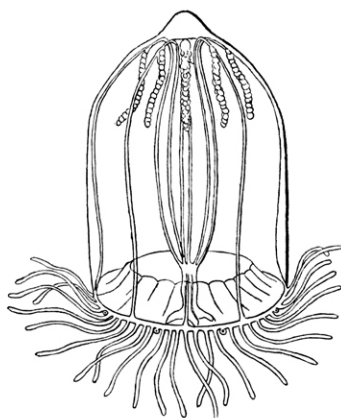


Fig. 328. *Aglantha digitale* (after MAYER, from BROCH).



Fig. 329. *Aglantha elata*  
 (after HAECKEL, from MAYER).

*Aglantha elata* (HAECKEL). 10–12 mm high, narrow, peduncle about half as long as bell cavity; stomach small; gonads issuing from about the middle of subumbrellar portions of radial canals; 40–48 tentacles; 16 statocysts. — South-East Australia. West Africa. (HAECKEL 1879 pp. 276, 277, Pl. 16, fig. 2, as *Agliscra elata* and *Aglantha elongata*; MAYER 1910 p. 404, textfig. 255, as *Aglantha elongata*; BLACKBURN 1955 p. 418, as *Aglantha elongata*).

*Aglantha intermedia* BIGELOW 1909. 15 mm high, 14 mm wide, with a small, conical apical projection; peduncle about half as long as bell cavity; stomach elongated; gonads long, sausage-shaped, close to base of peduncle; the radial canals on the peduncle are not straight but S-shaped and arranged in four pairs; 80–90 tentacles. — Eastern tropical Pacific. (BIGELOW 1909 p. 122, Pl. 29, figs. 4–10).

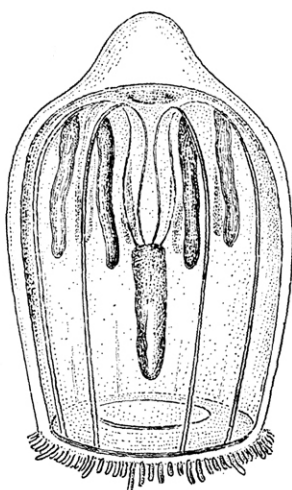


Fig. 330. *Aglantha intermedia* (from BIGELOW, redrawn by P. W.).

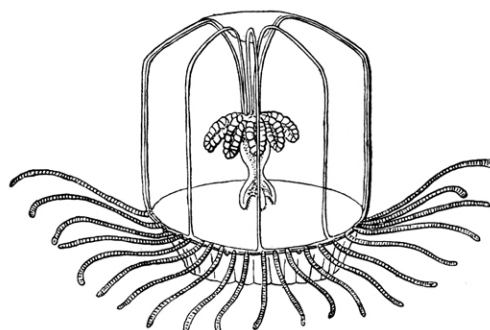


Fig. 331. *Aglaura hemistoma* (after MAYER, from BROCH).

*Aglaura* PÉRON & LESUEUR 1809. Rhopalonematidae with a slender gastric peduncle; with eight sausage-shaped gonads on the peduncle, not on the subumbrella; with numerous tentacles all alike; with free, club-shaped marginal statocysts.

*Aglaura hemistoma* PÉRON & LESUEUR 1809. 4–6 mm high, 3–4 mm wide, with a flat apex, jelly very thin; peduncle somewhat shorter than bell cavity; stomach small, mouth with four small, simple lips; gonads on the peduncle near stomach; 48–85 tentacles; eight statocysts. — Widely distributed in the warm and temperate parts of all the oceans between about 40° N. and 40° S.; Mediterranean. (MAYER 1910 p. 398, Pl. 46, figs. 4, 5, Pl. 49, figs. 3–7, Pl. 50, fig. 11, textfigs. 250, 251; KRAMP 1965 p. 127).

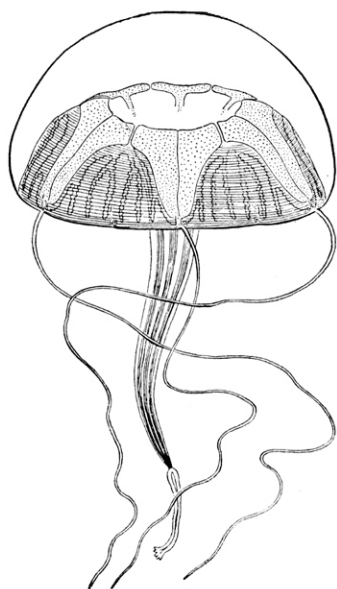


Fig. 332. *Geryonia proboscidalis* (from MAYER).

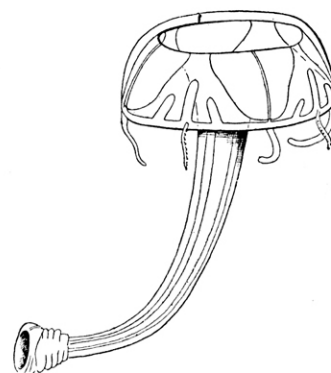


Fig. 333. *Liriope tetraphylla* (after VANHÖFFEN, from MAYER).

## Family Geryoniidae.

Trachymedusae with stomach with peduncle; with four or six radial canals; with centripetal canals; with flattened leaf-shaped gonads on radial canals; with marginal tentacles of two kinds, hollow and solid; with marginal sensory clubs enclosed in mesogloea.

*Geryonia* PÉRON & LESUEUR 1809. Geryoniidae with six radial canals and six gonads.

*Geryonia proboscidalis* (FORSKÅL 1775). 35–80 mm wide, almost hemispherical, jelly moderately thick; stomach small, on long conical peduncle; mouth with six simple lips; up to seven centripetal canals in each space between the six radial canals; gonads heart-shaped, very broad above; six long, hollow perradial tentacles with nematocyst rings, and six small, solid interrarial tentacles with adaxial nematocyst clusters; 12 statocysts. — Generally distributed in the tropical and subtropical parts of all the oceans, including the Mediterranean; mainly in the upper water layers. (MAYER 1910 p. 425, Pl. 53, figs. 1–3, Pl. 54, fig. 10, textfig. 282; KRAMP 1965 p. 136).

*Liriope* LESSON 1843. Geryoniidae with four radial canals and four gonads.

*Liriope tetraphylla* (CHAMISSE & EYSENHARDT 1821). 10–30 mm wide, almost hemispherical, jelly thick; stomach small, on peduncle of varying length; mouth with four simple lips; radial canals broad; 1–3 (or more) centripetal canals in each quadrant; gonads of very variable shape and size; four long, hollow perradial tentacles with nematocyst rings, and four small, solid interrarial tentacles with adaxial nematocyst clusters; eight statocysts. — Generally distributed in the warm parts of all the oceans, including the Mediterranean,

approximately between 40° S. and 40° N., in the Atlantic penetrating into the English Channel. (MAYER 1910 p. 413, Pl. 52, figs. 2–4, Pl. 53, fig. 4, textfigs. 263–66, as *L. exigua*; p. 414, textfig. 267, as *L. exigua* var. *mucronata*; p. 416, textfig. 268, as *L. hyperbolica*; p. 417, Pl. 52, fig. 1, textfigs. 269, 270, as *L. rosacea*; p. 418, Pl. 53, fig. 4, textfigs. 273, 273 a, as *L. tetraphylla*; p. 418, as *L. agaricus* and *canariensis*; p. 418, textfig. 272, as *L. lütkenii*; p. 419, Pl. 51, fig. 2, as *L. conirostris*; p. 420, Pl. 51, figs. 3, 4, textfigs. 274, 275, as *L. eurybia*; p. 420, textfig. 276, as *L. distanogona*; p. 421, Pl. 50, figs. 1–6, textfig. 277, as *L. catharinensis*; p. 421, as *L. indica* and *haeckelii*; p. 421, Pl. 50, figs. 7–10, Pl. 51, fig. 1, textfigs. 278, 280, as *L. scutigera*; p. 424, textfig. 281, as *L. minima*; p. 497, as *L. rosacea* and *haeckelii*; RUSSELL 1953 p. 419, Pl. 24, fig. 2, textfigs. 275–82; KRAMP 1965 p. 129).

## V. 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.

### Family Aeginidae.

Narcomedusae with interradiial, divided stomach pouches containing the gonads; with or without peripheral canal system; with primary perradiial 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 otoporopae.

#### Key to the genera of Aeginidae.

1. With only 2 tentacles ..... *Solmundella*  
     With 4 or more tentacles ..... 2
2. With 8 (or more) tentacles and twice as many stomach pouches; with secondary marginal tentacles ..... *Aeginura*  
     With 4–6 tentacles; without secondary tentacles ..... 3
3. With 4 tentacles, 8 peronia and 16 stomach pouches ..... *Aeginopsis*  
     With 4–6 tentacles, 4–6 peronia and 8–12 stomach pouches ..... *Aegina*

*Aegina* ESCHSCHOLTZ 1829. Aeginidae typically with eight, occasionally 10 or 12, stomach pouches; with peripheral canal system; with typically four, occasionally five or six, primary tentacles and same number of peronia; without secondary tentacles; without otoporopae.

*Aegina citrea* ESCHSCHOLTZ 1829. Up to 50 mm wide, hemispherical, jelly thick at apex; stomach large, circular; typically eight rectangular stomach pouches, sometimes with a small median notch; typically four tentacles issuing about midway between the apex and margin, a peronial strand from each tentacle base to margin of umbrella, dividing the margin into four lappets; numerous marginal statocysts; five- or six-rayed specimens occur rather frequently. — Widely distributed in the warm and temperate parts of the oceans, in the Pacific as far north as the Aleutian Islands and southwards to Chile and southern Australia, in the Atlantic from South Georgia to Iceland. Apart from a single record near the Antarctic Continent records from the Indian Ocean are alle from the areas north of 40° N. (MAYER 1910 p. 451, textfigs. 299, 300, as *Ae. citrea*; p. 452, Pl. 52, fig. 5, Pl. 54, figs. 11–11'', as *Ae. rhodina*; p. 453, as *Ae. eschscholtzii*, *brunnea* and *alternans*; p. 454, as *Ae. aeginoides*; RUSSELL 1953 p. 467, Pl. 28, fig. 1, textfigs. 308–10; NAUMOV 1960 p. 569, Pl. 30, fig. 8, textfig. 462; KRAMP 1965 p. 139).

*Aeginura* HAECKEL 1879. Aeginidae with 16 stomach pouches; peripheral canal system degenerate or absent; with eight primary tentacles and same number of peronia; with secondary tentacles on umbrella margin; without otoporphae.

**Key to the species of *Aeginura*.**

With 16 stomach pouches and 8 primary tentacles ..... *grimaldii*  
 With 22 stomach pouches and 11 primary tentacles ..... *beebei*

*Aeginura grimaldii* MAAS 1904. Up to 45 mm wide, hemispherical, central part fairly thick; stomach large, circular; 16 rectangular stomach pouches with indications of slight median clefts; primary tentacles large, at level of top of stomach, a peronial strand from each tentacle base to margin of umbrella; 3–5 small second-

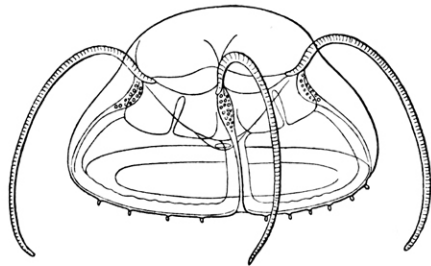


Fig. 334. *Aegina citrea* (after MAYER, from BROCH).

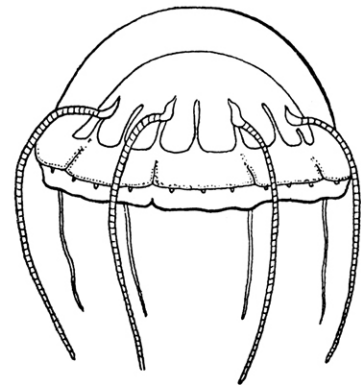


Fig. 335. *Aeginura grimaldii* (after MAAS, from MAYER).

dary tentacles on umbrella margin in each octant; one or two statocysts between adjacent secondary tentacles; colour of stomach and its pouches deep chocolate brown or purplish black. — Bathypelagic: Widely distributed in all the oceans except in the Mediterranean and in arctic and antarctic waters. (MAAS 1904 p. 38, Pl. 3, figs. 19–28; MAAS 1905 p. 77, Pl. 11, fig. 73, Pl. 12, fig. 76, Pl. 14, figs. 90–99, as *Ae. weberi*; RUSSELL 1953 p. 472, textfigs. 311, 312; NAUMOV 1960 p. 568, Pl. 30, fig. 7, textfig. 459; KRAMP 1965 p. 141).

*Aeginura beebei* BIGELOW 1940. 100 mm wide, 18 mm high, discoidal; 11 antimeres; 22 gastric pouches, interradiial notches much deeper than in the perradiial; 11 primary tentacles; on the margin of each of the 11 lappets 1–3 small secondary tentacles and 2–6 statocysts; gastric walls pale purplish (in formalin). — Pacific coast of Panama. (BIGELOW 1940 p. 309, textfigs. 17–20).

*Aeginopsis* BRANDT 1835. Aeginidae with 16 stomach pouches; peripheral canal system absent; with four primary tentacles and twice as many peronia; without secondary tentacles; without otoporphae.

*Aeginopsis laurentii* BRANDT 1838. Up to 25 mm wide, hemispherical or somewhat conical, apex thick, lateral walls very thin; stomach broad, lenticular; 16 rectangular stomach pouches (eight primary pouches deeply cleft); four large primary tentacles issuing at a very high level; four perradiial and four interradiial peronia; 2–3 statocysts in each octant. — Bering Sea; arctic circumpolar; surface to deep water. (HARTLAUB 1909 b p. 472, Pl. 76, figs. 7, 8; KRAMP 1942 p. 97; NAUMOV 1960 p. 568, textfig. 461).

*Solmundella* HAECKEL 1879. Aeginidae with eight stomach pouches; without peripheral canal system; with four peronia, but only two tentacles; without secondary tentacles; without otoporphae.

*Solmundella bitentaculata* (QUOY & GAIMARD 1833). Up to 12 mm wide, usually much smaller, higher than wide, apical jelly very thick; stomach broad, lenticular; stomach pouches rectangular; two opposite very long tentacles issuing from umbrella near the apex, which is keeled along the axis leading to the tentacles; the two tentacular peronia are deposited in deep grooves; usually 8–16 statocysts, but sometimes up to 32.



— Widely distributed and very common in the oceans; in the Pacific northwards to the Sea of Okhotsk and southern California; Atlantic everywhere south of 40° N; Mediterranean; circumpolar in antarctic waters; mainly in the upper water layers, particularly common in the southern hemisphere. (MAYER 1910 p. 455, textfigs. 301, 302; p. 456, Pl. 54, figs. 1–3, Pl. 55, fig. 4, as *S. bitentaculata* var. *mediterranea*; NAUMOV 1960 p. 571, textfig. 463; KRAMP 1965 p. 142).

*Aeginodiscus* HAECKEL 1879. *Doubtful genus and species*. Aeginidae with 16 peronial strands, eight tentacles and 32 (16 cleft) peripheral stomach pouches.

*Aeginodiscus actinodiscus* HAECKEL 1879. 40 mm wide, 13 mm high, lenticular; 16 peronial strands; mouth with four triangular lips; 32 (16 cleft) rectangular stomach pouches; eight tentacles. Description insufficient. — Zanzibar, E. Africa. (MAYER 1910 p. 486).

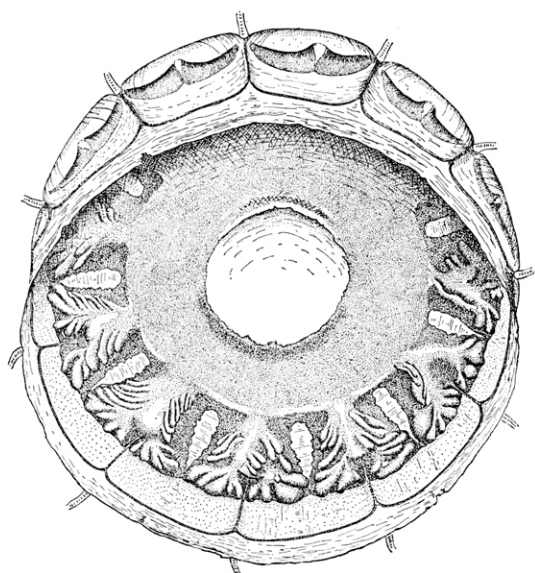


Fig. 336. *Aeginura beebei* (from BIGELOW).

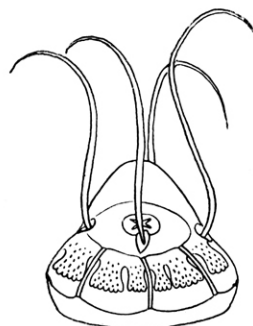


Fig. 337. *Aeginopsis laurentii* (after BRANDT, from MAYER).

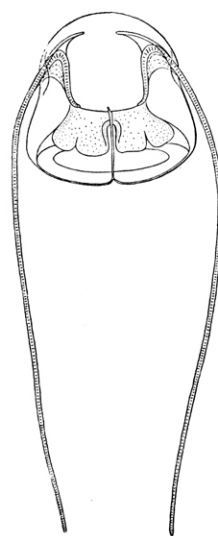


Fig. 338. *Solmundella bitentaculata* (from MAYER).

## Family Solmarisidae.

Narcomedusae without stomach pouches, genital products developed either as thickenings or as diverticula in the oral wall of the central stomach; with or without peripheral canal system; with numerous tentacles leaving umbrella at level of periphery of stomach; with or without otoporphae.

### Key to the genera of Solmarisidae.

With peripheral canal system and with otoporphae ..... *Pegantha*  
Without peripheral canal system and without otoporphae ..... *Solmaris*

*Pegantha* HAECKEL 1879. Solmarisidae with gonads forming diverticulae of the margin of the oral wall of the stomach; with peripheral canal system; with otoporphae. (Revision in KRAMP 1957, pp. 65–77).

### Key to the species of *Pegantha* represented in Indo-Pacific waters.

1. Exumbrella with deep radiating furrows and elevated ridges; 12–16 tentacles; otoporphae long ..... *triloba*
- Exumbrella smooth ..... 2
2. Some or all otoporphae long; peripheral canals narrow throughout their length ..... 3
- All otoporphae short; peripheral canals broad, at least in their lateral portions ..... 4

3. With 12–16 marginal lappets, each with usually 4 or 6 otoporpaе, the two middle ones long; canals very narrow *rubiginosa*  
 With about 20–40 marginal lappets, each with usually 3 or 5 long otoporpaе; canals fairly narrow ..... *clara*  
 4. Umbrella highly vaulted, thick; about 16 marginal lappets; lateral portions of peripheral canals broad at base, tapering outwards ..... *marlagon*  
 Umbrella flat, lenticular; 16–26 marginal lappets; peripheral canals very broad throughout ..... *laevis*

*Pegantha clara* R. P. BIGELOW 1909. Up to 50 mm wide and 20 mm high, jelly thick, lenticular, smooth; up to 40 marginal lappets, continuously increasing in number during growth of the individual, quadrate or somewhat longer than broad, usually tongue-shaped, each with 3–5 statocysts and long, linear otoporpaе,

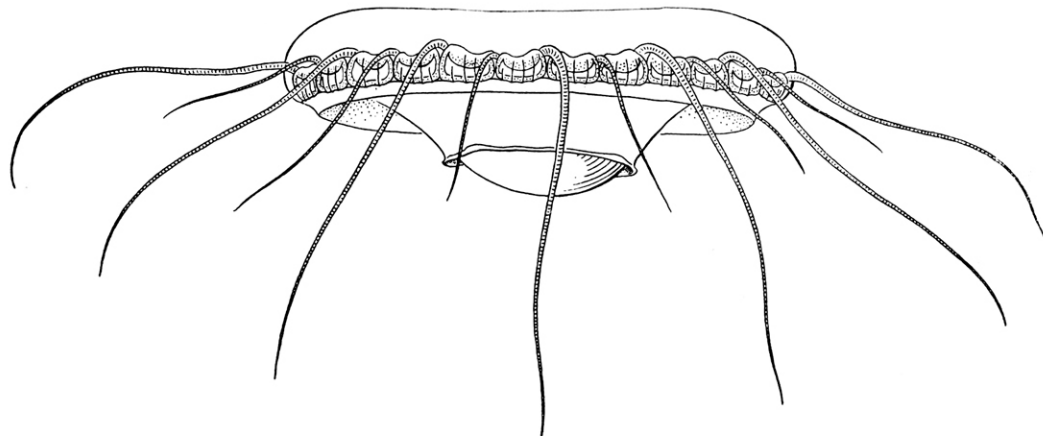


Fig. 339. *Pegantha clara* (from MAYER).

usually as long as the lappets; peripheral canals fairly narrow, of almost equal width throughout their length; gonads a simple, smooth or somewhat crenulated pouch in each lappet radius. — Widely distributed in the three great oceans between 40° S. and 40–50° N., mainly epipelagic. (R. P. BIGELOW 1909 p. 80, two textfigs.; H. B. BIGELOW 1909 p. 90, Pl. 14, figs. 1, 2, Pl. 19, figs. 1–9, Pls. 22–26, as *P. smaragdina*; KRAMP 1957 pp. 66, 67, 69, 73, 110 ff., 125, textfigs. 12, 13, Pl. 6, fig. 3; KRAMP 1959 a pp. 66, 198, fig. 304; KRAMP 1965 p. 147).

*Pegantha laevis* H. B. BIGELOW 1909. Up to about 40 mm wide, flat, lenticular, smooth; 16–22 (up to 26) marginal lappets, about as long as broad with rounded corners, each with 5–7 statocysts; otoporpaе shorter or slightly longer than the width of the transverse portion of the peripheral canals; canals very broad, especially in their lateral regions, of nearly the same width from their base to the outer edge of the lappet; gonads, when fully developed, sac-shaped with oval or papilliform processes. — Widely distributed, but not very common, in the warm and temperate parts of the oceans; mainly epipelagic. (BIGELOW 1909 p. 97, Pl. 16, fig. 1, Pl. 20, figs. 1–7; KRAMP 1957 pp. 66, 67, 69, 70, 73, 110 ff., 125, textfig. 11, map, Pl. 6, fig. 2; KRAMP 1959 a pp. 66, 198, fig. 303; KRAMP 1965 p. 147).

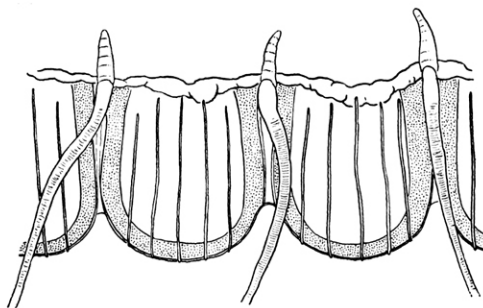


Fig. 340. *Pegantha clara*, marginal lappets (from KRAMP).

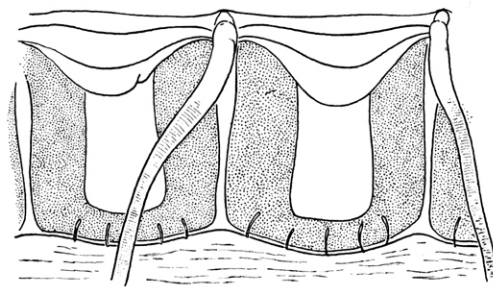


Fig. 341. *Pegantha laevis*, marginal lappets (from KRAMP).

*Pegantha martagon* HAECKEL 1879. Up to 30 mm wide, usually about 20 mm, hemispherical or higher, jelly thick, smooth; about 16 marginal lappets about as long as broad, square or evenly rounded, each with 5–7 (or 9) statocysts; otoporphae short and narrow, about twice as long as the width of the transverse portion of the peripheral canals; transverse portion of canals fairly narrow, lateral portions broad proximally, tapering distally; gonads simple or irregularly lobed sacs. — Generally distributed in the three great oceans from about 40° N., southwards almost to the Antarctic Continent; mainly epipelagic. (BIGELOW 1909 p. 83, Pl. 18, figs. 1–8; KRAMP 1957 pp. 66, 67, 98, 110 ff., 125, textfig. 10, map, Pl. 6, fig. 1; KRAMP 1959 a pp. 64, 197, fig. 302; KRAMP 1965 p. 145).

*Pegantha rubiginosa* (KÖLLIKER 1853). Up to about 16 mm wide, dome-shaped, jelly very thick, smooth; 12–16 marginal lappets, rectangular with rounded corners, each with four or six statocysts; the two middle

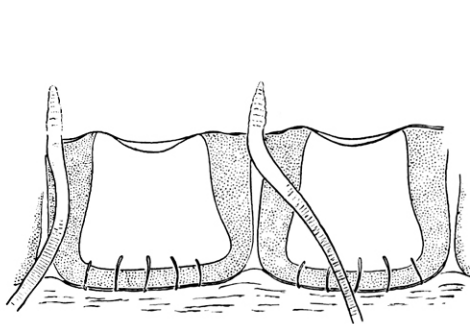


Fig. 342. *Pegantha martagon*, marginal lappets (from KRAMP).

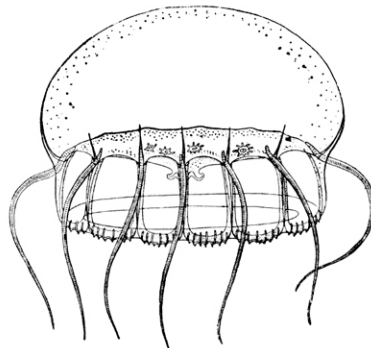


Fig. 343. *Pegantha rubiginosa* (from MAYER).

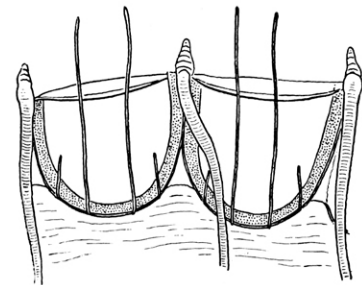


Fig. 344. *Pegantha rubiginosa*, marginal lappets (from KRAMP).

otoporphae long and narrow, frequently longer than the lappet, the lateral ones shorter; peripheral canals very narrow throughout their length; gonads without radial diverticulae. — South-East Australia<sup>1</sup>. Common in the Mediterranean; scattered occurrence in the Atlantic Ocean; mainly epipelagic. (MAYER 1910 p. 480, text-figs. 319–21, as *Cunina prolifera*; KRAMP 1924 p. 37, map, as *C. rubiginosa*; BIGELOW 1940 p. 303; KRAMP 1957 pp. 66, 67, 73, 76, 98, 125, Pl. 6, fig. 4; KRAMP 1959 a pp. 67, 198).

*Pegantha triloba* HAECKEL 1879. Up to 30 mm wide, hemispherical or somewhat flatter, jelly very rigid, exumbrella with deep radiating furrows from tentacle bases nearly to apex, surrounded by ribs and supplementary ridges; 12–16 tentacles and 12–16 marginal lappets, ovate, pointed, each with up to 20 statocysts; otoporphae long, tapering outwards; gonads with 2–4 lobes projecting into the lappet cavities. — Widely distributed in the three great oceans between about 30° N. and 30° S.; vertical distribution extensive. (BIGELOW 1909 p. 87, Pl. 14, fig. 3, Pl. 16, fig. 3, Pl. 20, figs. 1–3, Pl. 45, figs. 1–2; KRAMP 1957 pp. 66, 67, 77, 98, 125; KRAMP 1959 a pp. 68, 198, fig. 306; KRAMP 1965 p. 149).



Fig. 345. *Pegantha triloba* (from BIGELOW, redrawn by P. W.).

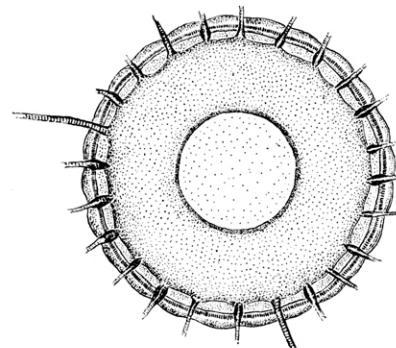


Fig. 346. *Solmaris rhodoloma* (from MAAS, redrawn by P. W.).

<sup>1</sup> The isolated record from Australia (BLACKBURN 1955 p. 423) seems doubtful.

*Solmaris* HAECKEL 1879. Solmarisidae with simple annular gonad; without peripheral canal system; without otoporphae.

**Key to the Indo-Pacific species of *Solmaris*.**

With 16–32 tentacles and marginal lappets ..... *rhodoloma*  
 With 11–14 tentacles and marginal lappets ..... *lenticula*

*Solmaris lenticula* HAECKEL 1879. 3–5 mm wide, 3 mm high; marginal lappets semicircular, not quite half as long as diameter of stomach, each with three statocysts; gonad a wide annulus on nearly entire subumbrellar wall of stomach; 11–16 tentacles somewhat longer than bell-diameter. — Coastal waters in India, Australia and the Malayan Archipelago; epipelagic. (HAECKEL 1879 p. 357; KRAMP 1965 p. 150).

*Solmaris rhodoloma* (BRANDT 1838). 2–7 mm wide, very flat, disk-like, thin and fragile; 16–32 tentacles; lappets varying in size, each with 1–2 statocysts. — Coastal waters in warm and temperate parts of eastern, central and western Pacific; epipelagic. (MAAS 1909 p. 39, Pl. 3 fig. 20; KRAMP 1923 p. 302; KRAMP 1965 p. 150).

## Family Cuninidae.

Narcomedusae with perradial and undivided stomach pouches; with or without peripheral canal system; with tentacles leaving umbrella opposite centre 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 otoporphae.

**Key to the genera of Cuninidae.**

With otoporphae ..... *Cunina*  
 Without otoporphae ..... *Solmissus*  
 (Doubtful genus *Cunissa* HAECKEL).

*Cunina* ESCHSCHOLTZ 1829. Cuninidae with or without peripheral canal system; with otoporphae.

**Key to the Indo-Pacific species of *Cunina*.**

1. With peripheral canals ..... 2  
    Without peripheral canals ..... 5
2. Stomach pouches tapering from broad base outwards, separated by wide triangular spaces ..... 3  
    Stomach pouches with nearly parallel sides ..... 4
3. With 8 marginal lappets very short, rounded; a thick pad of ectoderm below base of each tentacle; no medusa-buds ..... *tenella*  
    With 6–9 marginal lappets almost square; no ectodermal pad below base of tentacles; medusa-buds on subumbrellar side of stomach pouches ..... *frugifera*
4. Stomach pouches quadratic, more than twice as wide as septa between them; peripheral canals narrow; with 10–14 tentacles ..... *globosa*  
    Stomach pouches elongated, rectangular, hardly broader than spaces between them; lateral portions of peripheral canals very broad; with up to 29 stomach pouches, increasing in number with age ..... *duplicata*
5. With usually 8 stomach pouches, square; umbrella about 5 mm wide ..... *octonaria*  
    With usually about 12 stomach pouches, increasing with age, square or somewhat rounded distally; umbrella about 14 mm wide ..... *peregrina*

*Cunina octonaria* MCCRADY 1857. 5–7 mm wide, somewhat flatter than a hemisphere; 7–9, usually eight, stomach pouches, broad, square, very close together; no peripheral canals; tentacles projecting about midway between margin and apex; a thick and broad pad of ectoderm below base of each tentacle; 2–5, usually three, statocysts on each marginal lappet; otoporphae small; larvae developed in stomach pouches or attached

to other medusae. — Widely distributed in the warm parts of the oceans, including the Mediterranean; epipelagic. (MAYER 1910 p. 461, Pl. 55, figs. 1, 2, textfigs. 304, 305, as *Cunioctantha octonaria*; p. 464, Pl. 54, figs. 4–9, as *C. octonaria* var. *köl likeri*; p. 465, as *Cunioctantha parasitica*; KRAMP 1959 a pp. 69, 199, fig. 307; KRAMP 1965 p. 151).

*Cunina peregrina* BIGELOW 1909. Up to 14 mm wide, highly arched, jelly thick; 8–14 (usually 12) stomach pouches, increasing in number with age, in adult specimens square or slightly longer than wide, with narrow clefts between them; in young specimens, with few antimeres, the stomach pouches are well separated and more or less rounded distally; no peripheral canals; ectodermal pad below base of tentacle small; marginal lappets short and broad, each with 4–10 statocysts; otoporphae narrow, linear. — Widely distributed in the

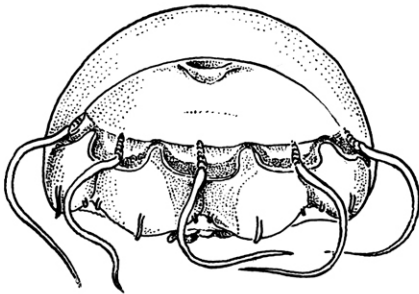


Fig. 347. *Cunina octonaria*  
(from MAYER, redrawn by P. W.).

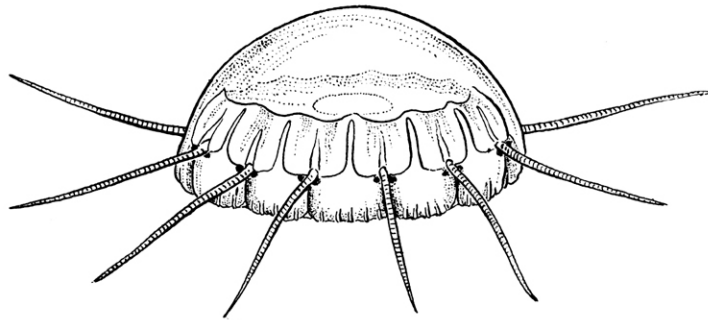


Fig. 348. *Cunina peregrina* (from BIGELOW, redrawn by P. W.).

warm parts of the great oceans; epipelagic. (BIGELOW 1909 p. 59, Pl. 1, fig. 6, Pl. 15, figs. 1, 2, Pl. 28, figs. 1–7, Pl. 45, fig. 8; KRAMP 1957 pp. 81, 84; textfig. 15, map; KRAMP 1959 a pp. 70, 199; KRAMP 1965 p. 152).

*Cunina frugifera* KRAMP 1948. About 8 mm wide, dome-shaped, apical jelly very thick; 6–9 stomach pouches, narrowing in width from base outwards, separated by wide triangular spaces; peripheral canals broad and flat; medusa-buds developing on subumbrella side of stomach pouches; no ectodermal pads below bases of tentacles; marginal lappets almost square, about as long as broad, each with four statocysts; otoporphae linear. — Widely distributed in the warm parts of the great oceans; epipelagic. (KRAMP 1948 b p. 18, Pl. figs. 1–6; KRAMP 1959 a pp. 69, 200; KRAMP 1965 p. 153).

*Cunina globosa* ESCHSCHOLTZ 1829. Up to 18 mm wide, conical or almost globular, jelly thick; stomach on a broad gelatinous peduncle; 10–14 stomach pouches wide, quadratic with rounded angles, more than twice as wide as septa between them; peripheral canals well developed; the tentacles arise a short distance only above the margin; no ectodermal pad below bases of tentacles; marginal lappets short and broad, each with three statocysts; otoporphae short and oval. — Scattered localities in the Pacific and Atlantic Oceans; epipelagic. (BIGELOW 1909 p. 57, Pl. 15, fig. 3, Pl. 17, figs. 3, 8; KRAMP 1959 a p. 201, fig. 312; KRAMP 1965 p. 154).

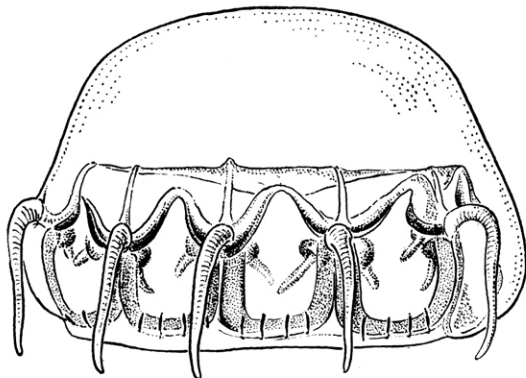


Fig. 349. *Cunina frugifera* (from KRAMP, redrawn by P. W.).

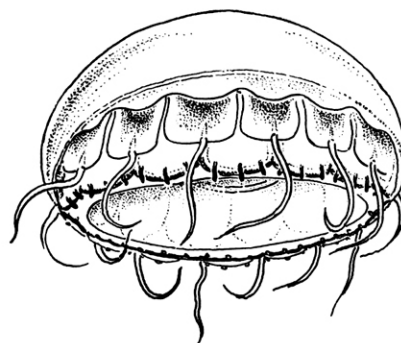


Fig. 350. *Cunina globosa*  
(from BIGELOW, redrawn by P. W.).

