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ANARE RESEARCH NOTES 8

A Guide to the Pelagic Tunicates of the Southern Ocean and Adjacent Waters

David O'Sullivan

ANTARCTIC DIVISION
DEPARTMENT OF SCIENCE AND TECHNOLOGY

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Species found south of the Subtropical Convergence will be dealt with in detail. Those occurring in more northerly waters but likely to be encountered on Antarctic voyages are included in identification keys.

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A GUIDE TO THE PELAGIC TUNICATES OF THE SOUTHERN OCEAN AND ADJACENT WATERS

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ABSTRACT

The characteristics of the Classes, Orders, Families and Genera of the pelagic tunicates found in the Southern Ocean and adjacent waters are given together with keys for their identification.

In the Southern Ocean 5 species of salps (Order Desmomyaria), 1 species of doliolid (Order Cyclomyaria) and 27 species, forms and types of larvaceans (Order Appendicularia) have been found. The synonymy, diagnostic characters, geographical and bathymetric distribution of each of these is given together with an illustration and a distribution map.

1. INTRODUCTION

Borradaile and Potts (1967) define the subphylum Tunicata (syn. Urochordata) as chordata without coelom, segmentation, or bony tissue, with a dorsal atrium in the adult; notochord restricted to the tail which is present in the larval organisation only; and a test, usually largely composed of a substance (tunicin) related to cellulose. The Tunicata is represented in the plankton by the classes Thaliacea (containing the orders Desmomyaria, Cyclomyaria and Pyrosomida) and Appendiculariae (syn. Larvacea). The free-swimming larvae (commonly known as tadpole larvae) of the Class Ascidiacea are also found in the plankton but will not be dealt with here.

In this guide only species found in the Southern Ocean are considered in detail. The Southern Ocean is that water that lies between the Antarctic Continent and the Subtropical Convergence and is divided into the Antarctic and Subantarctic by the Antarctic Convergence. Species found in adjacent waters (north of the Subtropical Convergence but south of 30° south) are included in the keys. The areas they have been found 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 South Africa, (In) for southern Indian Ocean and (Co) for cosmopolitan in all these areas.

Many of the major works of these groups (especially the Appendiculariae) were written in German, although Thompson (1942, 1948) published an excellent report on the "Pelagic Tunicates of Australia". The class, order, family, genus and species descriptions used here are from that report unless otherwise stated.

Author	Expedition	Pyroso-midia	Desmo-myaria	Cyclo-myaria	Appendic-ulariae
Herdman 1888	Challenger	X	X	X	X
Lohmann 1892	Plankton				X
Apstein 1894	Plankton		X		
Borgert 1894	Plankton			X	
Seeliger 1895	Plankton	X			X
Lohmann 1896	Plankton				X
Lohmann 1905					X
Apstein 1906	Deutschen Tiefsee		X		
Neumann 1906	Deutschen Tiefsee			X	
Apstein 1908	Deutschen Sudpolar		X		
Herdman 1910a	National Antarctic		X	X	X
Neumann 1913a	Deutschen Tiefsee	X			
Neumann 1913b	Deutschen Sudpolar	X		X	
Lohmann 1914	Valdivia				X
Buckmann 1924	Deutschen Sudpolar				X
Lohmann & Buckmann 1926	Deutschen Sudpolar				X
Lohmann 1928	Deutschen Antarktischen				X
Lohmann 1931	Deutschen Tiefsee				X
Garstang 1933	Terra Nova			X	
Garstang & Georgeson 1935	Terra Nova				X
Thompson 1954	BANZARE	X	X	X	X
Stadel 1958	Deutschen Antarktischen		X		
Udvardy 1958	Swedish Antarctic				X
Foxton 1961	Discovery		X		
Tokioka 1961	Japanese Antarctic				X
Tokioka 1964	Japanese Antarctic				X
Caldwell 1966	Eltanin		X		
Foxton 1966	Discovery		X		
Esnal 1970	Benito Goyena		X		
Foxton 1971	Discovery		X		

Table 1. Major works on pelagic Tunicates from the Southern Ocean.

2. PREVIOUS RECORDS

There have been a number of workers who have studied pelagic Tunicates from the Southern Ocean (Table 1). Most of this material was collected during the German Plankton, Tiefsee, Sudpolar, Valdivia and Antarktischen expeditions although areas other than the Southern Ocean were sampled.

Hardy and Gunther (1935) and Ealey and Chittleborough (1956) included some pelagic Tunicates in their general accounts of plankton from South Georgia and Heard Islands respectively. Studies from adjacent waters include southern Australia (Lohmann, 1909; Dakin and Colefax, 1940; Thompson, 1948; Taw, 1978), New Zealand (Bary, 1960), South America (Fagetti, 1959), South Africa (van Zyl 1959; Borgelt, 1968a,b; Lazarus and Dowler, 1979), and southern Indian Ocean (Ihle 1908, 1912).

3. SYSTEMATIC NOTES

Borradaile and Potts (1967) define the pelagic classes and orders as:

CLASS LARVACEA (Syn. Appendicularia). Tunicates in which the sexually mature form retains the organisation of the larva.

CLASS THALIACEA. Tunicates in which the adult has no tail, but it nas a degenerate nervous system, an atrium which opens posteriorly, a stolon of complex structure, and clefts which are not divided by external longitudinal bars.

Order Pyrosomida. Feeble muscles developed in complete rings round body but at end of body only.

Order Salpidae (Syn. Desmomyaria). Strong muscles but incomplete around body.

Order Doliolidae (Syn. Cyclomyarias). Strong muscles in complete rings round the body.

The general structure of each of these groups are shown in Figure 1.

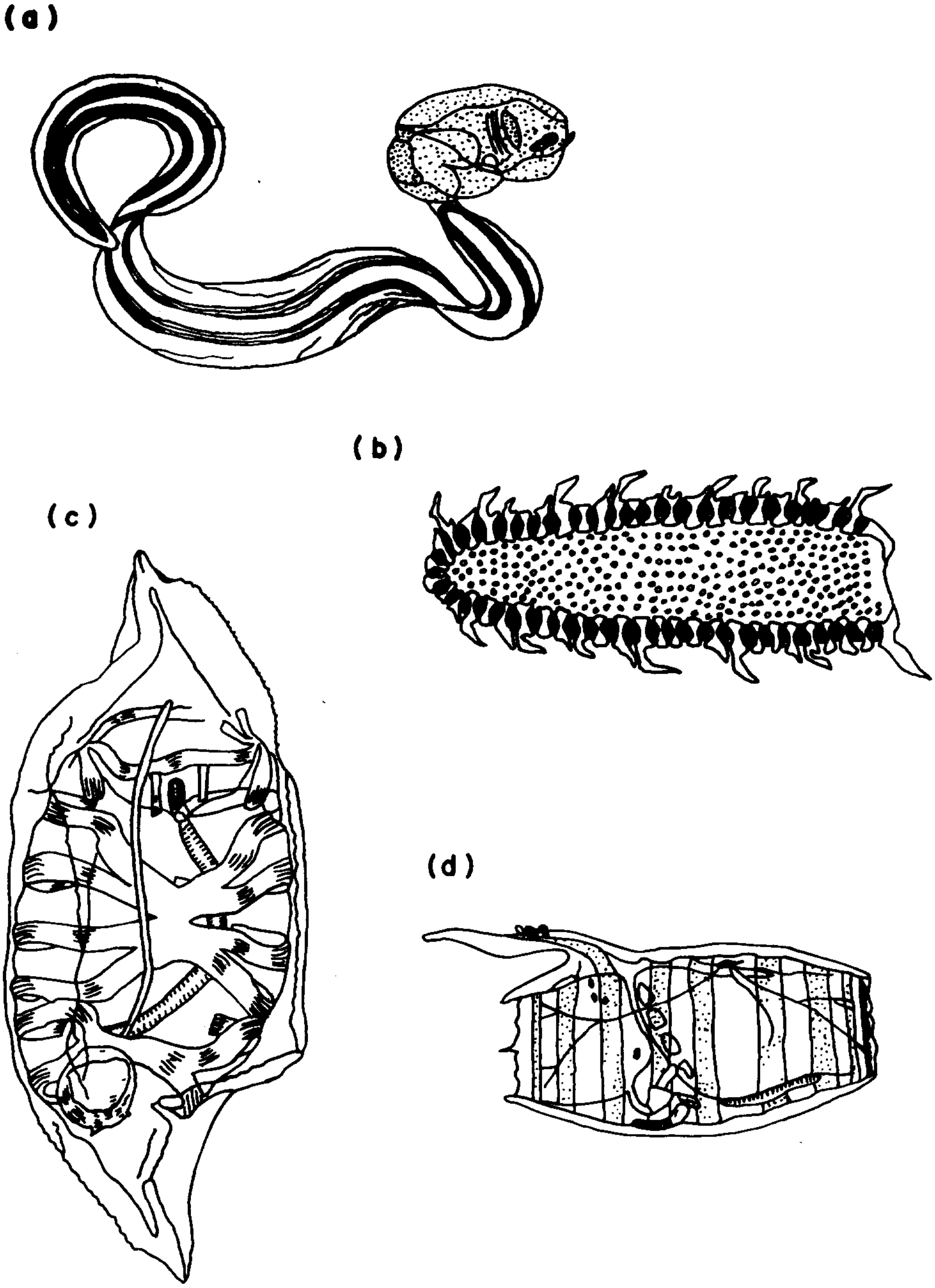


Figure 1. Characters of the classes and orders of tunicates (a) Larvacean, (b) Pyrosoma, (c) Salp, (d) Doliolid.

4. CLASS THALIACEA

The majority of the Thaliacea are highly characteristic, cylindrical, often barrel-shaped creatures of very transparent gelatinous substance (Dakin and Colefax, 1940). They differ from ascidians in having the buccal and atrial siphons at opposite ends of the body so that a water current through the body can be utilised not only for gas exchange and feeding but also for locomotion (Barnes, 1974). The classification of these forms into two groups is based on the character of circular bands of muscle fibres which run around the body. In the order Desmomyaria (salps) these muscle bands do not usually form completely closed rings but are open on the ventral side of the "barrel". In the Cyclomyaria (doliolids) there are eight or nine closed ring-forming bands of muscles and the organisms are more truely barrel shaped. There is a third section of the class, the order Pyrosomida, which is rather different. In this group a large number of individuals form a pelagic-living colony with a very definite shape, usually a long hollow cone with an open base.

5. ORDER PYROSOMIDA

5.1 FAMILY PYROSOMATIDAE

Genus Pyrosoma (Peron 1804)

(Figure 2)

Pyrosomida are pelagic, colony-forming Tunicates with intensive luminous organs. According to Metcalf and Hopkins (1919) they probably arose as a divergent group from social Ascidians (eg. Distomidea). Herdman (1910b) discusses the anatomy, development and life history of this group.

The colony of zooids usually has the form of a hollow cone or cylinder closed at the tip and open at the base; these are embedded in the test, in a single layer radially, so that the mouth opens towards the outside of the common test, the cloaca to the common central cavity and so that the ventral side is directed towards the closed end of the colony; the musculature of the zooids is limited to a sphincter at each of the two body openings and the cloacal muscle of the colony; a light organ is always present on each side of the anterior end of the branchial sac; colonies can attain a length of four metres, but are mostly from less than one to ten centimetres.

Pyrosomids are holoplanktonic forms found in the warmer seas from the surface to a depth of about 200 metres (rarely deeper). Neumann (1935) states that nine species and seven sub-species in all have been distinguished but many forms intergrade (Metcalf and Hopkins, 1919). Furthermore Thompson (1948) points out that subdivisions of species must to a certain extent be artificial, and a definitive classification is in a considerable measure a matter of judgement.

No species of Pyrosoma have been reported from south of the Antarctic Convergence. Thompson (1948) could only distinguish one species Pyrosoma atlanticum atlanticum, from Australia and he suggested that f. giganteum taken by the "Challenger" Expedition south of Australia (Herdman, 1888) may be only older colonies of atlanticum. P. atlanticum has also been reported from south

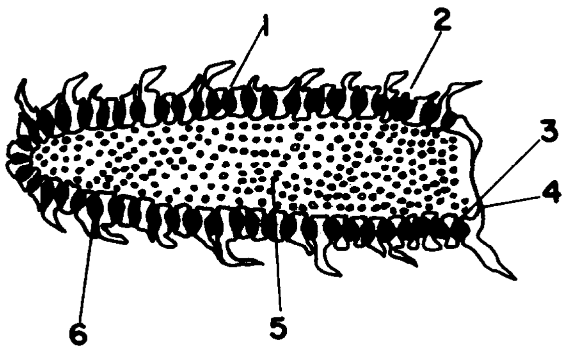
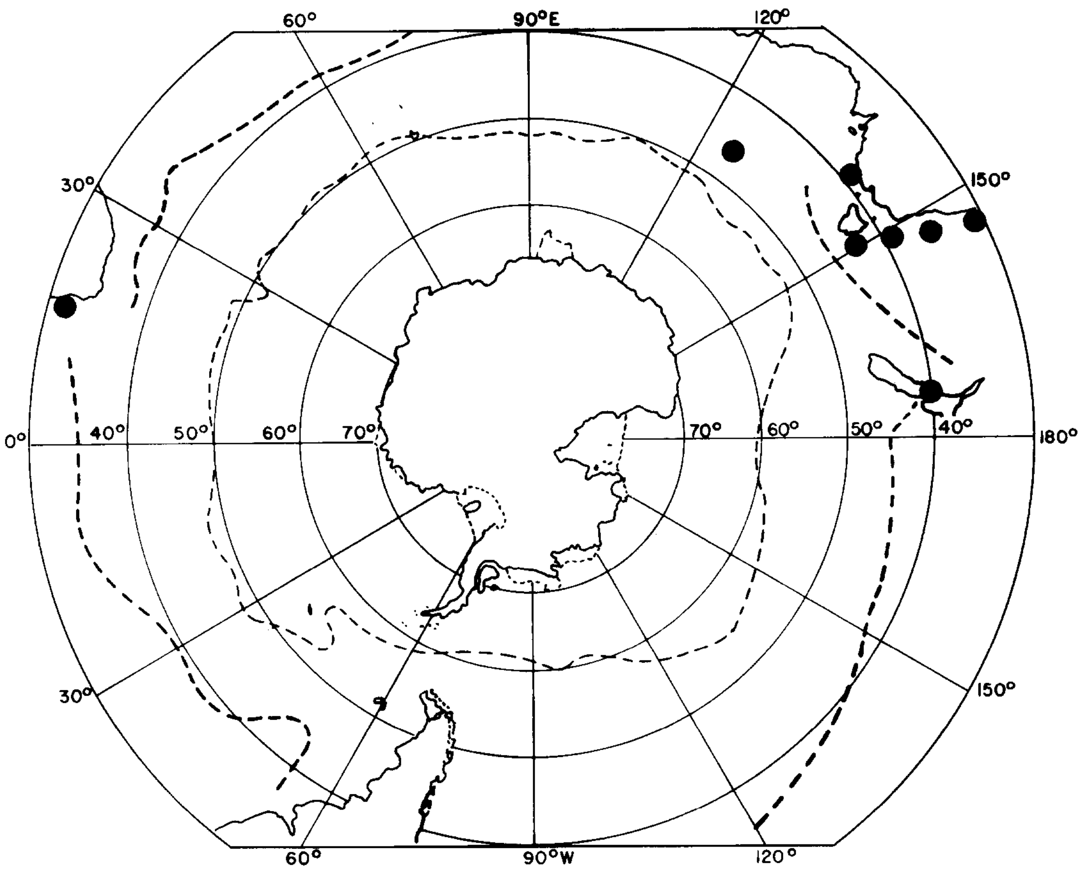


Figure 2. A colony of the thaliaceae <u>Pyrosoma</u> (longitudinal section) (1) mouth, (2) zooid, (3) cloacal aperture, (4) common aperture, (5) common cloaca, (6) branchial sac. Map of distribution.



eastern Australia (Dakin and Colefax, 1940; Thompson, 1954) and New Zealand (Bary, 1961). P. spinosum Herdman has been found in the south Atlantic Ocean (Herdman, 1888) and off New Zealand (Bary, 1961) and Pyrosoma sp. off South Africa (Lazarus and Dowler, 1979). Pyrosoma fragments were reported by Herdman (1888) from south of Australia.

