



AUSTRALIAN NATIONAL ANTARCTIC RESEARCH EXPEDITIONS

ANARE RESEARCH NOTES 4

A Guide to the Scyphomedusae of the Southern Ocean
and Adjacent Waters

David O'Sullivan

ANTARCTIC DIVISION
DEPARTMENT OF SCIENCE AND TECHNOLOGY

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A N A R E

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N O T E S

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A GUIDE TO THE SCYPHOMEDUSAE
OF THE SOUTHERN OCEAN AND ADJACENT WATERS

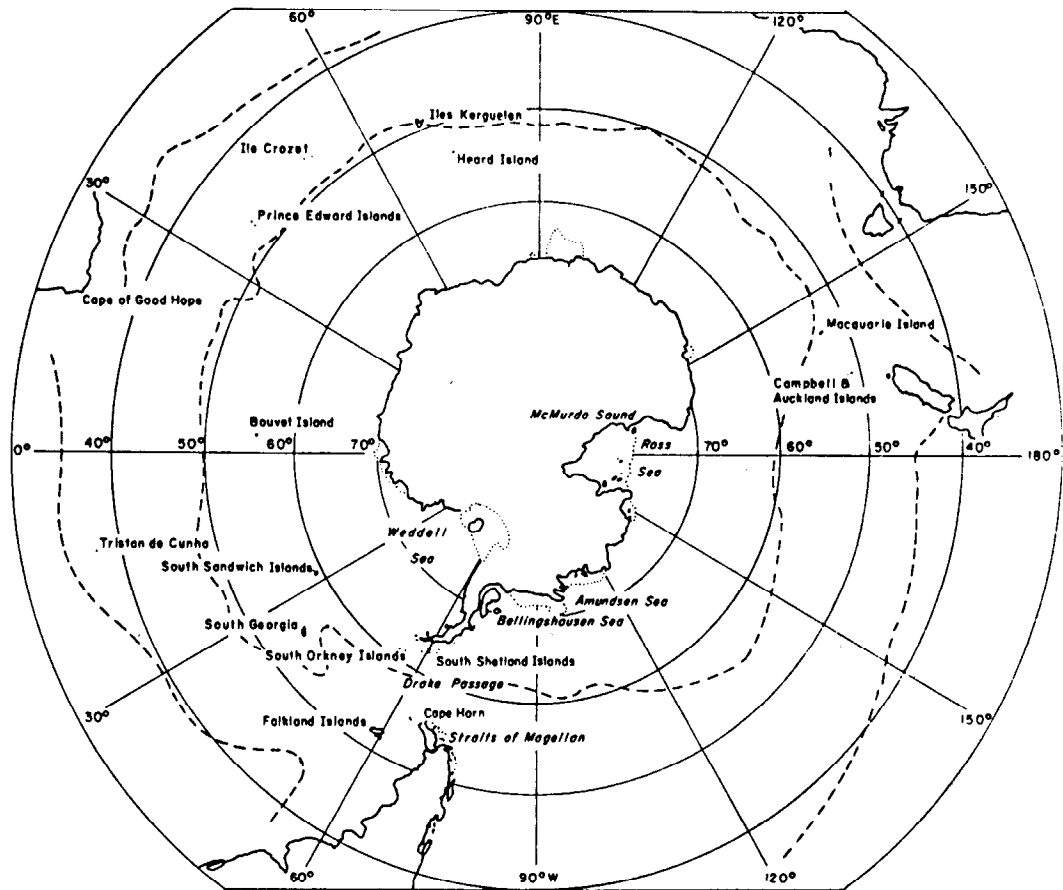
by David O'Sullivan,

Antarctic Division, Department of Science and Technology,
Kingston, Tasmania, Australia.

ABSTRACT

In the Southern Ocean there are eleven species of Scyphomedusae from two free-swimming orders (Coronatae and Semaestomeae), and one sedentary order (Stauromedusae). For each of these species, (Haliclystus antarcticus, Haliclystus kerguelensis, Lucernaria australis, Lucernariopsis vanhoeffeni, Atolla wyvillei, Pericolpa quadrigata, Periphylla periphylla, Desmonena chierchianum, Desmonena gaudichaudi and Diplumaris antarctica) the synonymy, vertical and horizontal distribution and diagnostic characters are listed. A distribution map and illustration is also given for each. Species not found in the Southern Ocean but in adjacent waters are included in the keys.

Map of Southern Ocean showing places mentioned in text.



1. INTRODUCTION

Scyphomedusae are the jellyfish or true medusae and differ from the Hydromedusae in that they are generally larger, and are more robust. They possess gastric tentacles and do not have a velum (except in Cubomedusae). Details of the general structure and morphology of the medusa form are given in the Guide to Hydromedusae of the Southern Ocean and Adjacent Waters (ANARE Research Notes Number 5). The medusa is the dominant and conspicuous stage in the life cycle, the polypoid form is restricted to a small larval stage. Although these cnidarians are typically free-swimming animals one order, the Stauromedusae, is sessile. In this group the exumbrellar surface is drawn out into the stalk (or calyx) by which the animal attaches to algae and other objects (Barnes, 1974).

The Class Scyphozoa is made up of five orders of which the Coronatae, Semaestomatae and Stauromedusae have representatives in the Southern Ocean. The Southern Ocean is defined as that area between the Antarctic continent and the Subtropical Convergence. It can be divided into the Antarctic and Subantarctic, separated by the Antarctic Convergence. The Cubomedusae and Rhizostomatae are found in waters adjacent to the Southern Ocean (south of 30° South), so both are defined and are included in the keys together with members of the other three orders which have been found in adjacent waters. The regions they have been found in are given in brackets: (Au) for southern Australia; (NZ) for New Zealand; (Pa) for southern Pacific Ocean; (SAm) for South America; (At) for southern Atlantic Ocean; (SA) for southern Africa; (In) for the southern Indian Ocean; and (Co) for cosmopolitan in adjacent waters.

Hyman (1940) gives a good account of the general morphology and physiology of the medusae. Russell (1970) gives a subject index to literature on Scyphomedusae biology and morphology. The first modern systematic monograph on the Scyphomedusae was that of Haeckel (1880). Early work was summarised in Mayer (1910). Up-to-date diagnoses of all known species are given by Kramp (1961) which includes a bibliography of papers published since 1910. In this handbook the diagnostic characters of the orders, families, genera and species and keys are taken from Kramp (1961) except where otherwise stated. In the synonymy only incorrect references from the Southern Ocean and adjacent waters are given.

Workers on the Scyphomedusae of the Southern Ocean include Haeckel (1880) ("Challenger" Expedition); Maas (1906) ("Belgica" Expedition); Browne (1908) ("Scotia" Expedition); Maas (1908) and Bedot (1908) ("Français" Collection); Vanhoffen (1908, 1912) ("Gauss" Collection); Browne (1910) ("Discovery" and "Southern Cross" Expeditions); Carlgren (1930) and Kramp (1948) (Swedish Antarctic Expedition); Stiasny (1934) ("Discovery" Collection); Kramp (1957a) (B.A.N.Z. Antarctic Research Expedition); Kramp (1957b) (Australian National Antarctic Research Expedition); and Uchida (1971) (Japanese Antarctic Research Expedition).

For each species a distribution map has been given. On these maps symbols represent the locations where a species has been found. In some cases they are only approximate as the author has specified a general area rather than an exact position. A question mark next to a symbol indicates a tentative identification or that subsequent authors have questioned the validity of the original identification. The positions of the Subtropical Convergence and the Antarctic Convergence are from Lomakina (1966).

2. STRUCTURE AND CHARACTERS OF PELAGIC SCYPHOMEDUSAE (after Russell, 1970)

The Umbrella

The umbrella is typically saucer-shaped or hemispherical, except in the Coronatae in which it may vary from the flat disc-like form of Atolla to the high conical bell of Periphylla. The mesogloea is usually thick and of solid consistency, being thickest in the centre of the umbrella and tapering off in thickness to the umbrella margin which is always interrupted by a number of clefts which result in the formation of separate lobes, the marginal lappets. According to whether the marginal lappets are situated next to a marginal sense organ or marginal tentacle they are known as rhopalar or tentacular lappets respectively. In the Cubomedusae the umbrella margin is turned inwards and terminates in a thin velum-like fringe the velarium.

In coronate medusae the thickness of the mesogloea does not taper evenly towards the umbrella margin, but the marginal zone of the umbrella is separated from its central disk by a circumferential furrow known as the coronal groove. The marginal zone of the umbrella beyond the coronal groove is also grooved by a number of radial furrows which divide the margin into a number of thickened areas known as pedalia. The pedalia may be rhopalar or tentacular according to whether they are situated at the base of a marginal sense organ or of a marginal tentacle respectively.

The exumbrellar surface may be quite smooth, or it may be roughened by the presence of numerous raised nematocyst warts. The nematocyst warts may also occur on the manubrium and its basal thickenings, but usually not on the subumbrella surface of the umbrella itself. The subumbrellar surface of the umbrella is characterised by the presence of the ectodermal musculature, composed of circular and radial muscle systems. The circular or coronal muscle may be continuous and very massive or divided radially into a number of separate fields. The radial muscles may be very strongly developed or absent.

Marginal Tentacles

The marginal tentacles, which may be solid or hollow, are usually very extensible and capable of contraction by direct shortening or spiral coiling. They can be situated either just on the margin of the umbrella or on the subumbrella in semaeostome medusae.

Gastrovascular System

Basically the gastrovascular system consists of a central stomach and a peripheral marginal zone, the gastrovascular sinus, or coronal sinus.

The central stomach leads to the exterior through a mouth or oral opening in the centre of a manubrium. The manubrium may be no more than four perradial well-formed lips as in the coronate medusae, but in all other scyphomedusae it consists of a shorter or longer pillar-like fused basal portion of solid consistency, the oral tube, which divides at its end into four elongated structures, the oral arms. The margins of these oral arms are often thin and much folded and frilled, or even curtain-like, and form mouth lips. In the Rhizostomeae the manubrium and upper arms are sometimes provided with swellings known as scapulets.