*Cunina duplicata* MAAS 1893. Up to 58 mm wide, rather flat and soft; up to 29 stomach pouches, increasing in number with age from nine in juvenile specimens, tongue-shaped or rectangular, somewhat longer than broad, with parallel sides, separated by spaces of about the same width or somewhat broader; the gonads form a continuous, folded band following the edge of the stomach with its pouches uninterruptedly; the stomach pouches are of unequal length and width, sometimes large and smaller ones alternate; marginal lappets rectangular, each with two or three statocysts; otoporphae very small; lateral portions of peripheral canals remarkably broad, transverse portion narrow. — Widely distributed in the Atlantic and Indian Oceans:

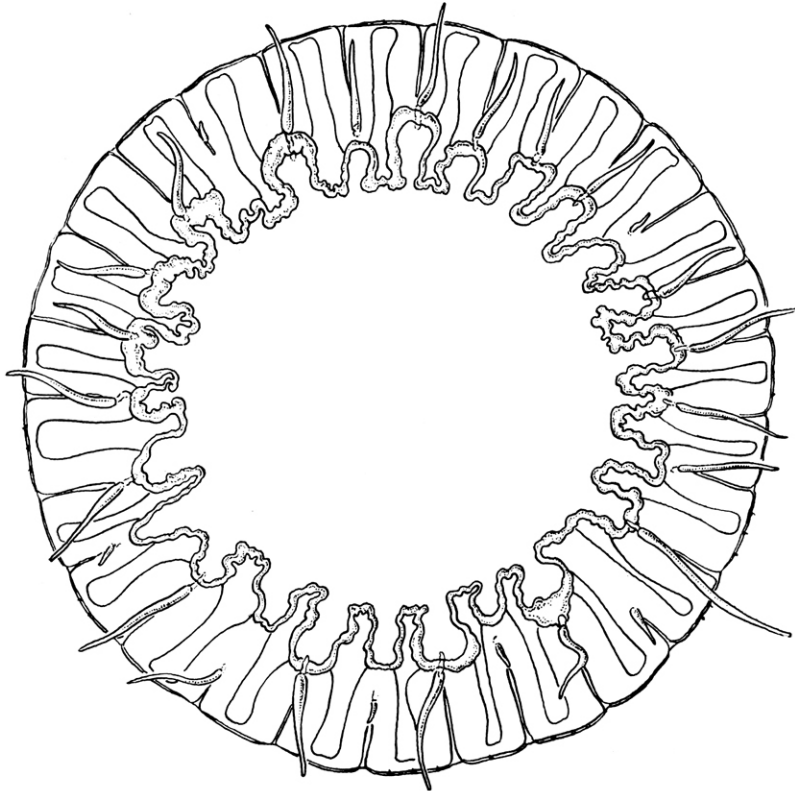


Fig. 351. *Cunina duplicata* (from KRAMP).

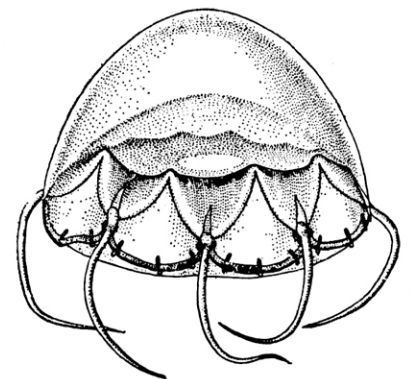


Fig. 352. *Cunina tenella* (from NAUMOV).

scattered localities east of Australia and off the coast of Peru; epipelagic. (MAAS 1893 p. 52, Pl. 5, figs. 9, 10; KRAMP 1957 p. 86, Pl. 6, fig. 5, Pl. 7, figs. 1, 2; KRAMP 1959 a pp. 70, 201, fig. 313; KRAMP 1965 p. 154).

*Cunina tenella* (BIGELOW 1909). 7 mm wide, higher than a hemisphere, apical jelly very thick; stomach deep, lenticular; eight stomach pouches, nearly triangular, pointed; peripheral canals well developed; a thick and broad pad of ectoderm below the base of each tentacle; marginal lappets very short, broadly rounded, each with three statocysts; otoporphae small, linear. — Pacific coast of Mexico; Ochotian Sea; epipelagic. (BIGELOW 1909 p. 54, Pl. 15, fig. 4, Pl. 16, fig. 2, Pl. 17, figs. 6, 7, as *Cunocantha tenella*).

*Solmissus* HAECKEL 1879. Cuninidae without peripheral canal system; without otoporphae.

#### Key to the Indo-Pacific species of *Solmissus*.

With about 16 stomach pouches, rectangular, close together; disk rigid ..... *marshalli*  
 With 20–40 stomach pouches, oval in outlines; disk soft and fragile ..... *incisa*

*Solmissus incisa* (FEWKES 1886). Up to 100 mm wide, flat, jelly soft and fragile, exumbrella smooth; 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. — Widely distributed in the Pacific and Atlantic Oceans between about 60° N. and 45° S.; near Ceylon in the Indian Ocean; mainly in deep water. (BIGELOW 1909 p. 67, Pl. 21, figs. 1–3, 5; RUSSELL 1953 p. 464, textfigs. 305–07; KRAMP 1959 *a* pp. 72, 203, fig. 316; KRAMP 1965 p. 155).

*Solmissus marshalli* AGASSIZ & MAYER 1902. Up to 62 mm wide, flat, gelatinous disk thick and rigid, lappet zone very thin, exumbrella smooth; 8–20, usually about 16 stomach pouches, rectangular, about as long as wide or slightly longer; marginal lappets square, as broad as long, margin hardly, if at all, incised in the peronial radii, each with up to 15 statocysts; tentacles long. — Widely distributed in the warm and temperate parts of the three great oceans; from surface into the abyssal region. (BIGELOW 1909 p. 64, Pl. 16, figs. 5,

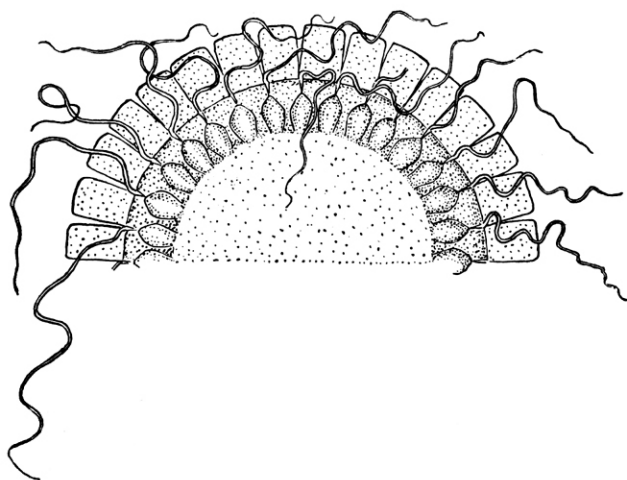


Fig. 353. *Solmissus incisa* (after FEWKES, from BROCH).

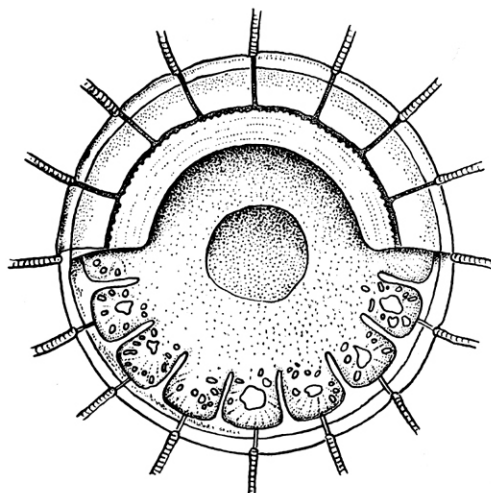


Fig. 354. *Solmissus marshalli* (from BIGELOW, redrawn by P. W.).

6, Pl. 21, figs. 4, 6–8; KRAMP 1957 pp. 78, 79, 110 ff., textfig. 14, map; KRAMP 1959 *a* pp. 71, 202, fig. 315; KRAMP 1965 p. 155).

*Cunissa* HAECKEL 1879. Cuninidae with nine or more tentacles and peronial strands; primary gastric pouches equal in number to tentacles, but cleft by the insertions of the tentacles so as to appear twice as numerous as the tentacles; peripheral canals? otoporphae?

With two uncertain species.

*Cunissa polyphera* HAECKEL 1879. 30 mm wide, 10 mm high, flat, shield-shaped; 32 lappets, oval, each with 5–7 statocysts; 32 tentacles. — Zanzibar, Indian Ocean. (HAECKEL 1879 p. 323).

*Cunissa polyporpa* HAECKEL 1879. 20 mm wide, 10 mm high, hemispherical; 16 lappets, semi-circular, each with 12–15 statocysts; 16 short tentacles. — Singapore, Indian Ocean. (HAECKEL 1879, p. 322).

## SECTION III. ZOOGEOGRAPHY

As I did in the paper on the hydromedusae of the Atlantic Ocean (in Dana Reports, 46, KRAMP 1959) I give here an account of the Indo-Pacific fauna of these animals from a zoogeographical point of view, not merely faunistical descriptions but also attempts at an explanation. The species are divided into three ecological groups: I, neritic species, II, slope species, III, oceanic species, the latter subdivided into the two groups epipelagic and bathypelagic. For further consideration, see the paper quoted above, p. 204, and introductory remarks to the treatments of these groups in the present paper.

### NERITIC SPECIES

The neritic region is the pelagic region above the continental shelves, generally estimated at depths within about 200 m. The neritic fauna of Hydromedusae mainly consists of meropelagic Leptolina, which are usually liberated from hydroids attached to objects on the bottom within the shelf region. The Trachymedusa *Ptychogastria polaris* should, however, be reckoned among the neritic forms, because it spends part of its life attached to the bottom by means of the adhesive disks of its tentacles. On the other hand, the medusae of the cosmopolitan genus *Obelia* are left out of consideration, because the species cannot be identified in their medusoid stage.

For the division into zoogeographical regions (as in the treatment of the Atlantic fauna) I again mainly follow EKMAN (1953), with slight alterations which are explained under the various headings. The extension of the regions is illustrated in the map, fig. 355, and reference is also made to the map, fig. 359.

### The Arctic Pacific Region.

Table I.

The Arctic Pacific Region is a rather restricted area, comprising the greater part of the Bering Sea and the Sea of Okhotsk. In table I is also included the coastal waters in the Polar Sea in the immediate neighbourhood of the northern entrance to the Bering Strait, i.e. the northern coast of the Siberian province Chukchi and the north coast of Alaska, where some collecting has been done near Point Barrow. As seen from Table I, 29 species of neritic Hydromedusae are recorded from the Arctic Pacific Region; more species might be expected in the future from these inhospitable waters, e. g. species penetrating northwards from the Pacific Boreal Region. A survey of the fauna of medusae in the northern Pacific waters was given by NAUMOV (1956).

The most pronouncedly arctic conditions are found in the Sea of Okhotsk; this is limited from the Pacific Ocean by the chain of the Kurile Islands, in which the hydrographical conditions are influenced by the left border of the warm Kuroshio Current and may be termed boreal conditions. The same applies to the Aleutian Islands. When the Kuroshio Current and its continuation, the North Pacific Current, reaches the West American coast, it divides into the southgoing California Current and the northgoing Alaska Current, which flows westward along the Aleutians and branches into the Bering Sea to form a rather complex circulation. The western side of the Bering Sea has colder water than the eastern side and from here the southgoing, cold Oyashio Current derives; in northern Japan the Oyashio Current meets the warm Kuroshio Current, establishing a rather sharp faunistical boundary, which is discussed below. The currents through the narrow and shallow Bering Strait are variable, but mainly northgoing and of great velocity, carrying considerable

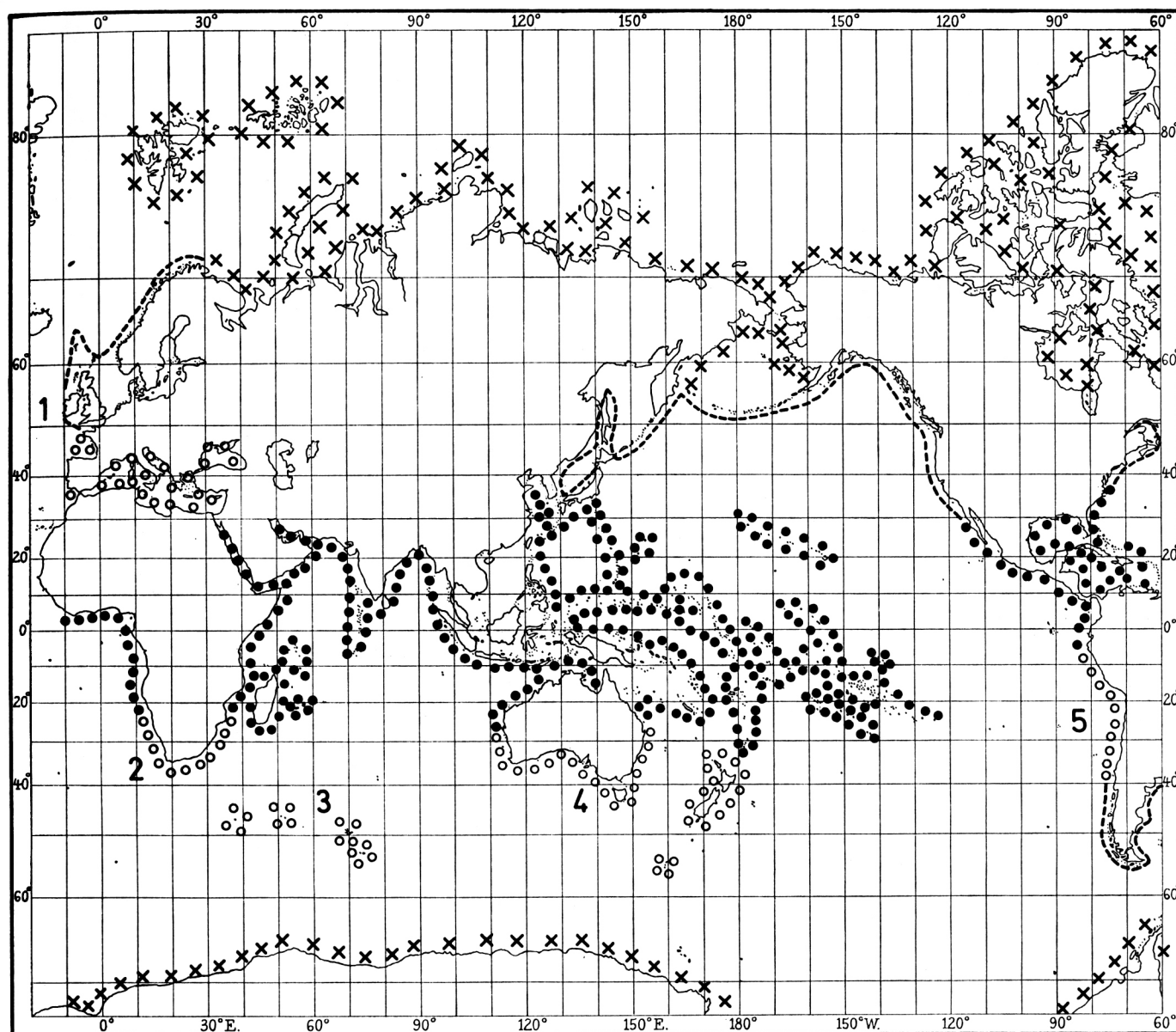


Fig. 355. Zoogeographical regions.

xx: arctic and antarctic regions. ---: boreal and antiboreal regions. ○○: 1 Mediterranean-, 2 South-African-, 3 Keguelen-, 4 South-Australian-New Zealand-, 5 Peru-Chilean regions. ●●: tropical regions.

masses of water into the Polar Sea and causing intensive mixing of the waters, especially in summer, being the fundamental factor in the hydrographical conditions of the Chukchi Sea.

In Table I the species are arranged according to their southward distribution in Pacific waters, which does not always correspond with their zoogeographical character in other waters; further investigations may alter the impression obtained from our present knowledge; it seems accidental, e. g. that *Bougainvillia principis* and *Leuckartiara nobilis* have only been found in the Polar Sea north of the mouth of the Bering Strait. The most interesting feature is the comparison between the present fauna and that in other areas, especially in the Atlantic and adjacent waters. It is immediately seen from the enumeration at the bottom of the table that the majority of the species under consideration are common to the two widely separated areas, which calls for an explanation, since ten of these species have a discontinuous distribution under the present conditions. A direct communication between a North-Atlantic and a North-Pacific marine fauna most probably existed in a former period, with conditions enabling an interchange, a problem discussed by several authors. This question is discussed under the Pacific Boreal Region.

Table I. The Arctic-Pacific Region.

	Arctic-Pacific			Pacific-boreal		Siberian Polar Sea	Atlantic-arctic		Atlantic-boreal	
	Polar Sea near Bering Strait	Bering Sea	Sea of Okhotsk	E.	W.		E.	W.	E.	W.
Platocnide borealis . . . . .	×	•	×	•	•	×	×	×	×	×
Ptychogastria polaris . . . . .	•	×	•	•	•	×	×	×	×	×
Halitholus cirratus . . . . .	×	×	•	•	•	×	×	×	×	×
Bythotiara depressa . . . . .	•	×	×	•	×	•	•	•	•	•
Tima saghalinensis . . . . .	•	•	×	•	•	•	•	•	•	•
Cladonema pacificum . . . . .	•	•	×	•	•	•	•	•	•	•
Meator rubatra . . . . .	•	×	×	•	•	•	•	•	•	•
Chiarella jaschnowi . . . . .	•	×	×	•	•	•	•	•	•	•
Bougainvillia principis . . . . .	×	•	•	•	•	•	×	×	×	×
Tiaropsis multicirrata . . . . .	×	×	×	•	•	•	×	×	×	×
Stauridiosarsia producta . . . . .	•	•	×	•	•	•	×	•	×	•
Polyorchis karafutoensis . . . . .	•	•	×	•	×	•	•	•	•	•
Ptychogena lactea . . . . .	•	×	×	•	×	×	×	×	•	×
Catablema multicirratum . . . . .	×	×	×	•	×	•	•	×	×	•
Halistaura cellularia . . . . .	×	•	•	×	•	•	•	•	•	•
Euphysa flammea . . . . .	×	×	×	×	•	×	×	×	•	×
Catablema vesicarium . . . . .	•	×	×	×	•	×	×	×	×	×
Leuckartiara brevicornis . . . . .	×	×	×	×	•	•	•	×	×	×
Staurophora mertensi . . . . .	•	•	×	×	×	×	×	×	×	×
Sarsia princeps . . . . .	×	×	×	×	×	×	×	×	•	×
Halitholus pauper . . . . .	•	•	×	×	×	•	•	×	•	×
Euphysa japonica . . . . .	•	×	×	×	×	•	•	•	•	•
Hybocodon prolifer . . . . .	•	×	×	×	×	•	×	×	×	×
Melicerium octocostatum . . . . .	•	×	×	•	×	•	×	×	×	×
Eutonina indicans . . . . .	•	×	×	×	×	•	•	•	×	•
Rathkea octopunctata . . . . .	×	×	×	•	×	×	×	×	×	×
Sarsia tubulosa . . . . .	×	×	×	×	×	×	×	×	×	×
Bougainvillia supercilialis . . . . .	×	×	×	•	×	×	×	×	×	×
Leuckartiara nobilis . . . . .	×	•	•	×	×	•	•	•	×	×
	13	19	24	12	15	11	16	18	17	18
	29						19		21	
							21			

According to EKMAN (in his Zoogeography of the Sea, 1953, pp. 157–159) “The cold-water fauna [of bottom animals] is considerably richer in the North Pacific than in the North Atlantic”, and “a considerable part of the North Atlantic boreal fauna and the Polar Sea arctic fauna is derived from the North Pacific”. As seen from Table I, 29 species of neritic Hydromedusae are known from the Pacific Arctic Region, 8 of which are endemic in the North Pacific, 21 also occurring in the North Atlantic; from the Atlantic Arctic Region 29 species are recorded, 8 of which are lacking in the Pacific. As far as the Hydromedusae are concerned, therefore, EKMAN’s statement is not confirmed.

The following 7 species are endemic in the Pacific area: *Tima saghalinensis*, *Cladonema pacificum*, *Chiarella jaschnowi*<sup>1</sup>, *Meator rubatra* and *Bythotia depressa*, all of which occur in the Sea of Okhotsk, two of them

<sup>1</sup> *Chiarella jaschnowi* as a new species of *Rathkea*, was described in 1956 by Professor NAUMOV, who kindly sent me a specimen; I found it indistinguishable from *Chiarella centripetalis* MAAS, and in my “Synopsis” (1961) I united the two species. *C. centripetalis* was recorded from the Gulf of California and the Pacific coast of Mexico; the species from the Bering Sea and the Sea of Okhotsk no doubt belongs to the same genus, but owing to the great distance and different ecological conditions of the two geographical areas I am now inclined to regard *Chiarella centripetalis* and *C. jaschnowi* as separate species.

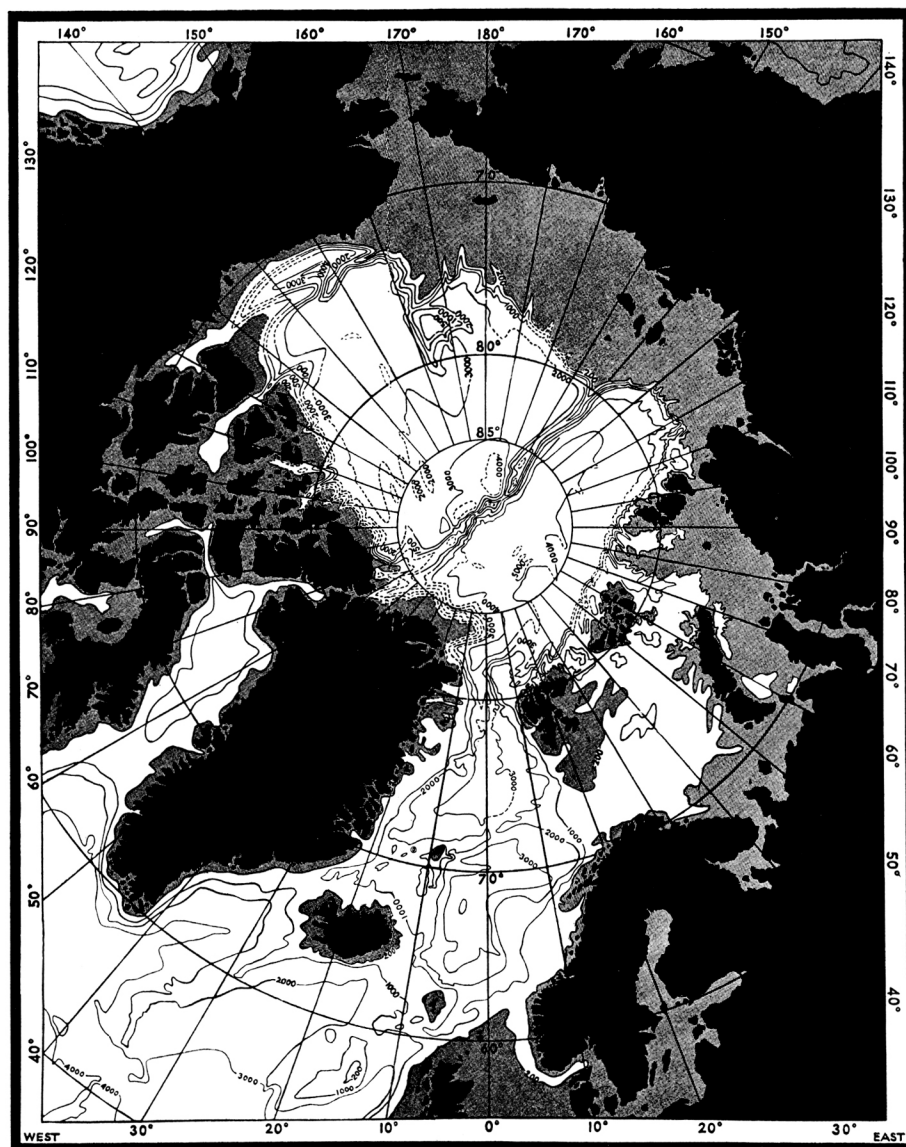


Fig. 356. The North-Polar region (from H.J. BROCH, 1961).

also in the Bering Sea and partly among the Aleutian and Kurile Islands; moreover *Euphysa japonica* which penetrates southwards to northern Japan and the Vancouver Island region on the American coast and *Hali-staura cellularia* which is recorded from the north and south coast of Alaska and the Vancouver Island region. *Bougainvillia bougainvillei* is an altogether doubtful species, recorded from the Bering Sea (BRANDT 1835).

Among these species eleven have been found in different localities along the north coast of Siberia and may have a circumpolar distribution, though they have not been recorded from the waters north of North America, which are incompletely investigated; only one of the species, *Euphysa flammea*, is recorded from the range between Hudson Strait and Point Barrow. The occurrence of several species off the Siberian coast, therefore, does not allow the conclusion that an exchange of the faunas in North Atlantic and North Pacific has taken place along the Siberian coast; several species may prove to be truly circumpolar. BROCH (1949) distinguishes between two groups of arctic species, an eastern arctic group of Atlantic origin and a western arctic group originating in the northern Pacific, and he comes to the conclusion that, owing to the directions of the currents in the Polar Sea, an eastern arctic species cannot develop into circumpolarity, its advance towards the east being blocked up at, or just beyond, the New Siberian Islands (see the map. fig. 356). Eight of the species

of Hydromedusae known from North Siberia, are, however, recorded from Point Barrow on the north coast of Alaska.

Ten species, common to the North Pacific and the North Atlantic, seem to have a discontinuous distribution, being unknown along the Siberian coast. One of them, *Catablema multicirrata*, is a decidedly west-arctic species; it occurs in the Sea of Okhotsk (penetrating southwards to northern Japan), in the Gulf of Alaska and the Bering Sea and also recorded from Point Barrow; in the Atlantic area its occurrence is restricted to the west coast of Greenland, where it is common from Cape Farewell to Upernavik, whereas it has never been found on the east coast. *Halitholus pauper* is likewise a predominantly arctic species with a western distribution in the Atlantic area, comprising the west coast of Greenland and the Hudson Strait, but it is also recorded from East Greenland and north-western Iceland; in the Pacific area it occurs in the Sea of Okhotsk, northern Japan and Vancouver on the American coast. All the other species with a discontinuous distribution are predominantly boreal; two of them, *Stauridiosarsia producta* and *Eutonina indicans*, are common in north-western Europe but unknown in western Atlantic waters, the remaining six species occur in boreal coastal waters on both sides of the Atlantic area; five of them also occur in the southern part of the west coast of Greenland. According to BROCH (1949, p. 133), western-arctic as well as eastern-arctic species "have a common playground in Greenland waters and along the coasts of Labrador as well as on the Newfoundland banks". The names of these species may be found in Table I.

Southward penetration (see Table I). Among the 29 species recorded from the Arctic Pacific Region 19 also occur in the Pacific Boreal Region, but the majority of these species have never been found further south than in northern Japan or in the Vancouver Island region on the American coast. As many as 13 of the species occurring in the Arctic Pacific Region have been found at the coasts of Hokkaido in northern Japan, only four of these somewhat further south, and none of them penetrating beyond the southern parts of the Japanese islands. In northern Japan the cold, south-going Oyashio Current meets the warm Kuroshio Current; the southward penetration of the arctic species is therefore blocked up here; the four species taken in southern Japan are predominantly boreal (*Rathkea octopunctata*, *Sarsia tubulosa*, *Bougainvillia superciliaris* and *Leuckartiara nobilis*). From numerous papers by prominent Japanese authors we have a rather thorough knowledge of the medusan fauna of Japan, but mainly from the eastern coasts, while we know very little about the somewhat colder western shores and nothing about the fauna on the Chinese side of the Sea of Japan, which is under direct cooling influence by the Liman Current flowing southwards from the western, coldest side of the Sea of Okhotsk.

Among the 9 species, which occur in the Arctic Pacific Region and have been found as far south as Vancouver, four are predominantly arctic (*Euphysa flammea*, *Sarsia princeps*, *Halitholus pauper* and *Catablema vesicarium*), while the five others are predominantly boreal species (*Euphysa japonica*, *Hybocodon prolifer*, *Leuckartiara nobilis*, *Leuckartiara brevicornis* and *Eutonina indicans*). The Vancouver Island region is interesting. A little further south the east-going North Pacific Current is divided into the south-going California Current and the north-going Alaska Current; arctic species extending their distribution southwards along the coast meet this current near Vancouver Island and therefore are unable to proceed further south, whereas boreal species like the five mentioned above, may proceed northwards as far as the temperature conditions are favourable. One predominantly boreal species, *Sarsia tubulosa*, is distributed from the arctic region beyond Vancouver to San Francisco. The Vancouver Island region also has a fauna rich in species, which do not occur further north on the American coast and is mentioned below. Apparently, the limit between an arctic and a boreal fauna is much sharper in the Pacific than in the Atlantic Ocean.

## The Pacific Boreal Region.

Table II.

The Pacific Boreal Region comprises the greater part of the eastern coasts of Japan, the Sea of Japan, the external sides of the Kurile and Aleutian Islands, and the American coast from Alaska to the northern part of the Californian Peninsula; in the southern part of Lower California the conditions should rather be regarded



as subtropical. Hydrographically the Asiatic side of the boreal region is mainly characterized by the warm, north-going Kuroshio Current along the eastern coasts of Japan, in the northern region meeting the cold currents from the Sea of Okhotsk and the Bering Sea, the American side characterized by the division of the North-Pacific Current into the north-going Alaska Current and the south-going California Current.

The neritic fauna in the boreal region consists of three groups of species; *a*: species of northern origin penetrating southwards into boreal waters, *b*: species indigenous in the boreal region, *c*: species of southern origin penetrating northwards from the Tropics into the boreal region.

It is shown below that species of southern origin are extremely few in the boreal part of the West-American coast. The east coast of Japan, however, is a mixed area, where several subtropical species of medusae penetrate more or less far northwards, occurring together with boreal species. As far as neritic-pelagic animals are concerned, a limit between two zoogeographical regions cannot be pointed out on the Japanese coast, but a boreal and a subtropical fauna can be distinguished, and from a zoogeographical point of view these two faunistic elements should be treated separately; in accordance herewith species, which actually belong to tropical or subtropical waters, are dealt with in the chapter on the Indo-West-Pacific Region and are listed in Table VII.

There are 19 species of neritic Hydromedusae which are common to the arctic and the boreal regions in the North Pacific (see Table I). Very few of these have been found further south than Hokkaido in northern Japan and Vancouver on the American coast; the few exceptions are: *Sarsia tubulosa*, *Rathkea octopunctata*, *Bougainvillia superciliaris* and *Leuckartiara nobilis*, which are recorded from southern Japan, partly also from the Yellow Sea, *Sarsia tubulosa* also proceeding southwards on the American coast as far as San Francisco. All these, and also *Eutonina indicans* (recorded from Vancouver as well as from northern Japan) are predominantly boreal species, indigenous in the northern part of the boreal regions, Atlantic as well as Pacific, and penetrating into arctic waters.

The total number of species recorded from the Pacific Boreal Region (apart from the subtropical species in Japan) is 67; the 19 species common to the arctic region are mentioned above. Among the remaining 48 species 14 also occur in tropical waters, some of them being boreal species which have extended their distribution into the Tropics. The region is divided into three subregions; the East-Pacific, the Aleutian-Kurile, and the North-Japanese subregions.

#### *The East-Pacific Subregion.*

Altogether 46 species of neritic Hydromedusae are recorded from the boreal part of the West-American coast, including 11 which also occur in the arctic region. Besides these northern species as many as 34 have been found in the coastal waters between Vancouver and Lower California. It is remarkable that of these 34 species no less than 24 are "endemic" in this subregion, in so far as they have not hitherto been observed anywhere else; among 35 species known from the Vancouver Island region 9 only have been observed there; 21 have been collected on the Californian coast, 10 of which are "endemic" there, and 10 species have been found in the Vancouver region as well as on the Californian coast.

In contradistinction to the fauna of the Japanese coasts (see below) only 6 of the species occurring along the West-American boreal coasts also occur in tropical waters, and all of them deserve special remarks. *Goniomemus vertens* is recorded from numerous localities along the coasts, from the Kurile Islands and Saghalin, Japan, China and further south to Vietnam and also from an increasing number of places in north-western Europe, the Mediterranean, and north-eastern America; it is undoubtedly carried along in the polyp stage attached to algae growing on ships-bottoms, whence medusae may be liberated and establish themselves in widely separated areas with favourable conditions. *Leuckartiara octona* is widely distributed in the temperate and warm parts of all oceans; it occurs on the Pacific coasts of Central and South America as well as on the Asiatic coasts from northern Japan to Vietnam and further eastwards and westwards in the Tropics. *Phialopsis diegensis* is widely distributed in the Atlantic Ocean, being partly oceanic, and is also recorded from East Africa and South Australia; other Pacific records are from Chile, Peru, the Galapagos Islands and near land in California, whence it was originally described. *Sarsia eximia* has a peculiar distribution; it mainly belongs

Table II. The Pacific Boreal Region.

	Subregions					Arctic Pacific	Warm East Pacific	Indo-West-Pacific	Atlantic arctic	Atlantic boreal
	Californian	Vancouver region	Aleutian-Kurile Isls.	Japanese						
				N.	S.					
Microcampana conica .....	×	•	•	•	•	•	•	•	•	•
Cladonema californicum .....	×	•	•	•	•	•	•	•	•	•
Cladonema myersi .....	×	•	•	•	•	•	•	•	•	•
Polyorchis haplus .....	×	•	•	•	•	•	•	•	•	•
Polyorchis montereyensis .....	×	•	•	•	•	•	•	•	•	•
Scrippsia pacifica .....	×	•	•	•	•	•	•	•	•	•
Ptychogena californica .....	×	•	•	•	•	•	•	•	•	•
Eucheilota bakeri .....	×	•	•	•	•	•	•	•	•	•
Eutimalphes brownei .....	×	•	•	•	•	•	•	•	•	•
Vallentinia adherens .....	×	•	•	•	•	•	•	•	•	•
Mitrocoma discoidea .....	×	×	•	•	•	•	•	•	•	•
Tiaropsidium kelseyi .....	×	×	•	•	•	•	•	•	•	•
Phialidium lomae .....	×	×	•	•	•	•	•	•	•	•
Eirene mollis .....	×	×	•	•	•	•	•	•	•	•
Polyorchis penicillatus .....	×	×	•	•	•	•	×	•	•	•
Sarsia rosaria .....	×	×	×	•	•	•	•	•	•	•
Calycopsis nematophora .....	•	•	×	•	•	•	•	•	•	•
Bougainvillia multitentaculata .....	•	×	•	•	•	•	•	•	•	•
Endocrypta huntsmani .....	•	×	•	•	•	•	•	•	•	•
Halimodusa typus .....	•	×	•	•	•	•	•	•	•	•
Leukartiara fontata .....	•	×	•	•	•	•	•	•	•	•
Stomotoca atra .....	•	×	•	•	•	•	•	•	•	•
Melicertum georgicum .....	•	×	•	•	•	•	•	•	•	•
Mitrocomella sinuosa .....	•	×	•	•	•	•	•	•	•	•
Phialidium bicophorum .....	•	×	•	•	•	•	•	•	•	•
Phialidium gregarium .....	•	×	•	•	•	•	•	•	•	•
Halistaura cellularia .....	•	×	•	•	•	×	•	•	•	•
Eperetmus typus .....	•	×	•	×	•	•	•	•	•	•
Stauridiosarsia japonica .....	•	•	•	×	•	•	•	•	•	•
Nemopsis dofeini .....	•	•	•	×	×	•	•	×	•	•
Spirocodon saltator .....	•	•	•	×	×	•	•	•	•	•
Olindias formosa .....	•	•	•	×	×	•	•	•	•	•
Euphysa japonica .....	•	×	×	×	•	×	•	•	•	•
Polyorchis karafutoensis .....	•	•	•	×	•	×	•	•	•	•
Neoturris pelagica .....	×	×	•	•	×	•	•	×	•	•
Proboscoidactyla flavicirrata .....	×	×	×	×	×	•	•	×	•	•
Climacocodon ikarii .....	•	•	•	×	×	•	•	×	•	•
Podocoryne simplex .....	•	•	•	×	×	•	•	×	•	•
Urashimea globosa .....	•	•	•	×	×	•	•	×	•	•
Pandeopsis ikarii .....	•	•	•	×	×	•	•	×	•	•
Bythotiara depressa .....	•	•	×	•	•	×	•	•	•	•
Gonionemus vertens .....	•	×	×	×	×	•	•	×	•	×
Ptychogena lactea .....	•	•	×	×	•	×	•	•	×	×
Catablema multicirrata .....	•	•	×	×	•	×	•	•	×	•
Sarsia princeps .....	•	×	×	×	•	×	•	•	×	×
Hybocodon profiler .....	•	×	×	×	•	×	•	•	×	×
Halitholus pauper .....	•	×	•	×	•	×	•	•	×	•
Staurophora mertensi .....	•	•	×	×	•	×	•	•	×	×
Sarsia tubulosa .....	×	×	•	×	×	×	•	•	×	×
Bougainvillia superciliaris .....	•	•	•	×	×	×	•	•	×	×
Rathkea octopunctata .....	•	•	×	×	×	×	•	•	×	×
Leuckartiara nobilis .....	•	×	•	•	×	×	•	•	•	×
Eutonina indicans .....	•	×	×	×	•	×	•	•	•	×

<sup>1</sup> Hawaiian.