6. ORDER DESMOMYARIA (Syn. Salpidae)

Single family made up of tunicates commonly known as "salps"; body more or less fusiform, with the long axis anterioposterior; the musculature of the body wall is in the form of transversly running bands which do not usually form complete independent rings; with no free-swimming larval stage but with two forms of adult individual - the asexual or solitary form and the sexual or aggregate form (Dakin and Colefax, 1940).

In the nomenclature, solitary and aggregate forms of the same speices have sometimes acquired different names. For example, Cuvier (1804) gives the name Salpa fusiformis for the aggregate forms of the same species S. runcinata. To link such forms, hyphenated names were subsequently employed eg. S. runcinata-fusiformis Chamisso-Cuvier. Today only one name, that having priority, is used. In this work the classification by Metcalf (1918) and by Ihle and Ihle-Landenberg (1935) is adopted as in Thompson (1948).

6.1 EXTERNAL STRUCTURE (After Thompson, 1948)

The body shape of both the aggregate and solitary forms varies greatly between genera but generally the aggregate form is dolioiform with a process at one or both ends while the solitary form is cylindrical with blunt ends (Figure 3).

The test is well developed. The muscle bands do not usually form complete rings and can join other bands dorsally or laterally. In the species description of this guide the body muscle bands are represented by the letter "M" followed by their number from the front of the salp (in Roman numerials). Thus MV is the fifth body muscle. The most satisfactory characters for specific identification are the number and arrangement of these muscle bands (which are characteristic from the early stages, 3 mm long and over), and the shape of the test (Fraser, 1947a).

The branchial and cloacal cavities form a continuous space in the anterior of the body, opening at or near the ends of the body by the branchial and atrial apertures respectively. The branchial aperture is surrounded with oral musculature. They are traversed obliquely from the dorsal and anterior to the ventral and posterior end by a long narrow vascular ciliated band known as the endostyle. The alimentary tract is placed ventrally with a stomach and intestines curled up to form a nucleus. The embryo can be found attached to the aggregate form near the posterior end of the body.

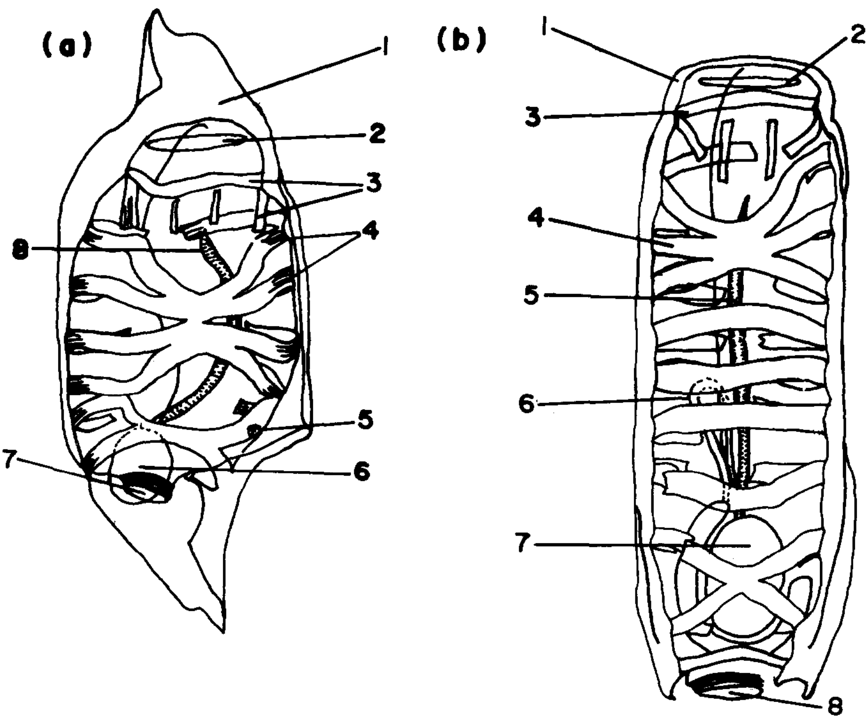


Figure 3. General structure of a salp (a) aggregate form (1) test, (2) branchial aperture, (3) oral musculature, (4) body musculature, (5) embryo, (6) intestinal nucleus, (7) atrial aperture, (8) endostyle; (b) solitary form (1) test, (2) branchial aperture, (3) oral musculature, (4) body musculature, (5) endostyle, (6) stolon, (7) intestinal nucleus, (8) atrial aperture.

6.2 LIFE HISTORY AND BIOLOGY

Salps have an alternation of generation in their life-history with two free-swimming stages. The solitary forms (="oozooids") are asexual, and these produce claims of aggregate sexual forms (="blastozooids" = "gonozooids") by means of budding by a stolon (Fraser, 1947a). The embryonic development is direct, no tailed larvae being formed as the embryo is united to the parent for a time by a "placenta" (Thompson, 1948).

All tunicates are filter feeders and Barnes (1974) outlines the feeding mechanism: the endostyle is the principle center for the elaboration of mucous, which is driven up in between the rows of stigmata. Plankton suspended in the stream of water passing through the stigmata become trapped on the mucous film. The food-laden mucous strands are carried downward toward the base of the pharynx and the oesophageal opening and thence to the stomach. He points out that this basic plan may be variously modified between the groups of tunicates but the process is generally similar. Salps are random filter feeders, the only dietary limitation possibly being the size of the oral aperature (Yount, 1958; Caldwell, 1966). They feed mainly on phytoplankton in inshore areas and zooplankton in off-shore areas (Van Zyl, 1959).

The majority of salps are found in the upper levels of the sea (Sewell, 1953). Ihle (1912) has pointed out that, as salps are mostly warm water inhabitants, they are but rarely found at depths greater than 400 m, almost the only exception being Salpa fusiformis f. aspera, that has been taken in a self closing net between 1000 and 2000 m (Sewell, 1953). However all of the species reported from the Southern Ocean by Caldwell (1966) also appeared at great depths and Caldwell included a photograph of an unidentified salp made at a depth of 4905 m.

In the Southern Ocean the salps are of special interest because they occur at certain seasons in dense concentrations or swarms and, as they are primarily herbivores (feeding predominately on marine diatoms - Caldwell, 1966), must play an important role in grazing down the phytoplankton, competing where distributions overlap, with such other key herbivores such as Euphausia superba (Foxton, 1971).

6.3 FAMILY SALPIDAE

With the characters of the order; 3 sub-families separated on the shape of the gut and intestine.

Key to Sub-families:

1a) Gut compact .... Sphaerodaea
 b) Gut not compact 2

2a) Gut elongated .... Dolichodaea
 b) Gut curved .... Circodea

Sub-family DOLICHODAEA

Gut elongated, intestine in the solitary forms is a straight tube dorsal to the gill, in the aggregated zooids it is either a straight tube or is bent into an open loop; solitary form with 6, aggregated form with 4 body muscles; a single genus, Cyclosalpa de Blainville with 5 species.

No species of this genus have been reported from the Southern Ocean but all have been found in adjacent waters (Thompson, 1948, Lazarus & Dowler, 1979). Thompson (1948) gives a key to the five species toegether with their synonymy and a description of their aggregate and solitary forms.

Sub-family CIRCODEA

Gut curved, in solitary forms not making a very compact nucleus, the course of the intestine can be traced without dissection, in the aggregated zooids the gut forms a nucleus in which, in most species, the course of the intestine can hardly be detected by superficial observation; eight genera, one of which has representatives in the Southern Ocean, but as certain species of the other genera have been found in waters adjacent to the Southern Ocean, each genera is defined separately.

Genus Brooksia Metcalf 1918

Solitary form with a long anterior protuberance below the mouth, containing two pairs of wide muscle bands; aggregated zooids very asymmetrical; solitary form with 7, aggregated form with 4 very asymmetrical body muscles; 1 species, B. rostrata (Traustedt) which has been reported from southern Australia (Thompson, 1948).

Genus Ritteriella Metcalf 1918

From 9 to 24 body muscles in the solitary form, asymmetrically continuous across the dorsal mid-line; 2 species of which R. picteti (Apstein) has been reported from southern Australia (Thompson, 1948), and R. amboinensis (Apstein) from the southern Atlantic Ocean (Apstein, 1904 as Salpa ambroinenis) and southern Australia (Thomson, 1948).

Genus Metcalfina Ihle 1935

Solitary form with a pair of long processes behind, and with 10 or 11 very broad body muscles forming an almost continuous layer, especially posteriorly; aggregated zooid showing 6 well-marked longitudinal ridges, and having 6 broad body muscles, of which the 5th and 6th are independent; 1 species M. hexagona (Quoy and Gaimard) which has been reported from South Africa (Herdman, 1910a as Salpa hexagona) and southern Australia (Thompson, 1948). Herdman (1910a) also tentatively identified a damaged specimen of M. hexagona (as S. hexagona) from McMurdo Bay but his identification is probably incorrect as the species has not been reported south of the Subtropical Convergence.

Genus Thetys Tilesius 1802

Solitary form with a pair of well-developed postero-lateral appendages; atrial siphon in both forms tubular; body muscles in both forms confined to the dorsal half of the body, numerous (from 16 to 22) in the solitary form, most of them interrupted both dorsally and laterally; 5 body muscles in aggregated form; one species, T. vagina Tilesius which has been reported from southern Australia (Thompson, 1948, 1954) and from the southern Pacific Ocean and off New Zealand (Herdman, 1888 as Salpa costata-tilessi).

Genus Thalia Blumenbach 1810

Solitary form with a pair of well developed postero-lateral appendages from half as long to about as long as the body; atrial aperture slit-shaped in both solitary and aggregated forms; 5 body muscles in each form, usually forming complete uninterrupted loops; 2 species of which T. democratica (Forskal) has been reported from the southern Pacific Ocean (Herdman, 1888, 1910a; van Soest, 1975); South Africa (Herdman, 1910a; van Zyl, 1959; Tokioka, 1964; Borgelt, 1968 a,b; van Soest, 1975); southern Australia (Herdman, 1888; Dakin and Colefax, 1940); South Africa (van Zyl, 1959; Lazarus and Dowler, 1979); southern Atlantic Ocean (Herdman, 1888); and South America (Herdman, 1888).

Genus Pegea Savigny 1816

Four body muscles in both forms, confined to the dorsal half of the body, and forming both an anterior and posterior X-shaped group; one species P. confoederata (Forskal) which has been reported from southern Australia (Dakin and Colefax, 1940; Thompson, 1948); the southern Pacific Ocean (Herdman, 1888); the southern Atlantic Ocean (Stadel, 1958; van Soest, 1975); New Zealand (Bary, 1961) and South Africa (van Soest, 1975; Lazarus and Dowler, 1979).

Genus Traustedtia Metcalf 1918

Solitary form with from 4 to over 20 tubular appendages from different parts of the body; aggregated forms with a single unequal pair of postero-lateral appendages; single species T. multitentaculata (Quoy and Gaimard) which has been reported from southern Australia (Thompson, 1948) and South Africa (Lazarus and Dowler, 1979).

Genus Iasis Lahille (Metcalf 1918)

Solitary form with 5 pairs of very broad muscle bands and a narrower shorter 6th on the dorsal surface behind them; body terminating behind in a sharp point whose enlarged base contains the gut; atrial aperture a horizontal slit. Aggregated zooid with similar atrial aperture, 3 to 5 embryos and 5 strong body muscles, nearly parallel, all but the first being continuous across the mid-dorsal line,; body pointed behind and narrowing to a truncated point in front, one species only.