The gastrovascular sinus can be divided into a number of partitioned areas or pouches by radial septa. These pouches can be replaced by a system of radial canals running from the stomach to the umbrella margin to communicate with a continuous ring canal. In the Rhizostomeae such a system can be a complicated network of anastomosing canals.

Gonads

In the Coronatae the gonads are eight in number, each situated approximately on an adradius. They arise as endodermal proliferations of the gastrovascular endoderm of the coronal sinus, and are thus peripheral to the central stomach. In the Semaestomeae and Rhizostomeae there are four gonads each situated interradially within the cavity of the central stomach. A genital sinus or ostia can develop in the subumbrellar endoderm of the stomach just peripheral to the gastric filaments. In the Cubomedusae, four pairs of leaf-shaped gonads are attached along the interradial septa and extend into the gastrovascular space.

Marginal Sense Organs

The marginal sense organ is a composite structure which may serve more than one function. In its most developed form as found in some of the Semaestomaeae, it is composed of a club-like body, the rhopalium, projecting from the umbrella margin and into which a small diverticulum from the gastrovascular system runs, the rhopalar canal.

The rhopalium consists of a solid terminal body whose endoderm is filled with crystals, the statocyst, and a hollow basal stem receiving the rhopalar canal. On the exumbrellar side there is an ectodermal pigment spot or ocellus, and there is an endodermal ocellus on the subumbrellar side.

Other less-developed marginal sense organs may lack ocelli, but the general form is the same throughout the Semaestomeae and Rhizostomeae.

In the Coronatae the marginal sense organ differs in that the rhopalium projects from a basal cushion on the umbrella margin and is not protected by a hood formed by an extension of the umbrella margin itself. The statocyst is, however, roofed over by a small spoon-shaped hood at the end of the rhopalium itself. In the Cubomedusae the sense organs are perradial situated within niches on the sides of the bell.

Thus the term 'marginal sense organ' includes a complex of sense organs each of which may serve a different function, e.g. the statocyst sensitive to gravity, the ocellus sensitive to light, and the exumbrellar and subumbrellar sensory pits whose functions are not known, but which may perhaps be sensitive to chemical substances.

3. LIFE HISTORY AND BIOLOGY (after Barnes, 1974)

With few exceptions, scyphozoans are dioecious, and the gonads are located in the gastrodermis, in contrast to the usual epidermal gonad in hydrozoans. In septate groups with gastric pouches, the eight gonads are located on both sides of the four septa. In semaeostomeae medusae, which lack septa, four horseshoe-shaped gonads lie on the floor of the stomach periphery when mature, and the eggs or sperm break into the gastrovascular cavity and pass out through the mouth. In some semaeostomes, the eggs become lodged in pits on the oral arms. This temporary brood chamber is the site of fertilization and early development through the planula stage.

Cleavage produces a hollow blastula that undergoes invagination to form a typical planula larva. After a brief free-swimming existence, the planula settles to the bottom and becomes attached by its anterior end. The attached planula then develops into a little polypoid larva called a scyphistoma.

The scyphistoma looks very much like a hydra, and it feeds and produces new scyphistomae by asexual budding, directly from the midcolumn wall. At certain periods of the year young medusae are formed. In some species (Cubomedusae) the scyphistoma transforms directly into a small medusa. In others, medusa formation is accomplished by transverse fission of the oral and of the scyphistoma, a process called strobilization. Buds may form one at a time (monostrobilization) so many simultaneously (polystrobilization) so that the immature medusae, called ephyrae, are stacked up like saucers at the oral end of the body stalk. As formation of the ephyrae is completed, they break away from the oral end of the scyphistoma one by one.

After strobilization, the scyphistoma may resume its polypoid existence until the following year, when formation of ephyrae is repeated. A scyphistoma may live for one or several years.

The ephyra is almost microscopic, has a deeply incised bell margin, and has incompletely developed adult structures. Ephyrae feed largely on small crustaceans, which are caught on the lappets and then wiped across the mouth and manubrium. An ephyra that has formed in the winter takes six months to two years to transform into a sexually reproducing adult medusa.

Modifications of the life cycle which avoid the necessity of a substratum are known. Some pelagic Scyphomedusae, such as species of Atolla and Periphylla, produce one adult from a single egg. In other species the larva is retained on the parent in cysts. Highly specialized cysts and scyphistomae occur in gastric brood chambers in some deep sea species. Further details on the life history of the Scyphomedusae are given in Russell (1970).

Swimming is effected by pulsation of the umbrella in which the coronal and radial muscles are concerned. The radial muscles are the first to contract and this tends to arch the summit of the umbrella. This is followed after a slight interval by the contraction of the coronal muscle by which the subumbrellar space is reduced and water is forced out through the now diminished subumbrellar opening. In this way the umbrella margin acts in much the same capacity as the velum of the Hydromedusae. This is probably typical of all Scyphomedusae, but the proportionate degree of development of coronal and radial muscles varies much from species to species.

Adult scyphozoans feed on all types of small animals, and several eat ctenophores or other medusae. Not many scyphozoans feed upon fish; in fact, larval fish of a number of species use certain species of scyphozoans for protection. As the medusa sinks slowly downward, prey is captured on contact with the tentacles or oral arms of the manubrium. Some species are actually suspension feeders for as they sink, plankton becomes entrapped in mucus on the subumbrellar surface, which is flagellated in these forms. Cilia then sweep the food to the bell margin, where it is scraped off by the oral arms. Ciliated grooves on the oral arms carry the food to the mouth and stomach. Members of the order Rhizostomeae, possess many small secondary mouths that open into the stomach by way of canals in the oral arms. Small animals trapped on the surface of the frilly oral arms are carried into the mouths within mucous cords.

Digestion is essentially as described in hydras. The gastric filaments are the source of extracellular enzymes, and the gastrodermal nematocysts are probably used to quell prey that is still active.

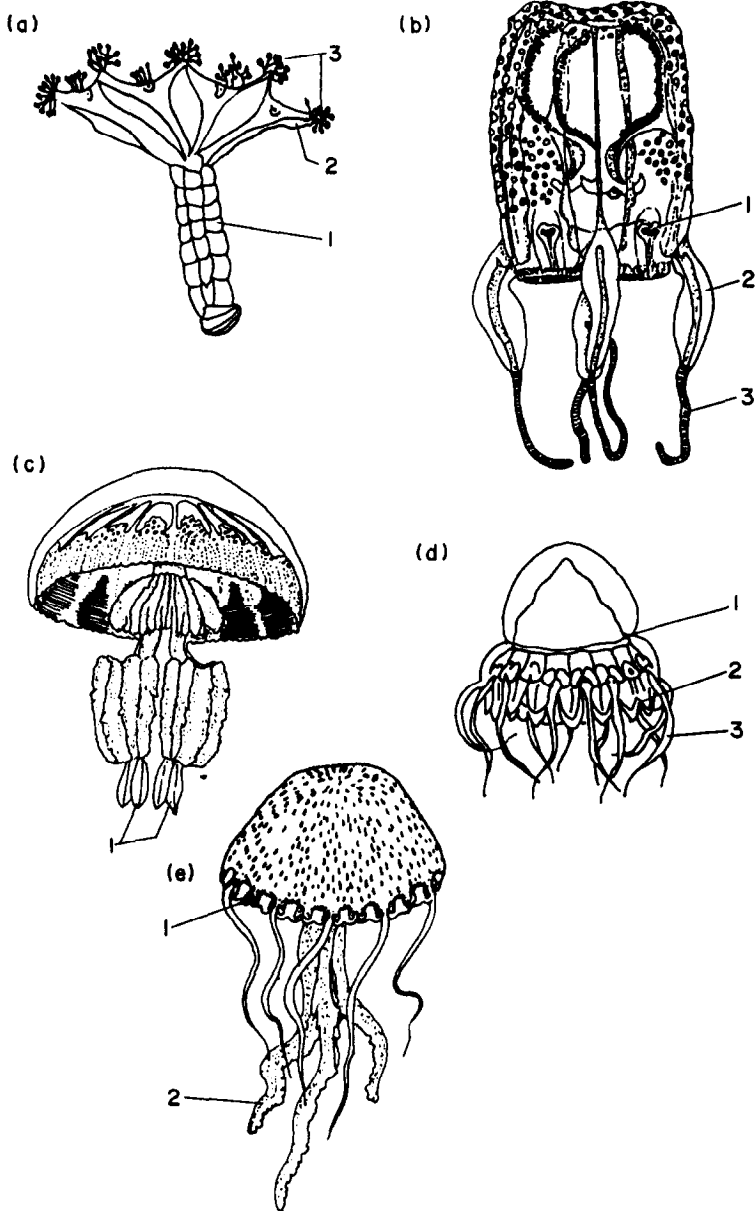


Figure 1. Diagnostic characters mentioned in the keys. a. (1) calyx, (2) arms, (3) tentacles; b. (1) sense organ, (2) pedalia, (3) tentacle; c. (1) mouths; d. (1) coronal furrow, (2) pedalia, (3) marginal tentacle; e. (1) marginal lappet, (2) lips.

4. KEY TO ORDERS

(Figure 1)

- 1a) Sessile, attached by a stalk on the aboral side of the trumpet-shaped body (Figure 1a) STAUROMEDUSAE
- b) Free-swimming medusae 2

- 2a) Bell cubical with four flattened sides and a velum (Figure 1b) CUBOMEDUSAE
- b) Bell discoidal or cone-shaped, not cubical, no velum present 3

- 3a) Numerous mouths with long oral arms, no marginal tentacles (Figure 1c) RHIZOSTOMEAE
- b) With a single mouth, marginal tentacles 4

- 4a) Bell of medusa with a deep circular groove or constriction (Figure 1d) CORONATE
- b) Bell without groove or constriction (Figure 1e) SEMAEOSTOMEAE

5. ORDER STAUROMEDUSAE

Scyphozoa developing directly from the scyphistoma, consisting of a calyx and a more or less distinct aboral peduncle attached to the substratum by an adhesive disk; typically with adradial marginal lobes (arms) carrying hollow, terminally knobbed tentacles; 2 families.