Table II. (Continued).

	Subregions					Arctic Pacific	Warm East Pacific	Indo-West-Pacific	Atlantic arctic	Atlantic boreal
	Californian	Vancouver region	Aleutian-Kurile Isls.	Japanese						
				N.	S.					
Melicerium octocostatum.....	•	•	•	×	•	×	•	•	×	×
Cladonema radiatum.....	•	•	•	×	×	•	•	×	•	×
Proboscoidactyla stellata.....	•	•	•	×	×	•	•	×	•	×
Stomatoca pterophylla.....	•	•	•	×	•	•	×	•	•	×
Leuckartiara octona.....	•	×	•	×	×	•	×	×	×	×
Bougainvillia muscoides.....	•	×	•	•	•	•	•	•	•	×
Pochella polynema.....	•	×	•	•	•	•	•	•	•	×
Sarsia eximia.....	×	×	×	•	•	•	×	×	•	×
Dipurena halterata.....	•	×	•	•	•	•	•	•	•	×
Euphysa flammea.....	•	×	•	•	•	×	•	•	×	×
Catablema vesicarium.....	•	×	×	•	•	×	•	•	×	×
Leukartiara breviconis.....	•	×	•	•	•	×	•	•	×	×
Phialopsis diegensis.....	×	•	•	•	•	•	×	•	•	×
Heterotiara anonyma.....	•	•	×	•	•	•	×	×	•	×
	21	35	16	28	17	19	6	13	14	24
	46			30					26	

to the coasts of north-western Europe and the Mediterranean, but the medusa is also recorded from the Polynesian Islands, where it was taken by the "Dana" Expedition, and from Chile, and, if the identification be correct, the hydroid occurs in California and near the Queen Charlotte Islands in British Columbia. The remaining three species are purely Pacific: *Polyorchis penicillatus*, which occurs all along the coast from Vancouver to Lower California, has been found near Hawaii; *Neoturris pelagica* has a very scattered distribution, being originally described from California and recorded again in the "Dana" Reports from off-shore localities outside the Californian coast and east of Japan; it has also been found in south-eastern Australia; *Polyorchis flavicirrata*, on the other hand, is entirely Amphi-Pacific, occurring from Kamchatka to Vietnam and from Vancouver to Lower California. The problem of the Amphi-Pacific distribution is further discussed below.<sup>1</sup>

It is characteristic that the fauna of neritic Hydromedusae in the boreal part of the west coast of North America almost completely consists of species with a strictly boreal character, belonging to temperate or even rather cold waters. Even the species mentioned above, which have been found more or less sporadically in tropical waters, are predominantly boreal in other regions of their occurrence; as a matter of fact, no warm-water species have settled anywhere along this coast. This is partly explained by the direction of the surface-water currents, but it also confirms the statement by EKMAN (1953 p. 142) concerning bottom animals, that the southern part of the Pacific coast of North America is cooled down by upwelling water from the bottom, with the result that practically no warm-temperate fauna exists there. A similar statement was made by GISLÉN (1944 p. 81), to the effect that, in comparison with Japan, "the conditions in California tend to make the shore life more stenothermic, more exclusive, more bound to low temperatures, but on the other hand, because of a rich amount of upwelling nutrients, it is very luxuriant". It is interesting that the composition of a fauna of neritic pelagic animals like the medusae shows a similar dependence of ecological conditions.

The comparison with the Atlantic fauna is discussed for the boreal region as a whole.

<sup>1</sup> *Aequorea aequorea* has been recorded from Vancouver and, with some doubt, from the Aleutians; the supposed occurrence of this medusa in the North Pacific is so peculiar that I am inclined to regard it as due to erroneous identifications; the specimens may have belonged to *Ae. coerulea*, which is known from southern and northern Japan.

*The Aleutian-Kurile Subregion.*

Comprises the chain of islands, the Aleutian and the Kurile Islands, bordering the predominantly arctic basins of the Bering Sea and the Sea of Okhotsk. The subregion contains very few species which do not also occur in arctic waters and these species were discussed above. The exceptions are as follows: *Calyropsis nematophora* is endemic in this subregion; *Sarsia rosaria* is recorded from the Kurile Islands and from Vancouver and California on the American coast; *Proboscoidactyla flavicirrata* is distributed from Kamchatka along the American as well as the Asiatic coasts to California and to Vietnam; these species are purely Pacific. *Sarsia eximia* and *Gonionemus vertens* are widely distributed species, and their occurrence was discussed above; *Heteroliara anonyma* is partly oceanic and very common in the tropical parts of the three great oceans; its occurrence in the Pacific (as known up to now) is rather peculiar; it is common in the Malayan Archipelago, recorded from outside the coast of Peru in South America and has been found in several localities along the Aleutian Islands and in the Gulf of Alaska, thus in widely separated areas. The number of species recorded from this subregion and also occurring in arctic waters amounts to ten (see Table I), and further investigations might considerably add to this number.

*The North Japanese Subregion.*

As briefly mentioned above the Japanese fauna of medusae is a mixed fauna. EKMAN (1953 p. 22) has pointed out a distinction between a boreal and a subtropical part of the Japanese coast at about 34° N. on the oceanic side of the islands. This limit, it is true, applies to bottom animals, and the medusae are pelagic animals, though mainly derived from bottom-growing hydroids, and many of them surpass the limit in either direction, being carried along with the currents; since, however, the occurrence of a considerable number of species is restricted to the southern parts of the islands, and a similar number is found only in the northern parts, the medusae tend to confirm EKMAN's statement. Species belonging to tropical or subtropical waters are discussed in the chapter on the Indo-West-Pacific Region and are listed in Table VII, although some of them may penetrate northwards to the northern parts of Japan, while species belonging to northern waters are listed in Table II, though some of them have extended their distribution to southern Japan.

The number of species enumerated in Table II as belonging to the South Japanese subregion amounts to 30, but in addition specimens of the following four species, belonging to tropical or subtropical waters, have been found in northern Japan: *Turritopsis nutricula*, *Eucheilota paradoxa*, *Phialella quadrata* and *Aequorea coerulescens* (see Table VII). Some conclusions concerning the currents may be drawn from the occurrence of these species (see later p. 164).

Numerous species of neritic Hydromedusae were first described from Japanese waters, but most of them have later on been observed in other regions; among the species enumerated in Table II only three are "endemic", *Stauridiosarsia japonica* in northern Japan, *Spirocodon saltator* and *Olindias formosa* which are generally distributed from the northern to the southern parts of the area, comprising also the South Japanese subregion, belonging to the Indo-West-Pacific Region. Among the 14 species common to Japan and the arctic waters the occurrence of 10 species is restricted to the northernmost area around Hokkaido, but four species have extended their distribution to southern Japan, partly even to the Yellow Sea; they have a predominantly boreal distribution in Atlantic as well as Pacific waters and are mentioned above (p.137). The species common to the North Japanese and the Aleutian-Kurile subregions also occur in arctic waters.

As many as 10 of the species listed in Table II as inhabitants of the North Japanese subregion are more or less widely distributed in tropical or subtropical waters. *Neoturris pelagica* was taken by the "Dana" in a locality east of Japan and it also occurs off California and in Australia (see above, p.139). All of the remaining 9 species occur in southern as well as in northern Japan.

How many of these species may be supposed to be indigenous in the boreal region, extending their distribution more or less into warmer areas, and how many may be regarded as belonging to tropical waters extending their distribution to Japan? Undoubtedly, the following 5 species belong to the first group: *Nemopsis doylei* is recorded from Chefoo in the Yellow Sea; *Urashimea globosa* to Formosa, *Climacocodon ikarii* and

*Proboscidactyla stellata* to Vietnam, and *Podocoryne simplex*, which has been found near the Palao Islands east of the Philippines; perhaps also *Staurodiscus gotoi*, which was described from southern Japan and has recently been recorded from one tropical locality, Sunda Strait between Java and Sumatra (in the "Dana" Reports, KRAMP 1965 p. 56). All these species are purely Pacific. *Proboscidactyla stellata* is an Atlantic boreal species, recorded from Vietnam and the Yellow Sea. *Stomatoca pterophylla* has a peculiar distribution, occurring in the tropical parts of the Atlantic (West Africa and the West-Indies) and on the Pacific coast of South America, and an isolated occurrence in Akkeshi Bay in northern Japan is recorded by UCHIDA (1940 p. 284). The only species which most probably is derived from truly tropical Pacific waters is *Pandeopsis ikarii*, originally described from Japan, later on recorded from several localities in the Indo-Malayan area and from the Kermadec Islands north of New Zealand (see the discussion on the nomenclature in KRAMP 1961 a, "Synopsis", p. 444).

#### *Amphi-Pacific Occurrence.*

Besides seven of the species, which occur in the arctic region, only the following 5 species are common to Japan and the boreal coasts of North America: the two widely distributed species *Leuckartiara octona* (occurring in tropical Indo-West-Pacific as well as in tropical East Pacific) and *Gonionemus vertens* (probably dispersed by ships as mentioned above), and three purely Pacific species, *Proboscidactyla flavicirrata* (with an almost continuous distribution from Vietnam via Japan and Kamchatka to Vancouver and California), *Eperetmus typus* (known only from northern Japan and Vancouver), and *Neoturris pelagica* (found in a few off-shore localities off Japan and California, besides in south-eastern Australia). The two last-named species, thus, are the only examples of a discontinuous Amphi-Pacific distribution; both are apparently rare species, perhaps occurring in other localities connecting the Japanese and Californian occurrences. *Eutima japonica* was described from Japan, and in the "Dana" Reports (KRAMP 1965 p. 85) it was recorded from a locality in the central part of the North Pacific, but not in the vicinity of the American Continent. It is remarkable that so few boreal species of neritic Hydromedusae are common to Japan and the American coast, and in no case needs an Amphi-Pacific distribution be explained by the fact that the Bering Strait in former days was dry land which prevented the cold Polar water from penetrating into the Pacific. As far as the warm-water species are concerned it is shown below (p. 164) that a direct exchange of neritic species between Japan and the American coasts seems highly improbable.

#### *Comparison with the Atlantic Ocean.*

The comparison of the Pacific boreal fauna to that of the Atlantic should be discussed. The majority of the species, which occur in arctic waters, have a circumpolar distribution and have extended their distribution through the Bering Strait into the boreal region; but some non-arctic species are also common to the northern parts of the two oceans; this applies to seven of the species in the East-Pacific and 5 of those in the North Japanese subregion. The explanations are different for the different groups of species. As mentioned above, the circumglobal, though scattered distribution of *Gonionemus vertens* is most probably due to transportation by ships. The occurrence of *Stomatoca pterophylla* on both sides of the isthmus of Panama is most probably due to direct communication before the isthmus was closed; its isolated occurrence in northern Japan seems inexplicable. Several species have an almost continuous distribution from the Atlantic through the Indian Ocean to the Indo-West-Pacific waters and have free access to the southern parts of Japan (which is discussed in the chapter on the Indo-West-Pacific Region, pp. 153 ff.); only one of them, *Leuckartiara octona*, also occurs in West-American boreal waters. *Heterotiara anonyma*, which is mainly oceanic, is likewise generally distributed from the Atlantic Ocean to the Malayan Archipelago, but its occurrence in the North Pacific is restricted to the surroundings of the Aleutian Islands (see above, p. 140). *Phialopsis diegensis*, which is partly oceanic, may have crossed the southern Pacific from Australia towards South America proceeding northwards to California, but unknown in the western Pacific. Special interest is attached to the predominantly boreal species, which do not occur in the Indian Ocean; they are not many: *Dipurena halterata*, *Bougainvillia muscoides*



and *Pochella polynema* are common species in north-western Europe and have been found at Vancouver; they are typical Atlantic-Boreal, and the only explanation of their occurrence in the North Pacific seems to be a direct communication north of Siberia in a previous period (see the map, fig. 356). The same probably applies to *Sarsia eximia*, provided that the determination of its occurrence at the coasts of Chile, California, British Columbia and the Aleutian Islands is correct. *Cladonema radiatum* and *Proboscoidactyla stellata* are likewise mainly boreal in the Atlantic area, and their occurrence in the Japanese subregion is difficult to explain.

The problem, whether the species common to the two oceans are of Atlantic or Pacific origin is discussed later (p. 188).

#### *Summary of the Pacific Boreal Region.*

The total number of species of neritic Hydromedusae belonging to this region amounts to 67, among which 19 species also occur in arctic waters, viz 11 in the East-Pacific subregion, 14 in the North Japanese subregion, 7 in both; usually they do not penetrate further south than to Hokkaido in Japan and Vancouver on the American coast; all of them are of northern origin, and 15 also occur in the Atlantic.

The East-Pacific subregion is inhabited by 46 species, the North Japanese subregion by 30. Apart from the arctic species no more than 5 species are Amphi-Pacific, occurring in both subregions; only in exceptional cases may a species cross the wide space of open ocean; the majority follow the coasts, their hydroids presumably being littoral, and the pelagic life of the medusae of too short duration (this was discussed above, p.141).

The difference in number of "endemic" species in the two subregions is very remarkable, 24 on the American coast and only 3 in northern Japan, and it should be noticed that keen observers have been present on both sides of the ocean.

It is also remarkable that very few of the species occurring in the American subregion have also been recorded from tropical waters, a hydrographic barrier (upwelling) evidently constituting an obstacle to an exchange of species across the limit between the boreal and the warm-water parts of the American coast, whereas no such barrier exists on the Asiatic coast. As far as demersal shelf animals are concerned, a limit between a subtropical and a boreal fauna may be pointed out at about 34° N on the oceanic coasts of Japan, but this limit may be surpassed by the free-swimming medusae; several tropical and subtropical species of medusae are recorded from the South Japanese subregion of the Indo-West-Pacific Region, and four of these have followed the Kuroshio Current far northwards, being collected in the surroundings of Hokkaido (evidencing a very intensive mixing of the water masses of the Kuroshio and the Oyashio Currents and formation of extensive eddies in this region); on the other hand, some species of northern origin have penetrated southwards to the southernmost of the Japanese islands or even into the Yellow Sea.

## The Hawaiian Region.

The Hawaiian Islands constitute an isolated group of islands in the central part of the North Pacific, situated within the belt of the north-east trade wind. According to "The Oceans" (p. 715) the region around the islands is a boundary region; the surface water current is directed towards the west and south-west, being part of the North Equatorial Current. The temperature of the surface water is constantly above 20°, but never reaching up to 30° C. The plateau is surrounded by deep water. According to EKMAN (1953 pp. 19 and 21) the shelf fauna is characterized by a relatively large number of endemic forms and shows a much closer relationship to the western Pacific than to America.

Very little is known about the medusae from this region; no more than 6 species of neritic Hydromedusae are recorded: *Staurocladia alternata* and *bilateralis* have not been found anywhere else; *S. acuminata* was likewise for a long time regarded as "endemic", until it was recorded from Japan (HARADA 1954), and *oahuensis* has been found on the coast of Chile (see below). *Pennaria armata* occurs in the Indian Ocean near Sumatra and the Nicobar Islands, *Polyorchis penicillatus* is an East Pacific medusa, occurring from Lower California to Vancouver. Our material, thus, is too scarce to confirm or reject EKMAN's statement.



## The East-Pacific Tropical Region.

Table III.

EKMAN has called this region the tropical West-American Region. It comprises the American coast from Lower California (including the entire Gulf of California) to a point, about 8° S. on the coast of Peru, where the north-going Peru Current leaves the coast, turning westwards as the South Equatorial Current. The northern limit of the region is determined by the westward turning of the California Current continuing as the North Equatorial Current; as mentioned above, the faunistic limit between the boreal and tropical faunas is rather sharply defined in that area. Along the coast between the northern and southern limits of the tropical region the currents are rather complicated, being influenced by local conditions.

The region has been divided into three provinces: the Mexican province, the Panama Bight, and the Equatorial province, but as far as the neritic Hydromedusae are concerned, no correlation can be pointed out between their occurrence in one or more of these provinces and their further geographical distribution.

The number of species recorded from the East-Pacific Tropical Region amounts to 28, seven of which are "endemic", being unknown elsewhere. As seen from the table ten of the species have been found in the Peru-Chilean Region further south on the South-American coast (to be discussed below), and four of these are species with an extensive geographical distribution. Eight species are known from the South-Australian-New Zealand Region.

Table III. East Pacific Tropical Region.

	Mexican	Panama Basin	Equatorial	Peru- Chilensis	Indo-West- Pacific	Australia	Medi- terranean	Warm Atlantic		Boreal Atlantic	
								W.	E.	W.	E.
<i>Chiarella centripetalis</i> .....	×	×	•	•	•	•	•	•	•	•	•
<i>Octophialucium bigelowi</i> .....	×	×	•	•	•	•	•	•	•	•	•
<i>Helgicirrha medusifera</i> .....	×	×	•	•	•	•	•	•	•	•	•
<i>Neoturris crockeri</i> .....	•	×	•	•	•	•	•	•	•	•	•
<i>Sarsia coccometra</i> .....	•	×	•	•	•	•	•	•	•	•	•
<i>Pachycordyle conica</i> .....	•	×	•	•	•	•	•	•	•	•	•
<i>Ectopleura sacculifera</i> .....	•	•	×	•	•	•	•	•	•	•	•
<i>Sarsia resplendens</i> .....	×	•	•	•	×	•	•	•	•	•	•
<i>Leuckartiara zacae</i> .....	•	×	•	×	×	•	•	•	•	•	•
<i>Bougainvillia fulva</i> .....	×	•	•	•	×	×	•	•	•	•	•
<i>Eutonina scintillans</i> .....	×	•	•	•	×	•	×	•	•	•	•
<i>Cytaeis tetrastyla</i> .....	•	×	×	×	×	×	×	×	×	•	•
<i>Heterotiara anonyma</i> .....	•	•	×	•	×	•	•	×	×	•	•
<i>Merga violacea</i> .....	×	•	•	×	×	•	×	×	•	•	•
<i>Zygocanna vagans</i> .....	•	×	•	•	×	×	•	•	×	•	•
<i>Proboscoidactyla ornata</i> .....	×	•	•	×	×	×	•	×	×	•	•
<i>Thamnostoma alexandri</i> .....	×	•	•	•	•	•	•	×	•	•	•
<i>Amphinema australis</i> .....	×	•	•	•	•	•	•	×	•	•	•
<i>Amphinema turrida</i> .....	×	•	•	×	×	×	•	×	•	•	•
<i>Stomotoca pterophylla</i> .....	•	×	×	×	•	•	•	×	•	•	•
<i>Eucheilota comata</i> .....	×	•	•	×	•	•	•	×	•	•	•
<i>Eucheilota duodecimalis</i> .....	×	•	•	•	•	•	•	×	•	•	•
<i>Gossea brachymera</i> .....	×	•	•	•	•	•	•	×	•	•	•
<i>Dipurena ophiogaster</i> .....	×	•	•	×	×	•	×	•	•	•	×
<i>Zanlea costata</i> .....	×	•	•	•	×	×	×	×	×	×	×
<i>Leuckartiara octona</i> .....	•	×	×	×	×	×	×	•	×	×	×
<i>Ectopleura dumortieri</i> .....	×	•	•	•	×	•	×	×	×	×	×
<i>Aequorea macrodactyla</i> .....	•	×	×	×	×	×	•	×	×	•	×
	17	12	6	10	15	8	7	14	8	3	5
	28							16		5	

Among about 180 species known from the Indo-West-Pacific Region (extending from Africa to the Polynesian Islands) only 15 are recorded from the East-Pacific Tropical Region, while a comparatively large number (amounting to 17) occurs somewhere in the Atlantic and adjacent waters.

Among the species occurring in the Atlantic 7 species are unknown (or only of sporadic occurrence) in other parts of Pacific or Indian waters. *Amphinema turrida* has been found off the coast of Chile and besides there are doubtful records from Japan and North Australia; *Stomatoca pterophylla* is said to have an isolated occurrence in northern Japan. The Atlantic occurrence of all these seven species is restricted to the warm coastal waters in the western Atlantic from the West-Indies and occasionally somewhat northwards as far as Cape Cod. It can hardly be doubted that the occurrence of these species on both sides of Central America is due to a former open connection across the Isthmus of Panama, as pointed out for many other marine animals.

The occurrence of *Heterotiara anonyma*, *Merga violacea*, *Proboscidactyla ornata*, *Zanclea costata* and *Ectopleura dumortieri*, which are unknown elsewhere in the eastern Pacific (except partly found on the coast of Chile), but occurring in the warm western Atlantic may also be derived from the former open connection across the Isthmus of Panama, like the seven species mentioned above.

Four species unknown in the Atlantic should also be mentioned. Three of these have a scattered distribution, and it seems futile to discuss their geographical connection with the East-Pacific region: *Sarsia resplendens* in southern Japan, *Leuckartiara zaca* near Sumatra and East Africa, *Eutonina scintillans* in the Gulf of Aden. The fourth species is *Bougainvillia fulva* (see below).

Finally six species, which are widely distributed in the Indo-West-Pacific Region shall be discussed; it holds good for most of them that there is a considerable gap between their Indo-West-Pacific distribution and their East-Pacific occurrence.

*Cytaeis tetrastyla* is a truly circumtropical species; it is partly oceanic because, though it has a littoral hydroid polyp, an asexual propagation also takes place in the pelagic medusa, either by direct budding of medusae on the stomach wall or by budding of polypoid structures, producing new generations of medusae (KRAMP 1959a p. 8). *Leuckartiara octona* and *Aequorea macrodactyla* have an almost continuous distribution from north-western Europe along the west coast of Africa and from East Africa to Japan and New Zealand, *L. octona* further east to the Marquesas Islands, about 140° W., *A. macrodactyla* to the Samoa Islands, about 170° W. besides an isolated record at about 120° W. They also occur in the western Atlantic. *Zycocanna vagans* and *Bougainvillia fulva* are unknown in the western Atlantic but continuously distributed and very common from East Africa eastwards into the Polynesian archipelago, but even the extensive collections of the "Dana" Expedition show that they have not been taken further east than Tahiti, about 150° W. Most probably the distribution of all these species is really continuous from the Indo-West-Pacific Region to the American coastal waters, the "gaps" being due to our lack of knowledge. *Dipurena ophiogaster* has a most peculiar distribution, since it is recorded from Mexico and Chile, the Indo-West-Pacific Region, the Mediterranean and north-eastern Europe, but is unknown in the western Atlantic and around Africa; a former connection through the Red Sea seems possible.

It is remarkable that a continuous distribution across the warm parts of the Pacific Ocean is restricted to such a small number of neritic species (presumably with littoral hydroids), considering the great number of such species which occur in the Indo-West-Pacific Region, many of them extending their distribution far eastwards among the Melanesian and Polynesian islands. They are dealt with below.

Evidently, the wide space of open sea with none or very few islands west of the American continent constitutes an effective barrier against a further eastward penetration of the vast majority of these animals which, accordingly, serves to confirm the establishment of the Indo-West-Pacific Region as a proper zoogeographical region as pointed out by EKMAN in 1934 and subsequent papers.

## The Peru-Chilean Region.

Table IV.

This is a well-marked region, comprising the Pacific coasts of Peru and Chile between about 6° S. (at Point Aguja) and about 42° S. The physical conditions are first and foremost characterized by the Peru Current, moving northwards along the coast. Antarctic and subantarctic water masses are circling around the Antarctic Continent in an easterly direction with the West-Wind-Drift, from which north-going branches flow along the western coasts of South America and South Africa and, to a less degree, Australia. Owing to its considerable southward extension the South American continent deflects particularly great quantities of the cold subantarctic water masses northwards along its western coast, giving rise to what is generally called the Peru Current. Distinction can be made between the narrow "Peru-Coastal-Current", which is directly derived from the West-Wind-Drift, and the "Peru-Oceanic-Current", which likewise moves northwards, but is broader and of less velocity than the coastal current and receives supplies of water from the subantarctic convergence. Owing to their southern origin these water masses have low temperatures, and their influence extends almost to the Equator, where they turn westwards constituting part of the South Equatorial Current. Within the zoogeographical region, the "Peru-Chilean Region" as here conceived (6° S. to 42° S.) the surface temperatures increase northwards from about 14° to 25° C. in February, 10° to 20° C. in August. The Chilean coast further south, with still lower temperatures, belongs to the "South-American-Antiboreal Region" (EKMAN 1953); this region is not discussed in the present paper, because not a single species of neritic medusae is known from

Table IV. Peru-Chilean Region.

	Peru	Chile	Subantarctic	Tropical East-Pacific	North Pacific	South Australian	Indo-West-Pacific	South African	Warm Atlantic		Boreal Atlantic	
									W.	E.	W.	E.
<i>Cosmetirella davisi</i> . . . . .	•	×	×	•	•	•	•	×	•	•	•	•
<i>Tiaricodon coeruleus</i> . . . . .	×	×	×	•	•	•	•	•	•	•	•	•
<i>Stomotoca pterophylla</i> . . . . .	×	•	•	×	•	•	•	•	×	•	×	•
<i>Eucheilota comata</i> . . . . .	•	×	•	×	•	•	•	•	×	•	•	•
<i>Amphinema turrida</i> . . . . .	•	×	•	×	•	•	×	•	×	•	•	•
<i>Leuckartiara zacaе</i> . . . . .	•	×	•	×	•	•	×	•	•	•	•	•
<i>Merga violacea</i> . . . . .	•	×	•	×	•	•	×	•	×	•	•	•
<i>Aequorea coerulescens</i> . . . . .	×	×	•	•	×	•	×	×	•	•	•	•
<i>Proboscidactyla ornata</i> . . . . .	•	×	•	×	•	•	×	•	×	×	×	•
<i>Aequorea macrodactyla</i> . . . . .	×	×	•	×	•	×	×	×	×	×	•	×
<i>Bougainvillia involuta</i> . . . . .	•	×	•	•	•	•	×	•	•	•	•	•
<i>Aequorea globosa</i> . . . . .	•	×	•	•	•	•	×	•	•	•	•	•
<i>Phialidium simplex</i> . . . . .	•	×	×	•	•	•	×	×	•	•	•	•
<i>Phialella quadrata</i> . . . . .	•	×	•	•	•	×	×	•	•	×	•	×
<i>Dipurena ophiogaster</i> . . . . .	•	×	•	×	•	•	×	•	•	•	•	×
<i>Sarsia eximia</i> . . . . .	•	×	•	•	×	•	×	•	•	•	•	×
<i>Leukartiara octona</i> . . . . .	×	×	•	×	×	×	×	×	•	×	×	×
<i>Staurocladia oahuensis</i> . . . . .	•	×	•	•	×	•	•	•	•	•	•	•
<i>Euphysa aurata</i> . . . . .	•	×	•	•	•	•	•	•	•	•	×	×
partly oceanic:												
<i>Heterotiara anonyma</i> . . . . .	×	•	•	•	×	•	×	×	×	×	•	•
<i>Cytaeis tetrastyla</i> . . . . .	×	•	•	×	×	•	×	×	×	×	•	•
<i>Euphysora furcata</i> . . . . .	•	×	•	•	•	•	×	×	×	×	•	•
	7	19	3	10	6	3	16	8	9	7	4	6
	22								11		8	
									14			

the Pacific side of this region. Within the Peru-Chilean Region the temperature of the upper water layers is generally increasing from the coast outwards. Close to the coast cooling of the surface water may be further intensified by upwelling cold water from moderate depths, while comparatively warm and light surface water is carried away from the coast by the prevailing winds; this phenomenon is emphasized by several authors and seems to be especially pronounced in the northern part of the region. On the Chilean coast it is apparently not a constant phenomenon (see below).

The marine fauna of the Peru-Chilean Region was previously very little known. As far as neritic medusae are concerned, our knowledge until recent time was restricted to a few scattered records by BIGELOW (1909), VANHÖFFEN (1913) BOONE (1938), and KRAMP (1952 and 1957). In 1958–1960, however, an extensive collection has been secured by the University of Concepción in Chile; a provisional account was given in a paper by FAGETTI & FISCHER, 1964 on the quantitative amount of zooplankton, and the medusae were dealt with in detail by the present author in a recent paper (KRAMP 1966), which greatly added to the number of species known from the Chilean coast. Probably, the number might be further increased by future investigations, but this new collection has made it possible to characterize the composition of the medusan fauna of this area.

The species now known to occur in the region are listed in Table IV. A few species, previously recorded from the region, should be omitted from the list: *Phialella falklandica* was recorded from two localities by VANHÖFFEN (1913), but numerous specimens of this genus examined by me all belong to *P. quadrata*, which probably also applies to the specimens recorded by VANHÖFFEN; a specimen referred to *Euphysora bigelowi* (KRAMP 1952) was in a crumpled state and may have been wrongly determined; in the same paper I described a hydroid with newly liberated medusae, which I determined as a new variety of *Podocoryne carnea* var. *chilensis*, but for geographical reasons I doubt the correctness of the identification; another mistake in the same paper was the record of three specimens of *Phialidium loma*; in my recent paper (KRAMP 1966) I stated that they belonged to *P. simplex*, which occurs in great numbers on the coast of Chile.

The list in Table IV comprises 19 species, which are truly neritic medusae; moreover *Heterotiara anonyma*, *Cytaeis tetrastyla* and *Euphysora furcata*, which are partly oceanic; the unknown hydroid of *Chromatonema erythronon* probably lives in deeper water, though the medusa has been found in several localities very close to the coast of Peru.

Considering the southern origin of the water masses of the Peru Current a fair number of antarctic or subantarctic species might be expected in the plankton; as a matter of fact, only two of the species belong to these southern waters; *Cosmetirella davis* is circumpolar in antarctic and subantarctic waters, and its distribution is extended northwards along the southern part of the west coast of Africa as well as along the Pacific coast of South America where, however, it has not been found further north than 37° S. *Tiarocodon coeruleus* occurs in the Weddell Sea and in the waters around Tierra del Fuego and is recorded from Valparaíso Bay in Chile and as far north as Callao in Peru.

Almost all the other neritic species are predominantly warm-water forms. Among the 19 truly neritic species 18 have been found on the Chilean coast, but only 5 on the coast of Peru (four in both areas), undoubtedly because the Peruvian area is particularly incompletely explored. Nine of the truly neritic species are known from the East-Pacific Tropical Region, and three of these are unknown in other parts of the Pacific (*Stomatopoda pterophylla*, *Eucheilota comata* and *Amphinema turrida*), whereas they occur in West-Indian waters, an occurrence most probably due to a former open connection across the Isthmus of Panama (see above, p.144). All the remaining six species common to the tropical eastern coasts of America and the Peru-Chilean Region also occur in the Indo-West-Pacific Region. As pointed out above (p.144), remarkably few Indo-West-Pacific neritic medusae have been found in the East-Pacific Tropical Region; it is remarkable, therefore, that no less than 12 Indo-West-Pacific species occur in the coastal waters of the Peru-Chilean Region (four of them also near New Zealand). The explanation may be that the easternmost of the Polynesian islands have a southern position (Easter Island about 30° S.), which makes it possible for these medusae, with the prevailing easterly currents at these latitudes, to cross the last open space towards the South American coast, perhaps in the hydroid stage attached to sea-weeds. These twelve species, however, represent only a small fraction of the numerous inhabitants of the Indo-West-Pacific Region (see later).

Only four of the Peru-Chilean species occur in the boreal parts of the North Pacific; all of them also occur in the Indo-West-Pacific Region, whence they have extended their distribution more or less northwards. Four species have been found in the surroundings of New Zealand. Rather peculiar is the occurrence of *Staurocladia oahuensis*, previously known only from Hawaii. Ten species of this genus of small, strictly littoral, crawling medusae have been described; none of them has been found in more than one or two widely separated localities, four of them in Hawaii, the others in antarctic or antiboreal waters; one species is recorded from Hawaii and Japan, one from South Australia and Graham Land in Antarctic, one from the Falkland Islands and (with some doubt) from New Zealand; the occurrence of an Hawaiian species on the coast of Chile is no more surprising than any of these other records, but no explanation can be given; the Chilean specimens are described and discussed in KRAMP 1952, p. 3.

The Peru-Chilean species which occur in Atlantic waters are mentioned in the discussion of the Indo-West-Pacific Region, where, with a few exceptions, all of them occur, except the three West-Indian species mentioned above, and the peculiar occurrence of *Euphysa aurata*. It is a very common medusa in north-western Europe, and it also occurs in the Russian and Siberian Polar Sea, on the west coast of Greenland, in the Massachusetts Bay in North America, and in the Mediterranean; moreover, there is a record from Chefoo in China (CHOW & HUANG, 1958 p. 174) and from the Patagonian Bank (THIEL 1938 p. 290). If this last record is correct, an occurrence in the southern part of the coast of Chile (KRAMP 1966) is not quite isolated.

In my recent paper on medusae from the coast of Chile (KRAMP 1966) I called attention to the fact that, at the time when the investigations were carried out, the occurrence of the neritic medusae was almost entirely restricted to the water of the narrow coastal current; these medusae are undoubtedly indigenous in the area. I concluded that the water of the Peru-Coastal-Current did not, or only to a very slight degree, spread outwards and did not mix with the waters of the Peru-Oceanic-Current; no surface water was carried away from the coast by the winds, and no upwelling of water from deeper layers took place during this period.

*Chromatonema erythrogenon*, on the other hand, was taken at rather considerable distances from the coast as well as near the coast of Peru; it is not a strictly neritic species, but rather a "slope species", the unknown hydroid probably occurring on the continental slope. *Heterotiara anonyma*, *Cytaeis tetrastyla* and *Euphysora furcata* are partly oceanic and widely distributed in the oceans.

## The Antarctic and Subantarctic Regions.

Table V.

The northern limit of the Antarctic Region is determined by the Antarctic Convergence, the position of which is about 50–55° S. around the Antarctic Continent. This northern limit of the region is marked by a sudden increase of the surface temperature brought about by the sinking of the cold antarctic surface water below the subantarctic surface water; it constitutes a rather effective barrier between the antarctic and the subantarctic faunas of neritic medusae. The temperature at the surface increases from about –1° C near the continent to +1° or 1–2° C at the convergence. The northern limit of the Subantarctic Region is constituted by the Subantarctic Convergence around the latitude of about 40° S., but it is less sharply defined. According to EKMAN, the South Island of New Zealand belongs to the Subantarctic Region (named by him the Antiboreal Region, see the map, fig. 357); as demonstrated below, however, the fauna of neritic hydromedusae at the coasts of the South Island is more closely related to the Australian than to the subantarctic fauna. The Kerguelen Islands, about 50° S. in the Indian Ocean are climatically antarctic, constituting an outpost of the Antarctic; as pointed out by EKMAN, the plateau around these islands possesses a high percentage of endemic species (mainly of fishes and echinoderms), and he regards it as a special sub-region; as pointed out below the same feature is indicated for the medusae. In the following discussion the Kerguelen plateau is regarded as belonging to the Antarctic Region.