Iasis zonaria (Pallas 1774)

(Figure 4)

(Salpa cordiformis zonaria Herdman, 1910a)

Diagnostic characters:

SOLITARY FORM.
External appearance: elongate, prismatic dorso-ventrally compressed in front; fore portion of body terminates squarely; the rear portion tapers to a point behind the atrial opening
Test: thick and rigid
Body muscles: 5, broad, interrupted both dorsally and ventrally, MV is rather narrower than the others
Alimentary canal: forms a rather tight circular loop
Stolon: spirally wound round the gut nucleus
Length: up to 65 mm.
AGGREGATE FORM.
External appearance; asymmetrical, elongate-oval with the back pressed flat; rear process occupies lateral position or the right side, varies in length, sometimes being as much as 1/3 or 1/2 as long as the body, but it is usually quite short in younger specimens
Test: thick and rigid

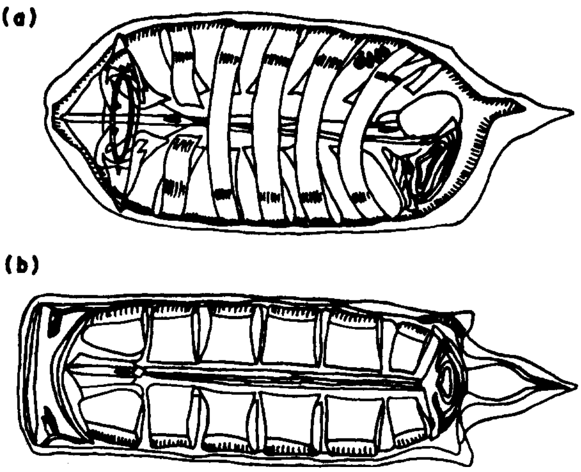
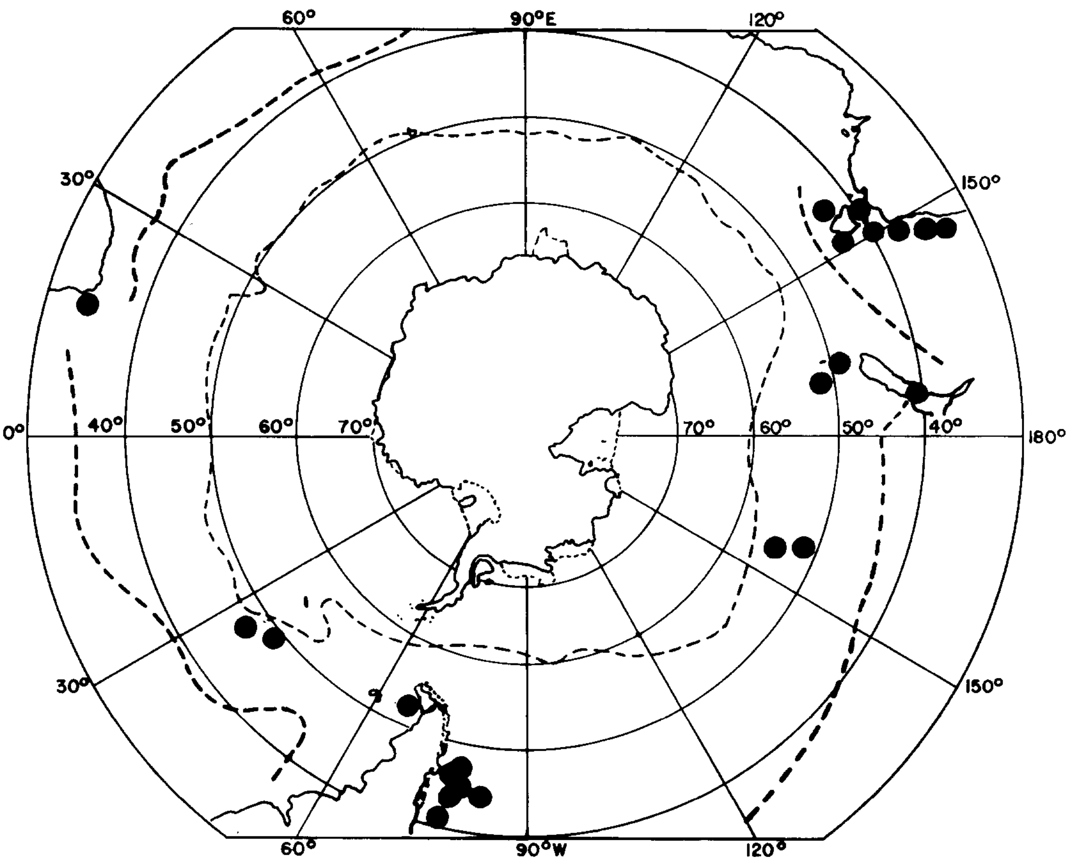


Figure 4. Iasis zonaria (a) aggregate form, dorsal view; (b) solitary form, dorsal view. Map of distribution.



Body muscles: 5, fairly broad, all but the first being continuous across the mid-line, all interrupted widely ventrally
Alimentary canal: forms a compact nucleus, but the course of the intestine can be traced without dissection
Embryos: up to 20mm long can be carried (Fraser, 1947a)
Length: up to 50mm.

This species is found in the deep cold waters of subtropical and tropical regions (Thompson, 1954). In Australian waters, Thompson (1948) regarded this as a surface or near surface species. It can be carried from tropical to colder waters by currents (Sewell, 1953) and it has been found in the Atlantic (Herdman, 1888; Caldwell, 1966) and Pacific (Caldwell, 1966) sectors of the Subantarctic.

Sub-family SPHAERODAEA

Gut in both forms making a compact nucleus, in which the course of the intestine cannot be clearly seen without dissection; 2 genera separated on body muscle shape and symmetry.

Key to Genera:

Body muscles in solitary form widely interrupted ventrally; body muscles in aggregate form not very symmetrical .... Salpa Forskal

Body muscles in solitary form complete uninterrupted loops; body muscles in aggregate form decidedly asymmetrical .... Ihlea Metcalf

Genus Salpa Forskal 1775

Body muscles in solitary form widely interrupted ventrally; aggregated form more or less pointed symmetrically in front and behind; body muscles not very asymmetrical; numerous species of which 6 are found in the Southern Ocean or adjacent waters.

Key to species (after Thompson, 1948; Foxton, 1961):

Aggregate Form

1a) Body muscles IV and V not in contact laterally (Au, Pa, SAm, SA, In) .... S. maxima Forskal
b) Body muscles IV and V in contact laterally 2

2a) Body muscles I to II and IV and V are fused dorsally to form two broad bands, which are in contact dorsally and may be united (Au, SA, In) .. S. cylindrica Cuvier
b) Body muscles I to IV and V and VI in contact dorsally, IV and V sometimes in contact laterally .... (S. fusiformis group) 3

3a) Test smooth; total fibre number 40 to 61 (Au, Pa, At, Sa, In) .... S. fusiformis Cuvier
b) Test serrated; total fibre number more than 113 .. 4

4a) Muscles IV and V approach but not in contact laterally (NZ Pa, At, In) .... S. aspera Chamisso
b) Muscles IV and V in contact laterally 5

5a) Muscle bands broad (ratio of body length: muscle width 18.9:1); total fibre number 140-235 .... S. thompsoni Foxton
b) Muscle bands narrow (ratio of body length: muscle width 27.6:1); total fibre number 113-159 . S. gerlachei Foxton

Solitary Form
1a) Body muscles about parallel, not in contact (Au, Pa, SAm, SA, In) .... S. maxima Forskal
b) Body muscles not parallel, some in contact dorsally 2

2a) Body muscles I to IV in contact dorsally (Au, SA, In) .... S. cylindrica Cuvier
b) Body muscles I to III in contact dorsally (S. fusiformis group) 3

3a) Test smooth; muscle bands I to III in contact dorsally; muscle fibres of muscle IV 19 to 40 (Au, Pa, At, SA, In) .... S. fusiformis Cuvier
b) Test serrated; muscle fibres of muscle IV 36 to 130 4

4a) Muscle bands VIII and IX parallel (or nearly so); test ridges "simple" (NZ, Pa, At, In) .... S aspera Chamisso
b) Muscle bands VIII and IX joined; test ridges "complex" 5

5a) Muscle bands broad (ratio of body length: muscle width 21.2:1); fibres of muscle IV 70 to 130 ..... S. thompsoni Foxton
b) Muscle bands narrow (ratio of body length: muscle width 35.8:1), fibres of muscle IV 36 to 71 .... S. gerlachei Foxton

Salpa thompsoni Foxton 1961

(Figure 5)

(Salpa antarctica Meyen, 1832)
(Salpa echinata Herdman, 1888 part)
(Salpa runcinata-fusiformis Herdman, 1888 part, 1910a)
(Salpa fusiformis var. echinata Apstein, 1906, part)
(Salpa funcinata-fusiformis var. echinata Herdman, 1910a part)
(Salpa fusiformis aspera Mackintosh, 1934; Hardy & Gunther, 1935; Stadel 1958)

Diagnostic characters (Foxton 1961):

SOLITARY FORM.
External appearance: with convex anterior end, posterior squarely cut off with pronounced spinose processes
Test: heavily serrated, firm, with thickened areas forming pronounced serrated ridges; complex arrangement of ridges (see Foxton, 1961)

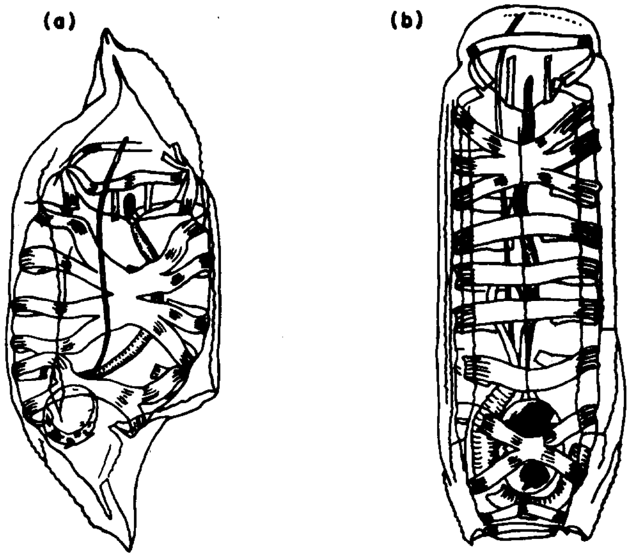
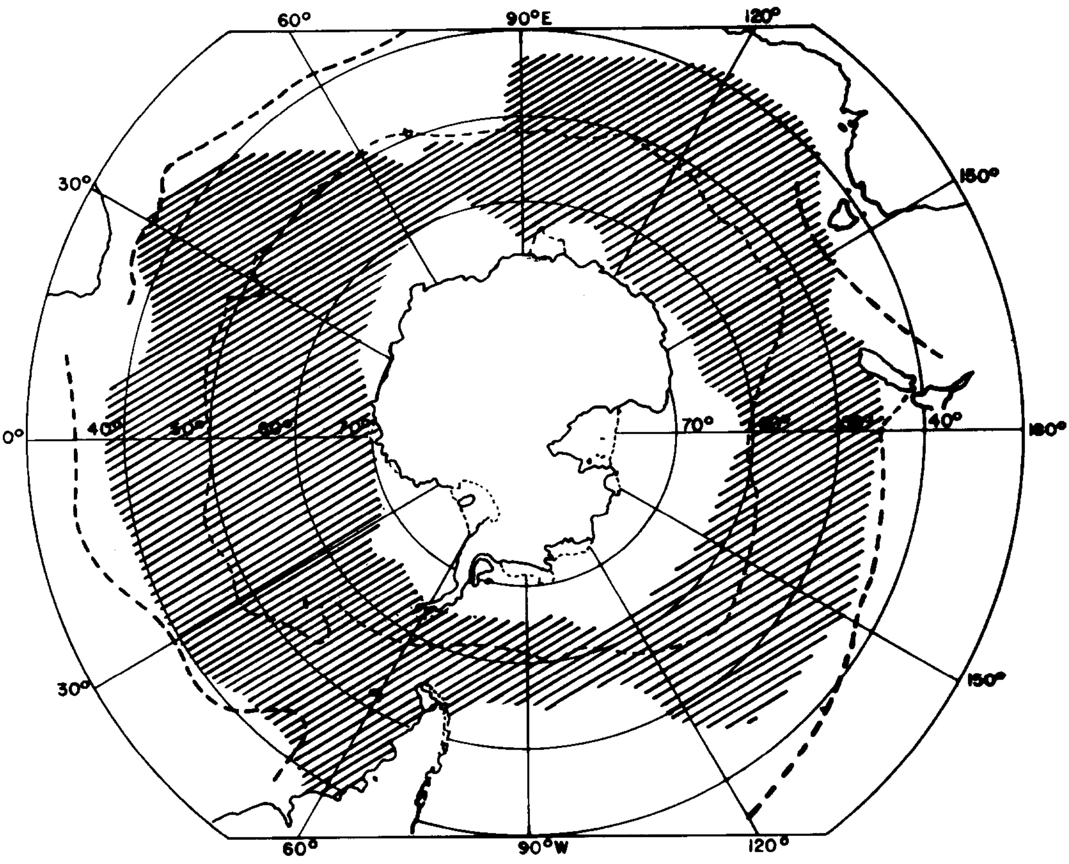


Figure 5. Salpa thompsoni (a) aggregate form, dorsal view; (b) solitary form, dorsal view. Map of distribution.



Body muscles: 9, broad, MI to III fuse medio-dorsally, MIV to VII are parallel, MVIII to IX fuse medio-dorsally
Alimentary canal: compact, oval nucleus
Stolon: proceeds forward past the level of MVII where it doubles back on itself
Length: up to 120 mm.
AGGREGATE FORM.
External appearance: barrel-shaped with conical anterior and posterior protuberances of the test; great variation in body form; anterior and posterior processes may be long giving a typical "fusiform" shape, or they may be shortened
Test: serrated, firm with a number of ridges
Body muscles: 6, broad, MI to IV and MV to VI fused to form two dorsal groups, MIV to V converge and join laterally
Alimentary canal: compact, oval nucleus
Embryo: single, behind MV at its point of lateral fusion with MIV
Length: up to 60 mm.

Salpa thompsoni is restricted to the Southern Ocean, and has a circumpolar distribution in moderate latitudes while in high latitudes it is restricted to the Atlantic, Indian and Australian sectors (Foxton, 1961). Its distribution and life history is studied in detail by Foxton (1966), who pointed out that it has a very patchy distribution with the greatest abundance between 45° and 55°S and only small numbers near the ice-edge.

This species is part of the "fusiformis group" (Foxton, 1961) together with Salpa fusiformis, S. aspera and S. gerlachei. These four closely related species can be separated on the external character of the test, the number of fibres per muscle band and the arrangement of the body muscles (see Table 2).