5.1 KEY TO FAMILIES:

With 4 simple, perradial stomach pouches ELEUTHEROCARPIDAE

With 4 perradial stomach pouches divided into an outer and an inner space by a transverse, circumferential membrane CLEISTOCARPIDAE

5.2 FAMILY ELEUTHEROCARPIDAE

Stauromedusae with four simple, perradial stomach pouches; 3 sub-families, separated on development of tentacles, presence or absence of muscles in the peduncle and the continuity of the coronal ring muscle.

Subfamily LUCERNARIINAE

Eleutherocarpidae with faintly or well developed marginal lobes; with eight adradial clusters of hollow, terminally knobbed tentacles; peduncle single-chambered or with four perradial chambers, with muscles in the septa; coronal muscle unbroken or divided into eight separate sectors; 3 genera of which 2 are found in the Southern Ocean.

Key to genera:

With perradial and interradial marginal anchors ... Haliclystus

Without perradial or interradial marginal anchors . Lucernaria

Genus Haliclystus Clarke 1863

Lucernariinae with eight perradial and interradial marginal anchors; peduncle with four perradial chambers; calyx with eight well developed marginal lobes (arms) about equidistant; coronal muscle divided into eight separate sectors; 6 species of which 3 are found in the Southern Ocean or adjacent waters.

Key to species:

- 1a) Calyx conical to pyramidal; peduncle about as long as height of calyx (SAm) H. auricula (Rathke)
- b) Calyx conical, flat 2

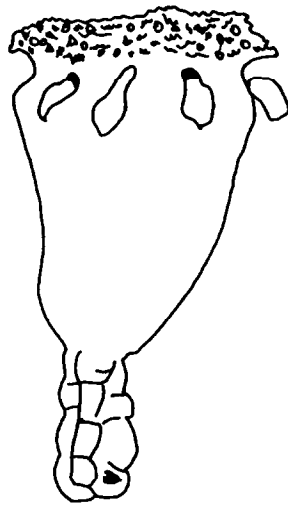
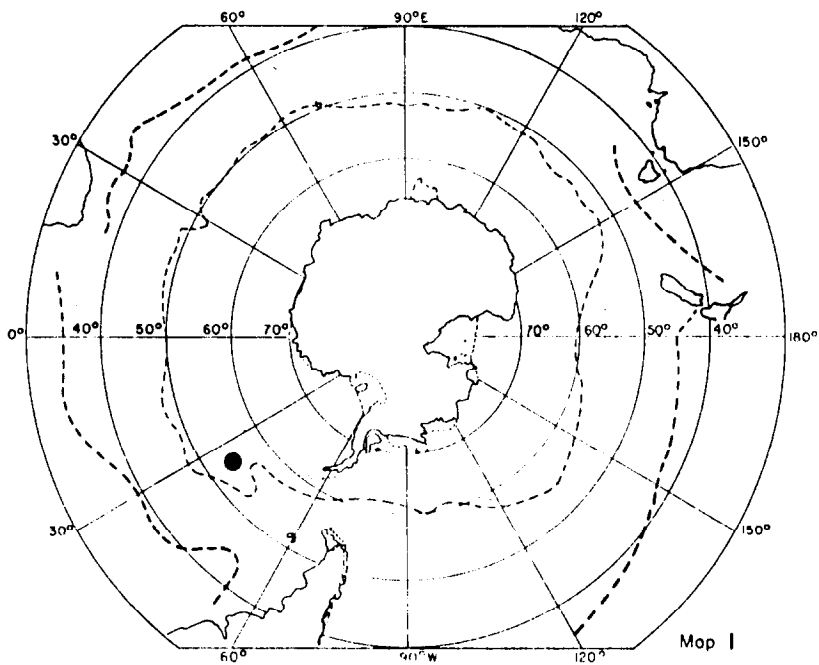


Figure 2. Haliclystus antarcticus, side view.



Map 1. Distribution of Haliclystus antarcticus.

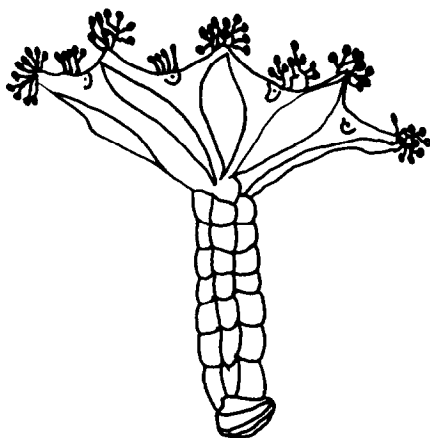
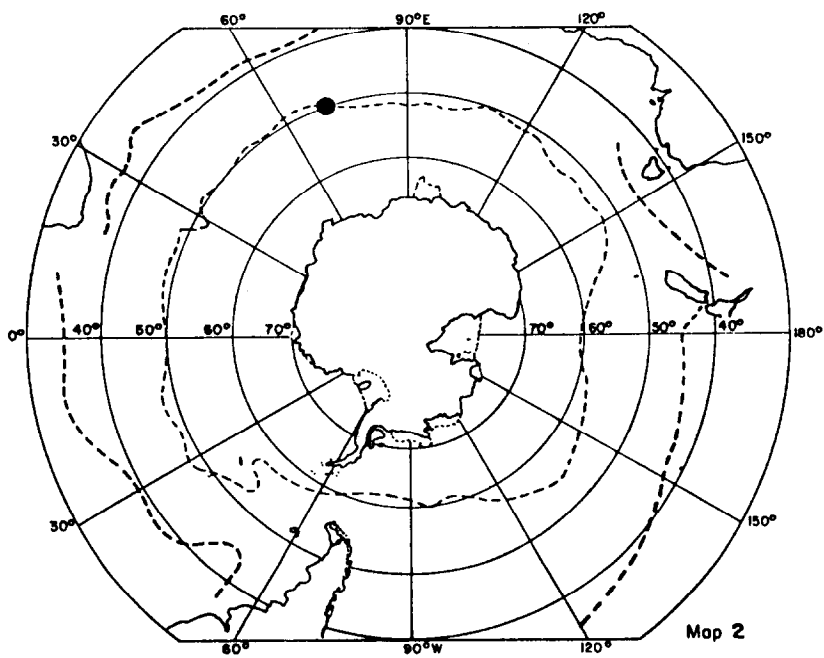


Figure 3. Haliclystus kerguelensis, side view.



Map 2. Distribution of Haliclystus kerguelensis.

- 2a) Peduncle one half to two-thirds as long as height of calyx H. antarcticus Pfeffer
 b) Peduncle about twice as long as height of calyx H. kerguelensis Vanhoffen

Haliclystus antarcticus Pfeffer 1889

(Figure 2, Map 1)

Diagnostic Characters:

Calyx conical

Size up to about 28 mm wide

Peduncle half to two-thirds as long as height of calyx

Arms fairly short, flat, equidistant, each with up to 100 or more tentacles

Marginal anchors very large, biscuit-shaped, each with a tentacular knot

Gonads wide, lancet-shaped, widely separated, extending to end of arms

Colour blue-violet, with lighter, somewhat reddish anchors and tentacles (Mayer, 1910).

Thiel (1928) compares Haliclystus antarcticus with H. kerguelensis.

Haliclystus kerguelensis Vanhoffen 1908

(Figure 3, Map 2)

Diagnostic Characters:

Calyx conical, flat

Size up to 27 mm wide

Peduncle about twice as long as height of calyx

Arms fairly short, equidistant, each with no more than 50 tentacles

Marginal anchors small, oval, each with a tentacular knob

Gonads wide, lancet-shaped, widely separated, extending to end of arms

Colour bell and peduncle sandy brown, gonads dark olive-brown, terminal knobs of the tentacles rose-red (Mayer, 1910).

This form is closely related to Haliclystus antarcticus, but has fewer tentacles, smaller anchors and apparently a longer peduncle (Mayer, 1910). The colours of the specimens are too variable to be relied upon as specific characters (Kramp, 1957a).

Genus Lucernaria O.F. Muller 1776

Lucernariinae without perradial and interradian marginal anchors or papillae; peduncle single-chambered; calyx with eight well developed marginal lobes; coronal muscle divided into eight separate sectors; with eight gonads in four interradian pairs; 7 species of which one is found in the Southern Ocean.

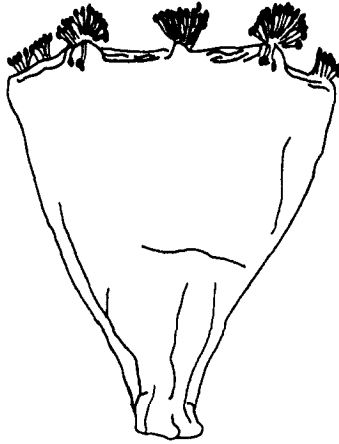
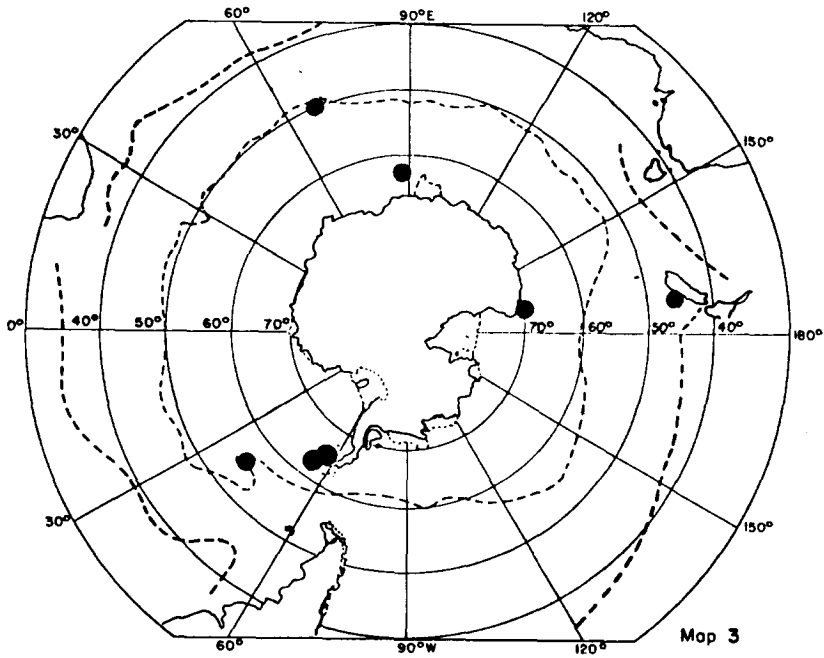


Figure 4. Lucernaria australis, side view.