Nearest to the Antarctic Continent the currents of the surface water are mainly directed westwards, but apart from this narrow coastal area the Antarctic as well the Subantarctic Regions are characterized by the



**Table V.** The Antarctic and Subantarctic Regions, Indo-Pacific sectors.

	Antarctic		Subantarctic		South Africa	South America	Tropical Atlantic	Arctic
	Indo-Pacific sectors	Atlantic Sector	Indo-Pacific sectors	Atlantic sector				
<i>Staurocladia charcoti</i> .....	×	•	•	•	•	•	•	•
<i>Staurocladia kerguelensis</i> .....	×	•	•	•	•	•	•	•
<i>Staurocladia hodgsoni</i> .....	×	×	•	•	•	•	•	•
<i>Margelopsis australis</i> .....	×	×	•	•	•	•	•	•
<i>Ptychogena antarctica</i> .....	×	×	•	•	•	•	•	•
<i>Phialidium iridescent</i> .....	×	×	•	•	•	•	•	•
<i>Calycopsis borchgrevinki</i> .....	×	×	•	×	•	•	•	•
<i>Laodicea pulchra</i> .....	×	•	•	×	•	•	•	•
<i>Zanclonia weldoni</i> .....	×	×	×	•	•	•	•	•
<i>Köllikerina maasi</i> .....	×	×	•	•	×	•	•	•
<i>Mitrocomella frigida</i> .....	×	×	•	•	×	•	•	•
<i>Bougainvillia macloviana</i> * .....	×	•	×	×	•	×	•	•
<i>Cosmetirella davis</i> .....	×	×	×	×	×	×	•	•
<i>Phialella falklandica</i> .....	×	•	×	×	•	×	•	•
<i>Phialidium simplex</i> .....	•	•	×	×	×	×	•	•
<i>Russellia mirabilis</i> .....	×	×	•	•	•	•	×	•
<i>Ptychogastria polaris</i> .....	×	×	•	•	•	•	•	×
	16	11	5	6	4	4	1	1

K. Kerguelen Islands only.

\* Artificially introduced to north-western Europe.

West-Wind-Drift, the upper water layers circulating eastwards around the continent, being deflected northwards along the western coasts of the three great continents, particularly South America, where subantarctic water also flows northwards along the east coast. EKMAN (1953 p. 229) is undoubtedly right, when he states that “the antarctic shelf has been a centre of development for marine animals during long geological periods”, and “the rich antarctic marine fauna lives in a polar region which for a very long time seems to have had a constant antarctic climate”. It remains to be seen, whether these views are confirmed by the occurrence of the medusae.

The conditions in the deeper water layers will be discussed in connection with the oceanic species.

Some species of neritic hydromedusae belonging to warm regions may occasionally appear in subantarctic waters. Table V, however, includes only such species which are indigenous in antarctic and subantarctic waters, their number amounting to 17 species (including the Trachymedusa *Ptychogastria polaris*, see above p.132), representing our present knowledge of the fauna of these animals in the regions, a comparatively small number which does not allow far-reaching conclusions. The distribution of the species, however, shows a tendency, which is in accordance with the views expressed by EKMAN and quoted above.

Up to now, only one of the species, *Phialella falklandica*, has not been found in the Antarctic Region, since the specimens recorded from the Kerguelen and Bouvet Islands by VANHÖFFEN (1911) proved to belong to *Cosmetirella davis*. An enumeration of the species shows that, among the 16 species recorded from the Indian and Pacific sectors, the distribution of 10 species is restricted to the waters south of the subantarctic convergence (most of them also occurring in the Atlantic sector); 6 species are strictly antarctic; 3 species also occur in subantarctic waters, two of them in the Atlantic sector only (*Calycopsis borchgrevinki* and *Laodicea pulchra*), *Zanclonia weldoni* also in the eastern Pacific west of Cape Horn. Among the remaining 7 species one is bipolar, viz *Ptychogena polaris*, and its occurrence in southern waters is restricted to the Antarctic Region (Graham



Land and the South Shetlands, Gauss Station about  $87^{\circ}$  E<sup>1</sup>). *Russellia mirabilis* occurs near Graham Land and the South Shetland Islands; it has an extensive vertical distribution and has also been recorded from deep water in the West-Indies. The other five species penetrate more or less north of the subantarctic convergence, following the north-going branches of the West-Wind-Drift: *Cosmetirella davisii* to Chile and South-West-Africa, *Köllikerina maasi* to the southern part of Madagascar, *Mitrocomella frigida* to a point west of Cape of Good Hope, *Phialella falklandica* and *Bougainvillia macloviana* to Buenos Aires in Argentina, following the Falkland Current.

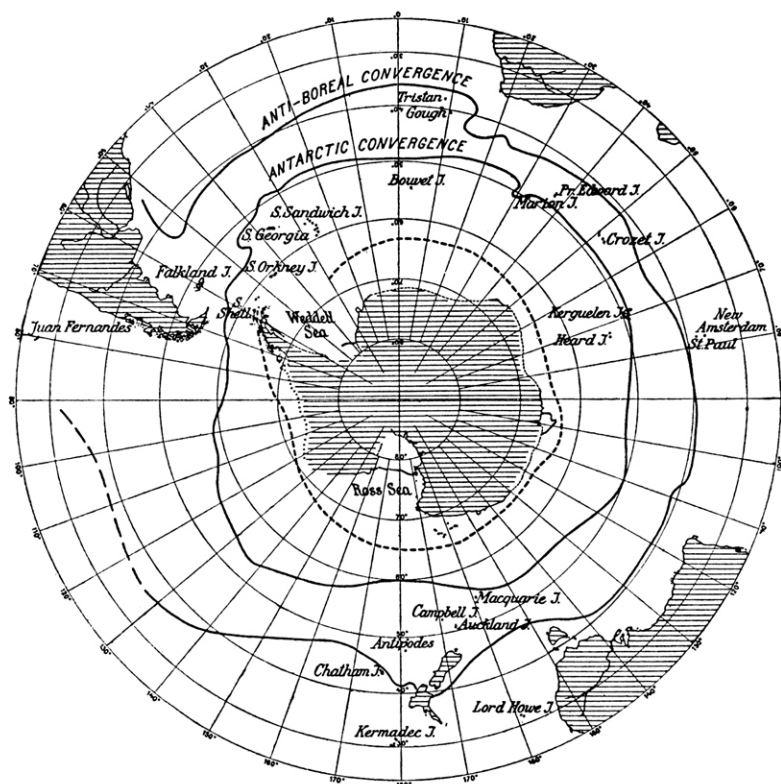


Fig. 357. The South Seas (from EKMAN).

With very few exceptions the fauna of neritic Hydromedusae occurring in the Indian and Pacific sectors of the Antarctic and Subantarctic Regions clearly belongs to these waters, and within these sectors very few species have been found on both sides of the Antarctic Convergence. More species may possibly appear during future investigations, but so far EKMAN's characterization of the marine fauna in the South-Polar areas as a separate fauna with a high percentage of endemic species can be confirmed. The paucity of neritic Hydromedusae in the Indian and Pacific sectors of the Subantarctic Region may partly be due to the scarcity of islands in these tracts.

In the Atlantic sector conditions are more complicated in accordance with the more complicated current systems (see KRAMP 1959 a p. 235). There are many more species (31, among which 14 are endemic, 9 species also found in the Indo-Pacific sections); the limit between the antarctic and subantarctic fauna is sharp (only four species common to the two regions), but in the south-western parts of the area several subantarctic species penetrate northwards, following the Falkland Current, while others, belonging to more northerly waters, are carried southwards along the South-American coast by the Brazil Current; the fauna in the subantarctic parts of the south-western Atlantic, therefore, is a mixed fauna. Nothing like these conditions occur in the Indian and Pacific sections of the Antarctic and Subantarctic Regions.

<sup>1</sup> *P. opposita* VANHÖFFEN 1912 is identical with *P. polaris*, and *P. antarctica* HAECKEL from Kerguelen is indeterminable, the type specimen in the British Museum, London, being mutilated.

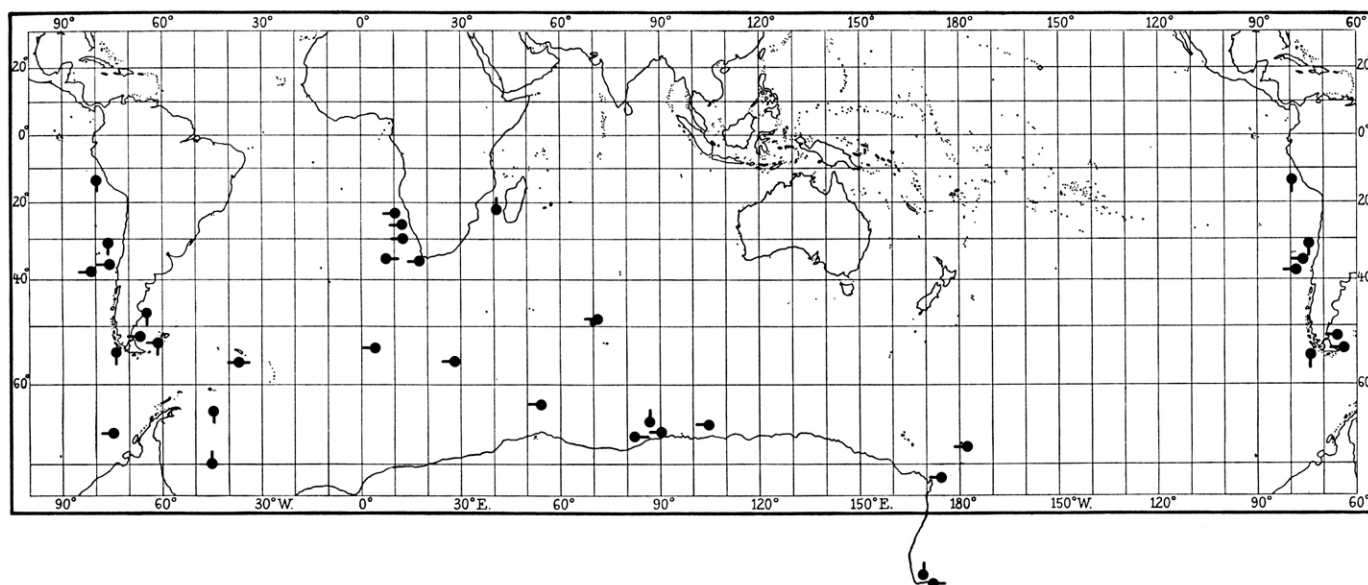


Fig. 358. Antarctic and subantarctic species.

● *Köllikerina maasi*. ● *Mitroconella frigida*. ● *Cosmetirella davisi*. ● *Tiaricodon coerulens*.

## The Southern Australian and New Zealand Region.

Table VI.

While the northern part of the Australian Continent have a tropical and subtropical climate and a marine fauna closely connected with that of the Indo-West-Pacific Region, the southern parts of the continent together with New Zealand constitute a temperate region. According to EKMAN (1953 p. 198) "... the South Australian coastal region is sharply divided from the more northern tropical-subtropical region and is very much sharply defined" (see the map, fig. 357 p. 149). As expected, the pelagic fauna of the southern districts is less sharply defined than the bottom fauna, on which EKMAN's statement was based. The fauna in the southern districts is mainly warm-temperate; the south coast of the continent is influenced by the cooling effect of the extreme northern boundary-line of the West-Wind-Drift, from which branches proceed somewhat to the north until they meet currents of warmer origin, forming transitional regions. According to EKMAN the limits between the sub-tropical and temperate shelf faunas are situated at about 29° S. on the west coast, about 32–34° S. on the east coast, slightly north of Sydney.

New Zealand stretches for a distance of 13° of latitude from north to south, the north point being in about the same latitude as Sydney. In the available maps the Subantarctic Convergence is placed between the two islands, thus the South Island might belong to the Subantarctic Region. As briefly mentioned above (p. 147) and further demonstrated below, however, its fauna of medusae is closely related to the Australian fauna. The currents around New Zealand are variable; water of the West-Wind-Drift may continue northwards along both sides, but the eastern coasts also receive deflections of the South Equatorial Current, and swirls in the Tasman Sea carry water masses from south-eastern Australia to the western coasts of New Zealand.

It might have been interesting to compare the faunas of medusae in the different parts of the neritic areas around Australia and New Zealand, but unfortunately the collecting of Hydromedusae seems to have been restricted to a few narrow sectors. Not a single species is known from the waters along the south coast of Australia west of Adelaide, or from the entire west coast and the north coast west of Cape Darwin; what is known from New Zealand is exclusively from the eastern coasts, mainly derived from the "Dana" collections. It is interesting, however, to compare the elements of the faunas along the coasts of New Zealand, South-East Australia, and North-East Australia and to study their association with the Indo-West-Pacific fauna, and "endemic" species appear to be remarkably few. In 1883–1890, it is true, R. VON LENDENFELD described several new Australian species, but most of them are unrecognizable; I once had the opportunity to examine

**Table VI.** The Southern Australian and New Zealand Region.

	New Zealand	Australia		Indo- West-Pacific	East Pacific	Atlantic
		South-east	North-east			
<i>Pelagohydra mirabilis</i> .....	×	•	•	•	•	•
<i>Tiaropsidium japonicum</i> .....	×	•	•	×	•	•
<i>Octophialucium indicum</i> .....	×	•	•	×	•	•
<i>Toxorchis polynema</i> .....	×	•	•	×	•	×
<i>Amphinema rugosum</i> .....	×	•	•	×	•	×
<i>Phialella quadrata</i> .....	×	•	•	×	×	×
<i>Cirrhovenia polynema</i> .....	×	•	×	×	•	•
<i>Eirene ceylonensis</i> .....	×	•	×	×	•	•
<i>Phialidium malayense</i> .....	×	•	×	×	•	•
<i>Bougainvillia fulva</i> .....	×	×	×	×	×	•
<i>Leuckartiara octona</i> .....	×	×	×	×	×	×
<i>Pandea conica</i> .....	×	×	•	×	×	×
<i>Aequorea macrodactyla</i> .....	×	×	×	×	×	×
<i>Phialidium hemisphaericum</i> .....	×	×	×	×	•	×
<i>Eutima orientalis</i> .....	×	•	•	×	•	•
<i>Turritopsis nutricula</i> .....	×	•	•	×	•	×
<i>Oceania armata</i> .....	×	×	•	×	×	×
<i>Eutimalphes pretiosa</i> .....	•	×	•	•	•	•
<i>Gonionemus hamatus</i> .....	•	×	•	•	•	•
<i>Pennaria adamsia</i> .....	•	×	•	•	•	•
<i>Pennaria rosea</i> .....	•	×	•	•	•	•
<i>Laodicea fertilis</i> .....	•	×	•	•	•	•
<i>Turritopsis lata</i> .....	•	×	•	•	•	•
<i>Staurocladia haswelli</i> .....	•	×	•	•	•	•
<i>Olindias singularis</i> .....	•	×	×	×	•	•
<i>Leuckartiara annexa</i> .....	•	×	•	×	•	•
<i>Neoturris papna</i> .....	•	×	•	×	•	•
<i>Laodicea indica</i> .....	•	×	×	×	•	•
<i>Tiaropsidium roseum</i> .....	•	×	•	×	•	•
<i>Eirene menoni</i> .....	•	×	×	×	•	•
<i>Neoturris pelagica</i> .....	•	×	•	•	×	•
<i>Zygocanna vagans</i> .....	•	×	•	×	×	×
<i>Phialopsis diegensis</i> .....	•	×	•	×	×	×
	17	22	10	24	9	11
		25				

the type specimens of some of his species in the British Museum in London; his descriptions, though brief and insufficient, might be fairly correct, but his figures were completely misleading.

#### *New Zealand.*

As seen from Table VI, only one species is endemic in the New Zealand waters, viz the peculiar floating polyp, *Pelagohydra mirabilis* DENDY, budding off medusae the further development of which is unknown; it has never been observed again, since it was described in 1902.<sup>1</sup>

Besides *Pelagohydra* 16 species of neritic Hydromedusae are recorded from New Zealand, 13 from the coastal waters of the South Island, only 4 from the North Island which, evidently, is not well investigated. Two of the species, *Turritopsis nutricula* and *Oceania armata* from the North Island, are partly oceanic (epipelagic). Nine of the species are also recorded from the coastal waters of Australia, where presumably also most of the others occur, since all of the 16 New Zealand species are more or less widely distributed in the Indo-West-Pacific Region. On the other hand, not a single species of the New Zealand Hydromedusae has been

<sup>1</sup> Many years ago I had the pleasure to meet Professor DENDY in London and he took me to his laboratory telling me that he wanted specialists to realize that *Pelagohydra* was not a fabulous animal.

observed in subantarctic or antarctic waters. The New Zealand fauna of these animals, accordingly, does not exhibit any subantarctic character, and this even applies to the fauna of the South Island, in spite of the position of the Subantarctic Convergence north of that island. The conditions may be different along the west coast from which, however, no Hydromedusae have been recorded.

The occurrence of a number of New Zealand species in the eastern Pacific and in the Atlantic is discussed below in connection with the Australian fauna.

#### *Southern Australia.*<sup>1</sup>

The total number of species of neritic Hydromedusae known up to now from the southern parts of the Australian continent amounts to 22, besides two (*Calycopsis chuni* and *Annatiara affinis*) which belong to the deeper water layers. No less than ten of these species were taken only by the "Dana" Expedition, the others being scattered records. Our knowledge of the fauna, accordingly, is very incomplete. Two species, described by HAECKEL (*Dicodonium dissonema* and *Pteronema darwini*), are only labelled "Australia"; they are left out of the discussion and are not included in Table VI. The occurrence of *Eutimalphes pretiosa* HAECKEL is likewise denoted as "Australia", but FLYNN (1927 p. 91) referred a medusa from Tasmania to the same species. *Staurocladia haswelli* was described from Port Jackson by BRIGGS (1920), *Gonionemus hamatus* from Henley in South Australia by KRAMP (1965<sup>2</sup> p. 274). With addition of four species described from New South Wales by LENDENFELD and considered valid species, the number of species which provisionally may be termed "endemic" in these waters amounts to seven (as mentioned above most of the species described by von LENDENFELD are unrecognizable).

Among the remaining 15 species 14 are widely distributed in the Indo-West-Pacific Region, except *Neoturris pelagica*, which belongs to the Californian waters and also was taken by the "Dana" Expedition in a locality east of Japan (KRAMP 1965 p. 35). All the four species recorded from the south coast likewise occur in the Indo-West-Pacific Region. No far-reaching conclusions can be drawn from the available scanty material, except that, apart from the "endemic" species, the fauna of neritic Hydromedusae along the south-eastern parts of the Australian coasts, so far as known up to now, consists of species with a predominantly tropical distribution. On the other hand, of the 46 species recorded from the north-eastern parts of Australia, 35 have not been found in the south-eastern areas. Provisionally, therefore, the south-eastern fauna of these animals can be designated at present as a southern offshot of a tropical fauna penetrating into warm-temperate waters, without simultaneous addition of southern elements from colder regions. This also seems to agree with the prevailing, southward direction of the coastal currents. EKMAN may be right that, as far as the demersal coastal and shelf fauna is concerned, the southern Australian region is sharply defined from the northern tropical-subtropical region, but pelagic animals may traverse the boundary area and proceed as far as the temperature conditions are tolerable. Future investigations may alter the views expressed above.

As seen from Table VI, nine species of neritic Hydromedusae, found in the Southern Australian and New Zealand Region, are also recorded from various parts of the East Pacific waters. Since none of these species inhabits subantarctic waters, the West-Wind-Drift is hardly responsible, except perhaps for the occurrence of *Phialella quadrata* and *Leuckartiara octona* along the coast of Chile. The others are found only in more northern East-Pacific localities. *Aequorea macrodactyla* and *Zygocanna vagans* are large medusae, presumably leading a pelagic life of fairly long duration, enabling them to drift to and fro between the Polynesian Islands and cross the gap towards the central parts of America. *Oceania armata* and *Pandea conica* are partly oceanic and have been found in the central part of the northern Pacific. All these species have a predominantly western distribution comprising the Indo-West-Pacific Region and the Atlantic. *Phialopsis diegensis* is likewise partly oceanic, widely distributed in the Atlantic and recorded from the east coast of Africa, its Pacific occurrence being restricted to three widely separated localities *viz* in California, south of the Galapagos Islands, and recently recorded from Adelaide in South Australia; this peculiar distribution cannot be explained.

<sup>1</sup> I prefer this expression for "South Australia", which is the name of a state.

<sup>2</sup> Some Medusae (mainly Scyphomedusae) from Australian Coastal waters. — Trans. Roy. Soc. South Australia, vol. 89. 1965.

Only two of the species common to southern Australia and eastern Pacific do not occur in the Atlantic: *Bougainvillia fulva* is generally distributed in the warm waters from Africa to Tahiti, including south-eastern Australia and New Zealand, with a single record from the Pacific coast of Mexico (MAYER 1910); *Neoturris pelagica* seems to be a rare species with a scattered distribution: off California, off Japan (recently recorded in the Dana Reports, KRAMP 1965 p. 34), and south-eastern Australia. In the discussion of the faunas of north-eastern Australia, more examples of Australian medusae occurring in the East Pacific will be given.

It applies to all the species which are common to the south-eastern Australian waters and the Atlantic Ocean that they are widely distributed in the Indo-West-Pacific Region, with an unbroken connection.

## The Indo-West-Pacific Region.

Tables VII and VIII.

The Indo-West-Pacific Region, as established by EKMAN, is an extensive region. As mentioned above, EKMAN's division of the coastal waters was based on the demersal fauna in the littoral and shelf regions, and, as a rule, the neritic medusae, most of which are derived from sessile hydroids, may be incorporated within the same limitations; it has also been emphasized, that the currents carry free-swimming medusae outside the borders of the shelf-regions. As pointed out below, this applies in particular to the faunas around the Australian and South Japanese sub-regions of the Indo-West-Pacific Region. The enumeration of the neritic Hydromedusae, in Table VII, seems to justify EKMAN's establishment of this extensive zoogeographical region and its sub-regions, also as far as the neritic Hydromedusae are concerned.

SCHOTT (1935) introduced another division of the Indian and Pacific Oceans into regions, but these regions are purely geographical and not zoogeographical, since they are mainly based on climatic conditions; his book however, contains a wealth of information on current-systems and other hydrographical conditions.

Provisionally, it should be emphasized that, as far as the neritic medusae are concerned, the Indo-West-Pacific Region has many more species in common with the Atlantic Ocean than with the eastern Pacific, which clearly confirms EKMAN's views.

The extension of the region and its division into subregions are seen in the adjacent map (fig. 359). In the western part of the Indian Ocean the Red Sea with the Gulf of Aden may be separated as a special subregion. EKMAN regards the entire Indian Ocean as one subregion, with exception of the coasts of the Malayan Islands and Australia facing the ocean. The sub-region of the Indian Ocean comprises the Iranian Gulf, the east coast of Africa as far south as Delagoa Bay, about 26° S., the western coasts of India, the Laccadive, Maldiva and Chagos Islands, the Bay of Bengal with the Andamans and the Nicobars, and the Strait of Malacca as far as Singapore, while the shelf fauna along the coasts of Sumatra and the Sunda Islands facing the Indian Ocean is regarded as belonging to the Indo-Malayan subregion. The limit between this subregion and the North-Australian may be placed in the channel between the Kei Islands and the Aru Islands, the latter being situated on the western border of the shallow-water area of the Arafura Sea.

The Indo-Malayan subregion further comprises the entire Malayan Archipelago, including the Philippines, Formosa, and the Riukiu Islands; further the Gulf of Thailand and the East-Asiatic coast as far north as Ningpo, 30° N., whereas the Hangchow Bay belongs to the South Japanese sub-region. SCHOTT (p. 257) regards the East-Asiatic marginal zone as a separate region owing to the rather considerable difference between the seasons, changing with the monsoons; I have been inclined to follow him in this longitudinal division of the Indo-Malayan subregion (see Table VII), but for reasons discussed below I have abandoned this division and prefer to regard the East-Asiatic marginal zone as belonging to the same sub-region as the Malayan Archipelago, thus agreeing with EKMAN.

I also agree with EKMAN in the limitation of the South Japanese subregion, comprising the Yellow Sea (with the west coast of Korea) and the oceanic coasts of southern Japan as far north as about 34° N., where a sub-tropical shelf fauna is rather sharply separated from a boreal fauna further north. In the composition of the pelagic fauna, however, the entire eastern coast of Japan is a mixed area, boreal species penetrating



**Table VII.** The Indo-West-Pacific Region.

	Subregions									North Pacific	Warm East Pacific		Mediterranean	Warm Atlantic		Boreal Atlantic	
	Indo-Malayan	North Australian	South Australian	Pacific Insular	Yellow Sea	South Japanese	North Japanese	Indian Ocean	Red Sea		Central America	South America					
<i>Euphysora abaxialis</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Euphysora valdiviae</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Pennaria grandis</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Pachycordyle globulosa</i> . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Pachycordyle lineata</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Zanclea dubia</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Podocoryne apicata</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Köllikerina octonemalis</i> . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Thamnostoma macrostomum</i> . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Protiara tropica</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Melicertoides centripetalis</i> . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Orchistomella applanata</i> . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Melicertissa malayica</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Staurodiscus vietnamensis</i> . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Phialidium chengshanense</i> . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Eucheilota diademata</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Eirene brevigona</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Zygocanna diploconus</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Nuarchus halius</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Olindias malayensis</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Lovenella cirrata</i> . . . . .	×	•	•	•	•	•	•	•	•	•	•	•	×	×	×	•	•
<i>Phialidium condensum</i> . . . . .	×	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Euphysora annulata</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Amphinema dinema</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	×	×	×	×	×
<i>Octotiar russelli</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Heterotiar minor</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eirene ceylonensis</i> . . . . .	×	×	×	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eirene palkensis</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eutima curva</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Aequorea conica</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Tiaropsidium roseum</i> . . . . .	×	•	×	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eutima orientalis</i> . . . . .	×	•	×	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Leuckartiara gardineri</i> . . . . .	×	×	•	•	•	•	•	×	×	•	•	•	•	•	•	•	•
<i>Phialidium simplex</i> . . . . .	×	×	•	•	•	•	•	×	•	•	•	×	•	×	•	•	•
<i>Merga violacea</i> . . . . .	×	×	•	×	•	•	•	×	•	•	×	×	×	×	•	•	•
<i>Laodicea indica</i> . . . . .	×	×	×	×	•	•	•	×	×	•	•	•	•	•	•	•	•
<i>Toxorchis polynema</i> . . . . .	×	•	×	×	•	•	•	×	•	•	•	•	•	•	×	•	•
<i>Phialidium hemisphaericum</i> . . .	×	×	×	×	•	•	•	×	•	•	•	•	•	•	×	•	×
<i>Phialidium malayense</i> . . . . .	×	×	×	×	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Phialidium rangiroae</i> . . . . .	×	×	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Octophialucium indicum</i> . . . .	×	×	×	×	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Phialucium mbenga</i> . . . . .	×	×	•	×	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eirene kambara</i> . . . . .	×	×	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Eirene menoni</i> . . . . .	×	×	×	×	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eutima levuka</i> . . . . .	×	×	•	×	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Zygocanna vagans</i> . . . . .	×	•	×	×	•	•	•	×	•	•	×	•	•	•	×	•	•
<i>Olindias singularis</i> . . . . .	×	×	×	×	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Zancleopsis tentaculata</i> . . . .	×	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Lizzia gracilis</i> . . . . .	×	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Leuckartiara annexa</i> . . . . .	×	•	×	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Neoturris bigelowi</i> . . . . .	×	•	•	×	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eucheilota ventricularis</i> . . . .	×	•	•	×	•	•	•	×	•	•	•	•	•	×	×	×	•



Table VII. (Continued).

	Subregions										Warm East Pacific			Warm Atlantic		Boreal Atlantic			
	Indo-Malayan	North Australian	South Australian	Pacific Insular	Yellow Sea	South Japanese	North Japanese	Indian Ocean	Red Sea		North Pacific	Central America		South America	Mediterranean	W.	E.	W.	E.
Cirrholovenia tetranema....	×	•	•	×	•	•	•	•	•	•	•	•	×	•	•	•	•		
Eirene elliceana .....	×	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•		
Euphysomma brevia .....	×	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•		
Aequorea globosa .....	×	•	•	×	•	•	•	×	•	•	•	×	•	•	•	•	•		
Bougainvillia platygaster ...	×	•	•	×	•	•	•	×	•	•	•	•	•	×	×	•	•		
Euphysora furcata .....	×	•	•	×	•	×	•	×	•	•	•	×	•	×	×	•	•		
Pandeopsis ikarii .....	×	•	•	×	•	×	×	•	•	•	•	•	•	•	•	•	•		
Euphysora bigelowi .....	×	×	•	×	×	×	•	×	•	•	•	•	•	•	•	•	•		
Zanclus costata .....	×	×	•	×	×	×	•	×	×	•	×	•	×	×	×	×	×		
Cytaeis tetrastyla .....	×	×	•	×	•	×	•	×	•	×	×	×	×	×	×	•	•		
Oceania armata .....	×	•	×	×	•	×	•	×	•	×	×	•	×	×	×	•	•		
Turritopsis nutricula .....	×	•	×	×	×	×	×	×	×	•	•	•	×	×	×	×	×		
Bougainvillia fulva .....	×	×	×	×	•	×	•	×	×	•	×	•	•	•	•	•	•		
Amphinema rugosum .....	×	•	×	×	×	×	•	×	•	•	•	•	×	×	•	×	×		
Halitiara formosa .....	×	•	•	×	•	×	•	×	•	×	•	•	•	×	•	•	•		
Leuckartiara octona .....	×	×	×	×	•	×	×	×	•	×	×	×	×	•	×	×	×		
Neoturris papua .....	×	•	×	×	•	×	•	×	•	•	•	•	•	•	•	•	•		
Pandea conica .....	×	•	×	×	•	×	•	×	•	×	•	•	×	×	×	•	•		
Cirrholovenia polynema ....	×	×	×	×	•	×	•	×	•	•	•	•	•	•	•	•	•		
Phialucium carolinae .....	×	×	•	×	×	•	•	×	•	•	•	•	•	×	•	•	•		
Eirene hexanemalis .....	×	×	•	×	×	×	•	×	•	•	•	•	•	•	•	•	•		
Aequorea australis .....	×	×	•	×	×	•	•	×	•	•	•	•	•	•	•	•	•		
Aequorea coerulescens ....	×	×	•	×	×	×	×	×	•	×	•	×	•	×	×	•	•		
Aequorea macrodactyla ....	×	×	×	×	•	×	•	×	•	•	×	×	•	×	×	•	×		
Proboscidaactyla ornata .....	×	×	•	×	•	×	•	×	•	•	×	×	•	×	×	•	×		
Ectopleura dumortieri ....	×	•	•	•	×	•	•	×	•	•	×	•	×	×	×	×	×		
Hybocodon forbesi .....	×	•	•	•	•	×	•	×	•	•	•	•	•	•	•	•	•		
Climacocodon ikarii .....	×	•	•	•	•	×	×	•	•	•	•	•	•	•	•	•	•		
Leuckartiara hoepflii .....	×	•	•	•	•	×	•	×	•	•	•	•	•	•	•	•	•		
Urashimea globosa .....	×	•	•	•	•	×	×	•	•	×	•	•	•	•	•	•	•		
Staurodiscus gotoi .....	×	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•		
Eucheilota paradoxa ....	×	•	•	•	•	×	×	•	•	•	•	•	•	×	•	•	•		
Eucheilota tropica .....	×	•	•	•	•	×	•	×	•	•	•	•	•	•	•	•	•		
Gonionemus vertens .....	×	•	•	•	×	×	×	•	•	×	•	•	×	•	•	•	×		
Proboscidaactyla abyssicola..	×	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•		
Proboscidaactyla flavicirrata .	×	•	•	•	×	•	×	•	•	×	•	•	•	•	•	•	•		
Proboscidaactyla stellata ....	×	•	•	•	×	×	×	•	•	•	•	•	•	•	•	•	×		
Phialella quadrata .....	×	•	×	•	•	•	×	•	•	•	•	×	•	•	×	•	×		
Helgicirrha malayensis .....	×	×	•	•	×	•	•	×	•	•	•	•	•	•	•	•	•		
Aequorea pensilis .....	×	×	•	•	•	×	•	×	×	•	•	•	•	•	•	•	•		
Ectopleura minerva .....	×	•	•	•	•	•	•	×	•	•	•	•	•	×	•	•	•		
Pennaria armata .....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Niobia dendrotentaculata...	×	•	•	•	•	•	•	×	•	•	•	•	×	×	•	×	•		
Staurodiscus tetrastaurus...	×	•	•	•	•	•	•	×	•	•	•	•	•	×	×	•	•		
Octophialucium solidum ....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Phialucium multitentacula- tum .....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Aequorea parva .....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Zygocanna buitendijki ....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Euphysora bigelowi .....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Köllikerina multicirrata ....	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•		
Heterotiara anonyma .....	×	•	•	•	•	•	•	×	•	×	×	•	•	×	×	•	•		

Table VII. (Continued).

	Subregions									North Pacific	Warm East Pacific		Mediterranean	Warm Atlantic		Boreal Atlantic	
	Indo-Malayan	North Australian	South Australian	Pacific Insular	Yellow Sea	South Japanese	North Japanese	Indian Ocean	Red Sea		Central America	South America					
Gotoea similis.....	×	•	•	•	•	•	•	×	•	•	•	•	•	×	•	•	
Leukartiara zacae.....	×	•	•	•	•	•	•	×	•	•	×	×	•	•	•	•	
Netocertoides brachiatus...	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	
Octophialucium aphrodite..	×	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	
Pelagohydra mirabilis.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Dicodonium dissonema.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Eutimalphes pretiosa.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Gonionemus hamatus.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Pennaria adamsia.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Pennaria rosea.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Laodicea fertilis.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Turritopsis lata.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Staurocladia haswelli.....	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	
Pteronema darwini.....	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
Meliceritissa orientalis.....	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
Eutima australis.....	•	×	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
Cirrhitiara superba.....	•	×	•	•	•	•	•	•	•	•	•	•	•	×	•	•	
Dipurena ophiogaster.....	•	×	•	×	•	×	•	×	•	•	×	×	×	•	•	×	
Amphinema turrida.....	•	×	•	•	•	•	•	•	•	•	×	×	•	×	•	•	
Bougainvillia ramosa.....	•	×	•	•	•	•	•	•	•	•	•	•	×	×	×	×	
Neoturris pelagica.....	•	•	×	•	•	×	•	•	•	×	•	•	•	•	•	•	
Zancleopsis gotoi.....	•	×	•	•	•	×	•	×	•	•	•	•	•	×	•	•	
Helgicirrho danduensis....	•	×	•	•	•	•	•	×	•	•	•	•	•	•	•	•	
Aequorea aequorea.....	•	×	•	×	•	•	•	×	•	•	•	•	×	×	×	×	
Tiaropsidium japonicum....	•	•	×	•	•	×	•	•	•	•	•	•	•	•	•	•	
Sarsia eximia.....	•	•	•	×	•	•	•	•	•	×	•	×	×	•	•	×	
Ectopleura pacifica.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Pennaria vitrea.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Cytaeis vulgaris.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Laodicea fijiana.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Laodicea marama.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Staurodiscus nigricans.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Phialidium ambiguum.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Phialidium uchidae.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Bougainvillia involuta.....	•	•	•	×	•	•	•	•	•	•	•	×	•	•	•	•	
Podocoryne ocellata.....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Dipleurosoma pacificum....	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	•	
Scolionema suvaense.....	•	•	•	×	•	×	•	×	•	•	•	•	×	×	•	•	
Sarsia resplendens.....	•	•	•	•	•	×	•	•	•	•	×	•	•	•	•	•	
Sarsia nipponica.....	•	•	•	•	×	×	•	•	•	•	•	•	•	•	•	•	
Sarsia polyocellata.....	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	
Eutima japonica.....	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	
Olindias formosa.....	•	•	•	•	•	×	×	•	•	•	•	•	•	•	•	•	
Bougainvillia bitentaculata..	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	
Podocoryne simplex.....	•	•	•	×	•	×	×	•	•	•	•	•	•	•	•	•	
Octorathkea onoi.....	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	
Nemopsis doffeini.....	•	•	•	•	×	×	×	•	•	•	•	•	•	•	•	•	
Amphinema physophorum..	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	
Spirocodon saltator.....	•	•	•	•	•	×	×	•	•	•	•	•	•	•	•	•	
Phialucium taeniogonia....	•	•	•	•	×	•	•	•	•	•	•	•	•	•	•	•	
Lovenella assimilis.....	•	•	•	•	×	•	•	×	•	•	•	•	•	•	•	×	
Podocoryne minima.....	•	•	•	•	×	•	•	•	•	•	•	•	×	×	•	×	

Table VII. (Continued).