Van Soest (1975) suggested that Salpa gerlachei could be clinal form of S. thompsoni as these taxa differ only biometrically, and more important, they show intermediates (cf. Caldwell, 1966; Esnal, 1970). This view concurs with the fairly general trend in salp species with a wide distribution to form clinal variation (van Soest, 1975). However, more work needs to be done to see if the two are synonymous, for though, Foxton (1961) points out that the change in fibre count for S. gerlachei is abrupt even in areas of common distribution, Caldwell (1966) found considerable overlap in this main distinguishing character for these two closely related species. For the present they will be considered as separate species.

Foxton (1966) showed that down to 500 metres both solitary and aggregate forms perform a diurnal migration with the animals approaching the surface in the hours of darkness. Below 500 m there is little or no tendency to migrate.

Van Zyl (1960) suggested that the solitary form is found in deep waters and the aggregate in surface or subsurface waters but this was not observed by Caldwell (1966). Although Mackintosh (1937) found that many plankters descended to greater depths in the winter in the Antarctic no seasonal trend for depths of capture of Salpa thompsoni was found by Caldwell (1966). In the upper 100 m layer, Foxton (1966) reported a winter minimum in abundance for the aggregate form, while the solitary form was taken in all months, though in smaller numbers than the aggregate form.

		Max. body length (mm)	External Character of the Test	Arrangement of the body muscles	Mean Number of Fibres	Width of Muscles	Distribution
S. fusiformis	Aggregate	25	Smooth	M IV-V laterally joined	51.8	-	) North of STC*
	Solitary	45	Smooth	M VIII-IX joined	29.4	-	)
S. aspera	Aggregate	60	Serrated	M IV-V separate	194.1	-	)
	Solitary	95	Serrated (simple)	M VIII-IX parallel or nearly so	100.7	-	) North of STC
S. thompsoni	Aggregate	60	Serrated	M IV-V laterally joined	177.7	Broad 18.9:1#	Middle latitudes of Southern Ocean. Circumpolar
	Solitary	120	Serrated (complex)	M VIII-IX joined	93.2	Broad 21.2:1#	Northern limit - STC
S. gerlachei	Aggregate	33	Serrated	M IV-V laterally joined	128.8	Narrow 27.6:1#	High latitudes of Pacific sector of Southern Ocean
	Solitary	75	Serrated (complex)	M VIII-IX joined	48.8	Narrow 35.8:1#	

*STC = Subtropical Convergence
#Ratio of body length : muscle width

Table 2. A summary of the features characterising the four species of the "fusiformis" group (from Foxton, 1961).

Salpa gerlachei Foxton 1961

(Figure 6)

(*Salpa runcinata-fusiformis* var. *echinata* Herdman, 1910a part)
(*S. fusiformis* var. *gerlachei* van Beneden & de Selys-Longchamps, 1913)

Diagnostic characters (Foxton, 1961):

SOLITARY FORM.
External appearance: elongate, similar to *S. thompsoni*
Test: heavily serrated, firm; pattern and number of serrated ridges identical with those in *S. thompsoni* (i.e. "complex")
Body muscles: 9, thin, MI to III converge and joint dorsally, MIV to VII parallel, MVIII to IX converge and join dorsally, area of contact of the muscles that join dorsally is much smaller than in *S. thompsoni*
Alimentary canal: compact, oval nucleus
Stolon: similar to *S. thompsoni*
Length: up to 75 mm.
AGGREGATE FORM.
External appearance: barrel-shaped with conical anterior and protuberances of the test, similar to *S. thompsoni*
Test: serrated, disposition of the serrated ridges is the same as in *S. thompsoni*
Body muscles: 6, thin, MI to IV and MV to VI fuse dorsally to form two muscle groups, MIV to V converge and join laterally
Alimentary canal: compact, oval nucleus
Embryo: single, as in *S. thompsoni*
Length: up to 33 mm.

Salpa gerlachei is confined to the high latitudes of the Pacific sector of the Southern Ocean, occurring mainly in a sector between 65°S and the ice-edge, roughly between 175°E and 80°W (Foxton, 1961). Caldwell (1966) extended the known range eastward into Drake Passage as far as 62°W and indicated a possible population situated at a great depth far north of the Southern Ocean in the Peru-Chile trench (around 8°S, 81°W,) though Foxton (1966) pointed out that it was tempting to assume that these were sterile expatriates. This species is remarkable in not having a circumpolar distribution (Foxton, 1966). Some of the specimens identified by Herdman (1910a) as *S. runcinata fusiformis* var. *echinata* from the Ross Sea were referred to this species by Foxton (1961).

Genus *Ihlea* Metcalf 1919

Body muscles in solitary form complete uninterrupted loops; in aggregated form decidedly asymmetrical. This genus was created to include 4 species which were previously assigned to the genus *Salpa*. The thin fragile test means that the animal is preserved in an unnatural collapsed state (Foxton, 1971). The body shape can be reconstituted by injecting the collapsed animal with molten agar through the atrial orifice (Foxton, 1965). Two species *Ihlea racovitzai* and *I. magalhanica* are found in the Southern Ocean and Foxton (1971) details the points of difference between the two (see Table 3).

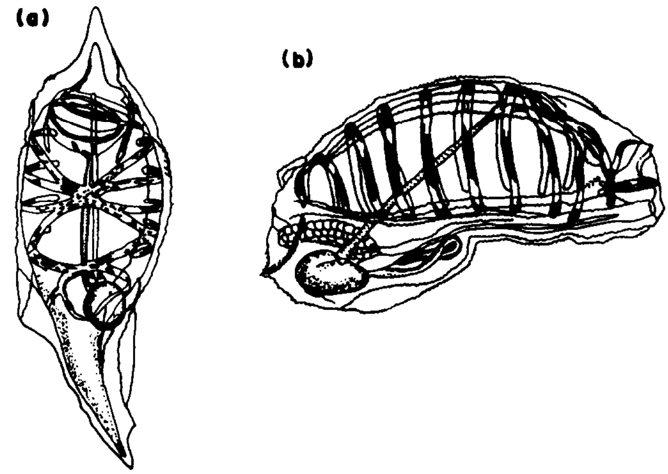
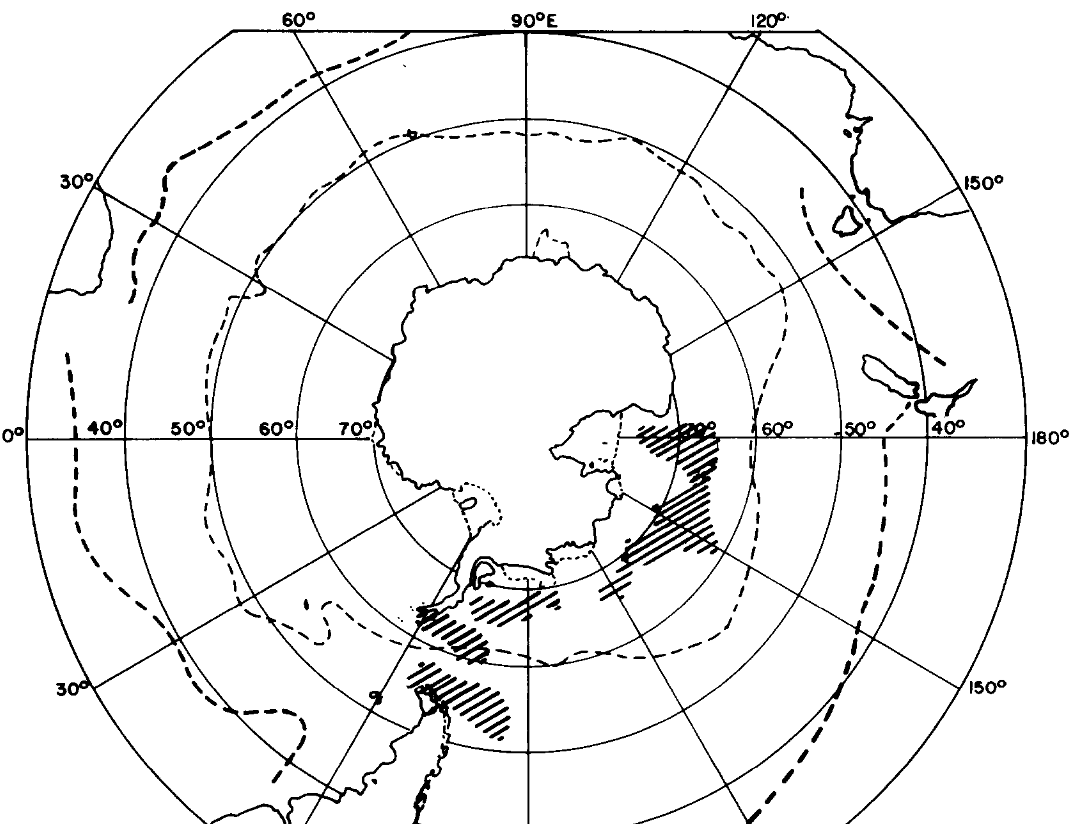


Figure 6. Salpa gerlachei (a) aggregate form, dorsal view; (b) solitary form, lateral view. Map of distribution.



	I. racovitzai	*I. magalhanica*
SOLITARY		
Oral retractor	Lateral tongue divided by a central zone of broad muscle fibres	Lateral tongue not so divided
MI to V (ventral)	Approach and touch medially	Only MI to IV approach and touch
Body muscle I (ventral)	Directed posteriorly as a prounounced spur to join MII	Joins MII but no spur
Muscle fibres	Structure of central zone precludes counting	MII 77-131 fibres mean 94.4 ± 15.9
Body form	Roughly cylindrical	Body reduces in width posteriorly
AGGREGATE		
Muscle fibres	MII 60-92. Mean 72.8 ± 8.3 (n = 20) Dolioliform	MII 25-40. Mean 31.5 ± 3.6 (n = 20) Cylindrical

Table 3. Points of significant morphological difference between the two Southern Ocean species of *Ihlea*. (Foxton, 1971).

Ihlea racovitzai (van Beneden 1913)

(Figure 7)

(Salpa magalhanica Apstein, 1906 part; Apstein, 1908 part)
(Salpa racovitzai van Beneden & de Selys-Langchamps, 1913)
(Ihlea magalhanica Stadel, 1958; Fagetti, 1959 part; Caldwell, 1966)

Diagnostic characters (Foxton, 1971):

SOLITARY FORM.
External appearance: elongate and roughly cylindrical; openings terminal, nucleus a compact ovoid
Test: extremely thin; soft and fragile
Body muscles: 7 of which MI to VI are broad and continuous; dorsally MI to IV and MV to VI touch over a wide area of contact to form two distinct groups, ventrally MI to V touch medially, although the area of contact is small, MI approach MII in the form of a pronounced and characteristic spur MIV and V approach and touch laterally, MVII divides into two lateral branches that are interrupted ventrally; muscles hyaline in texture
Oral musculature: although the lateral branch of oral retractor appears to be divided, this is due to a central area of a few relatively large muscle fibres that contrast with the upper and lower edges of the muscle; dorsally the oral retractor forms the first muscle of the upper lip and a branch of the second, while ventrally it divides to form two muscles of the lower lip, the intermediate muscle divides dorsally to contribute to the muscle of the upper lip and provides a narrow muscle that leads towards and divides just below the peripharyngeal groove; dorsally there are two horizontal muscles that originate just anterior to MI
Length: up to 70 mm.
AGGREGATE FORM.
External appearance: dolioform; pronounced asymmetry of anal orifice which is directed to the left or right according to the original position of the blastozooid on the stolon; short anterior and longer posterior process (Bary, 1961)
Test: thin and fragile
Body muscles: 5, dorsally MI to III meet and touch medially over a wide area as do MIV to V, thus forming two groups of muscles, MIV meets MIII laterally in one side or other depending on the asymmetry, MV on one side leads posteriorly over the nucleus and divides into two short branches; the other side provides two longer ventrally directed branches, which are interrupted; ventrally the musculature reveals further asymmetry, MII to III fusing with the left part of MI
Oral musculature: oral retractor provides two muscles of the upper lip and two of the lower; the intermediate muscle, which overlies the broad oral retractor is interrupted ventrally, narrowing as it leads dorsally where it divides into a short branch and a longer horizontal branch that turns abruptly to lead forward
Embryo: normally two behind MIV
Length: up to 20 mm.

Ihlea racovitzai van Beneden has been counsidered by nearly all later authors to be synonymous with I. magalhanica though Foxton (1971) believes both on morphological and distributional considerations, that van Beneden's species should be regarded as valid. It is an Antarctic form (van Soest, 1975) and is able to tolerate a temperature of 3.6° to -1.9°C and salinity up to 34.29 o/oo restricting its circumpolar distribution to waters south of the Antarctic Convergence (Foxton, 1971).