Map 3. Distribution of Lucernaria australis.

Lucernaria australis Vanhoffen 1908

(Figure 4, Map 3)

Diagnostic Characters:

Calyx thimble-shaped, with sloping sides

Size up to 9mm wide and slightly more in height

Peduncle almost rudimentary

Notches between arms, perradial ones are somewhat wider and deeper than interradial

Arms short, each with up to 100 short tentacles

Gonads very broad, extending to base of arms.

As this species was described from an immature specimen which had neither gonads nor peduncle, Mayer (1910) suggested that it was possible that this medusa may be a young Haliclystus, but as it has since been found in the Antarctic by Carlgren (1930), Kramp (1961) considers it a valid species.

Subfamily KISHINOUEINAE

Eleutherocarpidae with well developed marginal lobes; with eight adradial clusters of hollow, terminally knobbed tentacles; peduncle single-chambered, or four-chambered in lower portion, without muscles; coronal ring muscle discontinuous in each adradius; 3 genera of which 1 is found in the Southern Ocean.

Genus Lucernariopsis Uchida 1929

Kishinouyeinae without perradial and interradial marginal anchors of papillae (rarely papillae in young stages); peduncle single-chambered; 2 species of which one is found in the Southern Ocean.

Lucernariopsis vanhoeffeni (Browne 1910)

(Figure 5, Map 4)

(Lucernaria vanhoeffeni Browne, 1910; Stiasny, 1931a)

Diagnostic Characters:

Calyx funnel-shaped

Size 20 to 30 mm wide, 30 to 40 mm high

Peduncle not present (or very flattened, no true stalk, Browne, 1910)

Marginal lobes 8, equidistant, with equally developed notches between them

Tentacles 30 to 40 in each of the adradial clusters

Adhesive disk very broad and flat, separated from the calyx by a narrow constriction.

Uchida (1929) erected a new genus, Lucernariopsis, to take L. vanhoeffeni and L. campanulata (Lamouroux) both formerly in the genus Lucernaria O.F. Muller. The shape of the peduncle distinguished L. vanhoeffeni from the other species of the genus (Browne, 1910).

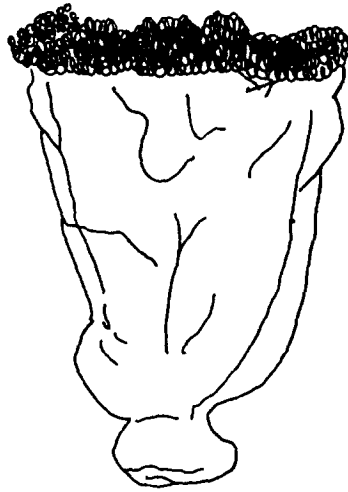
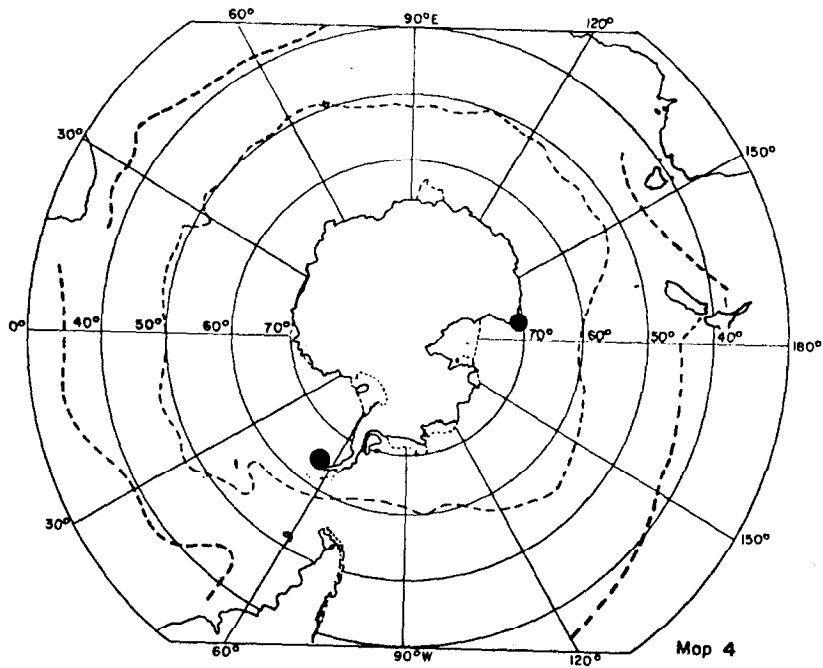


Figure 5. Lucernaria vanhoffeni, side view.



Map 4. Distribution of Lucernaria vanhoffeni.

Subfamily LIPKEINAE

Eleutherocarpidae with reduced tentacles; peduncle single-chambered, with muscles; coronal muscle unbroken; 1 genus.

Genus Lipkea Vogt 1886

Lipkeinae without perradial and interrarial marginal anchors or papillae; 3 species of which 1, Lipkea stephensoni Carlgren, has been found off South Africa (Carlgren, 1933).

5.3 FAMILY CLEISTOCARPIDAE

Stauromedusae in which the gonads are united by a transverse, circumferential membrane (claustrum) which divides each of the four perradial stomach pouches into an outer and an inner space; 3 sub-families of which 2 are found in waters adjacent to the Southern Ocean.

Subfamily DEPASTRINAE

Cleistocarpidae without, or with faintly indicated marginal lobes; adradial tentacles terminally knobbed, arranged in one or more rows around the bell margin; perradial and interrarial tentacles similar to adradial or papilliform; 2 genera of which one is found in waters adjacent to the Southern Ocean.

Genus Depastromorpha Carlgren 1935

Depastrinae with glandular cushions surrounding bases of the eight primary tentacles and some of the tentacles in the adradial group; with unbroken coronal muscle inside the primary tentacles; 1 species, D. africana Carlgren which has been found off South Africa (Carlgren, 1935).

Subfamily CRATEROLOPHINAE

Cleistocarpidae with eight radial lobes; with eight adradial clusters of terminally knobbed tentacles; without perradial or interrarial anchors or papillae; peduncle four-chambered, without muscles; 1 genus.

Genus Craterolophus Clarke 1863

With the characters of the family; 2 species, 1 of which (C. macrocystis von Lendenfeld) has been found off the east coast of New Zealand (von Lendenfeld, 1884).

6. ORDER CUBOMEDUSAE

Scyphomedusae with umbrella margin not cleft into lappets; with four interradial tentacles or groups of tentacles situated on gelatinous, wing-shaped or spatula-shaped structures (pedalia); with four perradial sense organs situated within niches on the sides of the bell; with four wide perradial sacs extending outwards from the central stomach into the subumbrellar cavity; incompletely separated by interradial septa; with four pairs of leaf-shaped gonads attached along the interradial septa and extending into the gastrovascular space; the opening of the bell cavity partly closed by an annular diaphragm (velarium); 2 families.

6.1 KEY TO FAMILIES: (Uchida, 1929; Bigelow, 1938)

Cubomedusae with 4 simple or tripartite interradial tentacles with pedalia; without diverticula of the 4 stomach pouches CARYBDEIDAE

Cubomedusae with 4 interradial tentacle clusters; with 8 diverticula of the 4 stomach pockets CHIRODROPIDAE

Southcott (1956) working on Australia Cubomedusae erected a new family Chironecidae, based on Chironex Southcott and containing that one genus, but Kramp (1961) included Chironex in the Chirodripidae.

6.2 FAMILY CARYBDEIDAE

Cubomedusae with four simple or tripartite interradial tentacles; four stomach pouches without diverticula; 3 genera of which 2 occur in adjacent waters to the Southern Ocean.

Key to genera:

Stomach flat, without mesenteries Carybdea

Stomach deep, connected to the subumbrella by well developed perradial mesenteries Tamoya

Genus Carybdea Peron & Lesueur 1809

Carybdeidae with four simple pedalia; stomach flat, without mesenteries; gastric cirri forming brush-like bundles at the interradial corners of the stomach, or (if expanded) crescentic areas extending horizontally; 1 species, C. alata Reynaud has been found off South Africa (Haeckel, 1880), in the southern Atlantic (Reynaud, 1830) and the southern Pacific Ocean (Agassiz & Mayer, 1902).

Genus Tamoya Muller 1859

Carybdeidae with four simple pedalia; stomach deep, connected with the subumbrella by well developed perradial mesenteries; gastric cirri in bands extending vertically along the walls of the stomach, in the interradial; 1 species, T. haplonema Muller has been found off south-west Africa (Ranson, 1949).

6.3 FAMILY CHIRODROPIDAE

Cubomedusae with four interradial clusters of tentacles; the four stomach pouches with eight diverticula; 3 genera of which 1 occurs in waters adjacent to the Southern Ocean.

Genus Chirodopus Haeckel 1880

Chirodopidae with eight branched, or feathered sac-like projections from the four perradial stomach pouches into the bell cavity; the free margins of the eight gonads have grape-like swellings; 1 species, C. gorilla Haeckel has been found off South Africa (Stiasny, 1931a).