	Subregions									North Pacific	Warm East Pacific		Mediterranean	Warm Atlantic		Boreal Atlantic	
	Indo-Malayan	North Australian	South Australian	Pacific Insular	Yellow Sea	South Japanese	North Japanese	Indian Ocean	Red Sea		Central America	South America		W.	E.	W.	E.
<i>Euphysa aurata</i> . . . . .	•	•	•	•	×	•	•	•	•	•	•	•	×	×	•	×	×
<i>Cladonema radiatum</i> . . . . .	•	•	•	•	•	×	×	•	•	×	•	•	×	×	•	•	×
<i>Sarsia conica</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Euphysa tetrabrachia</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Euphysora normani</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Hybocodon unicus</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Zanclaea orientalis</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Cytaeis herdmanni</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Rathkea rubence</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Köllikerina constricta</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Köllikerina elegans</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	×	•	•	•
<i>Köllikerina ornata</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Bythocellata cruciformis</i> . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Timoides agassizi</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Meliceritissa clavigera</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	×	•	•
<i>Meliceritissa platygastra</i> . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Tiaropsidium polyradiatum</i> . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Phialidium brunescens</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	×	•	•	•
<i>Phialidium gardineri</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eucheilota menoni</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Octocannoides ocellata</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Blackfordia virginica</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eirene tenuis</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Eutima hartlaubi</i> . . . . .	•	•	•	•	•	•	•	×	×	•	•	•	•	•	•	•	•
<i>Eirene viridula</i> . . . . .	•	•	•	•	•	•	•	×	×	•	•	•	×	•	×	•	•
<i>Eutonina scintillans</i> . . . . .	•	•	•	•	•	•	•	×	×	•	×	•	×	•	•	•	•
<i>Euphysilla pyramidata</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	×	•	•
<i>Calycopsis papillata</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	×	×	•	•
<i>Köllikerina maasi</i> . . . . .	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•	•
<i>Dicodonium cornutum</i> . . . . .	•	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•
<i>Eutima modesta</i> . . . . .	•	•	•	•	•	•	•	•	×	•	•	•	•	•	•	•	•
Total number of species . . . .	107	46	33	59	19	46	16	100	10	14	16	15	24	36	28	11	19
		68			56						23			45		21	
														48			

southwards, and sub-tropical species drifting northwards from warmer regions. These conditions are discussed below.

Another mixed area is the Australian waters. As mentioned above (p.150), nothing is known about the occurrence of Hydromedusae off the western part of Australia and, with the exception of endemic species, all the species hitherto recorded from south-eastern Australia and around New Zealand occur also in the tropical parts of the Indo-West-Pacific Region; all of them are therefore included in Table VII as well as in Table VI. As far as the demersal shelf faunas are concerned, the limits at 29° S. on the west coast and about 32–34° S. on the east coast of Australia as pointed out by EKMAN, may be valid, but not for the pelagic Hydro-medusae.

The last subregion of the IndoWest-Pacific Region is the Pacific Insular subregion, the extension of which is seen in the map (fig. 359), a very extensive area, in its western part comprising the greater part of

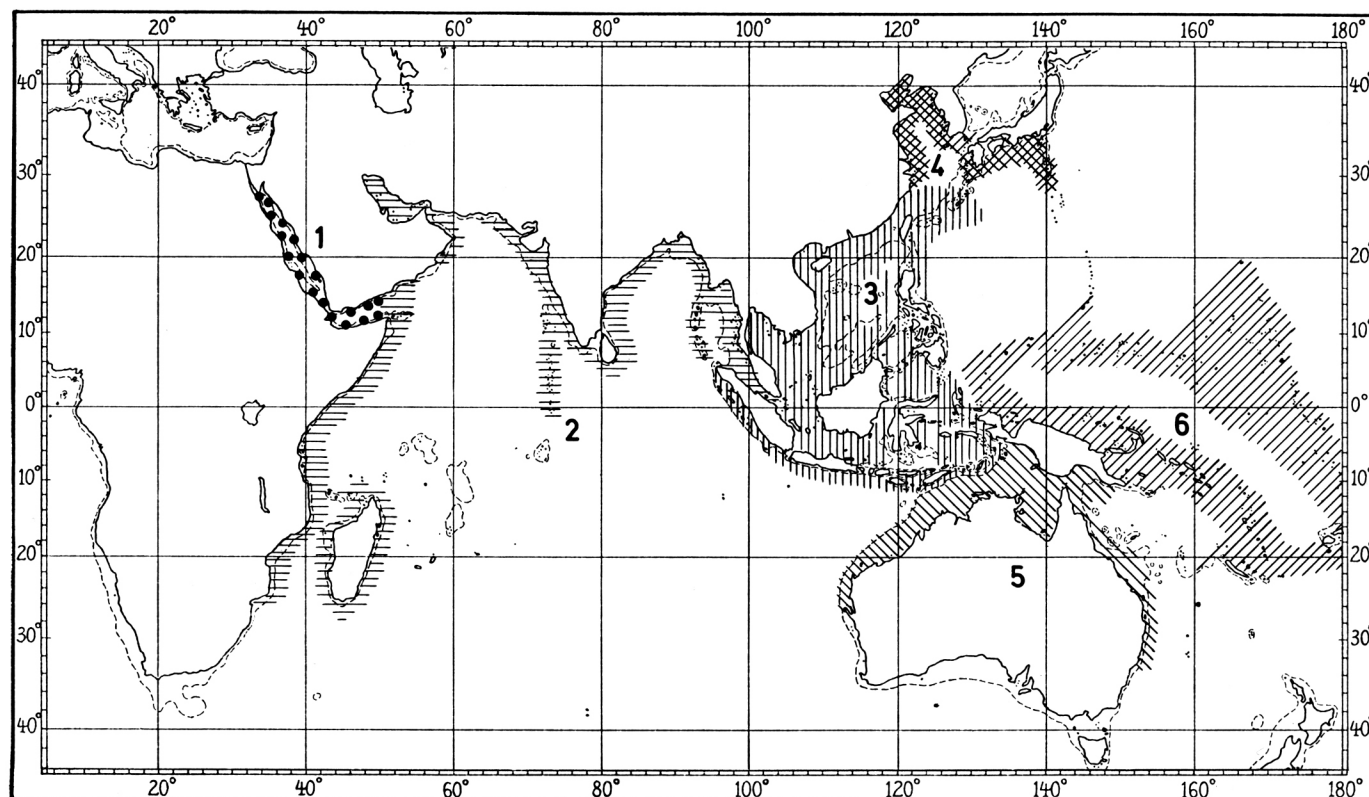


Fig. 359. The subdivision of the Indo-West-Pacific region.

 Red Sea subregion.
  Indian Ocean subregion.
  Indo-Malayan subregion.
  South Japanese subregion.
  North Australian subregion.
  Pacific Insular subregion.

the north coast of New Guinea and extending northwards towards southern Japan, the easternmost islands at no great distance from South America, but separated from this continent by a gap which, as briefly mentioned above (p.144) is insurmountable for the greater number of these medusae.

A further analysis of the occurrence of Hydromedusae in the subregions of the Indo-West-Pacific Region is given below. Although they are not equally well investigated, a comparison of the faunas in the different areas may lead to interesting considerations. The total number of species of neritic Hydromedusae in the entire region amounts to 187, a much greater number than found in any other zoogeographical region, the Atlantic regions included.

#### *The Indo-Malayan Subregion.*

This is the central and by far the richest of the subregions. As many as 108 species of neritic Hydromedusae are recorded, which is 57% of the species found in the entire Indo-West-Pacific Region and, as seen from the tables (Table VII and VIII), in all the other subregions the majority of their species (usually a vast majority) also occur in the Indo-Malayan subregion.

This is a tropical region. The mighty water masses of the North Equatorial Current wash the eastern coasts of the islands, proceeding partly northwards towards Japan, participating in the formation of the Kuroshio Current, partly southwards and eastwards as the narrow Equatorial Counter Current. Between the islands local currents are circulating, usually rather slowly, more or less influenced by the tides.

Between the islands the temperature of the surface water is always higher than 25° C (up to 28° or more) throughout the year, but in the marginal zone along the Asiatic coast two different seasons may be distinguished, changing in relation to the monsoons. The currents along the continental coast move southwards in February-March, northwards in August-September, and during the northern winter the temperature of the water decreases considerably in the coastal areas. The position of the 25° isotherm at the coast is as follows: in February

near Cape Cambodia in southern Vietnam, in May near Hongkong, in August in the Korea Bay, in November again near Hongkong; but at all seasons the temperatures are rather uniform, or slightly increasing, southwards in the open areas south of the actual position of the  $25^{\circ}$  isotherm. As mentioned above, I have been inclined to follow SCHOTT in regarding the East-Asiatic marginal zone as a separate subregion distinct from the Malayan Archipelago, but the composition of the medusan fauna shows that, in spite of the hydrographical differences, it cannot be regarded as a subregion from a zoogeographical point of view.

No less than 20 species of neritic Hydromedusae are "endemic" in this subregion, in so far as they have not been recorded from anywhere else; four of these species were found in the marginal zone, two of them only there (see Table VII). *Lovenella cirrata* (HAECKEL) was taken in the Java Sea by the "Dana" (KRAMP 1965 p. 66); it is fairly widely distributed in the Mediterranean and in the warm parts of the Atlantic, but has not been taken in other parts of the Indo-Pacific waters. The number of species taken within the archipelago proper amounts to 93, while 59 were found in the marginal zone, 45 common to both, and apart from the twenty "endemic" species 50 % are common to the two parts of the subregion.

A comparison between the numbers of species occurring in the six subregions and those common with other subregions is given in Table VIII. It is very natural that as many as 61 % of the Indo-Malayan species also occur in the Indian Ocean subregion; the numerical distribution of the species in the other subregions (apart from the Red Sea) is not very variable, but it is remarkable that 31 % of the Indo-Malayan species occur somewhere in the Atlantic, but only 15 % in the warm parts of the eastern Pacific. Among the 80 Indo-West-Pacific species which have not been found in the Indo-Malayan subregion, 52 are endemic in other subregions, as follows:

Australian and New Zealand .....	12
Pacific Insular .....	10
Japanese .....	10
Indian Ocean .....	18
Red Sea .....	2

Accordingly, leaving the endemic species out of consideration, only 28 Indo-West-Pacific species have not been found in the Indo-Malayan subregion, while 68 are common to this and one or more of the other subregions. An attempt is made in the following to find the range and routes of dispersal, also what species might have their origin in other regions, whence they invaded the Indo-Malayan waters.

The following species are so rare that it is futile to discuss their origin and further distribution (here listed in the same order as in Table VII): *Phialucium condensum*, *Euphysora annulata*, *Eirene kambara*, *Zancleopsis tentaculata*, *Eirene elliceana*, *Euphysomma brevia*, *Staurodiscus gotoi*, *Pennaria armata*, *Octophialucium solidum*, and *Phialucium multitentaculatum*. Their occurrence outside the Indo-Malayan subregion appears from the table.

The occurrence of some species is mainly concentrated within the Indo-Malayan subregion with (more or less scattered) offshots into the waters of Australia and the Insular subregion, a few towards Japan; but the majority are widely distributed in eastern as well as in western direction. Species with a wide distribution in Atlantic and/or Mediterranean waters (about twenty) are mentioned later on.

Among the 47 Indo-Malayan species, which occur in Australian waters, 25 have only been found in the northern parts of Australia, mainly in the well explored area of the Great Barrier Reef, but 22 have proceeded further south, 15 as far as to New Zealand. By far the greater number of the Indo-Malayan species in these waters are extensively distributed in the Insular Region and the Indian Ocean, their occurrence in the temperate parts of the Australian waters presumably being a secondary phenomenon. It is difficult to decide, whether any Indo-Malayan medusae should be regarded as immigrants from southern regions; if so, they might derive from western Australia whence, however, not a single species is known.

As many as 43 (40 %) of the species known from the Indo-Malayan subregion are recorded from the Pacific Insular subregion, twelve also from the warm parts of the East Pacific; whether their distribution is extended to the eastern Pacific or not, all the species occur only in a few scattered localities within the insular region; all of them are much more common in the Indo-Malayan waters. On the other hand, there are 16

“insular” species which are unknown in Indo-Malaya, ten of which are “endemic” in the Insular subregion; further remarks on the fauna of this subregion are given below.

The comparison between the Indo-Malayan and the Japanese faunas is also discussed below; 35 species are common to these two areas, and in this case there might be an exchange of species in both directions. *Leuckartiara gardineri* has a rather peculiar occurrence, viz in a locality in the northern Pacific, somewhat north-west of Hawaii; its further distribution comprises East Africa, north-eastern Australia, the South China Sea and Formosa.

The only Indo-Malayan species which have been found in sub-antarctic waters (apart from southern New Zealand, see above, p.152) are as follows: *Aequorea coerulescens*, widely distributed in the warm and temperate parts of the Indian and Pacific oceans with an isolated occurrence at the Falkland Islands in the southern Atlantic; *Aequorea macrodactyla*, widely distributed in Atlantic as well as Indo-Pacific waters and also found in a few localities off Patagonia near the southern end of South America; *Phialidium simplex*, which has been found in a locality rather far south of New Zealand and at the Falkland Islands, its further distribution comprising the tropical parts of the Indian Ocean, the Indo-Malayan waters, North-East Australia, and the coasts of Chile.

The tropical coasts of the Indian Ocean (*i.e.* the subregion as defined p.153) have a rich fauna of neritic Hydromedusae; at present 101 species are known, 18 of which are “endemic” (unknown elsewhere). The subregion has 67 species in common with the Indo-Malayan subregion (67 % of the Indo-Malayan species), a considerable number, it is true (see Table VIII), but, besides 20 “endemic” species, as many as 20 Indo-Malayan species have not been found in the Indian Ocean subregion; it is worth noticing that among these a considerable number occurs in Australian or Japanese waters. The five Indo-Malayan species which have been found in the Red Sea are widely distributed in the Indian Ocean.

#### *The Australian Subregion.*

According to EKMAN, the northern parts of the Australian Continent and the greater part of the south coast of New Guinea constitute a subregion of the Indo-West-Pacific Region; as far as the demersal shelf fauna is concerned, the southern limits of the subregion are rather sharply defined at about 32–34° S. on the east and about 29° S. on the west coast of Australia. As briefly mentioned above (p. 42), such limits cannot however be pointed out for the distribution of the neritic Hydromedusae. Apart from 12 “endemic” species the fauna of these animals recorded up to now from the southern as well as the northern parts of Australia and of New Zealand consists only of species which also occur in tropical parts of the Indo-West-Pacific Region, mainly in the subregions of the Indo-Malayan and Indian Ocean. Not a single antarctic or subantarctic medusa has been found near the Australian or New Zealand coasts, though some species may probably occur off the western coasts, carried there by the West-Wind-Drift as along the western coasts of South America and South Africa, but no information exists of Hydromedusae off the western coasts of Australia and New Zealand. The following discussion, therefore, only comprises the eastern parts of the Australian Continent and the coasts of New Zealand.

The total number of species of neritic Hydromedusae known from this subregion amounts to 68, 12 of which are unknown elsewhere (“endemic”), 46 being recorded from northern Australia, 33 from southern Australia and New Zealand. The number of species, thus, is diminishing in a southward direction, though not to any considerable degree.

The temperature of the water, naturally, is likewise decreasing towards region at higher latitudes, especially during the southern winter; in August the average temperature is 25° C in Torres Strait, 13° at Cape Howe in the south-eastern corner of the continent, but in February conditions are almost equal, 28–25° C right down to Sydney, 20° at Cape Howe. The currents are mainly moving southwards, partly from the Banda Sea, partly as more or less irregular deviations from the South Equatorial Current; in the Tasman Sea eddies carry water masses from eastern Australia to New Zealand. The Arafura Sea and Gulf of Carpentaria west of Cape York are shallow-water areas, the Torres Strait itself being particularly shallow, with many small islands, so that only a thin surface layer of water from the eastwards directed current may pass the strait



and penetrate into the Coral Sea, while southern deviations of the South Equatorial Current and currents from the Insular areas have free access through the Coral Sea to eastern Australia. An exchange of species between the Indo-Malayan subregion and the eastern Australian waters is natural, but the resemblance between their faunas may also be due to mutual communication with more easterly regions.

It should be borne in mind that the different parts of the coasts are not equally well investigated. From the periods before 1928 there are scattered records from the surroundings of Sydney (besides a considerable number of unrecognizable species established by VON LENDENFELD, about 1884), but our knowledge of the Australian marine fauna was greatly increased by the extensive investigations of the Great Barrier Reef Expedition in 1928–29, sponsored by the British Museum (Natural History); the present author had the great pleasure to work up the Hydromedusae from this expedition (KRAMP 1953), a collection containing 43 species (34 neritic and 9 oceanic), among which only eight species were previously known from Australian waters; three new species were described. Considerable additions to the fauna outside the southernmore coasts, however, are due to the “Dana” and the “Galathea” Expeditions, and in recent time collecting has been organized by the South Australian Museum, Adelaide. (KRAMP 1961 and 1965).

The Australian fauna of neritic Hydromedusae is decidedly an Indo-West-Pacific fauna; it contains 31 % of the species known in the entire region, and apart from endemic species all of them have been found in some of the other subregions. An enumeration shows that 29 of the Australian species occur in three of the other subregions, viz the Indo-Malayan, the Pacific Insular and the Indian Ocean (15 of these also in eastern Atlantic), and another 14 species occur in the Indo-Malayan and the Indian Ocean but not in the Insular subregion; very few species occur in only one of the other subregions, or in two of them (apart from the Indo-Malayan + Indian Ocean). Apparently, there is a predominance of species with a western distribution in comparison with Australian waters. For details, see the table at the end of the discussion of the whole Indo-West-Pacific Region (p. 168).

#### *The Subregion of the Pacific Insular Area.*

EKMAN did not give this subregion a proper name, but under the head-line “The islands of the Central Pacific excluding Hawaii” (1954 p. 18) he has given a clear characterization of it. This area partly coincides with SCHOTT’s “Region der süd-pazifische Inseln” (1935 p. 302) which, however, is a geographical region, extending westwards to the very eastern coasts of Australia and the Philippines, thus comprising the deep basins of the Coral Sea and the Philippine Basin, while the Indo-West-Pacific Region and its subregions as here discussed deal with the shelf regions and their faunas.

The subregion of the Pacific Insular area (abbreviated the Insular subregion) is characterized as an area consisting of numerous small islands separated by distances, which do not prevent a dispersal of animals belonging to the shelf or slope regions. Neritic medusae are particularly apt to disperse from one group of islands to another, dependent on the duration of their pelagic life.

The Insular subregion is situated entirely within the tropical belt. Its western limit is determined by the eastern limit of the Coral Sea, the north coast of New Guinea, and the eastern margin of the Philippine Basin; it comprises the Melanesian, the Micronesian, and the Polynesian islands, all the groups of islands eastwards to the Tuamotu or Low Archipelago. Some species may have been able to cross the distance to the isolated Easter Islands; this applies to some of the larger medusae. The Marianne and Marshall Islands and the Christmas and Palmyra Islands belong to the Insular subregion, but I agree with EKMAN that the Sandwich Islands with Hawaii constitute a separate region (see above, p. 142).

The hydrography of this extensive area is first and foremost characterized by the Equatorial Currents, carrying enormous quantities of water westwards across the ocean, though usually with no great velocity except under local conditions. The Equatorial Counter Current, moving eastwards between the North and South Equatorial Currents slightly north of the Equator, is narrow, but sometimes running at a considerable velocity. From the mighty South Equatorial Current deviations are directed towards south and south-west. Such deviations carry equatorial water masses to the eastern coasts of Australia and New Zealand (see above, p. 161). Water masses from the North Equatorial Current are directed towards the Philippine Basin, whence

they turn southwards and eastwards along the north coast of New Guinea to be mixed with the terminal branches of the South Equatorial Current, which results in complicated current conditions and great seasonal variations in the areas north and east of New Guinea with the island groups of New Britain and the Solomon Islands.

Up to recent time the different parts of the extensive Insular subregion were not equally well investigated; older collections were almost entirely concentrated around the Fiji Islands and Tahiti, but our knowledge was greatly augmented by the "Dana" and the "Galathea" Expeditions. The "Dana" came directly from Panama and cruised among the islands from the Marchesas to New Caledonia. The "Galathea" carried out investigations among the Solomon Islands and made several pelagic hauls during her passage from New Zealand along the Kermadec, Tonga and Samoa islands and further north towards Hawaii. Our present knowledge to some degree allows a comparison of the faunas in the different parts of the area, especially between the eastern and western parts, which is of importance for a zoogeographical discussion of the relation between the Insular subregion and other parts of the Indo-Pacific waters.

The pelagic fauna of this subregion is very rich, and future investigations will probably add to the number of species in a considerable degree, but some conclusions may be drawn from our present knowledge. The number of species of neritic Hydromedusae known up to now amounts to 59, which is 32 % of the number known from the entire Indo-West-Pacific Region. The numbers of species common with the other subregions are seen in Table VIII and, as might be expected, particularly many of the species also occur in the Indo-Malayan subregion (43, which is 72 %). Ten species are "endemic", two species (*Sarsia eximia* and *Bougainvillia involuta*) have not been found in any of the other subregions (but in the East Pacific), and it is characteristic that among the remaining 47 species no less than 60 % (28 species) occur in all the three other large subregions, the Indo-Malayan, the Australian and the Indian Ocean, the others in one or two of the subregions (for details, see Table IX, p.171). It is remarkable that only 14 of the species, in spite of the wide eastward extension of the Insular subregion, have been found in the warm East-Pacific regions, while 23 occur in the Atlantic (13 in the Mediterranean).

According to EKMAN (1953, p. 18, quoting other authors) certain groups of animals are impoverished eastwards, though the poverty of the eastern districts is less marked in some animal groups; it is admitted that the fauna is deficiently known, especially in the eastern island groups. The rich collections procured by the "Dana" and "Galathea" Expeditions however tend to show the richness of the fauna in different parts of the area. On the other hand the neritic Hydromedusae seem to indicate an eastward impoverishment, though nothing definite can be said as yet.

The number of species recorded up to now from different geographical longitudes within the Insular subregion may be summarized as follows:

130–140° E.	14	170° E.–180°	26	160–150° W.	7
140–150° E.	1	180°–170° W.	11	150–140° W.	6
150–160° E.	9	170–160° W.	7	140–130° W.	4
160–170° E.	8			130–120° W.	1

The species seem to decrease in number from the western towards the eastern groups of islands. The area on both sides of the 180° meridian evidently has a very rich fauna but the great number of species around the Fiji Islands may partly be due to the thorough investigations carried out in this area. On the other hand, the areas around Tahiti, 150° W, where comparatively few species have been found, were also rather well investigated. The poverty in the far eastern districts may partly be due to deficient knowledge. The apparent decrease in number of species east of the 180° meridian proceeds gradually, so that no demarcation line between a richer and a poorer fauna can be pointed out.

I also tried to count the number of species collected by the "Dana" at each of the stations during the passage from the Marchesas Islands to New Caledonia. Almost all the hauls were made with the 150 cm stramin net (S 150), also in the upper water layers; the stations were located in the channels between the islands above deep water, and every haul contained numerous oceanic species of medusae, while the neritic Hydromedusae

were rather scarce. At the first stations (St. 3564–3569) in the Marchesas only one species was taken (two specimens of *Leuckartiara octona*); at the stations between Tahiti (St. 3576) and St. 3590 near the Fiji Islands the number of species at each station varied from one or two to five, without any definite order in either direction; at each of two stations near the Fiji Islands (St. 3593 and 3601) 7 species were collected, and near the coast of New Caledonia (St. 3611), above deep water, no less than 10 species of neritic Hydromedusae were secured. The “Dana” collections, thus, indicate a richer fauna of these animals in the western than in the eastern districts, but the numbers are too scarce to serve definite proof.

Among the 59 species recorded from the Insular subregion only 14 have been found in the warm East Pacific regions, while 23 occur in Atlantic waters and 13 in the Mediterranean (discussed below). Most of the 14 species found in the East Pacific regions have an extensive distribution (see Table VII); *Bougainvillia involuta*, however, is a rare species, known only from the Palao Island and Chile; *Sarsia eximia* is mainly a North Atlantic and North Pacific species with a few scattered records from the Tonga and Samoa Islands and from Chile. *Merga violacea* occurs in the Mediterranean and is distributed from India to the Fiji Islands. All the others are widely distributed from the coasts of Africa more or less far eastwards into the Insular subregion, three of them (*Zanclea costata*, *Aequorea globosa* and *Proboscoidactyla ornata*) only to the Solomon Islands, 150–160° E, the remaining seven species at least to Samoa (about 170° W), some of them to Tahiti or still farther east, and only one of these (*Bougainvillia fulva*) does not occur in the Atlantic. *Euphysora furcata*, *Cytaeis tetrastyla* and *Oceania armata* are partly oceanic; *Aequorea coerulescens*, *Aequorea macrodactyla* and *Zygocanna vagans* are large medusae, presumably with a pelagic life of fairly long duration, and may easily have crossed the gap between the easternmost Polynesian islands and the American coast. Probably all these fourteen species do occur rather far east in the Insular subregion, though some of them have not yet been found there. Considering the large number of species occurring within the subregion, it is however remarkable that so few of them have extended their distribution to the East Pacific regions, and, as stated above, almost all these are extensively distributed in the western parts of the Indo-West-Pacific Region; undoubtedly, therefore, none of them has an American origin, but are derived from Indo-West-Pacific waters.

No more than 23 species are common to the Insular and the Japanese subregions; they are discussed below.

#### *The South Japanese Subregion.*

The limitation of this subregion of the Indo-West-Pacific Region was mentioned above (p. 153), and a characterization of the complete Japanese fauna of neritic Hydromedusae was given under the Pacific Boreal Region (p. 139), where it was pointed out that it is a mixed fauna, some of its species being derived from northern, partly even arctic seas, others which have their principal occurrence in tropical or subtropical waters. As far as the demersal shelf fauna is concerned, there is a rather sharp limit between a boreal and a subtropical fauna at about 34° N. on the oceanic coasts of Japan, but pelagic animals like the medusae may surpass this limit in either direction under certain conditions.

The area between the Japanese islands and the continental coast (the Sea of Japan) is considered part of the Boreal Region; its medusan fauna is deficiently known and is not discussed here. The oceanic side is characterized by the warm Kuroshio Current, which follows the Riukiu islands and closely along the oceanic coast of Japan as far as the large bend of the coast east of Yokohama, 35° N., where it turns east under the influence of the cold Oyashio (or Kurile) Current and proceeds across the ocean as the North Pacific Current. Where the two currents meet, there is an intensive mixing of the waters, and complicated eddies are formed.

The Yellow Sea, comprising the Chinese coast north of Shanghai and the west coast of Korea, is enclosed in the South Japanese subregion; it is a shallow-water area with great annual variations of temperature, and the salinity of the surface water is greatly reduced by the outflow of great rivers. Some medusae are recorded from the surroundings of Chefoo in the inner part of the Yellow Sea in a paper by CHOW & HUANG, 1958.

In all the Japanese areas (including the Yellow Sea) 74 species of neritic Hydromedusae have been found; fourteen of these species are recorded only from the northernmost parts of Japan, where three of them are “endemic”, the others belong to arctic waters; four other species (*Sarsia tubulosa*, *Rathkea octopunctata*,

*Bougainvillia superciliaris* and *Leuckartiara nobilis*) with a predominantly northern distribution likewise occur in northern Japan, but have extended their distribution to the southern parts of the Japanese islands. These 18 species are listed in Table II, but not in Table VII. The remaining 56 species are listed in Table VII as belonging to the South Japanese subregion of the Indo-West-Pacific Region, though 14 of these penetrate more or less north of the demarcation line at 34° N. Ten species are "endemic", three of them occurring in northern as well as in southern Japan, 6 only in southern Japan, and one (*Phialucium taeniogonia*) in the Yellow Sea.

Some species need special remarks. — *Phialucium carolinae*, *Aequorea australis* and *Ectopleura dumortieri* are widely distributed in tropical waters and have been found at Chefoo in the Yellow Sea, but not in Japan. *Climacocodon ikarii* seems to be a rare species, found in northern as well as southern Japan and on the south coast of Vietnam, presumably therefore a tropical species. The zoogeographical character of *Proboscoidactyla flavicirrata* is less certain; it also occurs in Vietnam and has been recorded from the Yellow Sea and the middle and northern parts of Japan, but also from Kamchatka and California. *Urashimea globosa* entirely belongs to the surroundings of Japan (on both sides of the islands) but is also recorded from Formosa and the southern part of Saghalin. *Neoturris pelagica* seems to have a scattered and partly oceanic distribution in the Pacific Ocean; it occurs in south-eastern Australia and off the coasts of California and Vancouver Island, and numerous specimens were collected by the "Dana" in a locality somewhat east of the southern part of Japan (KRAMP 1965 p. 34). A very peculiar record is the find of the common North-Atlantic medusa *Euphysa aurata* at Chefoo in the Yellow Sea, the only other record from Indo-Pacific waters being off the coast of Chile in South America.

The total number of 56 species of neritic Hydromedusae recorded up to now from the South Japanese subregion represents 30 % of the number recorded from the entire Indo-West-Pacific Region,<sup>1</sup> very nearly the same percentage as in the Australian and the Insular subregions. As seen from Table VIII, a considerable number of the South-Japanese species occurs in tropical Indo-West-Pacific subregions, 40 % in the Pacific Insular, 43 % in the Australian, 54 % in the Indian Ocean and no less than 62 % in the Indo-Malayan subregion, 29 % in all of these four subregions. This at once shows that the South Japanese fauna of medusae predominantly consists of tropical and subtropical species. Their demersal hydroids presumably occur in the coastal areas south of the demarcation line at 34° N, but several of the medusae are carried further north by the Kuroshio Current; it is remarkable that most of these were collected as far north as on the coasts of Hokkaido, about 42°–44° N. As mentioned above (p.163) the Kuroshio Current generally turns east at about 35° N, where it meets the Oyashio Current; the occurrence of so many southern species of medusae considerably farther north shows that the "eddies", mentioned by the hydrographers, may be of great extension, at least occasionally.

The occurrence of a number of South Japanese species in the eastern Pacific is almost exclusively due to a connection through tropical regions towards southern parts of the American coasts. A northern connection may have been established for *Proboscoidactyla flavicirrata* (see above); *Gonionemus vertens* has an almost continuous distribution from Japan via the Kurile and Aleutian islands to Vancouver, but as frequently pointed out, the extended distribution of this species presumably takes place in the polyp stage when it is attached to algae growing on ships-bottoms. *Oceania armata*, *Pandea conica* and *Neoturris pelagica* are partly oceanic, *Sarsia resplendens* is only known from two localities, Japan and Mexico. Arctic species have penetrated southwards to northern Japan as well as to the Pacific coast of North America, but a direct exchange of neritic species between southern Japan and the American coasts seems most improbable.

A few remarks should be made on the 19 species which have been recorded from Chefoo in the inner part of the Yellow Sea by CHOW & HUANG, 1958. As mentioned above (p.163) the Yellow Sea is a shallow-water area with reduced salinity of the surface water and with great variations of temperature. The occurrence of two of the species (*Podocoryne minima* and *Euphysa aurata*) may be regarded as doubtful, *Phialucium taeniogonia* was described as a new species; almost all the other species recorded from Chefoo have their principal occurrence in tropical seas and also occur in the Kuroshio Current, which flows across the wide outer part

<sup>1</sup> The oceanic coasts of Japan are particularly well investigated as far as medusae are concerned.



of the Yellow Sea, while great masses of water from Hwanho and other large rivers generally result in a preponderance of out-flowing water from the Gulf of Pechili into the Yellow Sea, and Chefoo is deposited in the strait between these two areas. The occurrence near Chefoo of the many medusae under consideration is regarded as evidence of the powerful eddies in the Yellow Sea created by the passing water masses of the Kuroshio.

#### *The Indian Ocean Subregion.*

From a geographical point of view the southern limit of the Indian Ocean may be placed at the Subtropical Convergence, about  $40^{\circ}$  S, but a fauna of shelf and neritic animals is produced only along the continental coasts and around the few scattered groups of small islands, all of which are situated north of about  $10^{\circ}$  S. As a subregion of the Indo-West-Pacific Region, as here defined, the Indian Ocean subregion thus comprises the east coast of Africa north of Dalagoa Bay (about  $26^{\circ}$  S), the Iranian Gulf, the western coasts of India, the Laccadive, Maldiva and Chagos Islands, the Bay of Bengal with the Andamans and the Nicobars, the Strait of Malacca as far as Singapore, while the shelf fauna along the coasts of Sumatra and the Sunda Islands facing the Indian Ocean were stated by EKMAN to belong to the Indo-Malayan subregion. In the present paper I have accepted this limitation of the subregion (see above, p. 153). From the waters west of Australia nothing is known about medusae; along the southern part of the African coast the fauna is sub-tropical, and this range of coastal water is united with the Atlantic coast of south-western Africa as one zoogeographical region, the South-African Region (see KRAMP 1959 a p. 205). The entire coastal areas of the Indian Ocean subregion, as here defined, thus have a tropical character.

The equatorial current systems of the Indian Ocean are more or less dependent on the monsoon winds and produce considerable annual variations; they are of particular interest for the distribution of the oceanic animals. In the two large gulfs, the Bay of Bengal and the Arabian Sea, the currents mainly follow the coasts, in different directions at different seasons. In the Bay of Bengal the currents are mainly derived from the westward directed North Equatorial Current in February-March, from the eastward directed Monsoon Current in August-September.

Along the African coast conditions are more complicated. North of the Mozambique Channel between Africa and Madagascar the Somali Current follows the coast, moving southwards in February-March derived from the North Equatorial Current, northwards in August-September derived from the South Equatorial Current, turning east off the Somali Coast to be united with the Monsoon Current, which has now replaced the North Equatorial Current at these latitudes. In the Mozambique Channel the current is generally southward directed, continuing further south as the Agulhas Current, finally turning around the south point of Africa. Upwelling water from deeper layers occurs in several places along the African coast. Outflow of water from the Red Sea into the Indian Ocean takes place in a similar way as that of Mediterranean water into the Atlantic, but intermittent and to a much smaller extent.

Owing to the complicated and seasonally varying conditions off the east coast of Africa I have been inclined to regard this area as a proper subregion. Among the 50 species of neritic Hydromedusae known from East Africa 12 have not been found in other parts of the Indian Ocean, and among 88 species in the other parts of the ocean 50 have not been taken off the East African coast. On the other hand, there are only 6 of the East African species, which have not been found in the Indo-Malayan subregion. Accordingly, there is no obvious contrast between the East African medusan fauna and that in other parts of the Indo-West-Pacific Region further east. The only East African species unknown further east are the following: *Euphysilla pyramidata* (found in the Mozambique Channel and in the Gulf of Guinea), *Calycopsis papillata* (north and south of Madagascar and in eastern and western parts of the tropical Atlantic), and the antarctic species *Köl likerina maasi* (found in the Mozambique Channel).

The "Dana" and "Galathea" Expeditions contributed in a considerable degree to our knowledge of the medusan fauna in the Indian Ocean; the predominant number of previous records was from the coasts of India and Ceylon and from the Maldiva Islands (BIGELOW 1904) and the Chagos Islands (BROWNE 1916). The "Dana" explored the waters west of the Malayan islands, proceeding across the Bay of Bengal to the surroundings of Madagascar; the "Galathea", on her cruise from Mombasa in East Africa, called at the

Seyshelles, the Maldives, Colombo, Tranquebar, Calcutta, and the Nicobars to Singapore. The present author was onboard the vessel during that part of the expedition and had the pleasure to collect numerous medusae and study them in fresh condition.

The number of species recorded up to now from the Indian Ocean subregion amounts to exactly 100, which is 53 % of the species known from the entire Indo-West-Pacific Region; 18 species are "endemic" (known from nowhere else); the actual as well as the percentage number, accordingly, is very similar to that of the Indo-Malayan subregion. The agreement between the two is further elucidated in Table VIII in the statement that 61 % of the Indo-Malayan species occur in the Indian Ocean, and 67 % of the species in the Indian Ocean occur in the Indo-Malayan subregion, percentages which exceed any of the other subregions. According to EKMAN (1953 p. 27) the enumeration of fishes, crabs, and crinoids has shown that in the Indian Ocean the number of species constantly decreases towards the west. Does an enumeration of the species of neritic Hydromedusae show a corresponding westward decrease?

The Indian Ocean may be divided into three sections as follows: I, the Bay of Bengal with the Andaman and Nicobar Islands, including Ceylon; II, the waters west of the south point of India with the Laccadive, Maldivé and Chagos Islands, including the Arabian Sea east of about 60° E; III, the Seyshelles and Amirante Islands, Madagascar, and the east coast of Africa. If we regard the species occurring in the Indo-Malayan subregion (excluding the "endemic" species) and count how many have been found in each of the three sections, we find that in section I the number amounts to 54, in section II to 37, in section III to 45. A westward decrease in number of Indo-Malayan species, accordingly, is only slightly indicated; the smaller number in section II in relation to section III is presumably due to lack of knowledge.