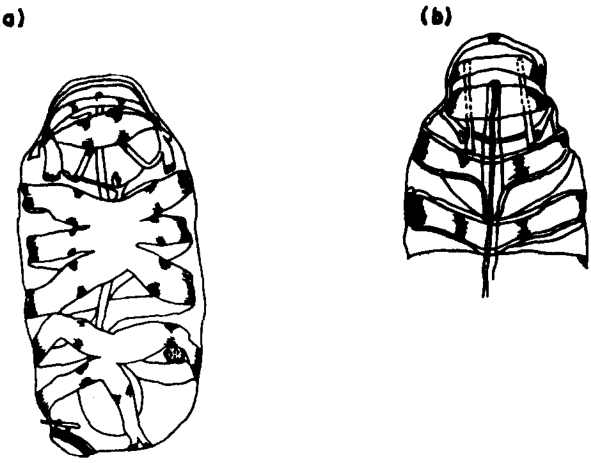
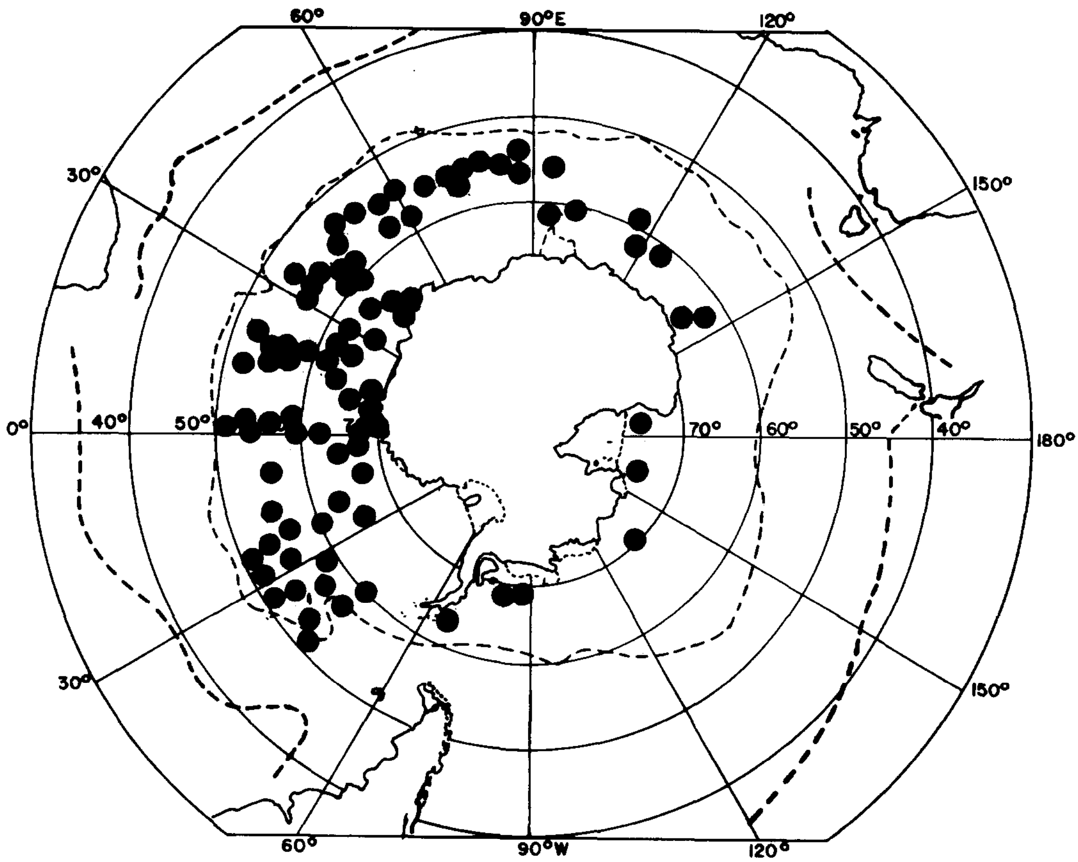


Figure 7. Ihlea racovitzai (a) aggregate form, dorsal view; (b) solitary form, in ventral aspect to show arrangement of oral muscles and body muscles I and II. Map of distribution.



Ihlea magalhanica (Apstein 1894)

(Figure 8)

(Salpa magalhanica Apstein, 1894, 1906 part, 1908 part; Streiff, 1908; Ihle, 1912)
(Apsteinia magalhanica Metcalf, 1918)

Diagnostic characters (Foxton, 1971):

SOLITARY FORM.
External appearance: elongate, inflated in region of MI to IV, marked reduction in width posterior to MIV; roughly dolioliform; oral and anal openings, nucleus and test as in I. racovitzai; stout, conical process posteriorly on test (Bary, 1961)
Body muscles: 7, MI to IV broad and continuous, MIII narrow; dorsally MI to IV approach and touch; similarly MV to MVI thus forming two groups; ventrally MI to IV approach and touch, MV and VI are separate; MVII divides into two ventral branches that separate; MVII divides into two ventral branches that are interrupted medially; MIV and V, touch laterally
Oral musculature: lateral branch of retractor not divided into two areas of broad muscle fibres; muscle arrangement as in I. racovitzai
Length: up to 35 mm.
AGGREGATE FORM.
External appearance: cylindrical; asymmetry of muscles and test as in I. racovitzai
Body muscles: broad, number and arrangements as in I. racovitzai, MII with more fibres than MII in I. racovitzai
Oral musculature: as in I. racovitzai
Embryo: two situated behind MIV
Length: up to 15 mm.

Ihlea magalhanica is a stenothermal, cold water species (Ihle, 1958) with a restricted high latitude distribution (Foxton, 1971). Its low tolerance to warm water conditions makes it a useful indicator of any northward extension of cold water (Thompson, 1948). Van Zyl (1959) reported the occurrence of I. magalhanica in South African waters and like Thompson presumes that this is attributable to a cold water intrusion from the South Atlantic. Bary (1961) however found a predominance of this species in warmer waters and postulated that it occurred in the warmest subantarctic water and the coldest subtropical water. Compared to I. racovitzai it is adapted to a greater temperature range 15.2 to 16.8°C, and a greater salinity range 33.86 to 35.44 o/oo (Foxton, 1971).

This species has been found by numerous workers in the Subantarctic waters and in adjacent waters and is considered to have a circumpolar distribution (Foxton, 1971). The only report of I. magalhanica from south of the Antarctic Convergence is that of Ealey & Chittleborough (1956) but this identification is doubtful (Foxton, 1971). It occurs in greater numbers than does I. racovitzai (Foxton, 1971).

The distribution of I. magalhanica and I. racovtzai, although circumpolar, are not contiguous being separated by a considerable area in which neither species has been recorded and this would seem to exclude that the possibility that the two species actually represent extremes of phenotypic variation in a single widely distributed species (Foxton, 1971).

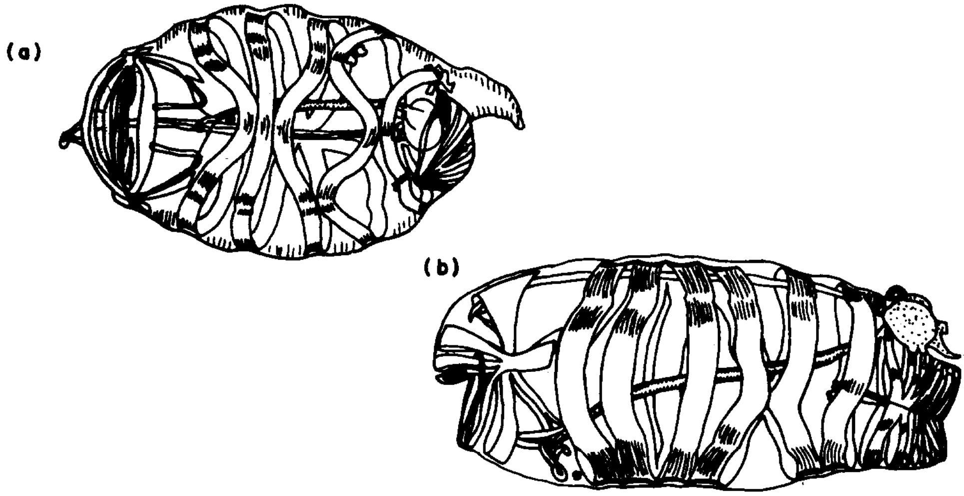
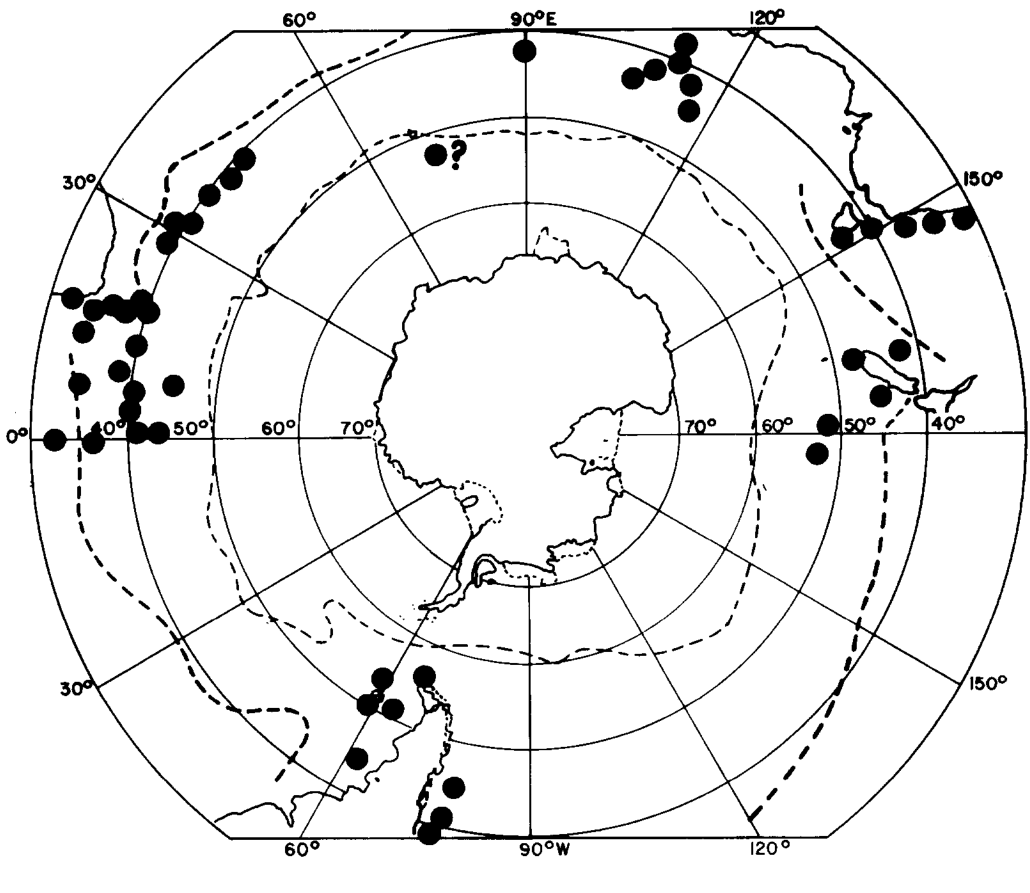


Figure 8. Ihlea magalhanica (a) aggregate form, dorsal view; (b) solitary form, lateral view. Map of distribution.



7. ORDER CYCLOMYARIA (Syn. Doliolidae)

Free swimming pelagic forms called doliolids exhibiting alternation of generations in their life history, the body is cask-shaped, and the musculature is mostly in the form of 8 or 9 complete circular bands surrounding the body.

7.1 EXTERNAL STRUCTURE

The adult sexual and asexual forms differ in only minor details of structure (see key below). The body is somewhat barrel-shaped with 8 or 9 complete circular muscle bands with terminal branchial and atrial apertures (Figure 9). The test is thin but tough. The branchial sac or pharynx is fairly large occupying the anterior half or more of the body. The alimentary canal or gut is placed ventrally, close to the anterior end of the cloacal cavity which is separated from the pharynx by the stigmata. The hermaphrodite reproductive organs lie ventrally near the intestine. The ovary is nearly spherical and the testis is elongated and may continue anteriorly for a long distance.

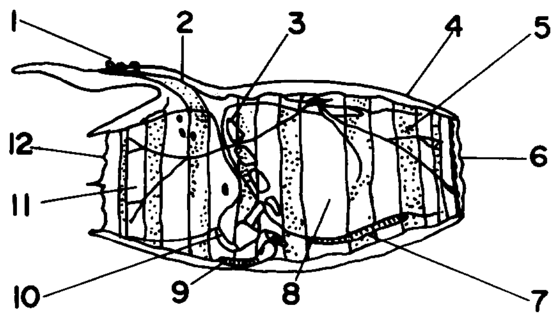


Figure 9. General structure of doliolid oozooid (1) buds, (2) dorsal stolon, (3) stigmata, (4) test, (5) body muscle, (6) branchial aperture, (7) endostyle (8) pharynx, (9) ventral stolon, (10) gut, (11) cloacal cavity, (12) atrial aperture.

Separation of free-swimming forms (Fraser, 1947b):

1a) With 8 muscle bands 2
 b) With 9 muscle bands (or continuous muscle sheet) and a dorsal process .... Oozooid

2a) A vestigeal ventral stalk, no gonads .... Phorozooid
 b) No outgrowth, gonads present .... Gonozooid

7.2 LIFE HISTORY AND BIOLOGY (after Fraser, 1947b; Thompson, 1948)

Doliolids have an alternation of generations in their life history. The asexual form (= "Oozooid") persists after the total disintegration of the viscera, and it is then known as an "old nurse" (=Amme). These have nine muscle bands but few sigmata, the latter being confined to the posterior end of the branchial sac. There is an otocyst on the left side of the body, and ventrally-placed complex stolon or "rosette organ", near the heart, from which the primary buds are produced by constriction.

These primary buds are constricted off while still very young and undeveloped; they migrate over the surface from their place of origin on the ventral stolon, multiply by fusion, and become attached in three rows - one median and two lateral - to the dorsal outgrowth or dorsal stolon, of the body of the nurse. This parent form has by this time become greatly modified. Its muscle bands develop greatly in width, and the branchial meshwork, endostyle and alimentary canal disappear.

The buds (="blastozooids") give rise eventually, after further division, to the sexual generation, which is polymorphic, having three distinct forms, in two of which the gonads do not develop. The three forms are:

a) nutritive forms (="gastrozooids" - "trophozooids"), which remain permanently attached to the oozooid;

b) free-swimming but sexless foster forms (="phorozooids"), which are eventually set free as cask-shaped bodies having the Doliolum appearance, with 8 muscle bands, but with a ventral outgrowth formed from the stalk by which the body was formerly attached to the oozooid;

c) on this ventral outgrowth the functional sexual forms ("gonozooids") are attached while still very young buds, and after the phorozooids are set free, these reproductive forms gradually attain their complete development, become sexually mature, and are finally separated off as cask-shaped bodies with 8 muscle bands.

The ova from the sexual generation produce tailed larvae. These have a relatively small tail but a large body in which the characteristic musculature begins to appear. These larvae after metamorphosis lose their tails and develop into oozooids (nurses).

7.3 FAMILY DOLIOLIDAE

Key to genera (gonozooids and phorozooids) (Garstang, 1933):

1. Alimentary canal forming an upright U or S shaped loop in the sagittal plane .... Doliolina
2. Alimentary canal extended horizontally in the sagittal plane, with a sub-terminal anus .... Dolioides*
3. Alimentary canal forming a close destral coil in the middle of the cloacal floor, with a median anus (Au, NZ, SA, In) .... Dolioletta
4. Alimentary canal forming a wide dextral arch round the cloacal floor, with anus parietal, on the right side (Au, NZ, Pa, SA) .... Doliolum+

The genus Doliopsis Vogt, represented by one rare species, D. rubescens Vogt (= Anchinia rubra Vogt) is not included above.