7. ORDER RHIZOSTOMEAE

Scyphomedusae with umbrella margin cleft into lappets; without marginal tentacles; without a central mouth opening, but with numerous mouths upon eight adradial, fleshy, branched, arm-like appendages arising from the centre of the subumbrella; with rhopalia between marginal clefts; 2 suborders separated on canal structure, shape of rhopalar pits and shape of subgenital ostia.

Suborder DAKTYLIOPHORAE

Mouth-arms three-winged; a network of anastomosing canals, issuing from the primary ring canal, does not communicate with the gastral cavity except through the radial canals; subumbrellar muscles annular; rhopalar pits with radial folds; subgenital ostia narrowed by papillae, five families of which 4 are found in waters adjacent to the Southern Ocean.

7.1 KEY TO FAMILIES:

- 1a) With eight pairs of scapulets on upper arms 2
- b) Without scapulets 3

- 2a) Mouth arms coalesced throughout entire length STOMOLOPHIDAE
- b) Mouth arms coalesced in proximal portion only RHIZOSTOMATIDAE

- 3a) Blind ending and non anastomosing canals LYCHNORHIZIDAE
- b) Anastomosing canals communicating with ring canal ... CATOSTYLIDAE

7.2 FAMILY LYCHNORHIZIDAE

Daktyliophorae with centripetal (usually blindly ending and non-anastomosing) canals between the 16 radial canals; with broad, much folded mouth-arms; 3 genera of which 1 occurs off southern Australia.

Genus Pseudorhiza von Lendenfeld 1882

Mouth-arms with very long terminal clubs, with or without filaments between the mouths; eight radial canals reaching bell margin, eight only reaching ring canal; in each of the 16 spaces 10 are centripetal unbranched, blind vessels; 2 species both of which have been found off southern Australia: P. aurosa von Lendenfeld (von Lendenfeld, 1882b) and P. haeckeli Haacke (Haacke, 1884; Thiel, 1926, Southcott, 1958). Southcott (1958) suggested that the 2 are possibly synonymous.

7.3 FAMILY CATOSTYLIDAE

Daktyliophorae with intracircular network of anastomosing canals communicating with the ring canal, but not always with the 16 radial canals; the eight rhopalar canals extending to the umbrella margin, the eight inter-rhopalar only to the ring canal; mouth-arms pyramidal; 6 genera of which 2 have representatives in waters adjacent to the Southern Ocean.

Genus Catostylus L. Agassiz 1862

With a broad, intracircular anastomosing network in direct communication with both rhopalar and inter-rhopalar canals and with the ring canal; mouth-arms without special appendages; 8 species, of which is one found off south-eastern Australia: C. mosaicus (Quoy & Gaimard), see Kramp (1961) for records.

Genus Leptobrachia Brandt 1838

The long, linear mouth-arms bear no frilled mouths near the middle of their length; but near their points of origin from the arm-disc there is a ventral row of mouths, and beyond the naked mid-region there are three lines of mouth, one ventral and two dorsal; mouth-arms terminate in a naked, pointed end. Doubtful genus with one species L. leptopus (Chamisso & Eysenhardt) which has been found north of New Zealand (as Leonura leptura) and off South America (as Leonura terminalis) by Haeckel (1880).

7.4 FAMILY RHIZOSTOMATIDAE

Daktyliophorae with mouth-arms coalesced in proximal portion only; without a primary mouth opening; manubrium with a complicated canal system; distal portion of arms three-winged usually with a terminal club; 3 genera of which 1 is found in waters adjacent to the Southern Ocean.

Genus Rhizostoma Cuvier 1800

Rhizostomatidae with small scapulets and short manubrium; mouth-arms without secondary clubs or filaments, but each with a single, club-like terminal appendage; usually with a ring canal; intracircular network of canals with few and large meshes; 2 species of which R. pulmo (Macri) has been found off South Africa (Mayer, 1910: as R. pulmo var. capensis).

7.5 FAMILY STOMOLOPHIDAE

Daktyliophorae with mouth-arms coalesced throughout their entire length; with a permanent primary mouth opening; manubrium with reduced canal system; lower arms dichotomously or irregularly branched, without terminal clubs; 1 genus.

Genus Stomolophus L. Agassiz 1862

Usually without ring canal; rhopalar canals thickened; large scapulets; with a very wide, long and small-meshed canal system, lying very near to the radial canals; 2 species of which S. meleagris L. Agassiz has been found off South America (Haeckel, 1880).

Suborder KOLPOPHORAE

Mouth-arms dichotomous and triangular or three winged, a network of anastomosing canals communicate with the central gastral cavity in several places between the radial canals; rhopalar pits smooth, without radial folds; subgenital osita without papillae; five families of which one is found in waters adjacent to the Southern Ocean.

7.6 FAMILY MASTIGIIDAE

Kolpophorae with short, pyramidal, three-winged mouth arms; with filaments on the arm-disc; 3 genera of which one is found in waters adjacent to the Southern Ocean.

Genus Phyllorhiza L. Agassiz 1862

Mouth-arms broad, leaf-shaped, with large window-like openings in the lateral membranes, lower parts of the mouth-arms with numerous filaments; intracircular mesh-work of canals never communicating with the perradial rhopalar canals; 3 species of which P. punctata von Lendenfeld has been found off south-eastern Australia (von Lendenfeld, 1884; Stiasny, 1924, 1931a).

8. ORDER CORONATAE

Scyphomedusae with the umbrella margin cleft into lappets; with a singular mouth opening provided with simple lips; with sense organs (rhopalia) and solid marginal tentacles arising from clefts between the lappets; with a circular, coronal furrow in the exumbrella, and peripheral to this a zone of gelatinous thickenings (pedalia) divided by radiating clefts alternating in position with the tentacles and rhopalia; six families of which three occur in the Southern Ocean and adjacent waters.

8.1 KEY TO FAMILIES: (after Russell, 1970)

- 1a) With more than eight marginal sense organs (rhopalia) and more than eight marginal tentacles, the sense organs and tentacles being equal in number ATOLLIDAE
- b) With eight or less rhopalia 2
- 2a) With eight rhopalia (four perradial and four interradial), eight adradial marginal tentacles NAUSITHOIDAE
- b) With four rhopalia (interradial) and 4 to 28 marginal tentacles PERIPHYLLIDAE

8.2 FAMILY ATOLLIDAE

Coronatae with numerous (more than eight) marginal sense organs (rhopalia) which alternate with an equal number of tentacles; marginal lappets twice as numerous as the tentacles; 1 genus.

Genus Atolla Haeckel 1880

Atollidae with eight adradial gonads and four interradial subgenital ostia; disc quite flat, central part lenticular, circular furrow deep; 4 species of which one has been found in the Southern Ocean. Atolla russelli has been described by Repelin (1962) from off the coast of south-west Africa (see Kramp, 1972 for a review on the distribution of all the species).

Atolla wyvillei Haeckel 1880

(Figure 6, Map 5)

(Colaspis achillis Haeckel, 1880)

(Atolla chuni Vanhoffen, 1902; Browne, 1908; Stiasny, 1934)

(A. verrilli Vanhoffen, 1908, Stiasny, 1934)

(A. bairdi Stiasny, 1934)

Diagnostic Characters:

Size up to 150 mm wide

Stomach basal attachment clover-shaped

Tentacles up to 32, usually about 22

Marginal septa diverging at their proximal ends, not completely covered by coronal muscle.

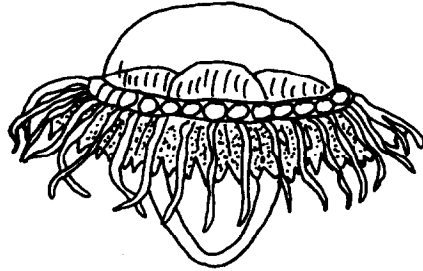
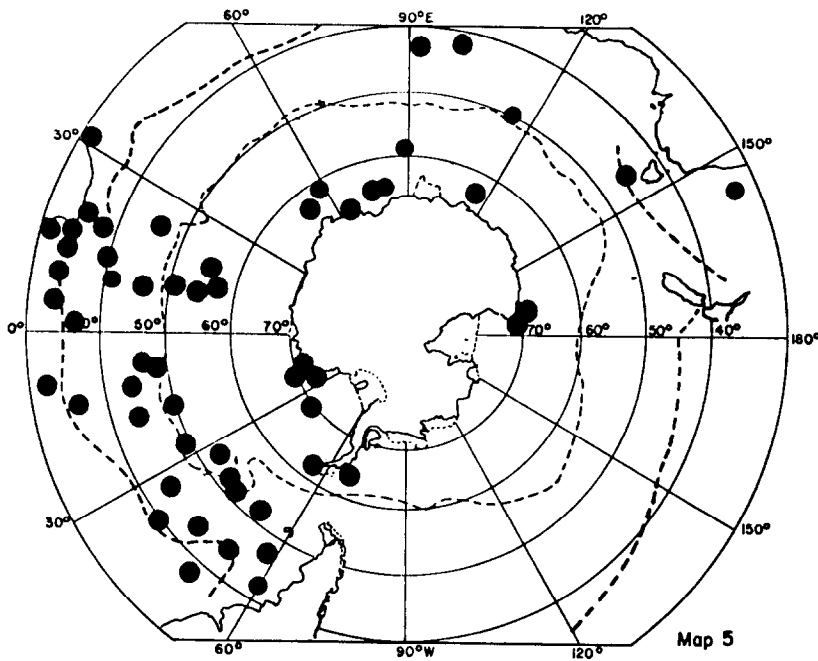


Figure 6. Atolla wyvillei, side view.



Map 5. Distribution of Atolla wyvillei.

This species has a cosmopolitan distribution, penetrating into Antarctic seas past 70° South (Kramp, 1948). It is predominantly bathypelagic being found below 1000 m (Kramp, 1957b). Russell (1970) gives details on the structure and habit of Atolla wyvillei and the other common species of the genus.