A comparison with the other subregions show (see Table VIII) that 46 % of the species known from the Indian Ocean have been found in the Australian, 37 % in the Pacific Insular, and 30 % in the Japanese subregion, percentages very similar to those of the Indo-Malayan subregion. We may state that the constituents of the fauna of neritic Hydromedusae in the Indian Ocean are very nearly the same as in the Indo-Malayan subregion, which means that it cannot be decided, whence the evolution of this fauna started; but its overwhelming richness in species and impoverishment to all sides show that the main contingent of the Indo-West-Pacific fauna of these animals was recruited from the tropical parts of the waters south of Asia, though perhaps not within a restricted area such as the Malayan region, which has sometimes been "regarded as the main development centre or even as the sole centre of origin and development for many animal groups", a supposition which by EKMAN (1953 p. 78), with full right was said to be exaggerated.

A considerable number of the species in the Indian Ocean (39 %) also occurs in Atlantic waters, the majority being species with an extensive distribution in both oceans. There are, however, also some species, common in the Indian Ocean, which have been recorded from only one or a few Atlantic localities; this question is discussed below in the general comparison between the Indo-Pacific and Atlantic faunas.

As briefly mentioned above (p. 165), three species found near the coasts of Madagascar have never been found further east in Indo-Pacific waters; they should evidently be regarded as immigrants, *Euphysilla pyramidata* and *Calyropsis papillata* from the tropical west coast of Africa, where both of them occur; *Köllikerina maasi* is an antarctic species; it is well-known that the West-Wind-Drift, circulating eastwards in the antarctic and subantarctic belts, is deflected northwards along the western coasts of the continents; presumably a deflection of the West-Wind-Drift has carried *Köllikerina maasi* to the south-west coast of Africa (though it has not yet been found there), and together with the two tropical species it has penetrated along the South-African coast northwards to Madagascar. The Agulhas Current generally moves south from the Mozambique Channel along the south-eastern coast of Africa, continuing around South Africa, finally to be united with the Benguela Current northwards along south-western Africa; but conditions may be more or less complicated by an Agulhas return current (DARBYSHIRE 1966), which may account for a northward penetration of pelagic animals along the south-eastern coast, and the occurrence of the said three species shows that such return movements of Agulhas water may be discerned as far north as the surroundings of Madagascar.

On the other hand, the medusae give no information of the outflow of water from the Red Sea, briefly mentioned above (p. 165), because very little is known about these animals in the Arabian Sea.



### The Red Sea Subregion.

Owing to the peculiar physical conditions in the long narrow Red Sea and the Gulf of Aden this area is regarded as a separate subregion. The greatest depth is 2000 m, but somewhat inside the narrow strait Bab el Mandeb the Red Sea is separated from the Gulf of Aden by a shallow sill, no more than 100 m deep, preventing the deep water of the Indian Ocean from penetrating into the Red Sea, but surface currents flow into the Red Sea in summer, out into the Indian Ocean in winter. The salinity of the surface water layers is exceptionally high, 40–41 ‰, owing to great evaporation and no supply of fresh water from rivers. An exchange of epipelagic organisms may take place through the narrow Bab el Mandeb; an exchange through the Suez Canal, which was opened in 1869, is also possible and may have been of some importance for certain groups of animals. According to EKMAN (1953 p. 88), "the similarity between the Mediterranean and the Indo-West-Pacific fauna does not depend upon the neighbouring Red Sea as much as the regions further to the east", viz during the Tertiary Period.

No more than 10 species of neritic Hydromedusae have been recorded from this subregion, and no conclusions can be drawn from this small number; the species may, however, be divided into characteristic groups. Two species are "endemic", *Dicodonium cornutum* in the northern end of the Red Sea, *Eutima modesta* near Bab el Mandeb. Two species are known from only a few localities, both were taken at Bab el Mandeb, *Eutima hartlaubii* also in the Nicobars, *Eutonina scintillans* at Djibouti in East Africa, on the coast of Mexico, and in the Adriatic Sea, thus a very scattered distribution. The following three species are widely distributed and very common in Indo-Pacific waters but unknown in the Atlantic or the Mediterranean: *Bougainvillia fulva*, *Laodicea indica* and *Aequorea pensilis*; they were taken in or just inside Bab el Mandeb. Three other species, however, are widely distributed and very common in the Atlantic and the Mediterranean: *Zanclea costata*, *Turritopsis nutricula* equally widely distributed in Indo-Pacific waters, *Eirene viridula* found in some localities in the Indian Ocean. On the other hand, up to now no species belonging to Atlantic or Mediterranean waters but unknown in Indo-Pacific have been found in the Red Sea.

### Summary of the Indo-West-Pacific Region.

A thoroughly tropical or subtropical region with a very rich fauna of neritic Hydromedusae, up to now comprising 187 species; their distribution within each of the six subregions is seen in Tables VII and VIII. In the entire region 72 species (40 ‰) are "endemic", and as seen from the enumeration at the bottom of Table VIII the percentage number of "endemic" species is very nearly the same in all the subregions. EKMAN pays considerable attention to the numbers of endemic species of various groups of animals in different regions, which does not seem important to me, since very often species, which have been regarded as endemic in a certain area, prove to occur in other localities.

The results of the present investigations show that the neritic Hydromedusae justify EKMAN in regarding this extensive region as one characteristic zoogeographical unity. As seen from the tables, the composition of the fauna is very similar in the various subregions (except in the Red Sea, from which only ten species are known), further illustrated in the adjacent table, in which "endemic" species are excluded, which shows that a great number of non-endemic species is common to two or three, or even four or five of the subregions:

	number of species	% of 112 non-endemic species
found in only one subregion.....	18	16
common to two subregions.....	34	30
- - three - .....	28	25
- - four - .....	16	14.5
- - five - .....	16	14.5

The total number of species in each subregion is decreasing very slightly from the Indo-Malayan subregion westwards into the Indian Ocean, somewhat more in other directions into the Australian, Insular and Japanese subregions.

**Table VIII.** Indo-West-Pacific Region.

Number of species in each of the six sub-regions and number of species common with any other sub-region, actual as well as percentage number	Sub-regions						North Pacific	Warm East-Pacific	Mediterranean	Atlantic
	Indo-Malayan	Australian	Pacific Insular	South Japanese	Indian Ocean	Red Sea				
Indo-Malayan . . . . .	<b>107</b>	47	43	35	67	5	11	16	14	33
0/0 . . .	..	44	40	33	61	5	10	15	13	31
Australian . . . . .	47	<b>68</b>	33	24	46	5	7	13	12	24
0/0 . . .	69	..	49	35	68	7	10	19	18	35
Pacific Insular . . . . .	43	33	<b>59</b>	23	37	4	7	14	13	23
0/0 . . .	72	56	..	39	63	7	12	24	22	39
South Japanese . . . . .	35	24	23	<b>56</b>	30	4	11	12	14	25
0/0 . . .	62	43	40	..	54	7	19	21	25	45
Indian Ocean . . . . .	67	46	37	30	<b>100</b>	8	8	17	15	39
0/0 . . .	67	46	37	30	..	8	8	17	15	39
Red Sea . . . . .	5	5	4	4	8	<b>10</b>	0	3	4	3
0/0 . . .	50	50	40	40	80	..	0	30	40	30
Entire region, <b>187</b> species . . . . .	107	68	59	50	100	10				
0/0 . . .	57	31	32	30	53	5				
“Endemic” species . . . . .	72	20	10	10	10	18	2			
0/0 . . .	40	19	18	17	18	18	20			

The southern limit of EKMAN's "North-Australian" subregion at 32-34° S. on the east coast of Australia may hold good for the demersal shelf animals, but is far surpassed by the free-swimming medusae; as demonstrated above (pp.159 and 160), the fauna of these animals in eastern and southern Australia (apart from "endemic" species) only consists of species which also occur in the tropical parts of the Indo-West-Pacific Region, many of them even penetrating to New Zealand, which is in accordance with the prevailing currents. Unfortunately, nothing is known about the medusan fauna in the western parts of Australia. — In the Insular subregion the fauna is similar to that of the Indo-Malayan subregion and northern Australia, apparently impoverished eastwards (see p.162); remarkably few of the species occur in the warm East-Pacific regions, and almost all are extensively distributed and derived from Indo-West-Pacific waters, while none of them has an American origin. — On the oceanic coast of Japan there is a rather sharp limit at about 34° N. between a subtropical and a boreal fauna of demersal shelf animals, but some medusae of northern origin may penetrate southwards to the southernmost islands, and several tropical and subtropical species follow the Kuroshio Current far north beyond the faunistic limit; their occurrence as far north as around the island Hokkaido evidences the formation of extensive eddies in the northern regions, where the Kuroshio meets the cold Oyashio Current (see p.164); in the same way the occurrence of many medusae belonging to the water masses of the Kuroshio in the inner part of the Yellow Sea is explained by extensive eddies in that basin. It is remarkable that as many as 54 % of the medusae in southern Japan occur as far away as in the Indian Ocean, another confirmation of the unity of the Indo-West-Pacific Region. It is also shown (p.164) that a direct exchange of neritic species of medusae between southern Japan and the American coasts is highly improbable. — In the Indian Ocean subregion the shelf region is purely tropical (p.165); the fauna of neritic Hydromedusae is very similar to that in the Indo-Malayan subregion; the possibility of the Malay region being regarded as a centre of origin of many animal groups is discussed (p.166); the occurrence near Madagascar of an antarctic and two Atlantic species is regarded as proof of a far northward penetration of water masses of the Agulhas return current, (p.166).

As seen from Table VIII it applies to all the subregions of the Indo-West-Pacific Region that a comparatively small number of species are recorded from the warm East Pacific, while numerous species occur in Atlantic waters, which are discussed in the following.

## Interchange of species between the regions.

Generally EKMAN's division of the shelf fauna into zoogeographical regions and subregions has been confirmed by the studies of the neritic Hydromedusae, though the limits are less sharp for these pelagic animals. As a matter of fact, there are characteristic differences in the composition of the faunas in the different regions, but some interchange of species between the regions naturally takes place. Numerically the difference between the regions is expressed in Tables I–VIII; in the concluding remarks the results obtained during the discussions of the various regions and subregions are summarized. An interchange between Indo-Pacific and Atlantic waters also takes place, but is discussed in a separate chapter.

As far as known up to now, the fauna of neritic Hydromedusae in the Arctic Pacific Region comprises 29 species, many of which also occur in the Siberian Polar Sea, free communication being possible through the Bering Strait; among the 29 species 19 also occur in the Pacific Boreal Region, 12 in the eastern and 15 in the western parts of this region. At a short distance south of Vancouver the east-going North Pacific Current is divided into the south-going California Current and the north-going Alaska Current, and it is difficult for arctic species to spread southwards against this current, while boreal species may easily extend their distribution from the Vancouver region northwards into arctic waters (see p.136). On the other hand, many of the medusae occurring in the arctic region follow the Oyashio Current southwards towards Japan, though usually not further south than to the northernmost of the Japanese islands, where the Oyashio Current meets the warm, north-going Kuroshio Current (p.136). A few tropical and subtropical species, which are numerous in southern Japan, occasionally follow the Kuroshio far northwards into the area, where the waters of the Kuroshio and the Oyashio are mixed during formation of extensive eddies (see p.164). There are also a few species indigenous in Japanese waters, which have extended their distribution more or less southwards along the asiatic coasts (see p.140). Apart from arctic species, very few neritic Hydromedusae are Amphi-Pacific (see p.114). From the Hawaiian Region only 6 species are known, and it is futile to discuss their origin. (p. 142).

There is a rather sharp limit between the eastern part of the boreal region and the East-Pacific Tropical Region, because the south-going California Current turns westwards and participates in the formation of the North Equatorial Current in the latitudes of Lower California, which obstructs a southwards penetration of boreal species and a northward penetration of tropical forms; in addition the southern part of the Californian coast is cooled down by upwelling water from the bottom, so that no warm-water animals can settle along this coast (see p. 143). On the other hand, the westward turn of the north-going Peru Current at about 8° S. constitutes a limit between the tropical region and the Peru-Chilean Region, though not a very sharp one. In comparison with the extremely rich fauna in the Indo-West-Pacific Region remarkably few of these numerous species have been found in the two East-Pacific regions, probably due to the wide gap of open sea west of the American coast (see p.146). The Peru Current has a southern origin, being partly derived from the West-Wind-Drift; a number of antarctic or subantarctic medusae could therefore be expected along the coast of Chile, but up to now only two such species have been found there (see p.146). Presumably, several antarctic species occur along the southernmost part of the South-American coast, i.e. in the South American Antiboreal Region, but no neritic Hydromedusae have ever been collected in this area. The Antarctic and Subantarctic Regions have their own special fauna (p.147), and very few of its medusae have been observed in other regions within the Pacific and Indian sectors; presumably, some species occur on the western coasts of New Zealand and Australia, but their fauna of medusae is entirely unknown; one species, *Köllikerina maasi*, has been found near Madagascar (p. 166), and two on the coast of Chile.

The fauna of neritic Hydromedusae in the eastern parts of the Southern Australian and New Zealand Region consists exclusively of species which are widely distributed in the tropical parts of the Indo-West-Pacific Region, decreasing in number from North towards South, some of them presumably derived from the Pacific Insular subregion, due to the south-western direction of the South Equatorial Current (p.161).

The extensive Indo-West-Pacific, Region has a very rich fauna of neritic Hydromedusae, and its central parts, the Indo-Malayan and parts of the Indian Ocean subregions, may probably be regarded as a centre of development of a considerable part of the tropical fauna of these animals (p.166), the number of species decreasing from there into all directions, southwards to Australia and New Zealand, eastwards through the Pacific Insular subregion, from which remarkably few species have extended their distribution to the American coasts; undoubtedly none of the Indo-West-Pacific species has an American origin (p.163). Many of the Indo-Malayan species penetrate northwards along the East-Asiatic coasts with the Kuroshio Current, usually only as far as southern Japan (p.164); a few species, indigeneous in Japan, have extended their distribution more or less into tropical waters (p.141); the few records of South-Japanese species from warm East-Pacific areas are probably due to connection through the tropical waters of the Indo-Malayan and Insular subregions, a direct exchange across the ocean being restricted to forms with an oceanic occurrence (p.164). The fauna along the tropical coasts of the Indian Ocean is very similar to that of the Indo-Malayan subregion, the number of species probably decreasing somewhat towards the West, though the apparent impoverishment may partly be due to deficient knowledge (p. 166); it is remarkable, however, that no more than six of the species recorded from the waters along the east coast of Africa have not been found in the Indo-Malayan subregion, and three of these are of Atlantic origin (p.165). The few species recorded from the Red Sea may all be derived from the Indian Ocean.

## Comparison with the Atlantic Fauna.

Table IX.

The interchange of the medusan faunas between the Atlantic and the Indian and Pacific Oceans was discussed in my paper on the Hydromedusae of the Atlantic Ocean and adjacent waters in the "Dana" Report No. 46, 1959. It was however expressly stated, that at the time being this interchange could not be discussed in details (l. c. p. 268). As the knowledge of the faunas in the Indian and Pacific Oceans has now been considerably added to, this discussion can be resumed. I shall however restrict myself in the present place to recapitulate the actual facts of the neritic species within the different zoogeographical regions, while attempts at an explanation of the facts is given under the oceanic forms.

Almost 50 % of the neritic species recorded up to now from Indo-Pacific waters have also been found in Atlantic waters but, as seen from Table IX, the numbers differ considerably within the different regions. In the following reference is made, in brackets, to the pages where these subjects were mentioned above.<sup>1</sup>

It is natural that the greatest percentage number of species common to the Atlantic and the other oceans are to be found within the arctic and antarctic regions with their uninterrupted ranges of coastal areas. Among the 17 species recorded from the Pacific and Indian-Ocean sectors of the Antarctic and Subantarctic Regions two are "endemic" in these waters; all the remaining species occur in the Atlantic sector (p. 33); on the other hand, several species occurring in the Atlantic sector have not been found further east, some of them being derived from more northerly waters, others which presumably may be found in the Indian and Pacific sectors when these regions are better investigated; probably the majority of the species indigenous in antarctic and subantarctic waters have a circumpolar distribution.

The number of species recorded from the Arctic Pacific Region amounts to 29, among which 5 species are "endemic" within the region; disregarding these, the vast majority of the remaining 24 species (87.5 %) are

<sup>1</sup> As previously remarked the medusae of the genus *Obelia* are left out of the discussion, because the species cannot be identified.

**Table IX.** Comparison between Indo-Pacific and Atlantic species of neritic Hydromedusae.

Indo-Pacific regions	Number of species	Also in Atlantic waters							
		Total		Arctic	Boreal	Mediterranean	Warm Atlantic		
		no.	%				W.	E.	(tot.)
Arctic-Pacific .....	29	21	72	19	21	2	1	1	2
Pacific Boreal .....	67	26	39	14	24	4	5	5	7
East Pacific Tropical .....	29	17	59	•	5	7	14	8	17
Peru-Chilean .....	22	14	64	•	8	5	9	7	11
Antarctic and Subantarctic .....	17	15	88	1	•	•	1	•	1
South Australian and New Zealand..	33	11	33	•	7	6	5	10	11
Indo-West-Pacific .....	187	48	26	1	21	24	36	30	45
Indo-Pacific total .....	208	105	50						

also occur in the Arctic Atlantic Region, but it is not certain that all of them have a circumpolar distribution, since practically nothing is known about the fauna of these animals in the waters north of the American continent (p.135). The number of species in the arctic Atlantic waters also occurring in the Arctic Pacific Region is almost the same in the opposite direction (p.134), and most of them are recorded from localities on the north coast of Siberia. Though many of the species found in the Arctic Pacific Region may also occur in boreal, some of them even in warmer regions, all of them are adapted to truly arctic conditions, and a direct interchange might take place through the arctic waters as they are today, in contradistinction to some boreal species, which now have a discontinuous distribution. The question, whether an exchange of species between the arctic regions of the two oceans has taken place in the one or the other direction, East–West or West–East, was touched upon in p. 135; this question is discussed in the Concluding Remarks.

Among the 67 species recorded from the Pacific Boreal Region no less than 32 are “endemic” within this region, mainly on the American side; when these are disregarded, 74 % of the remaining 35 species also occur in Atlantic waters, most of them in the Atlantic Boreal Region, but most of these also occur in arctic waters (see Table IX). An interchange may therefore take place under the present conditions in the Arctic. There are, however, some species, which are common to the northern parts of the two oceans though these species cannot live under arctic conditions (p.141). Some of these also occur in the warm parts of the oceans, and their simultaneous occurrence in Pacific and Atlantic boreal waters may, with more or less probability, be explained by some connection through southern regions (p.141). The discontinuous distribution of some distinct boreal species, however, is explained by a direct communication north of Siberia during a former period when higher temperatures prevailed in these northern tracts (p. 142).

Leaving out 7 “endemic” species of the 29 species recorded from the East Pacific Tropical Region 77 % of the remaining species have also been found in Atlantic waters, the majority in the western parts of the warm Atlantic, which undoubtedly can be explained by a former open connection across the isthmus of Panama (Table IX and p.144). The eight species occurring in the eastern parts of the warm Atlantic all have an extensive distribution including parts of the Indo-West-Pacific Region.

The fauna of the Peru-Chilean Region is insufficiently known, up to now comprising 22 species, 14 of which (64 %) occur in Atlantic waters; two of them are subantarctic species carried to the coast of Chile by the north-going branch of the West-Wind Drift (p.146); the former open connection across the isthmus of Panama is responsible for the occurrence in the West-Indies of only two or three species, while the distribution of all the others comprises the Indo-West-Pacific Region (p.146), the explanation of their occurrence in the Atlantic thus being of equal rank; most of them have been found in the eastern as well as in the western parts of the Atlantic (see Table IV).

All the species, which are common to the South Australian and New Zealand Region and the Atlantic Ocean, are widely distributed in the Indo-West-Pacific Region (p. 153).



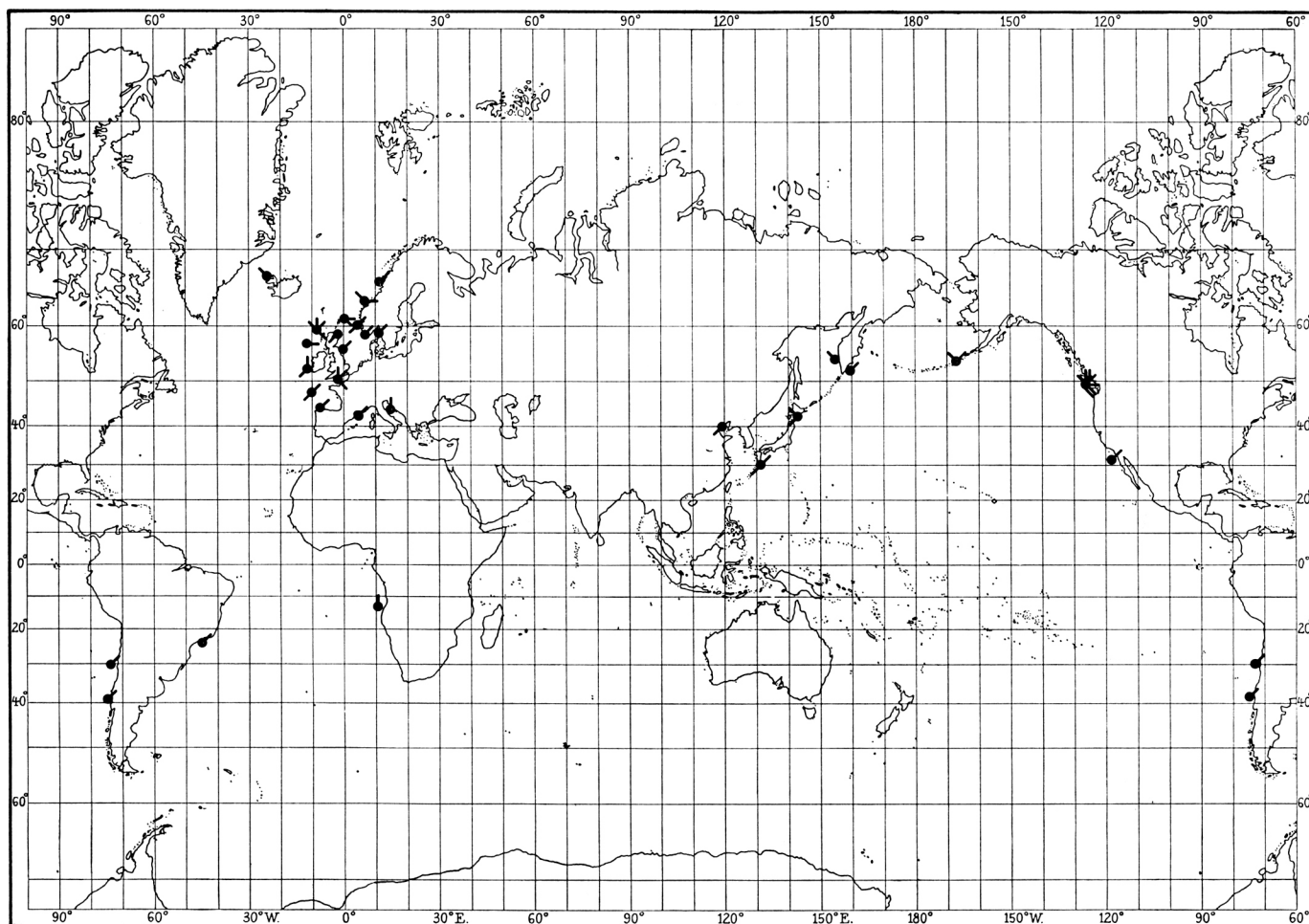


Fig. 360. Boreal species occurring in Atlantic and Pacific boreal regions, but not in Arctis. ● *Dipurena hallerata*.  
 ● *Sarsia eximia*. ● *Bougainvillia muscoides*. ● *Pochella polynema*. ● *Proboscidactyla stellata*. ● *Eutonina indicans*.

The distribution within the Indo-West-Pacific Region is particularly complicated; as a whole this is the region with the lowest percentage number of species in common with Atlantic waters (see Table IX), as many as 72 of its species are "endemic", and among the remaining 115 species 42 % have been found in the Atlantic and adjacent waters. The percentages are not very different within the different subregions, but the distribution of the species, in Pacific as well as in Atlantic waters, is subject to considerable distinction; many species occur in the Mediterranean, in the warm parts of the Atlantic they are almost equal in number in the western and eastern parts, most of them occurring in both sides of the ocean. There are also several species which have their principal occurrence in boreal waters, mainly in north-western Europe. These species might be divided into groups according to the possibilities of routes of communication. This was briefly mentioned in the treatment of the various subregions and is now discussed in more detail. Attempts on explanations, partly based on historical points of view, are given in the Concluding Remarks. For actual data on the distribution of each species see Table VII and Section I.

A. Rare species with scattered distribution: *Zancleopsis gotoi*, *Meliceritissa clavigera*, *Phialidium brunescens*.

B. Species probably distributed artificially, by ships: *Cladonema radiatum* (see p.142), *Gonionemus vertens* (pp. 137, 164), *Gonionemus suvaensis*.

C. Possible connection through the Polar Sea north of Siberia during a period with milder climate in these waters: *Sarsia eximia* (pp. 137, 142, 162), *Proboscidactyla stellata* (p. 141, see the map, fig. 360).

D. South of South America: *Phialidium simplex*, which is widely distributed in the Indian Ocean and recorded from Australia and New Zealand and from the coast of Chile, the only Atlantic records being from



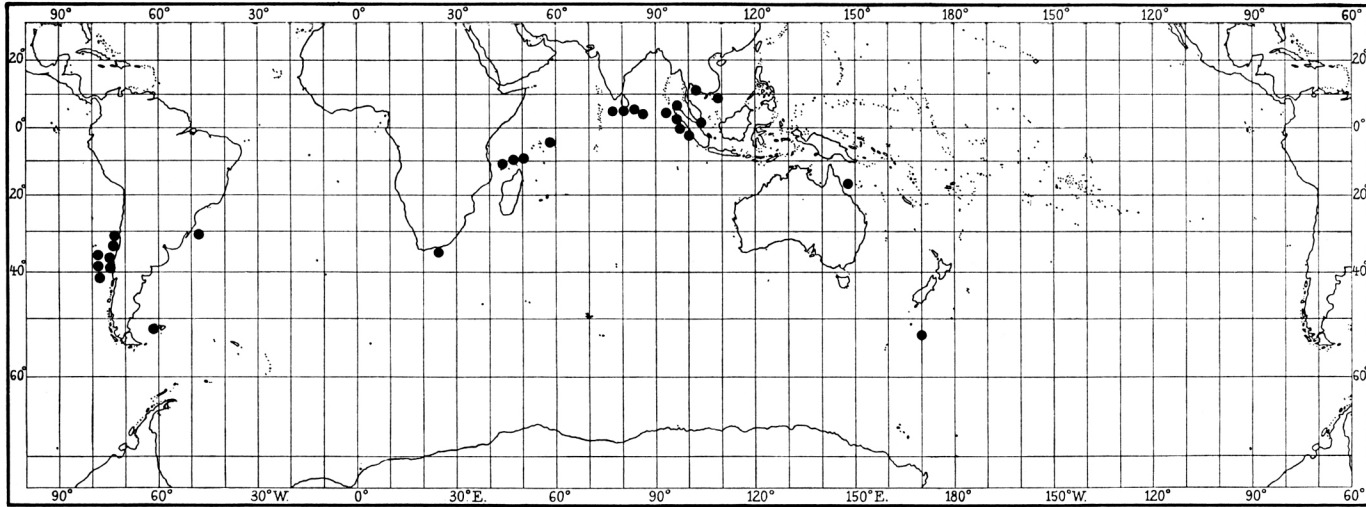


Fig. 361. Distribution of *Phialidium simplex*.

the Falkland Islands and from a point on the coast of the southern part of Brazil, undoubtedly derived from the Falkland Current. (p. 160, see the map, fig. 361).

*E.* Direct connection south of Africa under the present conditions. This is the largest group, comprising 20 species, all of them occurring in the Indian Ocean, and, with one exception (*Bougainvillia platygaster*), also off the southern part of the west coast of Africa south of the Equator. They may be divided into minor groups, as follows:

*E. a.* Common in the Indian Ocean, rare in the Atlantic: *Gotoea similis*, *Eucheilota ventricularis*, *Toxororchis polynema*, *Aequorea macrodactyla* (pp.144,160), *Aequorea coerulescens* (p.160), *Zygocanna vagans* (p.144), *Probosciodactyla ornata* (p. 144, perhaps also a former connection through the isthmus of Panama).

*E. b.* Common and widely distributed in both oceans: partly or mainly oceanic, *Euphysora furcata*, *Cytaeis tetrastyla*, (p.144), *Bougainvillia platygaster* (widely distributed in tropical Atlantic and along the east coast of Africa), *Pandea conica*, *Oceania armata*, *Heterotiara anonyma* (pp.140,144), *Turritopsis nutricula*; strictly neritic: *Leuckartiara octona* (pp.137,144,152), *Ectopleura dumortieri* (pp.144,164) and *Phialidium hemisphaericum* (these three species occur in the Mediterranean and are particularly common in north-western Europe.)

*E. c.* Rare in the Indian Ocean: *Phialopsis diegensis* (widely distributed in the eastern Atlantic, a few localities on the east coast of Africa, its further penetration *via* South Australia and the Insular subregion to California, see pp.137,141), *Aequorea aequorea*, and the two species *Euphysilla pyramidata* and *Calycopsis papillata*, which have only been found near Madagascar besides in some Atlantic localities (pp.165,166). The species of *E. c* are undoubtedly derived from the Atlantic.

*F.* Unknown in the eastern Atlantic but occurring in West-Indian waters, 8 species:

*F. a.* Found in a few localities in the eastern Pacific besides in Australian or Indo-Pacific areas: *Halitiara formosa*, *Amphinema turrida* (pp. 144, 146).

*F. b.* Unknown in the eastern Pacific, but occurring in the Indian Ocean and/or Indo-Malayan and Australian waters: *Ectopleura minerva*, *Köllikerina elegans*, *Cirrhitiara superba*, *Niobia dendrotentaculata* (also in the Mediterranean), *Eucheilota paradoxa*, *Phialucium carolinae* (p.164). In spite of their absence in the eastern parts of the Pacific these species may formerly have crossed the Isthmus of Panama.

*G.* Distribution in Atlantic and Indo-Pacific waters completely isolated under present conditions, 14 species. With two exceptions all these species occur in the Mediterranean; their occurrence in the Atlantic is very diversified. — Unknown in the Mediterranean: *Staurodiscus tetrastaurus* (north-western Africa and Florida), *Phialella quadrata* (north-western Europe, Gulf of Guinea p.152). Mediterranean alone: *Eutonina scintillans* (Indo-Pacific only Red Sea and Mexico), *Cirrholovenia tetranema*. Mediterranean and Florida: *Merga violacea*. (p.144). Warm Atlantic East and West: *Lovenella cirrata* (p.159). Atlantic East and West, mainly boreal,

principal occurrence in north-western Europe: *Euphysa aurata* (pp.147,164, Indo-Pacific only in Yellow Sea, if determination correct), *Zanclea costata* (p.167), *Bougainvillia ramosa* (Indo-Pacific Australia only), *Amphinema dinema* and *Amphinema rugosum*. Unknown in western Atlantic: *Eirene viridula* (p.167, also in West Africa), *Podocoryne minima*, *Dipurena ophiogaster* (p. 144).

## SLOPE SPECIES

As in my paper on the Hydromedusae of the Atlantic Ocean (KRAMP 1959 p. 238) attention is called to a number of species which are neither neritic nor oceanic, mainly occurring in the deeper water layers, but presumably meropelagic, being derived from hydroids attached to the bottom of the continental slopes outside the neritic areas. These "slope species" do not constitute a sharply defined ecological group, since some of them may occasionally ascend towards the upper strata, preferably near the coasts, where upwelling water from the deep layers takes place, but their geographical distribution cannot be explained by the directions and extension of the sea-currents in the upper water layers.

There are eleven species of Antho- and Leptomedusae, but also one of the Trachymedusae, *Ptychogastris polaris* ALLMAN should be mentioned here, though it has no hydroid stage, but the medusa itself is attached to the bottom by its sucker-bearing tentacles, occasionally swimming towards the surface; its distribution is bipolar, it is circumpolar in arctic and subarctic waters and is recorded from the Aleutian Islands; its antarctic occurrence comprises the South Shetland Islands and a point about 90° East near the Antarctic Continent (as *P. opposita* VANHÖFFEN); *P. antarctica* HAECKEL from the neighbourhood of the Kerguelen Islands is an altogether doubtful species; it is interesting, however, that another species of the same peculiar genus, *P. asteroides* (HAECKEL) occurs in the Mediterranean.

Most of the slope species of Antho- and Leptomedusae have an extensive distribution in the deep and intermediate water layers of the Atlantic Ocean and a more or less scattered occurrence in the Indian Ocean and the western Pacific, *Annatiara affinis*, *Bythotia murrayi* and *Calyropsis chuni* as far east as Australia or New Zealand (the latter also found in the Gulf of Panama), *Sibogita geometrica* to the Malayan Archipelago. The following three species likewise have an extensive distribution from North to South in the Atlantic Ocean, but their penetration into the Indo-Pacific takes place within a narrow zone along the border of the Antarctic Continent, *Tiaranna rotunda* as far as 140° E., *Chromatonema rubrum* and *Pandea rubra* to about 110° E. This latter species has however also been found near Ceylon and in the northern Pacific (San Francisco, Alaska, Kamchatka, with a shoal of juvenile specimens near the surface in the central part of the North Pacific).

There are, however, also some species with entirely, or almost entirely, belong to Indo-Pacific waters; *Chromatonema erythronon* (BIGELOW) occurs in the intermediate layers in the eastern tropical Pacific from the Gulf of California to the Gulf of Panama and off Peru (*Chromatonema hertwigi* (VANHÖFFEN) described from the Bay of Bengal seems to be a doubtful species); *Calyropsis simulans* (BIGELOW) is recorded from intermediate depths in the Gulf of Panama and the Malayan Archipelago and was collected by the "Dana" in two localities in the Indian Ocean; *Calyropsis bigelowi* VANHÖFFEN was taken by the "Dana" in several localities in the Malayan Archipelago; it was originally described from the Gulf of Aden, and it has turned around the corner of South Africa, being recorded from two localities immediately west of the Cape of Good Hope.

Finally, the peculiar little medusa *Russellia mirabilis* KRAMP should be mentioned, which has been found in more or less deep water in the West-Indies and among the antarctic islands South Sandwich and South Shetland Islands in the south-western Atlantic and also on the Pacific Side of Graham Land.

Some of these so-called slope-species may, of course, appear in new localities in the future, but their distribution as known up to now comprises so scattered and different parts of Indo-Pacific waters that no reliable zoogeographical conclusions can be drawn from their occurrence.

## OCEANIC SPECIES

Introductory remarks on oceanic species of Hydromedusae were given in my paper on the Atlantic forms in the Dana Report no. 46 (KRAMP 1959 p. 241), to which I refer, pointing out a few statements of principal importance. The species require certain physical conditions; they are carried along with the sea-currents, which may sometimes carry them to areas with unfavourable conditions, where they are found as stray visitors, and they may also be caught by descending or upwelling water masses; medusae observed outside their usual habitat become valuable indicators of displacements of the water masses. The majority of the oceanic medusae are the holopelagic Trachymedusae and Narcomedusae, which are not directly dependent on the coastal shelves. There are, however, also a few of the meropelagic Anthomedusae and Leptomedusae which, for various reasons, may spread widely over the oceans; they are treated separately in the following. The Indo-Pacific species of oceanic Hydromedusae are listed in Tables X and XI, comprising the epipelagic species (belonging to the upper water layers down to about 150–250 m below the surface) and the bathypelagic forms in the intermediate and deep strata respectively; the comparatively few eurybathic species are mentioned under both headings.

### The epipelagic zone.

Table X.

The epipelagic species are partly exposed to the same currents as the neritic species, but in the Indo-Pacific as well as in the Atlantic waters the division into zoogeographical regions may be more simplified (see Table X) comprising arctic, north-temperate, warm-water, south-temperate and antarctic conditions; for comparison with the Atlantic and adjacent waters the occurrence of Indo-Pacific species in the Mediterranean Sea is included in the table, which may be of importance in a discussion of the interchange of species between the oceans. It is seen from Table X that the vast majority of the Indo-Pacific epipelagic species also occur in Atlantic waters.