*Found in the Mediterranean only.
+Some specimens found in the Atlantic sector of the Southern Ocean were tentatively referred to Doliolum tritonis Herdman and D. denticulatum Quoy and Gaimard by Neumann (1906).

Genus Doliolina

Alimentary canal forming an upright U or S-shaped loop in the sagittal plane; five species of which only one has been reported from the Southern Ocean and adjacent waters although Garstang (1933) found D. mulleri Krohn off the north coast of New Zealand.

Doliolina intermedium var. resistible Neumann, 1913

(Figure 10)

(?Doliolium sp. Herdmann, 1910a)
(Doliolum resistible Neumann, 1913b)

Garstang (1933) gives the definition of Doliolina resistible Neumann as: Gill-septum vertical, slightly arched, with numerous gill-slits (12 to 45 pairs), which dorsally and ventrally begin on the 4th intermuscular space. He points out that the differential character of this and other so-called "species" (Dolioina intermedium Neumann), i.e. the limiting attachment of the gill septum, is probably no more than environmental modification. He goes on to suggest that resistible is simply a large varient of intermedium and should be referred to as D. intermedium var. resistible.

This species has been found in the Antarctic by Neumann (1906, 1913b), Garstang (1933) and possibly by Thompson (1954). Some imperfect specimens from the Southern Ocean, tentatively identified as Doliolium sp. by Herdman (1910a) may actually be D. intermedium var. resistible.

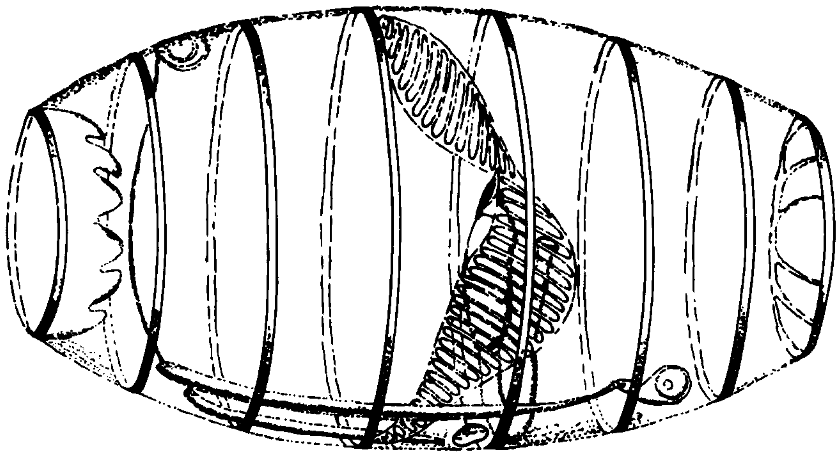
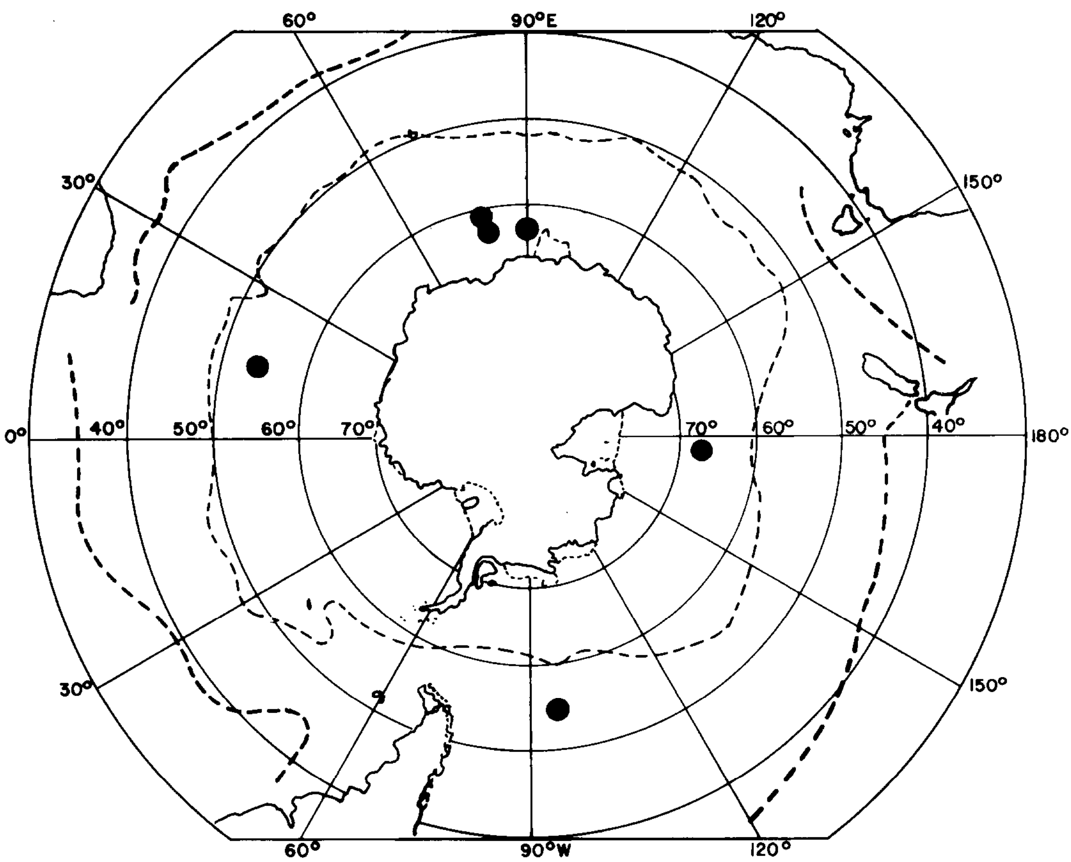


Figure 10. Doliolina intermedium var. resistible. Map of distribution.



8. CLASS APPENDICULARIA (Syn. Larvacea, Copelata)

Tunicata in which the sexually mature forms are small free-swimming larva-like individuals with conspicuous tail and a median axis called the urochord (Dakin and Colefax, 1940). These animals differ from the Ascidian tadpole larvae in that the tail begins at the middle of the body rather than the end and the distal extremity of the tail falls on the same side of the mouth. The three families are separated on the shapes of the body and endostyle and the length of tail.

8.1 EXTERNAL STRUCTURE (after Herdman, 1910b)

Appendicularians are usually damaged during capture and it is very difficult to relate the descriptions and figures in the literature to the specimens seen under a microscope. New students of this group may also become confused by the various names given by different authors to the same structure. Table 4 gives the names used in this guide together with the corresponding names used by the major workers in this group: Lohmann, Herdman, Thompson and Tokioka. In the text these alternative names are given in parenthesis.

The body of an Appendicularian can be divided into two sections, the trunk and the tail (Figure 11). The trunk is clothed in an ectoderm cell layer known as the oikoplast epithelium. The occurrence of specific cell groups (i.e. Fol's and Eisen's oikoplast) in this layer can help to identify species but it is often damaged or lost during capture. These tracts of glandular cells possess the power of forming with great rapidity (often within an hour), an enormously large (many times the size of the body) investing gelatinous layer known as the "house". This probably corresponds to the test of the other Tunicate groups, although it is doubtful whether it contains cellulose and it differs in having no migratory cells and its temporary nature. Fenaux (1977) gives an account of the "house building" of the genus Oikopleura.

The house is only loosely attached to the body, and is frequently thrown off soon after its formation. The volume of the house is about three hundred times the volume of the trunk of the animal (Fenaux and Hirel, 1972). Its function is probably protective and possibly to some extent hydrostatic and it is also used in straining nutritive particles from the large volumes of water which pass through the "filter" formed from the complicated passages and perforated folds of the house.

The trunk proper is usually either compact and ovoid or elongated and rod-like. The length of this portion which houses the organs varies from 0.3 up to 25 mm. The nervous system consists of a large dorsally placed ganglion and a long nerve chord, which stretches backwards over the alimentary canal to reach the tail, along which it runs on the left side of the urochord.

The mouth is in front of the trunk and in some species it has a prominent lower lip. It leads into the simple pharynx (branchial sac). There are no tentacles, though in the Fritillaridae a snout is formed in front of the mouth which often carries several lobe-like lip processes. A dorsal hood is also present in this group of Appendicularians.

In front of the pharynx is a short endostyle, a tube closed at both ends, having about four longitudinal rows of buccal (oral) gland cells. The wall of

STRUCTURE	LOHMANN	HERDMAN	TOKIOKA	THOMPSON
Trunk (body)	rumpf			
Oikoplast epithelium	Oikoplasten-epithel	"oikoplasts"		
House (shell)	gehausen lage			
Urochord	chorda			
Mouth	mundoffnung			
Pharynx		branchial sac		branchial sac, cavity
Lip	randfalte angedeutet			
Hood	Kapuze			
Endostyle	endostyl			
Spiracles	kiemenoff-nungen	stigmata		branchial aperture
Atrial opening			external gill opening	
Anus	after			
Oesophagus	speiserohre			
Stomach	magen			
Intestine	darm			
Rectum	enddarm			
Ovary	escistock			
Testis	hoden			
Buccal glands	munddrusen	oral gland		
Fol's oikoplast	Folschen oikoplasten			
Eisen's oikoplast	Eisenschen oikoplasten			
Tail	schwanze			
Tail fin	schwanzflosse			
Tail musculature	schwanz muskulatur			
Subchordal cells	subchord-alzellen			
Amplichordal cells	amphichordal zellen			
Giant cells	riesenzellen			
Middle cells	mittelzellen			subsidary cells
Desquamation bodies	hautungskorpern			
Martinis field	Martinis feld			
Branchial canal	kiemenganze	ciliated funnel		branchial passage

Table 4. Differences in the names of the morphological structures of the Appendicularia as given by Lohmann, Herdmann, Tokioka and Thompson. A blank indicates that the authors used the same name.

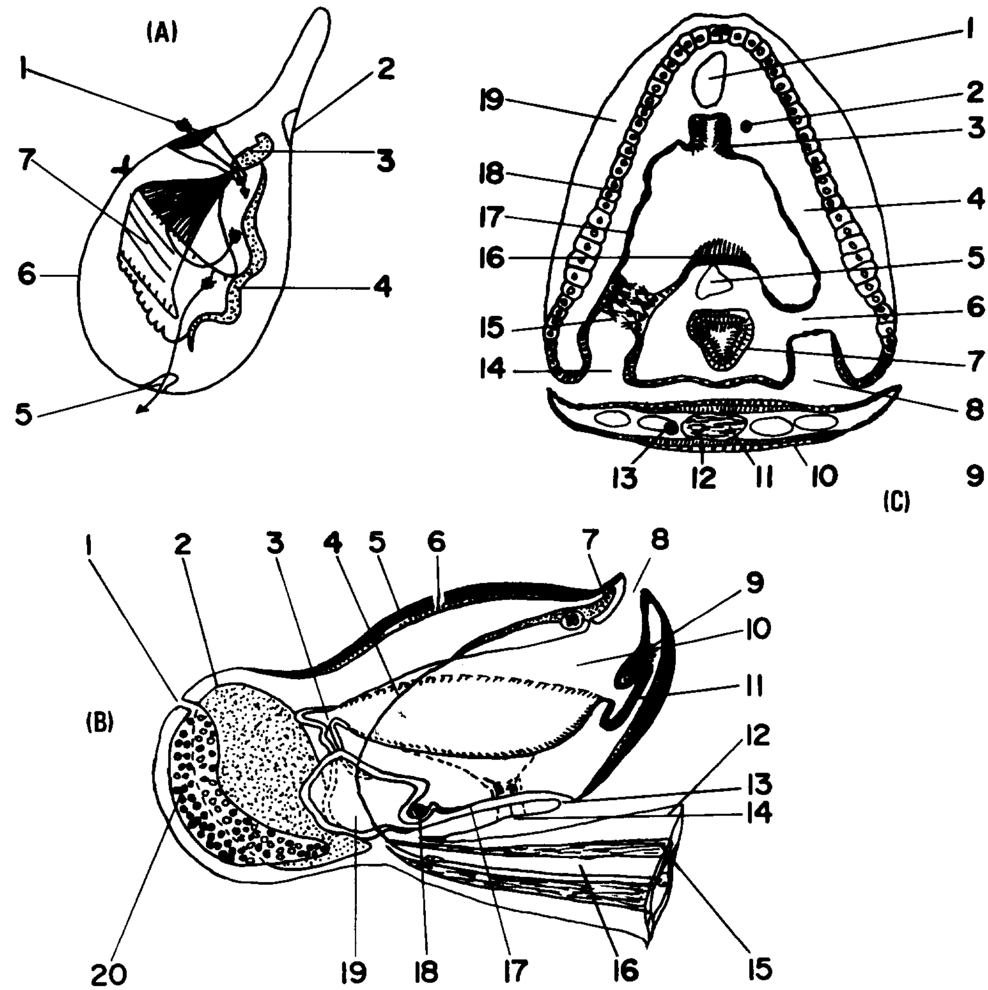


Figure 11. General structure of larvaceans. (a). The larvacean Oikopleura albicans with arrows showing path of water currents through the house (1) inhalent orifice, (2) emergency exit, (3) body, (4) tail, (5) exhalent orifice, (6) house, (7) filter; (b). Longitudinal optical section of Oikopleura (part of the tail is cut off) (1) genital opening, (2) testis, (3) oesophagus, (4) nerve, (5) test, (6) ectoderm, (7) nerve ganglion, (8) mouth, (9) buccal gland, (10) pharynx, (11) endostyle, (12) tail fin, (13) anus, (14) atrial opening, (15) tail muscle, (16) urochord, (17) intestine, (18) heart, (19) stomach, (20) ovary; (c). Cross section through Oikopleura body and tail (1) blood-space, (2) nerve-chord, (3) epipharyngeal cili bands, (4) gelatinous layer between ectoderm and endoderm, (5) blood-space, (6) bridge of gelatinous tissue in front of spiracle closing pharynx off from atrial tube, (7) rectum, (8) atrial tube, (9) blood-space, (10) ectoderm, (11) notochord in tail, (12) muscular tissue on inner surface of ectoderm of tail, (13) nerve chord in tail, (14) atrial tube, (15) spiracle, (16) hypopharyngeal ciliated band, (17) endoderm, (18) ectoderm, (19) test.

the simple pharynx has only two cilitated apertures called spiracles (stigmata or branchial apertures) placed far back on the ventral surface, one on each side of the middle line, and leading into short funnel-shaped tubes, the branchial canals, which open on the ventral surface of the body behind the anus via the atrial (gill) opening.