8.3 FAMILY NAUSITHOIDAE

Coronatae with eight rhopalia, eight tentacles and 16 marginal lappets; with sac-like pouches upon the subumbrella; 16 radiating stomach pouches; 2 genera.

Genus Nausithoe Kolliker 1853

Nausithoidae with eight adradial gonads; 3 species have been found in waters adjacent to the Southern Ocean: N. albatrossi (Maas) off Chile (Kramp, 1952), N. challengerii (Haeckel) off Tristan de Cunha (Haeckel, 1880) and N. punctata Kolliker off the Cape of Good Hope (Stiasny, 1934).

Genus Palephyra Haeckel 1880

Nausithoidae with four interradial gonads; 2 species occur near the Southern Ocean: P. antiqua Haeckel off Australia (Haeckel, 1880) and P. indica Vanhoffen off New Zealand (Stiasny, 1940).

8.4 FAMILY PERIPHYLLIDAE

Coronatae with four interradial rhopalia and with four or more (up to 28) tentacles; 2 genera occur in the Southern Ocean.

Key to genera:

- With 4 perradial tentacles Pericolpa
With 12 tentacles (four perradial and eight adradial) Periphylla

Genus Pericolpa Haeckel 1880

Periphyllidae with four perradial tentacles; eight adradial lappets; eight gonads, adradial or on both sides of the four interradial; 1 species occurs in the Southern Ocean and two in adjacent waters: P. compana (Haeckel) off New Zealand (Haeckel, 1880) and P. tetralina (Haeckel) south of Australia (Haeckel, 1880).

Pericolpa quadrigata Haeckel 1880

(Figure 7, Map 6)

(Pericolpa tetralina (?) Haeckel, 1880)

(P. galea Haeckel, 1880)

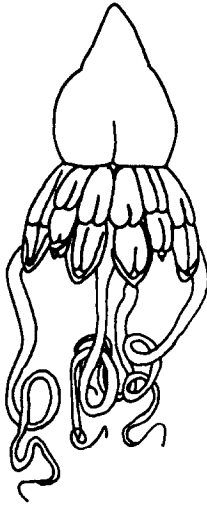
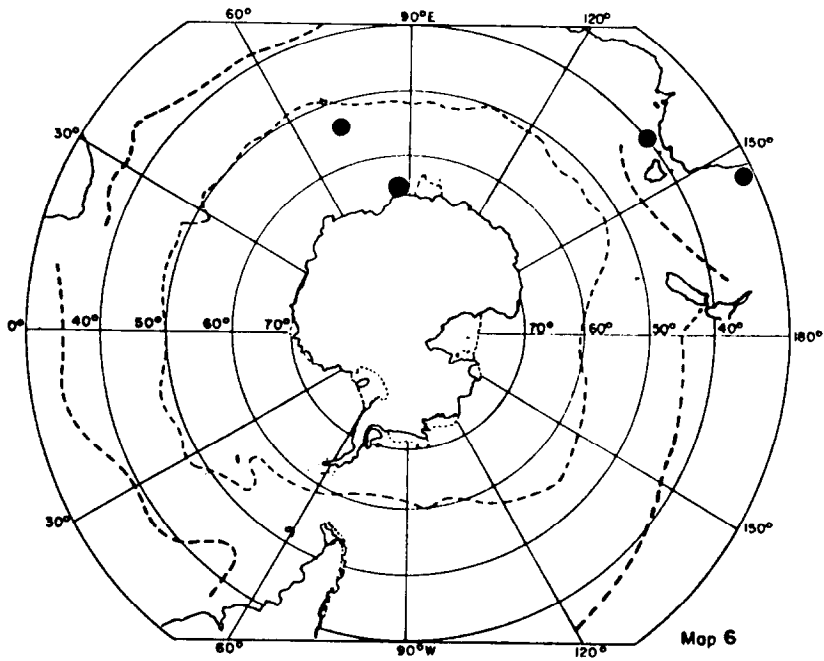


Figure 7. Pericolpa quadrigata, side view.



Map 6. Distribution of Pericolpa quadrigata.

Diagnostic Characters:

Size 30 mm wide, 40 mm high

Umbrella dome like apex pointed

Tentacular pedalia 4, perradial, somewhat wider than the 4 interradial, rhopalar ones and somewhat longer than the marginal lappets

Marginal lappets elongate, somewhat pointed

Gonads in 4 pairs, their inner ends close together near the interradial, diverging outwards.

Pericolpa galea Haeckel and P. tetralina Haeckel are probably identical with P. quadrigata (Mayer, 1910).

Genus Periphylla Haeckel 1880

Periphyllidae with 12 tentacles (four perradial and eight adradial), 16 marginal lappets, and eight gonads; 1 species only.

Periphylla periphylla (Peron & Lesueur 1809)

(Figure 8, Map 7)

(Periphylla hyacinthina Stiasny, 1934, 1940)

(P. dodecasbostrycha Browne, 1910; Vanhoffen, 1908; Stiasny, 1934)

(P. regina Vanhoffen, 1902, 1908; Stiasny, 1934)

(P. mirabilis Haeckel, 1880; von Lendenfeld, 1884)

Diagnostic Characters:

Umbrella usually higher than wide, with a pointed or dome-shaped apex

Size up to 200 mm wide

Marginal tentacles in groups of three between adjacent interradial marginal sense organs (Russell, 1976)

Gonads U-shaped

Colour stomach and subumbrella purple or violet.

The generic and specific names of this medusa are discussed by Kramp (1947). Periphylla periphylla is a large, oceanic medusa and it has an almost cosmopolitan distribution; it is occasionally carried by currents into the Arctic regions, and it is recorded from several localities in the Antarctic seas, penetrating right into the coastal areas of the Antarctic continent (Kramp, 1948). It is a bathypelagic medusa which occasionally may ascend towards the surface water, especially in cold areas (Kramp, 1957a). Russell (1970) gives details of the structure of the adult.

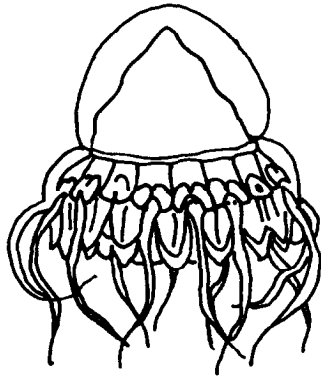
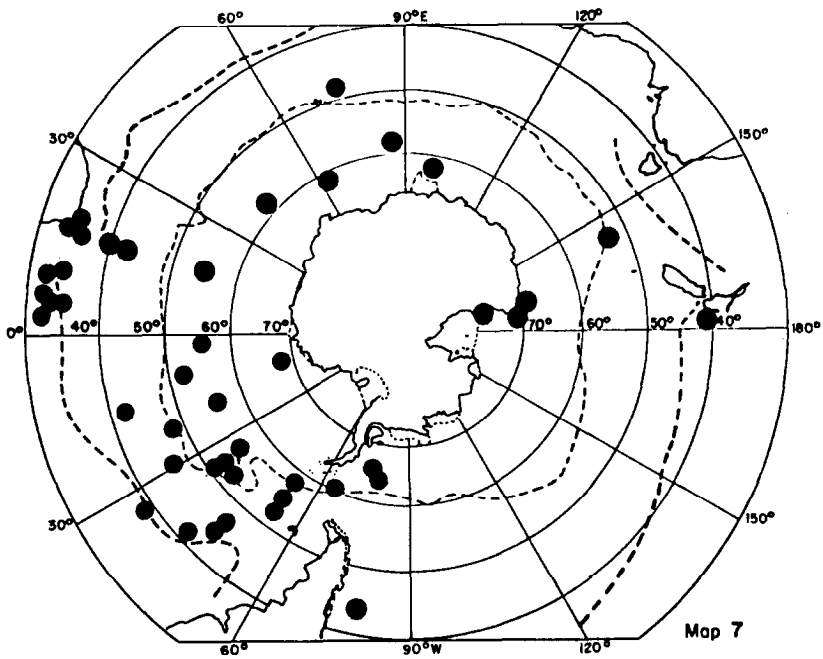


Figure 8. Periphylla periphylla, side view.



Map 7. Distribution of Periphylla periphylla.

9. ORDER SEMAEOSTOMEAE

Scyphomedusae with umbrella margin cleft into lappets; without a coronal furrow and without pedalia; with or without hollow marginal tentacles and with marginal rhopalia; with a single central mouth opening provided with four large curtain-like or gelatinous lips; with gonads in sac-like folds of the endodermal wall of the subumbrella; 3 families, all of which have representatives in the Southern Ocean or adjacent waters.

9.1 KEY TO FAMILIES:

- 1a) With ring canal ULMARIDAE
- 1b) Without a ring canal..... 2

- 2a) Central stomach gives rise to radiating pouches which in turn give rise to numerous branching, blind canals in the marginal lappets CYANEIDAE
- 2b) Central stomach gives rise to completely separated, unbranched radiating pouches PELAGIIDAE

9.2 FAMILY PELAGIIDAE

Smaeostomeae in which the central stomach gives rise to completely separated, unbranched radiating pouches; without a ring-canal; tentacles arise from the umbrella margin between the clefts of the lappets; oral arms long, pointed, much folded; 3 genera of which 2 are found in waters adjacent to the Southern Ocean.

Key to Genera:

- With 32-48 (or more) simple lappets Chrysaora
- With 16 marginal lappets Pelagia

Genus Chrysaora Peron & Lesueur 1809

Pelagiidae with 32-48 (or more) simple marginal lappets; with eight marginal sense-organs; with three to nine tentacles between each successive pair of marginal sense-organs; with 16 radial stomach pouches; in the marginal zone the eight rhopalar stomach pouches are much narrower than the eight tentacular pouches; exumbrella with numerous minute nematocyst warts. All the specific characters are vague and variable; 3 species are found in waters adjacent to the Southern Ocean: C. plocamia (Lesson) off South America (Haeckel, 1880; ? Vanhoffen, 1888), C. africana (Vanhoffen) off South Africa (Vanhoffen, 1902) and C. fulgida (Reynaud) off South Africa (Reynaud, 1830; Stiasny, 1934, 1939). It is possible that C. africana is synonymous with C. fulgida (Stiasny, 1939).