#### *The Pacific Arctic Region.*

No more than three epipelagic species of Hydromedusae occur in this region, and only one of them, *Aeginopsis laurentii*, is purely arctic, circumpolar; the second species, *Aglantha digitale*, is likewise circumpolar, but its distribution is extended far southwards into north-temperate waters in the Pacific as well as in Atlantic waters; both species are eurybathic, requiring cold water, which in arctic regions is present at any depth. The third species is *Cunina tenella*, which is recorded from only two widely separated localities, the Ochotian Sea and the Pacific coast of Mexico.

#### *The North-Temperate Region.*

With 13 species; only one of them is "endemic" in this region, *Crossota pedunculata*, which is known from only one locality in the Vancouver Island region; all of the others are indigenous in warmer regions, all of them widely distributed in Pacific as well as in Atlantic waters, their occurrence in the north-temperate part of the Pacific being more or less sporadic. *Cunina globosa* may be left out of the discussion, since it has a very scattered distribution (Saghalin, Sea of Japan, Mexico, Gilbert Islands and north of New Zealand in tropical Pacific, Chile, South Africa, West of Ireland, and perhaps in the Mediterranean). Among the thirteen species enumerated as occurring in the Pacific north-temperate region only two can be said to have an indigenous population in this region, viz. *Aegina citrea* (as far north as along the Aleutian Islands) and *Rhopalonema velatum* (to about 42° N); both of them occur in both sides of the north-temperate region, and both are eurybathic. None of the other species has been found further north than 35–38° N. All of them occur off the coasts of Japan, and it is characteristic that, with two exceptions, they occur equally far north in the eastern Pacific. The two exceptions are *Solmundella bitentaculata* (in East Pacific very common south of 20° N.) and *Pegantha martagon* (from 5° N. southwards into the Antarctic); the occurrence of these two species in the western parts of the north-temperate region is due to a northward penetration from tropical

Table X. Oceanic species in the epipelagic zone.

		Pacific					Indian			Atlantic					
		Arctic	North-temperate	Warm-water	South-temperate	Antarctic	Warm-water	South-temperate	Antarctic	Arctic	North-temperate	Mediterranean	Warm-water	South-temperate	Antarctic
*Aeginopsis laurentii.....		×	•	•	•	•	•	•	•	×	•	•	•	•	•
*Aglanta digitale.....		×	×	•	•	•	•	•	•	×	×	•	•	•	•
Cunina tenella.....		×	•	E	•	•	•	•	•	•	•	•	•	•	•
Crossota pedunculata.....		•	E	•	•	•	•	•	•	•	•	•	•	•	•
*Rhopalonema velatum.....		•	×	×	×	•	×	×	•	•	×	×	×	×	•
*Aegina citrea.....		•	×	×	×	•	×	×	(×)	•	×	•	×	×	×
Aglaura hemistoma.....		•	(×)	×	×	•	×	×	•	•	×	×	×	×	•
Liriope tetraphylla.....		•	×	×	×	•	×	×	•	•	×	×	×	×	•
Geryonia proboscoidalis.....		•	(×)	×	(×)	•	×	×	•	•	•	×	×	×	•
Solmundella bitentaculata...		•	(×)	×	×	×	×	×	×	•	(×)	×	×	×	×
Cunina globosa.....		•	(×)	×	×	•	•	•	•	•	E	•	•	SE	•
Aglantha intermedia.....		•	•	E	•	•	•	•	•	•	•	•	•	•	•
Aeginura beebei.....		•	•	E	•	•	•	•	•	•	•	•	•	•	•
Petasiella asymmetrica.....		•	•	W	•	•	•	•	•	•	•	•	•	•	•
Solmaris rhodoloma.....		•	•	×	×	•	•	•	•	•	•	•	•	•	•
Solmaris lenticula.....		•	•	W	•	•	×	•	•	•	•	•	•	•	•
Amphogona pusilla.....		•	•	W	•	•	W	•	•	•	•	•	•	•	•
Amphogona apsteini.....		•	•	×	•	•	×	•	•	•	•	•	E	•	•
Pegantha triloba.....		•	•	×	×	•	×	•	•	•	•	•	×	×	•
Pegantha clara.....		•	(×)	×	×	•	×	×	•	•	×	•	×	×	•
Pegantha laevis.....		•	×	×	•	•	×	×	•	•	(×)	•	×	×	•
Pegantha martagon.....		•	(×)	×	×	×	×	×	•	•	•	•	×	×	×
*Solmissus mashalli.....		•	•	×	×	•	×	×	•	•	×	•	×	×	•
Cunina octonaria.....		•	•	×	×	•	×	×	•	•	•	×	×	×	•
Cunina frugifera.....		•	(×)	×	×	•	×	×	•	•	•	•	×	×	•
Cunina peregrina.....		•	•	×	×	•	×	×	•	•	•	•	×	×	•
Cunina duplicata.....		•	•	×	•	•	×	×	•	•	•	•	×	×	•
*Sminthea eurygaster.....		•	•	×	×	•	×	•	•	•	(×)	×	×	×	•
*Persa incolorata.....		•	•	•	W	•	E	•	•	•	•	×	×	×	•
Pantachogon scotti.....		•	•	•	•	×	•	•	×	•	•	•	•	•	×
		3	13	25	17	3	20	14	3	2	11	8	18	18	3
Leptolina	Heterotiara anonyma....	•	×	×	•	•	W	•	•	•	•	•	W	E	•
	Pandea conica.....	•	×	×	W	•	×	W	•	•	•	×	×	×	•
	Cytaeis tetrastyla.....	•	•	×	•	•	×	•	•	•	•	×	×	•	•
	Bougainvillia platygaster.	•	•	W	•	•	×	W	•	•	•	•	×	•	•

\* Eurybathic species.

waters, while all the others, including *Rhopalonema velatum*, have a well marked northern limit of distribution at about 35–38° N. right across the northern Pacific, *i. e.* in the water mass of the North Pacific Current (see the map, fig. 367).

#### The Pacific Warm-Water Regions.

The vast majority of the 34 species recorded from these waters occur right across the warm parts of the ocean, in eastern as well as in western parts, only somewhat differing in their northward and southward extension, and without exception these species are widely distributed in the warm parts of the Indian and Atlantic Oceans.

Some remarks should be made on seven species with more or less restricted areas of distribution. *Aglantha intermedia* and *Aeginura beebei* have been found only in the easternmost part of the Pacific equatorial waters, the latter in only one locality (Panama). *Petasiella asymmetrica*, *Solmaris lenticula* and *Amphogona pusilla* only occur in the western tropical Pacific waters and in a few scattered localities in the Indian Ocean. *Solmaris rhodoloma* and *Amphogona apsteini* are fairly common in the western tropical Pacific and have been found in a few localities in the East Pacific. Among the seven species listed here only one, *Amphogona apsteini*, is recorded from the Atlantic, viz. in the Gulf of Guinea, and none of the seven species has been found in the Mediterranean.

*Persa incolorata*, which is eurybathic, is widely distributed in the Atlantic and the Mediterranean and recorded from only two Indo-Pacific localities, South-East Australia and the Sunda Strait.

#### *The Indian Ocean Warm-Water and Temperate-Water Regions.*

There is no characteristic difference between the warm-water and the South-Temperate faunas of medusae in the Pacific Ocean (see Table X). Without exception all the epipelagic Trachy- and Narcomedusae occurring in these waters are widely distributed in the Pacific as well as in the Atlantic oceans, mainly in their warmer parts.

The three species recorded from the Antarctic Region in the Pacific and Indian Oceans are widely distributed in the oceans and are only occasionally dispersed into antarctic waters. Finally, *Pantachogon scotti* should be mentioned. It is a purely antarctic medusa, presumably circumpolar; it is recorded from the Ross Sea in the Pacific, Queen Mary Land in the Indian, and the Weddell Sea in the Atlantic sector of the Antarctic Continent.

#### *Epipelagic, Oceanic Leptolina.*

As briefly mentioned above (p.175), a few species of Anthomedusae and Leptomedusae are so widely distributed in the central parts of the oceans, far from the coasts, that they should be designated as "partly oceanic" and exposed to the same currents and physical conditions as the Trachylina. In the epipelagic zone this applies to four species (see Table X). All of them may presumably possess sessile hydroids belonging to the shelf areas. As far as two of the species are concerned, their ability to spread is due to the production of medusa-buds on the manubrium of the medusa; this applies to *Cytaeis tetrastyla* and *Bougainvillia platygaster*; both are almost generally distributed in the warm parts of the Atlantic and Indian oceans, *Cytaeis* also right across the Pacific, while *B. platygaster* has not been found further east than at the Fiji Islands, 180°. The two other species, *Heterotiara anonyma* and *Pandea conica*, have no medusa-buds, their partly oceanic distribution may either be due to a comparatively long pelagic life or to transportation of their unknown polypoid stages by drifting objects. Both are widely distributed in the warm parts of the Atlantic and Indian oceans; *Heterotiara anonyma* also occurs off the coast of Peru and in the boreal part of the North Pacific (see above, p.140). *Pandea conica* has been collected in several localities in the North Pacific, partly near Japan and near California, but also about midway between these distant areas, adults as well as a shoal of young stages, thus in the water mass of the North Pacific Current (see p.153). The Anthomedusa *Euphysora furcata*, which is eurybathic and may be found in coastal waters as well as in open sea areas, has been mentioned among the "slope species" (p. 174).

## The bathypelagic zone.

Table XI.

Among the 40 species listed in Table XI as many as seven may be designated as eurybathic (marked with an \*) and are also included in Table X. The occurrence of the remaining species is normally restricted to the intermediate and deep water masses below the epipelagic zone, i. e. at depths exceeding 150–250 m, though some of them may occasionally be met with at somewhat higher levels, indicating upwelling of water from the

**Table XI.** Oceanic bathypelagic species.

	Pacific Ocean					Indian Ocean		Atlantic Ocean				Mediterranean
	Arctic	North of ca. 40° N.	Warm-water		Antarctic	Warm-water	Antarctic	Arctic	Warm-water		Antarctic	
			E.	W.					E.	W.		
*Aeginopsis laurentii .....	×	•	•	•	•	•	•	×	•	•	•	•
*Aglantha digitale .....	×	×	N	N	•	•	•	×	N	N	•	•
Crossota norvegica .....	•	•	•	•	•	•	•	×	•	•	•	•
Botrynema ellinorae.....	•	•	•	•	•	•	•	×	•	•	•	•
Crossota rufobrunnea .....	•	×	•	N	•	•	•	•	N	N	•	•
Colobonema typicum .....	•	•	×	•	•	•	•	•	•	•	•	•
Colobonema igneum .....	•	•	×	•	•	W	•	•	•	•	•	•
Chromatonema hertwigi .....	•	•	•	•	•	N	•	•	•	•	•	•
Aglantha elata.....	•	•	•	S	•	•	•	•	×	•	•	•
*Aegina citrea .....	•	×	×	×	•	×	×	•	×	×	×	•
*Solmissus marshalli .....	•	•	×	×	•	×	•	•	×	×	•	•
*Rhopalonema velatum.....	•	•	×	×	•	×	•	•	×	×	•	×
*Sminthea eurygaster .....	•	•	×	S	•	×	•	•	×	×	•	×
*Persa incolorata .....	•	•	•	S	•	E	•	•	×	×	•	×
Solmissus incisa.....	•	×	×	×	•	×	•	•	×	N	•	•
Aeginura grimaldii .....	•	×	×	×	•	×	•	•	×	×	•	•
Rhopalonema funerarium .....	•	•	×	×	•	×	•	•	×	N	•	•
Colobonema sericeum.....	•	•	×	×	•	×	•	•	×	×	•	•
Halitrephes maasi.....	•	•	×	×	•	×	•	•	×	×	•	•
Haliceas minimum .....	•	×	×	×	•	×	×	•	×	×	×	•
Crossota brunnea .....	•	•	×	×	×	×	×	•	×	S	×	•
Pandea rubra.....	•	×	N	•	•	×	×	•	×	×	×	•
Botrynema brucei.....	•	×	•	S	•	×	×	•	×	×	×	•
Pantachogon haeckeli .....	•	×	•	×	×	×	×	•	×	×	×	•
Haliscera bigelowi.....	•	•	×	S	•	•	•	•	×	•	•	•
Tetrorchis erythrogaster .....	•	•	×	S	•	•	•	•	×	•	•	•
Bythotiara murrayi .....	•	•	•	S	•	×	•	•	×	•	•	×
Annatiara affinis.....	•	•	•	S	•	×	•	•	×	×	•	•
Amphogona apicata .....	•	•	•	S	•	W	•	•	×	S	•	•
Crossota alba .....	•	•	•	×	•	•	•	•	×	•	•	•
Pantachogon militare.....	•	•	•	•	•	•	•	•	×	•	•	•
Ransonia krampi .....	•	•	•	•	•	•	•	•	×	•	•	•
Haliscera conica .....	•	•	•	S	E	•	×	•	×	S	×	×
Tiaranna rotunda .....	•	•	•	•	•	S	×	×	×	×	•	•
Chromatonema rubrum .....	•	•	•	•	•	•	×	×	×	×	×	•
Haliscera racovitzae.....	•	•	S	S	E	•	•	•	•	S	×	•
Arctapodema ampla.....	•	•	•	•	E	•	×	•	×	S	×	•
Arctapodema antarctica .....	•	•	•	•	•	×	×	•	•	S	×	•
Arctapodema australis.....	•	•	•	•	•	×	×	•	•	•	•	•
Euphysora gigantea.....	•	•	•	•	•	•	•	•	S	S	×	•
	2	9	18	25	5	23	12	6	31	26	12	5
		28				26			33			
		30							36			
* Eury bathic												

\* Eurybathic.

deep strata. Owing to inexact knowledge of the actual depths at which the animals are captured, a distinction between an upper and a lower bathypelagic fauna cannot be made. Some bathypelagic animals are able to ascend or descend actively to other levels, but the medusae are not "good swimmers", so their vertical movements are generally due to physical conditions. Geographically the configuration of the bottom of the oceans



consists of a number of deep depressions or basins, separated by more or less complex ridges; if the distribution of the bathypelagic Hydromedusae is plotted for comparison with *e. g.* the 3000 m bathymetrical curve it appears that they all occur above the ridges as well as over the basins with depths exceeding 3000 m, and across these ridges there is free communication, except with the arctic basins, between the water masses of the oceans.

The hydrographical conditions in the bathypelagic zone are rather uniform within extensive areas, and the circulation is slow. Two cold-water areas, arctic and antarctic, and a warm-water region can be distinguished.

In the paper on the Atlantic Hydromedusae (KRAMP 1959 *a*) the "warm" region was subdivided in order to notify a northern and a southern temperate ("boreal") region, and I have felt inclined to do the same in the present paper, mainly because a considerable number of the species belonging to the warm, deep water in the Pacific Ocean seem to be absent in the northern part of this ocean; there is reason to believe, however, that this is merely due to lack of knowledge.

For further introductory remarks, see the paper on "The Hydromedusae of the Atlantic Ocean and adjacent waters" in the Dana-Report No. 46, KRAMP 1959 *a*.

#### *The Arctic Deep-Sea Region.*

The deep-water areas around the North Pole are divided into four basins with depths exceeding 2000 m and separated by shallow ridges (see the map. fig. 356). Baffin Bay between the northern part of Baffinland and Greenland is effectively cut off from the Polar Sea by narrow straits between North Greenland and the arctic Canadian islands; the Norwegian Sea between Norway and East Greenland communicates with the Polar Sea through a narrow strait with depths of less than 1000 m; the central Polar Sea itself is divided into two almost equal parts by a narrow ridge from Ellesmere Land across the north Pole towards the New Siberian Islands. Two species of Hydromedusae, *Aglantha digitale* and *Aeginopsis laurentii*, occur in these deep basins. Both of them are, however, eurybathic and have a circumpolar distribution in the upper and intermediate strata, *Aglantha* penetrating rather far into boreal waters, while *Aeginopsis* is purely arctic (see above, p.175). Up to now no other Hydromedusae have been collected in the arctic basins north of Asia and America, but two decidedly bathypelagic species are recorded from the "Atlantic" sector of the arctic region, *Crossota norvegica* in the Norwegian Sea and *Botrynema ellinorae* in the Norwegian Sea and Baffin Bay.

#### *The Warm-Water Region.*

Since there are only five Atlantic (besides one Mediterranean) bathypelagic species, which have not been found in Indo-Pacific waters, these species are included in Table XI, which thus comprises 40 species; it is seen from the table that the majority occur in all of the three great oceans, which is further discussed below.

While in the Atlantic the vast majority of the bathypelagic species in the warm-water region are distributed northwards to the submarine ridges separating the region from the two cold-water basins (or nearly so), several Pacific species are apparently absent in the northern part of that ocean; some of them are rare species, which should be left out of the discussion, but a number of common and widely distributed species which, with one exception, occur in the tropical belt, have also been found along the Aleutian and Kurile Islands but in no other parts of the northern Pacific; they are listed in Table XI in a separate column "north of about 40° N". *Crossota rufobrunnea* does not occur in tropical regions, but is a well-marked northern species in the Pacific as well as in the Atlantic; the other species in this column occur in the tropical belts in all three oceans. The only two species which in the Pacific have been found around the 40° northern latitude as well as in the tropical belts, are the widely distributed *Rhopalonema velatum* and *Solmissus marshalli*, which are eurybathic. The apparent absence of any other bathypelagic Hydromedusae in an extensive part of the northern Pacific is probably due to insufficient investigations across this part of the ocean, while the ranges along the Aleutian and Kurile Islands have been explored by American and Russian expeditions. Unfortunately, most of this collecting was done by vertical hauls, giving no information of the depth, at which the animals were captured, so no conclusions may be drawn concerning a possible upwelling of water from the deep strata.

As far as the other parts of the warm deep-water region are concerned, it is advisable to distinguish between the occurrence in the eastern or western areas, and also, in some cases, to notify whether a species is recorded only from the northern or from the southern parts. The expeditions by the "Dana" and the "Galathea" have contributed much to our knowledge of the distribution of these animals in the Indian and Pacific oceans.

Some species, recorded from only one or a few, scattered localities, should be omitted from the discussion. *Colobonema typicum* (MAAS 1897, not 1905) was found off the Pacific coast of Central America and has also been recorded, erroneously, from Japan, the Philippines and Bermuda, at a time when it was considered identical with *C. sericeum* (see KRAMP 1947 p. 19). *Colobonema igneum* VANHÖFFEN was described from deep sea north of Madagascar, found near the Galapagos Islands in eastern Pacific by the "Dana" (KRAMP 1965 p. 121, considered a valid species). *Chromatonema hertwigi* (VANHÖFFEN), taken only between the Nicobars and Ceylon. *Arctapodema macrogaster* (VANHÖFFEN), in the central part of the Indian Ocean is probably identical with *A. australis* (VANHÖFFEN). *Aglantha elata* (HAECKEL) in two widely separated localities: near the west coast of Africa and near Tasmania.

As mentioned above (p.179), the configuration of the bottom of the oceans does not present any effective barriers preventing free communication of meso- and bathypelagic medusae between the different parts of the oceans except the bridges separating the arctic basins from the warm-water regions in northern Atlantic and northern Pacific. Moreover, the conditions of temperature and salinity are rather uniform within extensive areas of the deep-sea; accordingly a division of the deep-sea areas into "regions", similar to the regions in the epipelagic zone, seems superfluous. Even the communication between the three oceans south of the continents is independent of the configuration of the sea-bottom. The plateau south-east of South America, surrounding the South Shetlands and South Orkneys and other groups of islands, might be expected to prevent a communication between the South Atlantic and the South Pacific but, as a matter of fact, several species have been collected above this plateau, which, accordingly, cannot explain the absence of most of these species in the southern Pacific. Special attention should, however, be paid to the water masses surrounding the Antarctic Continent, which are discussed below. In the following account, as well as in Table XI, considerations of comparison between the Indo-Pacific and the Atlantic bathypelagic fauna is included.

Obviously the eurybathic species have particularly easy conditions for being extensively distributed. Among the five eurybathic warm-water species listed in Table XI four have a circumglobal distribution; they are almost generally distributed in the Atlantic, from north to south; *Aegina citrea*, *Solmissus marshalli* and *Rhopalonema velatum* also occur in the northern Pacific, while *Sminthea eurygaster* has not been found further north than in the Gulf of Panama in the Pacific; *Persa incolorata* is widely distributed in the Atlantic, but seems to be rare in the Indian Ocean (only found near Java) and in the Pacific (south-eastern Australia). Three of these species also occur in the Mediterranean. Even among the eurybathic medusae, there is thus a limit for a world-wide distribution, and hardly on account of the physical conditions of the water masses; already here a diminution of the fauna from Atlantic waters eastwards is indicated (see below).

The following predominantly bathypelagic species have a circumglobal distribution in the warm areas. All of them are widely distributed in the Atlantic Ocean and are also more or less common in the Indian and Pacific Oceans: *Solmissus incisa* (apparently rare in the Indian Ocean but common in northern and eastern Pacific), *Aeginura grimaldii*, *Rhopalonema funerarium*, *Colobonema sericeum*, and *Halitrephes maasi*; none of these has been found in the antarctic or subantarctic areas, while the following five species occur in antarctic waters: *Halicreas minimum* (almost generally distributed in all three oceans), *Crossota brunnea* (widely distributed in the southern hemisphere, never found north of 10° N. except in one locality in southern Japan), *Pandea rubra*, *Botrynema brucei*, and *Pantachogon haeckeli* (the three latter species occur in the northern Pacific, but have not been found in the warm parts of the eastern Pacific). *Haliscera bigelowi* and *Tetrorchis erythrogaster* occur in the Atlantic Ocean and are fairly common in the eastern Pacific off the South-American coast, also recorded from New Zealand but apparently absent in the Indian Ocean, which may be accidental.

There are thus 12 bathypelagic species which may be termed circumglobal in the warm region. The following four species, however, which are widely distributed in the Atlantic, are rare in the Indian Ocean, and in

the Pacific only found in the surroundings of New Zealand: *Bythotiara murrayi*, *Annatiara affinis*, *Amphogona apicata*, and *Crossota alba* (this latter also found near Japan).

In this connection it may be mentioned that two species, *Pantachogon militare* and *Ransonia krampi*, are recorded from several localities in the eastern tropical Atlantic, off the west coast of Africa, but not found in Indo-Pacific waters. Besides these only one purely Atlantic species of bathypelagic Hydromedusae, *Euphysora gigantea* is known, and it belongs to the south-western corner of this ocean and is discussed under the antarctic fauna. The remaining species all occur in the waters near the Antarctic Continent; some of them are widely distributed in the Atlantic Ocean, but within Indo-Pacific waters they are not, or only very sporadically, recorded from somewhat warmer areas.

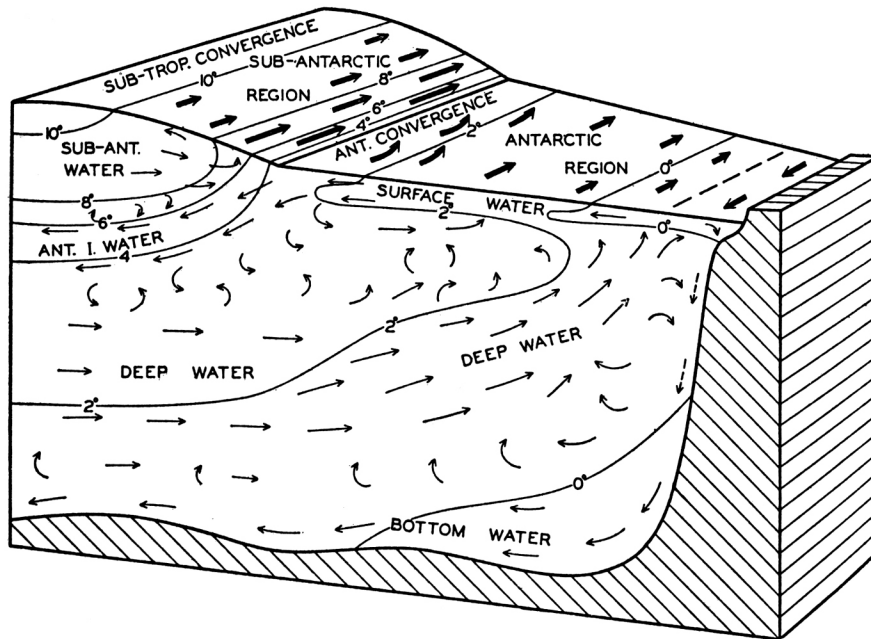


Fig. 362. Schematic representation of the currents and water masses of the Antarctic region and the distribution of temperature (from "The Oceans").

#### *The Antarctic Deep-Sea Region.*

In earlier papers the medusan fauna of the antarctic and subantarctic waters has been dealt with, mainly in the "Discovery Reports" (KRAMP 1957 pp. 98–104 and p. 106), with additional records in the reports of the BANZAR Expedition (KRAMP 1957 b) and in some degree in the "Dana Reports" (KRAMP 1959 a pp. 235–238, 251–252, 260–262 and 269). Since no new records are available, and neither the "Dana" nor the "Galathea" approached these southern latitudes, I restrict myself, in the present paper, to give a brief general survey of the occurrence of bathypelagic Hydromedusae in the waters around the Antarctic Continent. The neritic forms were discussed above (pp. 147–149, the oceanic epipelagic species p. 177).

In contradistinction to the arctic basins the water masses of the deep-sea with their contents of medusae and other pelagic organisms have free admission towards the slope of the Antarctic Continent, and the southward distribution of the bathypelagic medusae depends only on the sensibility of each single species to the gradually decreasing temperatures. Moreover the configuration of the sea-bottom does not prevent a free communication around the continent, or slightly so for the species living at the greatest depths. The water masses surrounding the continent, however, are partly of antarctic, partly of oceanic origin, as illustrated in the well-known block-diagram in "The Oceans", p. 620, here reproduced in fig. 362. We may try to elucidate to which of the water masses the various species do belong and trace their ways of dispersal, but to divide the deep water masses into an antarctic and a subantarctic (or antiboreal) "region" as I did before (in the "Dana" Report pp. 260–262) is inadequate.

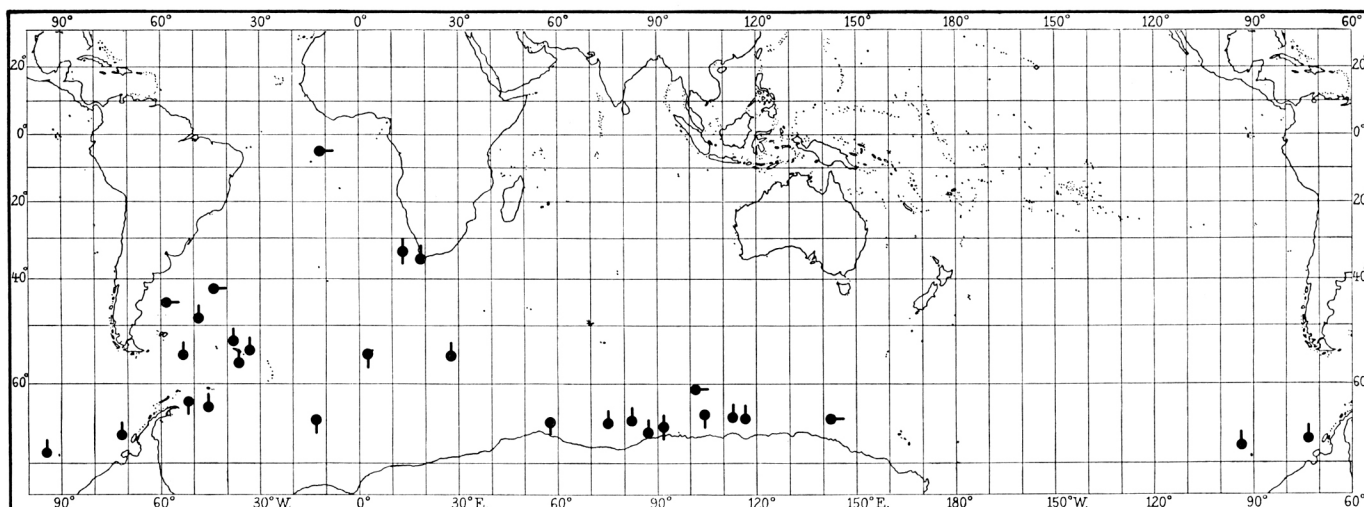


Fig. 363. ● *Haliscera conica*. ●● *Tiaranna rotunda*. ●● *Chromatonema rubrum*.

The thirteen species of bathypelagic Hydromedusae, which up to now have been recorded from the antarctic deep-sea region, may be divided into three groups (see Table XI and the maps, figs. 363, 364), according to their further distribution. Almost all of them occur in the Atlantic and Indian-Ocean sectors of the area, while only five species have been found in the Pacific sector which, however, is insufficiently investigated. For details see the "Discovery" paper quoted above.

A. Species with an extensive distribution in the warm deep water in all the three oceans: *Haliereas minimum*, *Botrynema brucei*, *Pandea rubra*, *Pantachogon haeckeli*, and *Crossota brunnea*; they all occur in the Atlantic sector and along a considerable part of the continental slope of the Indian-Ocean sector, and the two last mentioned species have also been found in one locality in the Pacific sector, 69° S., 126° E., in a haul from a depth of 1000 m ("Discovery").

B. Three species with an extensive distribution in the Atlantic Ocean, but unknown in the warm-water regions of the Indian and Pacific oceans (map, fig. 363): *Haliscera conica*, *Tiaranna rotunda* and *Chromatonema rubrum*. The first mentioned species, *Haliscera conica*, mainly belongs to intermediate water layers and occurs in the Mediterranean and along the west coast of Africa. It has been collected in several localities around the Scotia Sea area in the south-western Atlantic and also in the Pacific Antarctic Basin west of Graham Land, besides in several localities in the Indian-Ocean sector of the antarctic slope region. The two other species of this group are distinctly bathypelagic, widely distributed in the deep parts of the Atlantic from Greenland waters southwards, *Tiaranna* to the northern slope of the South Georgia plateau, *Chromatonema* into the Weddell Sea, and both have been collected in deep hauls in the Indian Antarctic Basins, partly rather near the continental slope, but in the "warm" deep water (see the block diagram), but they have not been found in the Pacific sector, and none of them has extended its distribution northwards in the Indian and Pacific oceans. If their occurrence in the Indian antarctic sector is due to immigration from the Atlantic Ocean, their further penetration into the Pacific may, in this particular case, possibly have been prevented by the Indian Antarctic Rise south of Australia acting as a blockade for these pronounced deep-sea medusae, though their apparent absence in the Pacific sector may perhaps be due to insufficient knowledge of the South Pacific fauna.

The species mentioned above as belonging to groups A and B undoubtedly are inhabitants of the "warm deep-water region" of one or more of the oceans, whence they have spread into the antarctic region following the influx of these water masses towards the continental slope (see the block diagram); from their dominance in the Atlantic Ocean it can be concluded that all of them are of Atlantic origin, being more or less successful stragglers in the other oceans.

C. The third group of species have a predominantly southern distribution in or near the antarctic region, whence, however, they penetrate more or less northwards into the oceans. There are five species; they behave in dif-

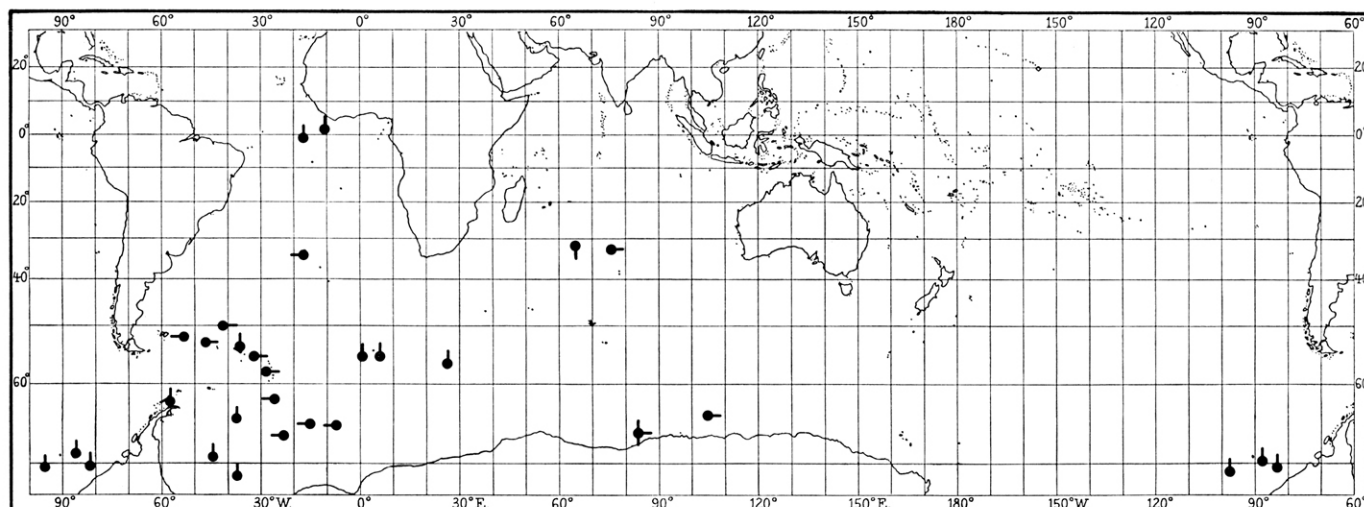


Fig. 364. ● *Arctapodema ampla*. ● *Arctapodema antarctica*. ● *Arctapodema australis*. ● *Euphysora gigantea*.

ferent ways, and none of them is known from any great number of localities. *Haliscera racovitzae* is not strictly bathypelagic; it was first described from Bellinghausen Sea in south-eastern Pacific near the coast of Graham Land, and it occurs in the Weddell Sea; the "Dana" has taken it east and west of New Zealand (KRAMP 1965 p. 108), and a specimen was found near the coast of Chile (by a mistake not mentioned in my recent paper on medusae from the coast of Chile, KRAMP 1966). The species of the genus *Arctapodema* have given rise to much doubt and discussion (see the map, fig. 364); there are probably only three species, all of them occurring in antarctic waters (see KRAMP 1957 a p. 55). *Arctapodema ampla* is recorded from a locality in the Indian sector, about 90° E. near the coast of the continent, it occurs in the Pacific sector west of Graham Land, and in the Weddell Sea in the South Atlantic, whence its distribution is extended to some localities at about the latitude of 55° S. south of Africa, probably also to equatorial waters between Africa and South America; two records from the Mediterranean, however, seem doubtful. *Arctapodema antarctica* is recorded from deep water near South Georgia and the South Sandwich Islands and from the Indian sector of the antarctic region and also from a locality in the central part of the Indian Ocean between Australia and South Africa. Finally *Arctapodema australis* has been found in only two localities, about 90° E. near the Antarctic Continent and about 30° S. and in 70° in the Indian Ocean. The Anthomedusa *Euphysora gigantea*, which is strictly bathypelagic, is restricted to the South Atlantic, the Weddell Sea and the Scotia Sea, but was also found in a locality further north, about 35° S., 19° W. In my paper on the "Discovery" medusae (KRAMP 1957 a p. 6), where this species was first described, I expressed the view that the specimen from this locality was taken in the layer of antarctic intermediate water, which flows northwards below the warmer subantarctic water.

While the species of groups A and B undoubtedly are of oceanic, and presumably of Atlantic, origin and should be regarded as immigrants in antarctic waters, the latter five species, group C, are original inhabitants of the waters adjacent to the Antarctic Continent, but all of them have extended their distribution more or less northwards into the warm water region of one or two of the oceans. Since the exact depth, at which the specimens were captured, is not stated, it is difficult to decide whether they belong to the antarctic bottom water or to the slightly warmer "deep water" with temperatures above 0° C. As, however, in all instances, where data are available, they were collected together with warm-water species, as *Haliceas minimum*, *Pantachogon haeckeli* and *Colobonema sericeum*, their habitat is presumably the layer of "warm deep water" above the antarctic bottom water. A strictly antarctic bathypelagic fauna of Hydromedusae does not exist, and no bathypelagic species of Hydromedusae are endemic in antarctic waters.

The specimens of *Haliscera racovitzae* and *Arctapodema ampla* taken in the Pacific sector near Graham Land are probably derived from the Scotia area in South Atlantic through the Drake Strait; the populations



of *Arctapodema ampla* and *antarctica* in the Indian sector may be derived from the South Atlantic following the same eastward movement along the continental slope as the species of groups A and B.

The analysis given of the fauna of bathypelagic Hydromedusae confirms the statement above (p.179) that, with exception of the arctic basins, there is free communication between the deep water masses with their contents of medusae.