The remainder of the alimentary canal consists of oesophagus, stomach (which may have a glandular diverticulum in the Fritillaridae), intestine and rectum. The heart lies below and in front of the stomach, and is formed by the differentiation of the outer ends of epithelial cells into muscular fibrillae. Two specially large glandular cells are placed at opposite ends of the heart in the Fritillaridae. There are no blood-vessels except the remains of the primary body-cavity (blastocoel) which form blood spaces. All species, but one, are hermaphroditic, and the large ovary and testis are placed at the posterior end of the body behind the alimentary canal, except in Tectillaria tertilis. The number and shape of the gonads vary in the genera and very often among the species also (Fenaux, 1977).

The tail is attached to the ventral surface of the body, and is bent downwards and forward, so that it usually points more or less anteriorly, and is twisted through an angle of 90° so that the dorsal edge lies to the left. The tail is the locomotory appendage by which the animal moves in a characteristic vibratory manner.

The tail consists of a fin in which there is a median axis, the urochord, consisting of a homogeneous rod flanked on either side by a sheath or bank of muscles. The tail fin may be thin or quite broad and is usually several times longer than the trunk section of the body, growing up to 20 mm in length. Species can be recognised by the presence or absence of cell groups in various patterns within different parts of the tail. Subchordal cells occur in Oikopleuridae within the muscle bands while amphichordal cell groups occur in Fritillaridae in the tail fin proper.

Although for the most part transparent, and usually almost invisible in seawater, some larvaceans may have certain parts of the body (alimentary canal, endostyle, gonads, etc.) brilliantly pigmented (violet, red or yellow). In O. longicauda, the colouration most frequently observable is a faint purplish tint found on the stomach and intestine, while the rectum is usually seen yellowish orange by its contents (Tokioka, 1961). This colouration can often be seen on living specimens of many other species.

8.2 LIFE HISTORY AND BIOLOGY (after Herdman, 1910b)

Only sexual reproduction occurs in the Appendicularia with development leading to a free-swimming tadpole larva that undergoes metamorphosis without settling (Barnes, 1974). All species except one (O. dioica Fol) are hermaphroditic. The products of the ovary are expelled through the genital opening at the rear of the body as there is no proper oviduct but there is a spermiduct. The spermatozoa mature and are generally shed before the ova, so self-fertilisation is prevented. The spawning is followed by the death of the animal (Fenaux, 1977). The free gametes fertilize in the sea (Fenaux, 1976). For detailed studies on the life history and development of some species of Appendicularians see Fenaux (1976a, 1977 and 1983).

Essenberg (1926) studied the death and disintegration of some species of Appendicularia stating that these animals degenerate and die by degrees, the anterior end preceeding the posterior end. If the anterior end is separated from the posterior one, all the organs in the anterior end stop functioning immediately, while the posterior half may live several hours with all its organs functioning. She also reported the gradual degeneration of some organs coincident with the extreme development of the ovaries and testes of certain genera.

The beating of the tail of the animal creates a water current that passes through the house and is strained of plankton by a grid or screen of fine fibers often called the filter. The cilia of the spiracles rotate bringing water into the pharyngeal cavity through the mouth. Particles of food on the filter are transported by this current into the mouth where they adhere to secreted mucus and are passed through the oesophagus into the stomach (Fenaux, 1977).

Water passing out the exhalent opening of the house creates a jet which drives the animal in the opposite direction. The animal leaves the house by breaking through the lower front wall which is particularly thin (Fenaux, 1977).

The important part of the appendicularian population lies in the upper 200 m layer as generally more than 80% of the number are caught in the upper 75 m in trawls from 100 m to the surface (Fenaux, pers. comm.). Some species such as O. parva, Frit. tenella, Frit. megachile and Folia gracilis often penetrate into much deeper layers (Tokioka, 1961). In the Antarctic sea the densest population may be found in some cases in 100-200 m or 200-300 m layers (Lohmann, 1933).

Many individuals of appendicularians floating in the surface water layers can be blown together to form enormously dense swarms at some place, under special topographic condition, in much the same way as "red tides" or Noctiluca and other phytoplankton (Tokioka, 1955). Such a swarm of Oikopleura was described by Seki (1973).

8.3 KEY TO FAMILIES (Fenaux, pers. comm.)

Body ovoid; endostyle straight, spiracles in the rectal area; tail thin and never indented at the tip .... OIKOPLEURIDAE

Body elongated or flattened dorso ventrally; endostyle curved; spiracles in the anterior part of the pharyngeal cavity; tail broad and short, sometimes indented in the median part of the fore edge .... FRITILLARIDAE

Body short; endostyle and heart missing; no spiracles; elongated branchial appertures; tail elongated with a willow sliver shape .... KOWALEVSKIIDAE

The Antarctic fauna contains some endemic species in addition to warm water species which are evidently carried there from adjoining antiboreal or south temperate regions (Tokioka, 1961). Lohmann (1928) found that in the Weddell Sea the Antarctic endemic species were confined to the cooler upper 100 m layer while the warm water species were found in the lower layer deeper than 100 m and with the temperature slightly higher than the surface layer. However

Tokioka (1961) points out that it is impossible that such distributions are wholly attributable to the difference of temperature, because some Antarctic endemic species may sometimes be distributed far north to the West Wind Drift and moreover the temperature difference between these two layers is too small to be regarded significant in usual cases.

The rich Antarctic pelagic fauna seems attributable to the rather invariable state of the waters maintained for a long historial age and caused by the characteristic topography of the Antarctic continent, the hydrographic conditions around it and also by the existence of the cyclone zone of the Antarctic front (Tokioka, 1961).

Identification of some species is not easy for the beginner. Fritillarians are much smaller than Oikopleurians and so are not usually caught in nets with a large mesh. They are also often overlooked in plankton collections due to their small size. The classification of the Appendicularia followed below is generally in accordance with that of Lohmann (1933), with certain amendments by Thompson (1948).

8.4 FAMILY OIKOPLEURIDAE

Body ovoid, with compact alimentary tract; endostyle is straight; stomach wall beset with very numerous small and a few large glandular cells; Fol's oikoplast group is present on either side of the oikoplast epithelium, and consists of a row of giant cells with three rows of secondary or subsidiary cells lying closely behind them; the spiracles are connected to the pharynx by several passages; a gelatinous house encloses the body; the tail is usually several times as long as the body; 2 sub-families separated by shape of spiracles, position of the subsidiary cells of Fol's oikoplast and position of the oikoplast epithelium.

Key to sub-families (Lohmann & Buckmann, 1926):

The oikoplast epithelium stretched on the abdominal side up to the anus, which is just before the spiracles, its back is more or less pedimentally erected; the subsidiary cells on the Fol's oikoplast lie behind the giant cells .... Oikopleurinae

The oikoplast epithelium is limited ventrally to a very small belt like the Fritillarids, the anus is situated far behind it, while the spiracles lie in front of the anus, right behind the belt; the oikoplast epithelium is very flat dorsolaterally and not pedimentally erected; the subsidiary cells of the Fol's Oikoplast lie in front of the giant cells; the intestinal loop with its opening to the front lies horizontal with the exception of the rectum, a gigantic left stomach lobe protrudes from the middle section .... Bathochordaeinae

Sub-family Oikopleurinae

Spiracles not sharply separated from the pharynx but opening into it by broad funnels; alimentary canal simply tube-shaped; oikoplast epithelium directed outwards dorsally, more or less steeply, in gable-like fashion, and reaching ventrally well posterior to the anus; the subsidiary cells of Fol's oikoplast lie behind the giant cells; 7 genera of which Chunopleura has not been reported from the Southern Ocean or adjacent waters. The genera and species of the Oikopleurinae are usually separated by the structure of the alimentary canal.

Key to Genera:

1a) Alimentary canal compactly coiled into a thick and massive nucleus .... Oikopleura
b) Alimentary canal not compactly coiled 2

2a) Alimentary canal incompletely developed through the absence of one or both lateral pouches 3
b) Alimentary canal forms only a loop which stands vertically and is broadly open to the front, no left stomach process 4

3a) Stomach compact and roundish, with well-developed left lobe only .... Folia
b) Stomach smooth and extensive, the left lobe being more or less strongly reduced so that only the median portion remains (Au) .... Megalocercus

4a) Midportion of intestinal loop modified to serve as stomach, situated vertically along the sagittal axis of the body .... Pelagopleura
b) Stomach separate from intestinal loop 5

5a) Stomach compressed sideways .... Stegosoma
b) Stomach not compressed 6

6a) Stomach located horizontally above the level of the gonad (At, Au) .... Althoffia
b) Stomach situated vertically along the left lateral body wall in the posterior half of the body .... Sinisteroffia

Garstang and Georgeson (1935) reported an un-named Oikopleuridaen from the New Zealand sector of the Antarctic with two striking rows of amphicordal cells running the whole length of tail and a pair of well developed oblong and lobulated buccal glands. This combination of characters was unique that they couldn't refer the specimen to a known genus.

Genus Oikopleura Mertens 1830

Body compact, organs within it tightly packed; oikoplast epithelium extends dorsally over the coil of the gut, ventrally to the anus; spiracles on both sides of rectum; stomach a broad transversal sack, in the posterior part divided into a right and a left lobe by an aboral notch; oesophagus leads into the dorsal edge of the left stomach lobe; rectum in the median plane below or in front of the unpaired middle part of the stomach (Buckmann 1969); eighteen species of which some are probably synonymous (Thompson, 1948).

This genus is often divided into 2 subgenera: Subgenus Vexillaria Lohmann characterised by buccal glands on both sides of the endostyle and subchordal cells in the tail, and Subgenus Coecaria Lohmann without buccal glands and subchordal cells. The Southern Ocean species Oikopleura gaussica Lohmann and

O. parva Lohmann belong to the former and O. fusiformis Fol and O. longicanda (Vogt) to the latter. Subgeneric differentiations will not be given in the synonymy.

Key to species (after Lohmann & Buckmann, 1926):

1a) Buccal glands and subchordal cells exist; the area of the pharynx flat; endostyle horizontal; mouth at the front end of body; shell nearly always with d-bodies[1]; postcardial blindsac of the stomach mostly small, if large then not dorsally ascenting (subgenus Vexillaria) 2

b) Buccal glands and subchordal cells are missing; the area of the pharynx is well formed and reaches into the region of the sides, they are mostly roundish and swollen; mouth opening transferred to the dorsal end of body; d-bodies are always missing; post cardial blindsac is often very strongly developed and dorsally erected .... (subgenus Coecaria) 7

2a) Left stomach lobe roundish or pocket-shaped; d-bodies shaped like a rod, tube or plate, their lines always stretch from the bottom end of the Fol's Oikoplast back toward the dorsal end 3

b) D-bodies are missing or are arranged in rows which are directed toward the mouth; left stomach lobe without post cardial blindsac; body arched steeply, like a pediment; only one or two subchordal cells 6

3a) Martini's field with 7 large middle cells; gonads of bow shape growing on the side of the intestinal coil; left stomach lobe is roundish; subchordal cells forming a long half-duct of about 15 cell pairs; d-bodies formed from tailed rods and arranged in two complete erect loops; oikoplast epithelium so short that the largest part of the intestinal coil remains uncovered; body length up to 3.9 mm .... O. gaussica Lohmann

b) D-bodies string-like tubes which develop in one type like plates or bands; Martini's field not with 7 large middle cells 4

4a) D-bodies are not numerous, they are a few bodies shaped like bands or plates and are situated in the back part of the oikoplast-epithelium; left stomach lobe is a diagonally situated pocket of a rhomboidal shape; buccal glands very large; subchordal cells lie in one row (about 8 cells); gonads when fully developed

1. Only known in the Vexillaria group are strange additions to the shell which Lohmann and Buckmann (1926) named Desquamation Bodies (d-bodies) because they seemed to play an important role in the development of the shell of the animal, which has similarities to desquamation procedures in other cuticularly covered animals. They are missing with O. rufescens and mediterranea. Most types have them prominently developed and they appear either as small rod or box-shaped bodies or as tube-like strings.

are mostly in the lower part of body; body length up to 1.35 mm (Au, SA, In) .... O. cophocerca Gegenbaur

b) D-bodies numerous tube-like strings, partly running parallel to each other 5

5a) Only one parallel row of d-body strings is formed, it climbs diagonally from the front and the lower section to the back; left stomach lobe roundish; muscles of the tail above the urochord very thin; four spindle-shaped subchordal cell groups; body length up to 0.8 mm ...... O. parva Lehman

b) 2 rows of stringlike d-bodies running parallel to each other are formed, the rows lie close to each other without forming a loop, strings stored close together and very numerous; left stomach lobe is pocket-shaped, stretching toward the front with a small postcardial blindsac; subchordal cells numerous and arranged into two cell rows that lie close to each other (one row dorsoventral over the other) which sometimes stretch backwards to the tail root, with the body fluids running between them; body length up to 5 mm (Au, At, SA) .... O. albicans Leuckart

6a) Left stomach lobe having a semicircular outline; no d-bodies; rectum stands up straight and is very thick; d-bodies are missing; one large linear or spindle-shaped subchordal cell; the dorsal part of the body has depression between intestinal coil and atrial opening; body length up to 1.8 mm (Co) .... O. rufescens Fol

b) Left stomach lobe is cut off near the lower section, just behind the oesophagus, in a straight line; intestine under the right stomach lobe with protruding blindsac; Fol's oikoplast with 9 'giant cells' and Eisen's oikoplast with 7 main cells (in all other types 8 or 6 resp.); endostyle formed on both sides from only one ciliated cell and one glandular cell; Martini's field large, bow shaped and cells very small; two spindle-shaped subchordal cells; unisexual, not hermaphroditic as in the other species; body length up to 1.29 mm (Au, NZ, SA) .... O. dioica Fol

7a) Hood well developed, covering the whole oikoplast epithelium; Eisen's oikoplast is missing completely; postcardial blindsac finger-shaped and situated close to the oesophagus and is directed upwards and rounded off on the top; body length up to 12 mm .... O. longicauda Vogt

b) Hood is missing or only just indicated as a small wrinkly lip; Eisen's oikoplast present, its subsidary cells lie dorsally 8