Genus Pelagia Peron & Lesueur 1809

Pelagiidae with 16 marginal lappets; with eight marginal sense-organs; with eight tentacles alternating with the marginal sense-organs; with 16 radial stomach pouches, all alike, each terminating in a pair of unbranched canals entering the marginal lappets; exumbrella with numerous nematocyst warts; one species only.

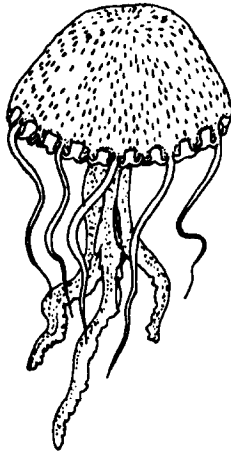
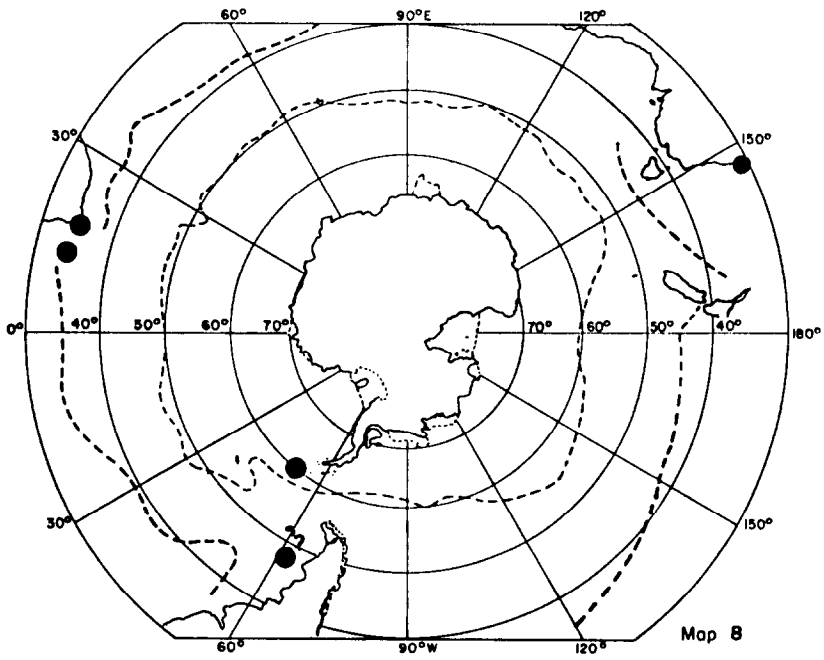


Figure 9. Pelagia noctiluca, side view.



Map 8. Distribution of Pelagia noctiluca.

Pelagia noctiluca (Forskal 1775)

(Figure 9, Map 8)

(Pelagia discoidea Eschscholtz, 1829; Vanhoffen, 1888)

(P. placenta Haeckel, 1880; Vanhoffen, 1888)

Diagnostic Characters:

Size up to about 65 mm wide (to 100 mm, Russell, 1978)

Marginal tentacles with longitudinal muscle furrows embedded in mesoglea (Russell, 1978)

Nematocyst warts on exumbrella, very variable in size and number

Colour very variable

Stiasny (1934) discusses the twenty different species or varieties of the genus Pelagia pointing out that there is probably only a single species with a world-wide distribution, to which the oldest name (noctiluca) ought to be applied. Pelagia noctiluca is a warm temperate oceanic species with direct development and only occurs in coastal areas when it has drifted in (Russell, 1978).

9.3 FAMILY CYANEIDAE

Semaeostomeae in which the central stomach gives rise to radiating pouches which in turn give rise to numerous branching, blind canals in the marginal lappets; without a ring-canal; with gonads in complexly folded, interradial eversion of the wall of the subumbrella at some distance from the margin; 3 genera of which 2 are found in the Southern Ocean or adjacent waters.

Genus Cyanea Peron & Lesueur 1809

Cyaneidae with eight rhopalia; with eight adradial clusters of tentacles, each cluster containing several rows of tentacles; both radial and circular muscles in the subumbrella; 1 species C. capillata (Linne) has been reported from south-eastern Australia (von Lendenfeld, 1882a - as C. annaskala; Stiasny, 1931b; Pope, 1953b - as C. capillata var annaskala; Pope, 1953a).

Mayer (1910) says that Cyanea is common in Antarctic waters but I can find no records from this area except for Uchida (1971) who found a juvenile off Enderby Land. Two doubtful species, C. annasethe (Haeckel) and C. muellerianthe Haacke have been found off south-west Africa (Haeckel, 1880) and south-east Australia (Haacke, 1887; Stiasny, 1922; Southcott, 1958) respectively.

Genus Desmonema L. Agassiz 1862

Cyaneidae with eight rhopalia and with eight adradial clusters of tentacles; no radial muscle strands in the subumbrella; 2 species both of which are found in the Southern Ocean.

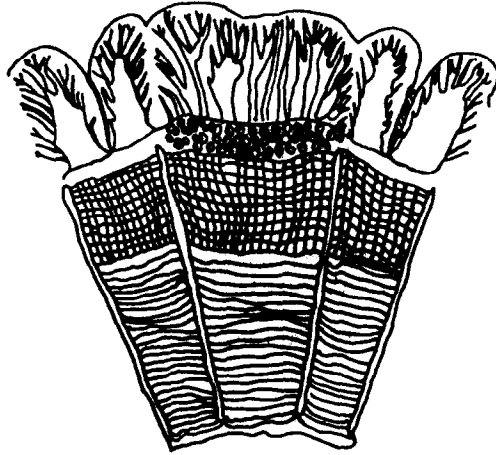
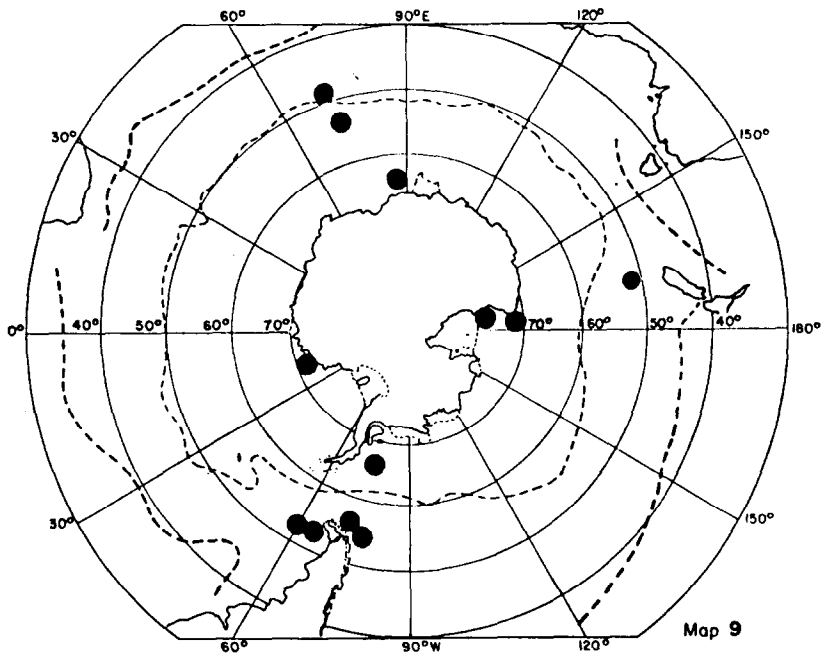


Figure 10. Desmonema chierchiana, sector of the bell with many canals in the lappets after injection with Delafield's haemotoxylin, many rows of thin tentacles (torn away).



Map 9. Distribution of Desmonema chierchiana.

Key to species:

Numerous narrow canals in the lappets, tentacles in several rows in each cluster D. chierchianum Vanhoffen
Few broad canals in the lappets, tentacles in a single line in each cluster D. gaudichaudi (Lesson)

Desmonema chierchianum Vanhoffen 1888

(Figure 10, Map 9)

Diagnostic Characters:

Size about 300 mm wide

Canals numerous, narrow in the lappets, branching towards both sides

Tentacles long and thin in several rows in each cluster.

There has been some discussion whether this species and D. gaudichaudi (Lesson) are in fact separate species (see Kramp, 1957b), but most workers believe that the two species should be kept apart. They can be separated by the number and thickness of the tentacles: D. chierchianum has a very large number of tentacles, up to sixty in each group and they are thin and slender, about 2 mm in diameter while D. gaudichaudi has no more than 7 tentacles in each group and these tentacles become very thick, 5 mm or more in diameter (Browne, 1910). Stiasny & Maaden (1943) emphasized the following distinguishing characters: D. chierchianum has many long and thin tentacles in each of the eight bundles, and they are placed in several rows; the canals in the marginal lappets are numerous, narrow and bilaterally branched; D. gaudichaudi has few tentacles (5 to 6 in each bundle), very thick and placed in one row; the canals are few and broad the lateral ones in each lappet unilaterally branched. Kramp (1957b) does not agree that the tentacles of D. chierchianum are placed in several rows, rather the lack of space between them causes the tentacles to become more or less displaced in a zig-zag like manner which may give the impression that they issue in more than one row.

According to Browne (1910), D. gaudichaudi is an Antarctic species occurring south of 60°S, whereas D. chierchianum is Subantarctic occurring north of 60°S but as pointed out by Kramp (1957b) they occur together in the vicinity of Tierra del Fuego and the Falkland Islands. D. chierchianum is a decidedly neritic species and has a circumpolar distribution within the Subantarctic belt (Kramp, 1957b).

Desmonema gaudichaudi (Lesson 1830)

(Figure 11, Map 10)

(Chrysaora gaudichaudi Lesson, 1830)

(Couthouyia ? sp. Maas, 1906)

(C. gaudichaudi Maas, 1908)

Diagnostic Characters:

Size 500 to 600 mm wide

Tentacles only 5 to 7 in a single line in each cluster

Canals a few in lappets, broad, the lateral ones unilaterally branched.