The total number of bathypelagic species (including eurybathic) of Hydromedusae listed in Table XI amounts to 40, of which 30 were found in the Pacific Ocean, 26 in the Indian, and 36 in the Atlantic with adjacent waters; there are accordingly 10 species which were not found in the Pacific, 14 species unknown in the Indian Ocean, and only four which are not recorded from the Atlantic; these are rare species each of them being taken in only 1–3 localities in the other oceans, while the three purely Atlantic species were all found in several localities. There is accordingly a distinct uniformity in the composition of the bathypelagic fauna of medusae in the three great oceans, and a clear predominance of the Atlantic fauna. As far as the Hydromedusae are concerned we must contradict STIASNY (1931 p. 137) that “die frühere Auffassung der Einheitlichkeit der Tiefseefauna (ist) als überwundener Standpunkt zu betrachten”.

One bathypelagic species, *Solmissus albescens*, is endemic (and very common) in the Mediterranean; the five other bathypelagic species occurring in the Mediterranean and listed in Table XI occur in all three great oceans.

## CONCLUDING REMARKS

In the preceding I have given faunistic descriptions of the various parts of the Indo-Pacific waters and tried to correlate the occurrence of the species and the composition of the fauna with hydrographical conditions and the directions of currents. The most important problems of zoogeography are, however, to trace the origin of the species and determine how their present time distribution was attained. It is true, however, that many geographical areas are insufficiently explored, so that future investigations may reveal species in unexpected localities. Uncertainty in the identification of the species may change our views; I want to stress the importance of taxonomic work as a basis for biology and ecology.

Our attempt to trace the ways of dispersal of these pelagic animals over great distances becomes easier, when a species has a continuous distribution agreeing with our knowledge of the currents and other hydrographical conditions; explanations are more difficult, when the distribution of a species appears to be discontinuous; in some cases this is simply due to insufficient knowledge of the actual occurrence of that species, and therefore species, recorded from only a few, scattered localities, should be left out of the discussion; but in other cases a discontinuous distribution should be regarded as an established fact, and in such cases we must agree with EKMAN in his concluding remark (1953 p. 374) that “biogeography . . . must also proceed historically”.

Such problems were discussed in my paper on the Atlantic Hydromedusae; with our present increased knowledge of the Indo-Pacific fauna special attention can be given to the interchange between the faunas of the Atlantic and the Indian and Pacific Oceans, and it is natural to commence with the oceanic faunas, for which the conditions are less complicated than for the neritic forms.

The oceanic, bathypelagic fauna (see Table XI) consists of 40 species, one of which is endemic in the Mediterranean. With exception of the arctic basins (with three endemic species) there is free communication between the deep water masses in the oceans, the ridges between the deep basins being surmountable for the medusae while drifting with the slowly moving currents in the deep water masses. All of the five eurybathic warm-water species listed in the table have a continuous distribution. The species occurring in antarctic and subantarctic waters likewise have a continuous distribution from south-western Atlantic eastwards, but most of them are still unknown in the Pacific. The distribution of the truly bathypelagic species is continuous in almost all instances, but several of them, though occurring in the western parts of the Pacific,



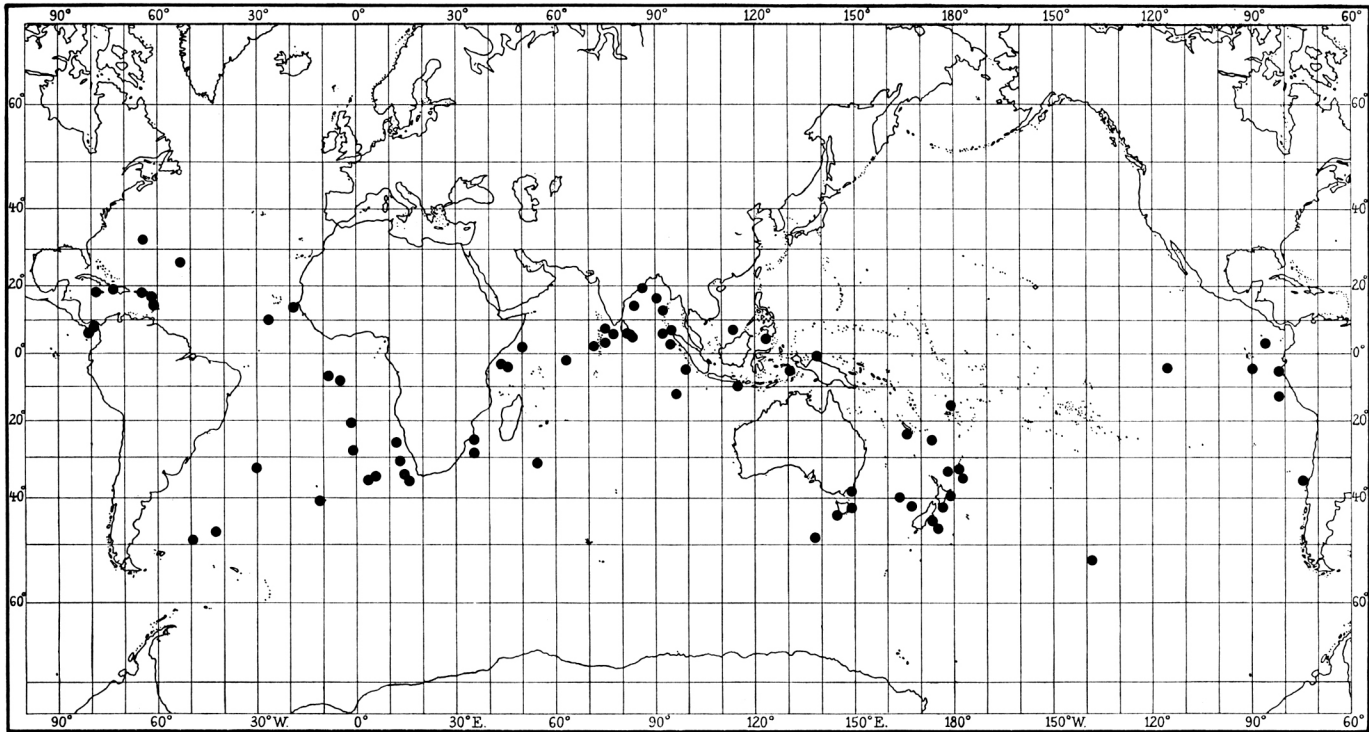


Fig. 365. Distribution of *Halitrephes maasi*.

have not been found in East-Pacific waters; the apparent absence of three species in the Indian Ocean is presumably due to lack of knowledge, since they occur in the Pacific as well as in the Atlantic. Only three species are unknown outside the Atlantic. No submarine barriers, except those bordering the arctic basins, have prevented the medusae living in the deep water masses from extending their distribution throughout the oceanic basins, so former geological structures and formations may be left out of consideration. Nevertheless, the historical point of view should be considered. The bathypelagic medusan fauna seems to be an ancient fauna, since no less than ten genera of Hydromedusae are endemic in the bathypelagic zone, having no representatives in the upper water layers; the bathypelagic genera and species have had plenty of time to extend their distribution over great areas, and with one exception (*Ransonia*) all of the ten endemic genera are represented in all the three great oceans. Some species probably arose in antarctic regions, presumably in the Atlantic parts, whence they are still spreading northwards and eastwards; all tends to show that the Atlantic Ocean has been the centre of origin of the bathypelagic fauna of Hydromedusae (see above p.182), whence their distribution gradually was extended to the other oceans, but several species have not yet accomplished their migration. The distribution of *Halitrephes maasi* may serve as a typical example (fig. 365).

These considerations are in good accordance with the statement by SVERDRUP (1940, in BANZARE Rep. vol. III, P. 2): "In the Indian and the Pacific Oceans the deep water and the bottom water are renewed very slowly by admixture of Atlantic deep water and Antarctic bottom water. The stratospheric layers of the Indian, and especially the Pacific Oceans, are almost motionless as compared to the corresponding layers in the Atlantic Ocean . . . water masses of Atlantic origin are added to the Antarctic circumpolar flow, from which the deep water and bottom water in the Indian and Pacific Oceans are slowly renewed . . ." Once again the occurrence of medusae has proved to be valuable in corroborating hydrographical views.

The oceanic epipelagic fauna (Table X and pp. 175–177) is exposed to considerable variation of hydrographical conditions, which might be supposed to establish insurmountable barriers to the distribution of the species. Table X contains 34 species occurring in Indo-Pacific waters, 11 species unknown in the Indo-Pacific increases the total number of oceanic epipelagic species to 45, among which 26 are common to the Atlantic and the Indo-Pacific waters, and almost all of these have a continuous distribution.

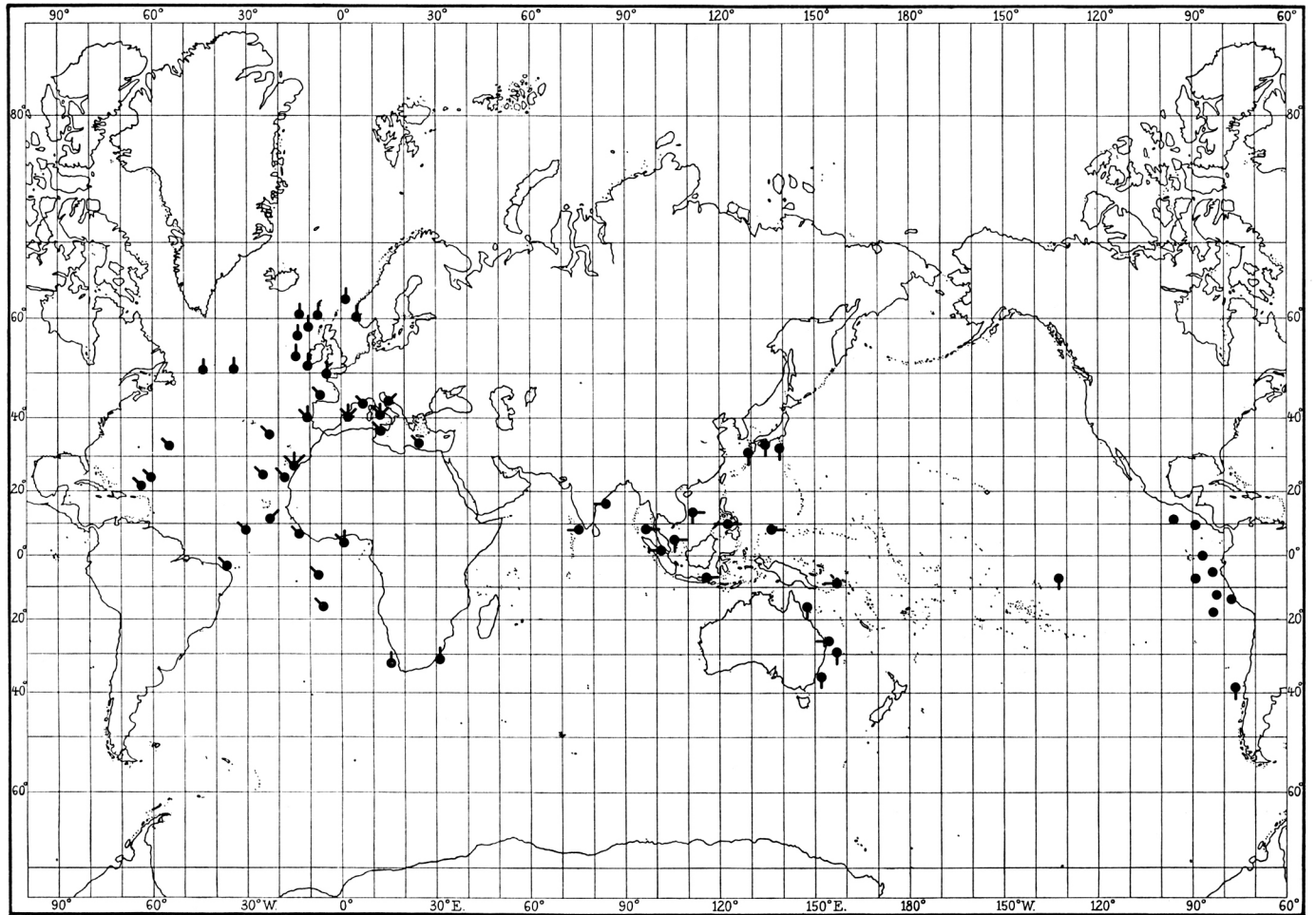


Fig. 366. Epipelagic species with restricted distribution. ● *Solmaris corona*. ● *Solmaris flavescens*. ● *Pegantha rubiginosa*. ● *Aglantha intermedia*. ● *Petasiella asymmetrica*. ● *Solmaris lenticula*. ● *Solmaris rhodoloma*.

Ten species (5 Indo-Pacific and 5 Atlantic or Mediterranean) are excluded from the following discussion, because they have been found in only one or two localities each. Three species are endemic in the Mediterranean (see below). Two arctic species are circumpolar, one of them (*Aglantha digitale*) penetrating into the boreal parts of the Pacific as well as of the Atlantic Ocean. It applies to the Hydromedusae as well as to all other groups of epipelagic animals that none of them is endemic in boreal waters (cf. EKMAN p. 341).

Among 8 Atlantic species unknown in the Indo-Pacific five are rare, but the three others are very common; among 8 Indo-Pacific species unknown in the Atlantic four are rare, while the four others are of common occurrence within restricted areas.

All of the remaining species are inhabitants of warm-water regions, and for these there has been free communication south of Africa and Australia and through the Indo-Malayan areas; only three of them (*Aegina citrea*, *Solmundella bitentaculata* and *Pegantha martagon*, also occur in antarctic waters and may have been able to traverse the Drake Strait south of South America. *Persa incolorata* is common in the Atlantic but rare in the Indo-Pacific (Java and south-eastern Australia), *Amphogona apsteini*, on the other hand, is common in the Pacific and Indian Oceans, recorded only once in the Atlantic (Gulf of Guinea). It is probably accidental that *Cunina globosa* has not been observed in the Indian Ocean. All the others have a continuous circumglobal distribution in the warm parts of all of the three oceans.

One might ask, whether the interchange of these species between the Atlantic and the Indian Oceans might in some degree be due to a former connection through the Mediterranean Sea across south-western Asia, *i. e.* through the Tethys Sea. It might seem possible, but is not a necessary explanation of the community of the faunas, I would even say that it is improbable. Among 17 species recorded from the Mediterranean 8 have

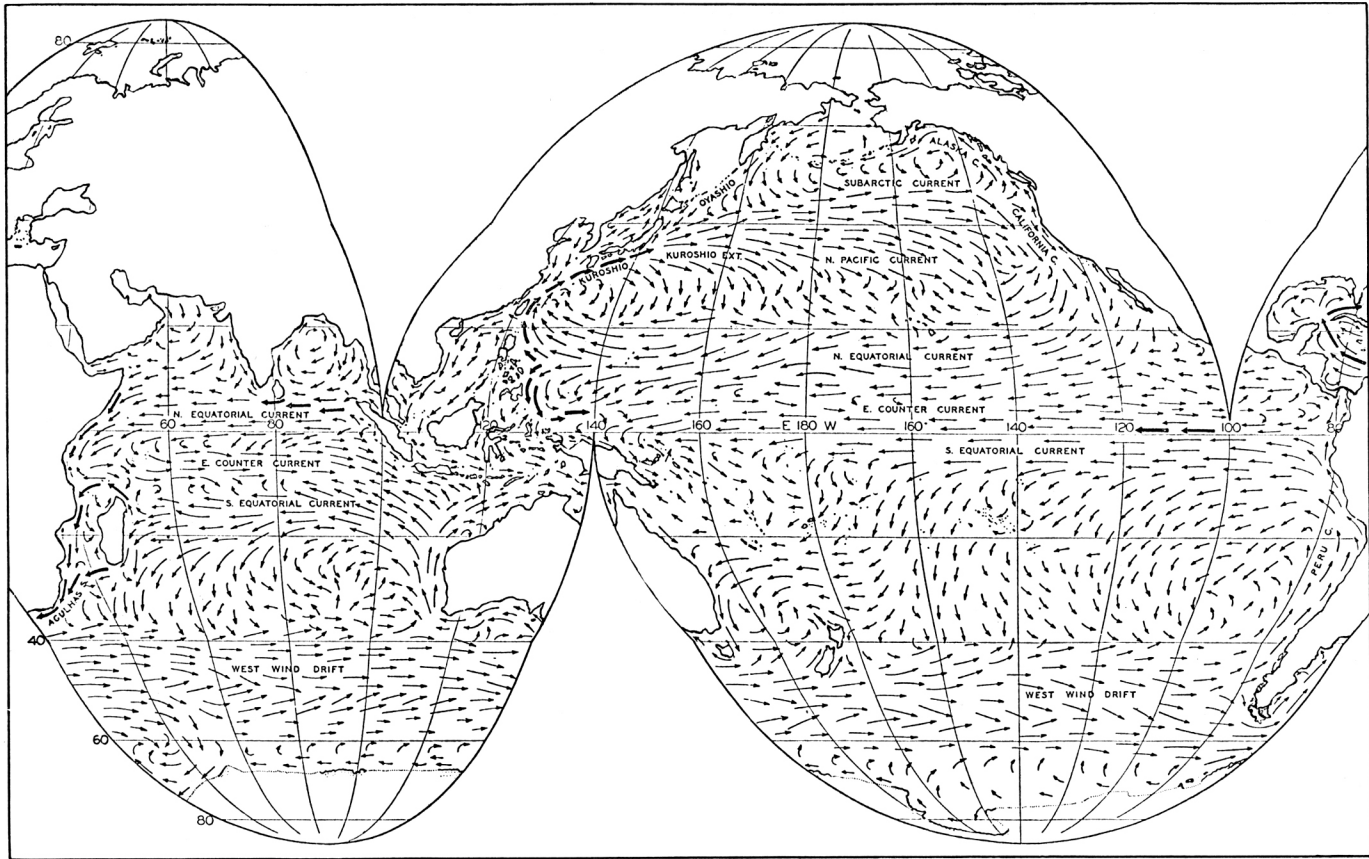


Fig. 367. Surface currents in the oceans.

a cosmopolitan distribution in all warm areas, 9 Mediterranean species do not occur in the Indian Ocean, and 16 species occurring in the Indian Ocean are absent in the Mediterranean.

The numerous warm-water species with a circumglobal distribution are almost equally common throughout the extensive areas (also right across the Pacific Ocean, in contradistinction to the bathypelagic forms, see above, p. 184); it is difficult, therefore, to say anything definite about the origin of this fauna.

A comparatively small number of species, however, occur in restricted areas and have evidently arisen there (see the map, fig. 366). This applies to three Atlantic and four Indo-Pacific species (rare species omitted). *Solmaris corona*, *Solmaris flavescens* and *Pegantha rubiginosa* (the latter with a doubtful record from South-East Australia) are common in the Mediterranean and in extensive parts of the eastern Atlantic, whence their distribution has been slightly extended towards the western Atlantic. One Pacific species, *Aglantha intermedia* (in my opinion a valid species, see p.177) is recorded from several localities in the eastern tropical Pacific, off the coasts of Mexico, Colombia and Peru, evidently originated in this area, whence it has not extended its distribution. The centre of origin of the other three species was undoubtedly the Indo-Malayan Region; the occurrence of *Petasiella asymmetrica* has not been extended beyond this region; the occurrence of *Solmaris lenticula* is slightly extended, westwards to India, eastwards to the Solomon Islands and East Australia; *Solmaris rhodoloma* also occurs in the waters of East Australia and southern Japan, and it is recorded from a locality near the Marqueses Islands (KRAMP 1956 p. 4); it was first described from the coast of Chile by BRANDT, 1838 (its affinity discussed in KRAMP 1953 p. 302).

Seven oceanic epipelagic species are thus known, most of them Narcomedusae, with demonstrable centres of evolution: in the eastern Atlantic (three), in the eastern Pacific (one), and in the Indo-Malayan Region (three).

The neritic fauna. A comparison between the Atlantic and Indo-Pacific faunas of neritic Hydromedusae was made above (pp.170–174) with reference to actual statements of the conditions within each of the zoogeographical regions. Since the neritic fauna of these animals consists of meropelagic Leptolina derived, as far

as we know, from hydroids attached to the bottom (or to objects on the bottom) within the shelf regions along the coasts, their dependance on the surrounding conditions is much more complicated than that of the oceanic forms; when tracing the ways of conveyance of the neritic forms attention should be paid to many other local conditions, and the distributional features of the neritic forms should be compared with those of the oceanic forms. Historical points of view should be taken into consideration in several cases. For details reference is made to the account pp. 170–174 and also reference to previous remarks.

In the arctic as well as in the antarctic regions the Atlantic and Pacific sections are connected by uninterrupted coastal stretches and therefore also uninterrupted routes of distribution of such species, which can endure low temperatures, also under the present conditions, and, as a matter of fact, the vast majority of the arctic and antarctic neritic species have, or may be presumed to have, a circumpolar distribution. It is hardly possible to point out any centre or centres of evolutionary origin of the arctic and antarctic faunas.

The zoogeographical problems are much more complicated as far as the boreal faunas are concerned. As emphasized by EKMAN, and confirmed by the occurrence of the medusae (see above, p.186) there are very few, if any, purely boreal species among the oceanic epipelagic animals; but as far as the neritic forms are concerned, the boreal regions have numerous endemic species, and this applies to the Atlantic as well as to the Pacific boreal regions, which seems to indicate that these faunas are of ancient origin. The species of Hydromedusae which are common to the boreal parts of both oceans are mainly such which are able to endure the present low temperatures in the arctic regions, whence they penetrate more or less into the boreal waters, besides some immigrants from southern areas. The problem arises, when some species are found to be common to the Atlantic and the Pacific boreal regions, though they do not occur in intervenient waters, either in the Arctic or in the Indian Ocean (see above, pp. 142, 171); their discontinuous occurrence in the two widely separated boreal regions probably is derived from a direct communication north of Siberia, which may have been possible during the postglacial period, when a milder climate prevailed (EKMAN p. 162).

As to the question of an Atlantic or a Pacific origin of the boreal fauna opinions are very different (cf. EKMAN p. 159). If the species and genera of Hydromedusae in the two boreal regions are counted, we find that the total number of species amounts to 67 in the Pacific, 108 in the Atlantic, thus an overwhelming number in the Atlantic, but this includes northern and southern immigrants as well as endemic species; the difference in number of genera is somewhat less conspicuous, as follows:

Genera in Pacific 46, common with Atlantic 28 (60 %)  
Genera in Atlantic 62, common with Pacific 28 (45 %)

The Hydromedusae, thus, are in strong contradistinction to the statement by EKMAN (p. 157) that "The cold-water fauna is considerably richer in the North Pacific than in the North Atlantic" and further (p. 158) "Of the temperate shelf fauna of the northern hemisphere the Pacific . . . contains a several times greater number of species and genera than the Atlantic region . . .", from which it might be concluded that "a considerable part of the North Atlantic boreal fauna and the Polar Sea arctic fauna is derived from the North Pacific". EKMAN's considerations, it is true, refer to the shelf fauna, but the meropelagic neritic Hydromedusae are derived from demersal hydroids belonging to the shelf and may be regarded in the same way.

During the Tertiary period, still into the Pliocene, the Polar basin had a comparatively warm climate; a rich fauna may have originated there, spreading into the North Pacific as well as into the North Atlantic, supplying these two regions with a "boreal" fauna. When separated by adverse climatic and hydrographical conditions, the two faunas developed analogously to each other, but not in identical directions, producing closely related, but not identical species replacing each other<sup>1</sup>. In the North Pacific this fauna was not exposed

<sup>1</sup> Number of species of some more important genera in the boreal regions.

	Atlantic	Pacific	common
Sarsia . . . . .	6	4	3
Bougainvillia . . . . .	8	3	2
Leuckartiara . . . . .	3	4	3
Phialidium . . . . .	6	3	1
Aequorea . . . . .	5	0	0

to particularly great climatic fluctuations; in the Atlantic, on the other hand, climatic and hydrographical conditions were subjected to great, partly disastrous changes followed by periods with conditions favourable to a further evolution of the existing "boreal" fauna and moreover open to a greater invasion of southern genera and species than in the Pacific (see above, p.142), which may account for the presence of a particularly rich fauna of certain groups of animals (e. g. medusae). The many identical species common to the Atlantic and the Pacific Boreal Regions is due to a direct interchange in present and post-glacial time, but the predominance of species in the North Atlantic (of medusae) or in the North Pacific (of some other groups of animals as stated by EKMAN) does not allow the assumption that the "boreal fauna" is derived from one or the other of the two oceans. The original boreal fauna is most probably derived from the Tertiary polar basin, evolved in different ways and to a different extent in the two boreal regions, while these were in open connection with the Polar Basin, the contents of identical species being due to mutual interchange in recent time.

The neritic fauna of the East-Pacific Tropical and the Peru-Chilean Regions is imperfectly known; it may be characterized as a greatly impoverished Indo-West-Pacific fauna with addition of Atlantic, mainly West-Atlantic, species. The Hydromedusae, therefore, confirm the supposition of a former open connection across the isthmus of Panama (see pp.144,146,171). The fauna of neritic Hydromedusae in the South-Australian and New Zealand Region entirely consists of species belonging to the Indo-West-Pacific Region, in contradistinction to other groups of animals for which it constitutes a distinct zoogeographical region.

The Indo-West-Pacific Region. As previously pointed out this is the region with the richest marine fauna in the world, and this also applies to the Hydromedusae. In the account, pp.172-173 the species of the Indo-West-Pacific Region were divided into groups according to their distribution in other regions or subregions; the first groups, A-D, comprise special cases which need no further considerations than those made on p. 172. Group E consists of species, for which a direct communication south of Africa is possible under the present conditions, and it is the largest group which, however, were divided into three minor groups: E, a, 7 species which are common and indigenous in the Indian Ocean, but rare in the Atlantic, where they may be regarded as immigrants following the Agulhas Current. E, b, 9 species, which are common and widely distributed in both these oceans; most of them are partly oceanic, and a mutual interchange of these species between the oceans is easy to understand; three species of this group are, however, strictly neritic and need special comments (see below). The species of the groups E, a, and E, b are examples showing that a continuous distribution gives no problems. The third of these groups, E, c, consists of only four species, undoubtedly of Atlantic origin; one of them, *Phialopsis diegensis*, is partly oceanic and seems to have immigrated along the same route as some of the oceanic, epipelagic species, south of Africa and Australia to the west coast of South America and further north to California; *Aequorea aequorea* may have followed the same route as far east as Australia. The two others have not been found further east in the Indian Ocean than in the surroundings of Madagascar. — Group F (p.173) comprises 8 species which crossed before the establishment of the Panama isthmus, in the one or the other direction; all of them are unknown in the eastern Atlantic but occur in the West-Indies, more or less widely distributed in Indo-Pacific waters, mainly within the Indo-West-Pacific Region, therefore probably of Indo-Pacific origin.

Finally, there are 14 species with a discontinuous distribution, their occurrences in Atlantic and Indo-Pacific areas being completely isolated and very different (see p.173); almost all of them occur in the Mediterranean, and this leads to a discussion of a possible interchange of species through former open connections between the oceans.

These questions were discussed in my paper on the Atlantic medusae (1959), but with our increased knowledge of the Indo-Pacific fauna the discussion may be resumed.

Among the species enumerated under group G, p.173, the following five species should be excluded from the discussion, either because they are rare, being found in only a few localities, or because the Indo-Pacific records are more or less doubtful: *Podocoryne minuta*, *Eutonina scintillans*, *Euphysa aurata*, *Bougainvillia ramosa* and *Lovenella cirrata*. Among the others there is only one, *Staurodiscus tetrastaurus*, which has not been found in the Mediterranean. Two species, *Merga violacea* and *Cirrholovenia tetranema*, occur in the Mediterranean but not in north-western Europe, and they have not been found on the coasts of Africa, while



they are rather common in the Indo-Malayan region; presumably these two species are derived from the Indo-Malayan waters. The remaining six species occur in the Mediterranean, but within the Atlantic waters they have their principal occurrence in north-western Europe; most of them are absent in the southern parts of Africa, rare or entirely absent in the western part of the Indian Ocean, but more or less common further east, mainly in the Indo-Malayan region. An interchange south of Africa seems most improbable for these species under the present conditions; another explanation of their occurrence in both oceans must be given. There are three questions: the route of dispersal, the time when an interchange was possible, and the geographical regions, from which the species are derived.

During the greater part of the Tertiary Period, towards the end of it, though with interruptions, there was a widely open connection, the Tethys Sea, from the middle Atlantic across the present position of the Mediterranean and parts of south-western Asia to the Indian Ocean. It is beyond doubt that the Tertiary Tethys Sea gave origin to a fairly homogeneous fauna which, however, underwent considerable alterations in conformity with geographical and geological changes. The distribution of several groups of marine animals gave rise to the supposition that the similarity of the fauna in the Indian Ocean and that in the Mediterranean and in the adjacent, non-tropical part of the Atlantic Ocean is due to such open connections, and this at any rate applies to families and genera, but as regards the species, the millions of years should be taken into consideration. In comparison with the great abundance of species of Hydromedusae in the Indian Ocean and Indo-Malayan waters the number of species which also occur in the Mediterranean-Atlantic waters is not considerable and, as pointed out above, many of them may have been dispersed from one ocean to the other south of Africa; some species, however, need an explanation. The fact that the majority of such species occur in the Mediterranean as well as in the Atlantic Ocean might confirm the view that they are derived from the Tethys Sea. As emphasised by me in the "Atlantic" paper (p. 270), if the species under consideration "really are remnants of the ancient Tethys fauna, they must be very conservative, since their specific characters have not been visually altered during the ages after their geographical separation". There must be other possibilities.

In early Quaternary Period there was a narrow opening between the Mediterranean and the Red Sea, but this opening was not of importance for an interchange of species between the Indian and the Atlantic Oceans.

As pointed out above (p. 187) the oceanic, epipelagic species of Hydromedusae common to the Atlantic and the Indo-Pacific waters may all have been spread directly south of Africa, and it seems improbable that any of them have traversed the Mediterranean basin of the Tethys Sea. As far as the neritic species are concerned, the following may be stated:

a. Among the 187 species known from the Indo-West-Pacific Region 26% have been found in the Atlantic Ocean, but only 13% in the Mediterranean (see Table IX); this does not suggest that the fauna common to the two regions is derived from the Tethys Sea, which comprised the Mediterranean.

b. Many species, which undoubtedly are of Indo-Pacific origin but also have been found in the Atlantic, do not occur in the Mediterranean.

c. Species, which in the Atlantic have their principal occurrence in north-western Europe, all occur in the Mediterranean.

d. Among six species with a partly oceanic occurrence and more or less widely distributed in the oceans, three occur in the Mediterranean and three are absent there.

Evidently, therefore, the Mediterranean fauna of these animals is much more closely allied to the Atlantic than to the Indo-Pacific fauna.

In my opinion the present occurrence of identical species of neritic Hydromedusae common to Atlantic and Indo-Pacific waters is not derived from the Tertiary connection through the Asian-Mediterranean basin of the Tethys Sea but is of a later date and, like the dispersal of the oceanic-epipelagic fauna, it has taken place around South Africa.

The only objection to this view is the present discontinuous distribution of a limited number of species, *viz.* those listed in group G, p. 173.



With exclusion of the species mentioned p. 173 (as rare or with uncertain Indo-Pacific records) the discussion comprises 8 species with a predominantly northern distribution in Atlantic waters, whose dispersal was probably obstructed by the tropical or subtropical temperatures of the South African waters. All of them, however, occur under truly tropical conditions in the Indian and Malayan regions. A possible explanation might be that their transgression around South Africa, in one or the other direction, was accomplished in the early Quaternary Period, when the waters west of Africa had low temperatures at the same time as arctic conditions prevailed in the North Atlantic. In the postglacial periods the Atlantic populations of these species penetrated northwards into boreal waters and adapted themselves to low temperatures, while the populations in the Indian Ocean retained their tropical adaptation, thus a physiological, though not a visual, structural difference of the populations evolved. The possibility, however, also exists that some of these species may later be found in localities effacing the distances between the habitats as known up to now.

I am aware that the views expressed above do not agree with my views in the "Atlantic" paper (1959 *a*), since increased knowledge of the Indo-Pacific fauna has now been obtained.

As to the much discussed Mediterranean problem opinions still differ. STEINITZ's (1929) strongly maintained the Tethys origin of the fauna of the "Mediterranik", and not until this broad basin had shrivelled into the present Mediterranean Sea and lost its connection with the Pacific Ocean, did the Atlantic fauna increase, so that it surpassed the Mediterranean fauna, which gave rise to the erroneous conception that the Mediterranean fauna was an impoverished Atlantic fauna. STEINITZ's views may hold good for the higher systematic categories as families and genera, but not for the species. At least for the Hydromedusae I maintain my former views, as expressed in my Atlantic paper (1959 *a*, pp. 267–268) of the Mediterranean fauna as an impoverished Atlantic fauna.

## FINAL CONCLUSIONS

Finally, it is discussed to what extent the distribution of the Hydromedusae may elucidate "the origin of the zoogeographical conditions of the present age". In an instructive chapter EKMAN (1953 pp. 77 ff) discussed this problem of the Atlantic fauna being derived from the Indo-Pacific or *vice versa*.

As shown above (p. 188) free communication has been possible in arctic and antarctic regions, and a circumpolar interchange of species has occurred at any time and in both directions. The origin of the North Pacific and the North Atlantic boreal faunas was discussed pp. 188–189, both presumably derived from the Tertiary Polar basin during a warm period, each of them further evolved independently, an interchange being resumed in post-glacial time. The crucial point is the relation between the Indo-Pacific and the Atlantic warm-water faunas. The interchange across central America, before the isthmus of Panama was closed, applied to rather few species, and there is reason to believe that most of them were of Pacific origin.

The diverging opinions mainly concern the importance of the Indo-West-Pacific Region and its comparison with the Atlantic fauna. "The great abundance of species found in the Indo-West-Pacific, and in particular the Malay region, has often been accorded an exaggerated importance, these regions having been regarded as the main developmental centre or even as the sole centre of origin and development for many animal groups . . ." (EKMAN p. 78), and further: "It has been asserted that the Atlantic fauna represents an impoverished offspring of the Indo-Pacific fauna". EKMAN is strongly opposed to these views; during the ages the oceans have been exposed to great geographical and climatic alterations, and this mainly applies to what we now call the Atlantic Ocean, while the Indo-Malayan region retained its "inherited richness". The Hydromedusae tend to show that this region and its surroundings were really the centre of origin of the faunas in peripheral parts of the Indo-West-Pacific Region, but its influence on the Atlantic fauna of these animals may be elucidated by the following considerations, in which I compare the Indo-West-Pacific fauna with that of the warm, eastern Atlantic; the boreal fauna is composed of species of southern and northern origin and is therefore left out of consideration in this connection, and the relation between the East-Atlantic and the West-Atlantic fauna was discussed in detail in my paper on the Atlantic Hydromedusae (1959 *a*).

In the Indo-West-Pacific Region 67 genera of neritic Hydromedusae are represented, among which 40, *i. e.* 64 %, are represented in the warm eastern Atlantic; among 73 genera in the warm eastern Atlantic 59 % also occur in the Indo-West-Pacific, thus a considerable similarity as far as genera are concerned; but no more than 16 % of the Indo-West-Pacific species have been found in the warm eastern Atlantic. This confirms the supposition expressed above (p.190) that when the two regions were finally separated towards the end of the Tertiary period, the species in both regions developed independently of each other and gave rise to diverging populations (in agreement with UMBROVE, 1930); the great climatic alterations in the Atlantic may even have accelerated the evolution of new species. The community of species at the present time is due to an interchange around South Africa; for some species it can be decided, whether they are derived from one or the other of the oceans. For species with a circumglobal distribution and which are about equally common in the three oceans nothing definitely can be said about their origin; this applies to 6 species; rare species and species with doubtful Indo-Pacific records should also be left out of consideration; but among 21 species with a prominent occurrence in one or the other of the regions 12 can be said to be of Atlantic and 9 of Indo-West-Pacific origin, thus no great difference. The following conclusions can be made:

No species of recent Hydromedusae has been dispersed from one ocean to another through the Tertiary Tethys Sea, which is only responsible for similarity between higher systematic categories.

The populations of Indo-Pacific and Atlantic neritic Hydromedusae in the warm-water regions have been developed independently since the termination of the Tertiary period; in Quaternary time a limited interchange of species has taken place around South Africa in both directions.

An interchange of oceanic epipelagic species, mainly south of Africa, has comprised the majority of the existing species, and many have obtained a circumglobal distribution, their Atlantic or Indo-Pacific origin being uncertain, but presumably of almost equal importance; some few species, arisen in separate Pacific, Malayan or Atlantic areas, have given origin to local populations without being dispersed to other oceans (p. 187).

The bathypelagic fauna of Hydromedusae is entirely of Atlantic origin (p. 185).

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