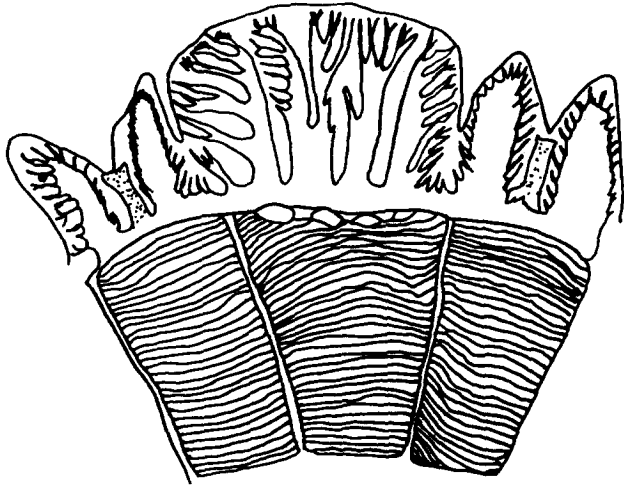
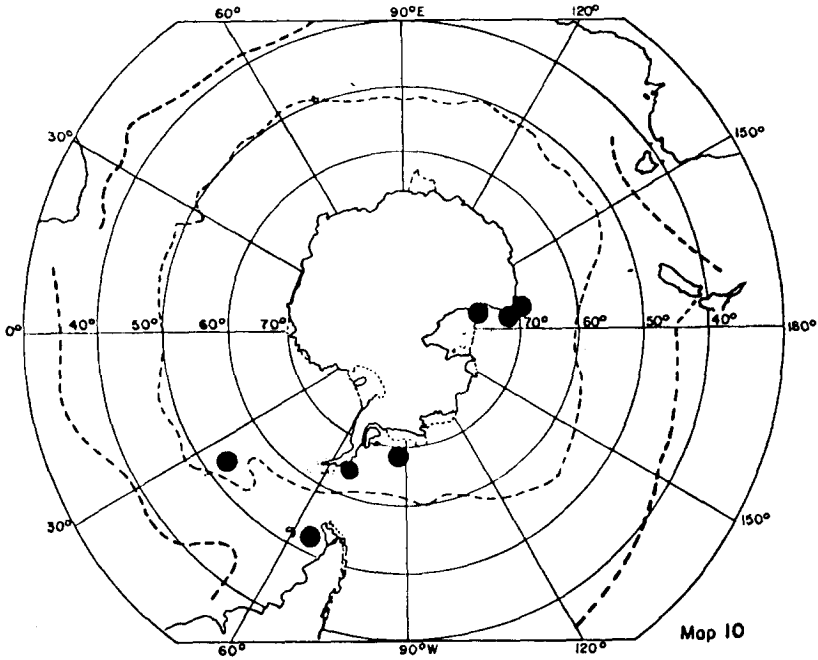


Figure 11. *Desmonema gaudichaudi*, sector of the bell with a few canals in the lappets after injection with Delafield's haemotoxylin, one row of a few thick tentacles (torn away).



Map 10. Distribution of *Desmonema gaudichaudi*.

The differences between this species and Desmonema chierchianum have already been discussed. Browne (1910) considered Vanhoffen's (1908) specimen of D. chierchianum to be a young D. gaudichaudi but Kramp (1961) gives Vanhoffen's identification as correct. Maas (1906) found a specimen which he tentatively identified as Couthouyia ? sp. Browne (1910) pointed out that this is probably synonymous with Desmonema and so it has been included on map 10.

9.4 FAMILY ULMARIDAE

Semaeostomeae with simple or branched radial canals and a ring-canal; with or without subgenital pits, 4 sub-families separated on the position of origin of the tentacles and lappets, the position of the gonads and the presence or absence of sub-genital pits.

Subfamily AURELIINAE

Ulmaridae in which the tentacles and lappets arise from the sides of the exumbrella above the margin; invaginated gonads with external subgenital pits; 2 genera of which 1 is found in waters adjacent to the Southern Ocean.

Genus Aurelia Peron & Lesueur 1809

Aureliinae with four unbranched mouth-arms; bell margin divided into eight or 16 broad velar lobes; some or all radial canals give rise to anastomosing branches; 7 species of which 3 are found in waters adjacent to the Southern Ocean: A. aurita (Linne) off southern Australia (Southcott, 1958); A. coerulea von Lendenfeld, off south-eastern Australia (von Lendenfeld, 1884; Stiasny, 1924; Stiasny, 1931b, Dakin & Colefax, 1933); and A. colpota Brandt off South Africa (Brandt, 1838).

Subfamily STHENONIINAE

Ulmaridae in which the tentacles arise in linear clusters from the subumbrella; with protrusive sac-like gonads; without subgenital pits; 3 genera of which 1 has been found in waters adjacent to the Southern Ocean.

Genus Phacellophora Brandt 1835

Sthenoniinae with 16 rhopalia alternating with 16 clusters of tentacles; radial canals in the rhopalar radii branched, in the tentacular radii simple; four gonads; 1 species, P. camtschatica Brandt has been found off Chile (Kramp, 1952) and off southern Argentina (Browne, 1908, 1910 - as P. ornata).

Subfamily ULMARINAE

Ulmarinae in which the tentacles arise from the clefts between the marginal lappets; with protrusive, sac-like gonads; without subgenital pits; 6 genera of which one is found in the Southern Ocean.

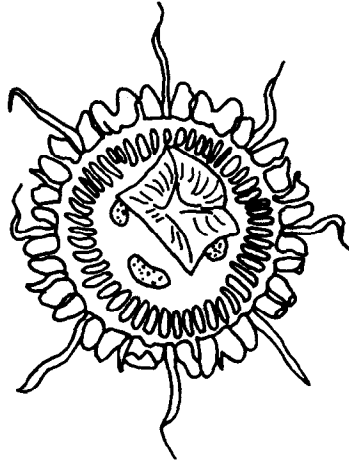
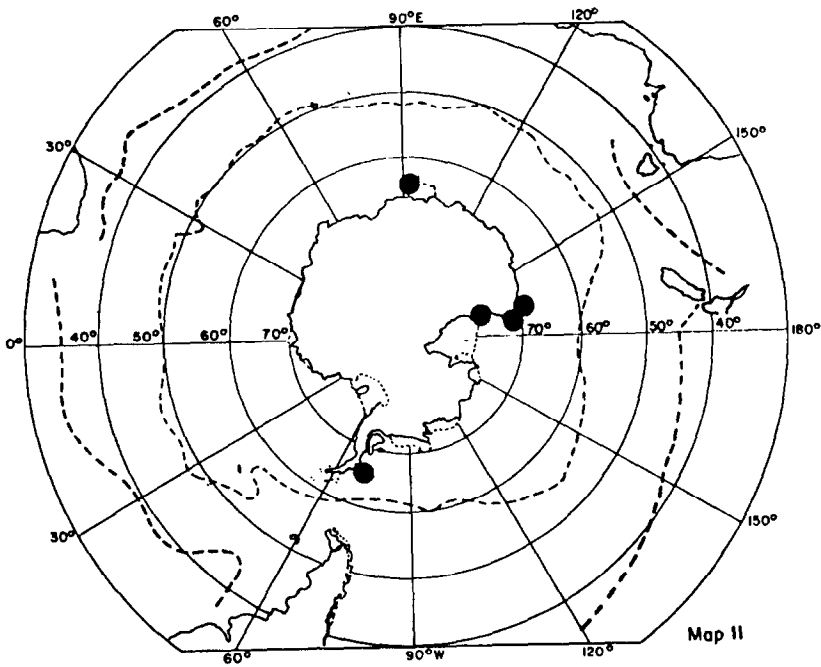


Figure 12. Diplulmaris antarctica, aboral view.



Map 11. Distribution of Diplulmaris antarctica.

Genus Diplulmaris Maas 1908

Ulmarinae with 16 rhopalia, 16 tentacles and 64 lappets; 16 rhopalar canals branched, 16 simple tentacular canals; 2 species of which one occurs in the Southern Ocean.

Diplulmaris antarctica Maas 1908

(Figure 12, Map 11)

(Ulmaropsis drygalskii Vanhoffen, 1908)

(Diplulmaris (?) gigantea Browne, 1910)

Diagnostic Characters:

Size up to 42 mm wide

Marginal lappets pointed

Tentacular canals as broad as rhopalar canals, canals without anastomoses.

A few months after the appearance of Maas' (1908) report, Vanhoffen (1908a) described a medusa under the name of Ulmaropsis drygalski but Diplulmaris antarctica has priority (Browne, 1910).

10. SOURCES OF FIGURES AND MAPS

AUTHOR	FIGURE NUMBER
Haeckel (1880)	7
Mayer (1910)	1a,d,e, 3, 6, 8, 9, 12
Carlgren (1930)	2, 4, 5
Stiasny (1934)	1b, 10, 11
Russell (1978)	1c

AUTHOR	MAP NUMBER
Eschscholtz (1829)	8
Lesson (1830)	10
Haeckel (1880)	5, 6, 7, 8
Lendenfeld (1881)	6
Vanhoffen (1888)	8, 9, 10
Pfeffer (1889)	1
Vanhoffen (1902)	5, 7
Maas (1908)	10, 11
Browne (1908)	5, 9
Maas (1906)	10
Vanhoffen (1908b)	2, 3, 5, 7, 9, 11
Browne (1910)	4, 5, 7, 10, 11
Carlgren (1930)	1, 3, 4
Stiasny (1931a)	4, 5, 10
Stiasny (1931b)	5, 8
Dakin & Colefax (1933)	8
Stiasny (1934)	5, 7, 8, 9, 10
Stiasny & Maaden (1934)	9
Stiasny (1940)	7
Kramp (1948)	5, 7
Kramp (1957a)	2, 5, 7
Kramp (1957b)	7, 9

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