8a) Post cardial blindsac is strongly developed and has a dorsally directed extension 9

b) Post cardial blindsac is not directed dorsally; left stomach lobe trapezoid or triangular in shape, growing out into a blindsac behind the cardiac portion of the stomach; stomach lobes ventrally much diminished; body length up to 0.37 mm (Au) .... O. gracilis Lohmann

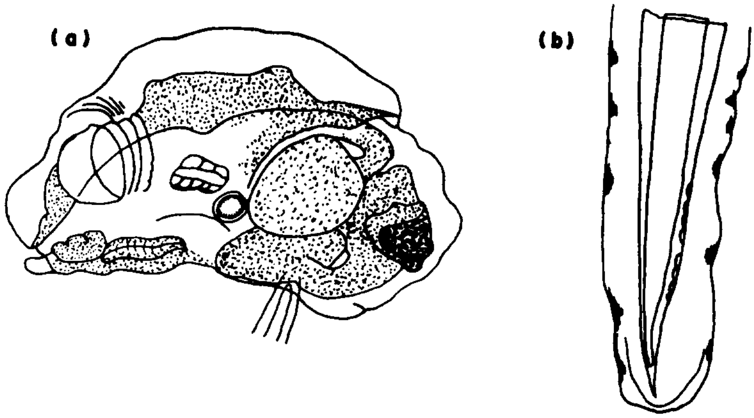
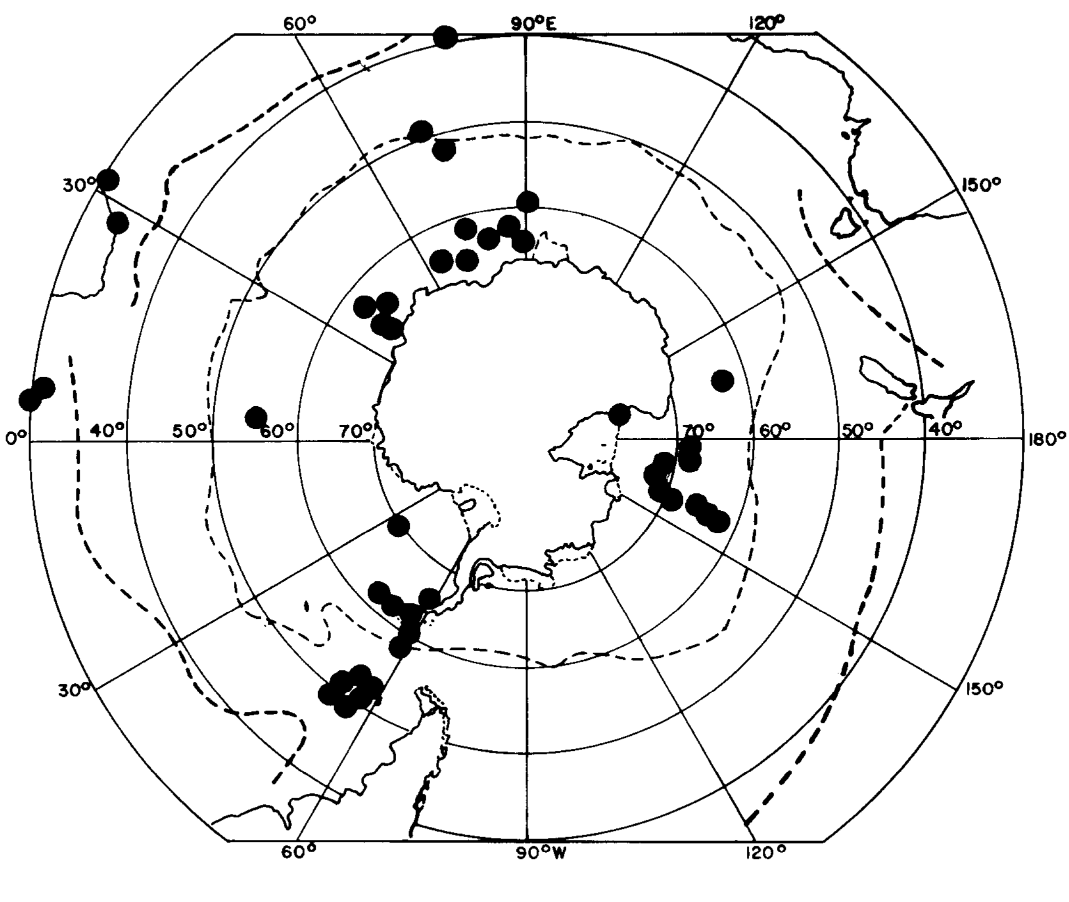


Figure 12. Oikopleura gaussica (a) trunk, lateral view; (b) tail, dorsal view of end. Map of distribution.



9a) Extension short, finger-like rising behind the cardiac region of the gut, separated from the cardia by a round bight; intestinal coil standing far apart between the left stomach lobe and the large intestine, the resulting sinus is bridged by the bowl-shaped spreading gonads; body length up to 2.12 mm (Au, At, SA) .... O. intermedia Lohmann

b) Extension long, horn-shaped, directed diagonally to the rear 10

10a) Extension stiff, linear, veil arranged as a small wrinkly flap; the front section of the body is short and stubby; tail fin broad; body length up to 2 mm (Au, SA) .... O. cornutogastra Aida

b) Extension bent, no wrinkly flaps; front section of the body very slim and elongated; body length up to 1.5 mm .... O. fusiformis Fol

The Antarctic oikopleurids seem to shown much more extensive variability than the Arctic oikopleurids, but some described species may be nothing but variants or one or two distinct species (Tokioka, 1961). Lohmann and Hentschel (1939) named seven new Antarctic endemic oikopleurdis without giving descriptions or figures. Tokioka (1961) lists them as Oikopleura falklandica, O. fridida, O. magellanica, O. meteori, O. oblonga, O. rigata and O. simplex saying they are invalid as well as pointing out that nothing is known about their systematic affinities.

There are four species of Oikopleura that have been found in the Southern Ocean. These are O. gaussica Lohmann, O. parva Lohmann, O. fusiformis Fol and O. longicauda (Vogt). A specimen of O. mirabilis was tentatively identified by

Lohmann and Buckmann (1926) from the southern Atlantic Ocean but no other information was given. Herdman (1910a), Hardy and Gunther (1935) and Tokioka (1964) all found specimens in the Southern Ocean which they could only identify to genus level (i.e. Oikopleura spp.).

Garstang and Georgeson (1935) tentatively referred some species from the New Zealand sector of the Antarctic to O. rufescens Fol but pointed out certain peculiarities which with fuller material might justify the definition of a new species intermediate between O. rufescens and O. dioica Fol.

Oikopleura gaussica Lohmann 1905

(Figure 12)

(Oikopleura valdiviae Lohmann, 1905; Lohmann and Buckmann, 1926; Garstang and Georgeson, 1935; Thompson, 1954; Udvardy, 1958)
(Oikopleura drygalski Lohmann and Buckmann, 1926)
(Oikopleura weddelli Lohmann, 1928)

Diagnostic characters (Tokioka, 1964):

Trunk: ovoidal, considerably elongate
Oikoplast epithelium: dorso-posterior edge attains the level of the posterior margin of the alimentary organ in smaller individuals but ends before it,

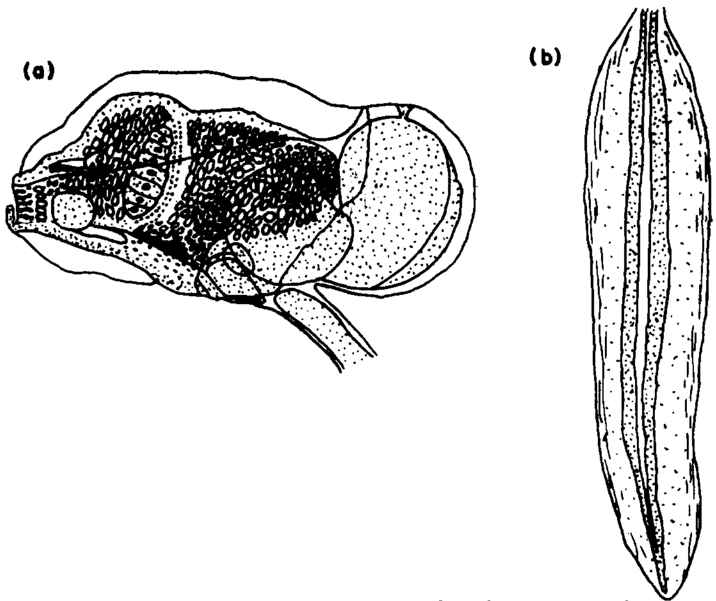
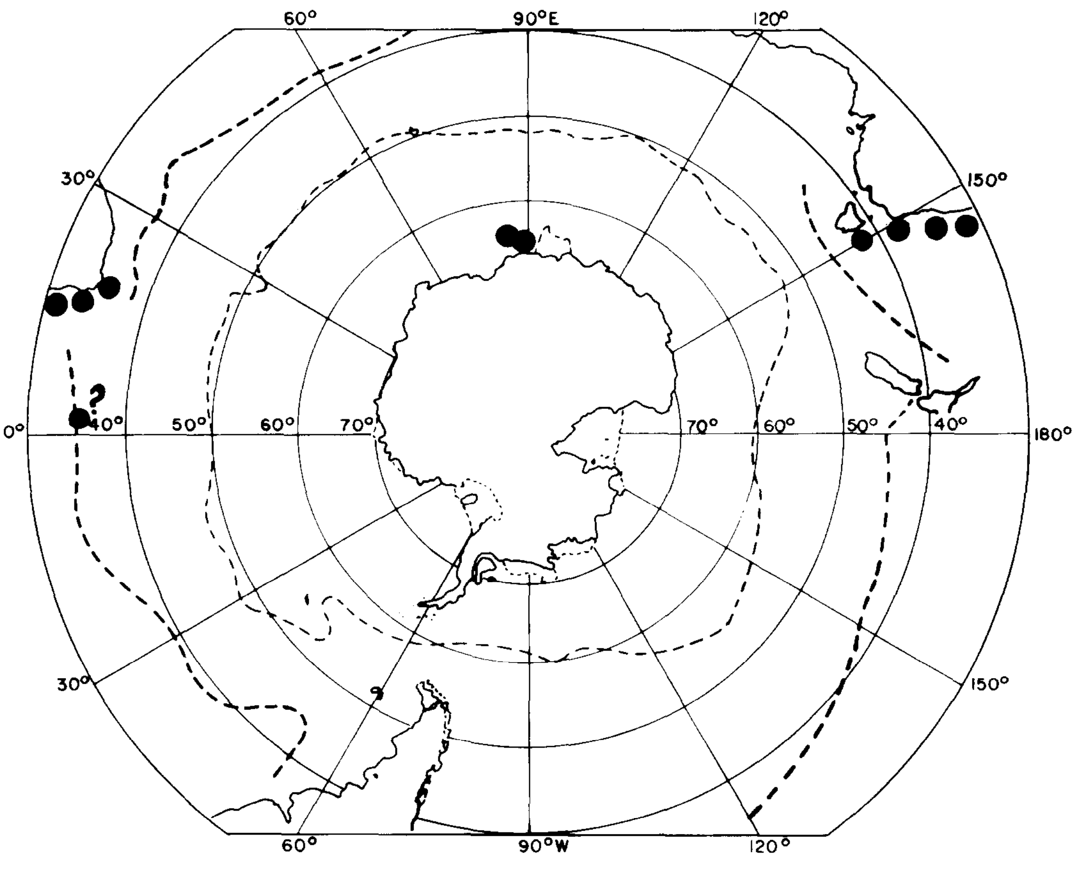


Figure 13. Oikopleura parva (a) trunk, left side; (b) tail. Map of distribution.



reaches near the posterior margin of the organ in larger ones
Buccal glands: large, oval in small to medium individuals, but become more or less lobated along the periphery in larger individuals
Endostyle: elongate
Oesophagus: enters left stomach lobe at its dorso-posterior end
Stomach: occupies the posterior half of trunk left lobe is roughly oval in outline, without any blind-sac, being slightly elongate antero-posteriorly
Rectum: nearly horizontal
Anus: opens before anterior edge of stomach
Gonad: retains triangular shape even in most mature individuals
Tail fin: long and pointed
Subchordal cells: 6 to 14, most frequently oval and vascular
Length: body to 4.1 mm; tail to 17 mm (Garstang and Georgeson, 1935).

The validity of four described species of Oikopleura reported from the Antarctic Seas (O. gaussica, O. valdiviae Lohmann, O. drygalski Lohmann and Buckmann and O. weddelli Lohmann) is discussed by Tokioka (1964):
O. drygalski was described on the basis of a few imperfectly preserved specimens and may be nothing but an individual of O. gaussica or valdiviae sexually matured in spite of a small body. Only three immature specimens of O. weddelli are known and this species is only separated from O. gaussica and O. valdiviae by a character which varies considerably in arrangement and structure. O. weddelli most closely resembles O. valdiviae in having a similar oikoplast-epithelium and a tail with then capsular subchordal cells and with a wide musculature. The two remaining species O. valdiviae and O. gaussica resembled each other so closely that Tokioka (1964) considered them identical, stating that the specific name gaussica should be retained after the page priority.

O. gaussica has been reported from the Southern Ocean by numerous workers and Tokioka (1961) considers it to be endemic. Garstang and Georgeson (1935) detail the maturation process for this species and describe the principal gelatinous and membranous elements of the house rudiments.

Oikopleura parva Lohmann 1896

(Figure 13)

Diagnostic characters:

Trunk: elongated in form, but very small
Oikoplast epithelium: extends backwards so as to cover the oesophagus and a portion of the stomach (Buckmann, 1969)
Buccal glands: one pair, large
Endostyle: short and narrow, close to front of stomach (Buckmann, 1969)
Stomach: left lobe round, posterior edge protrudes only slightly beyond the cardia (Buckmann, 1969)
Ovary: single, median
Testes: paired, lateral together in roundish mass behind the gut coil
Tailfin: long and usually much curved
Tail musculature: fairly broad, but delicate and rather transparent
Sub-chordal cells: four, spindle-shaped, on left side of notochord near tip of tail
Length: body up to 0.8 mm; tail up to 4 mm.

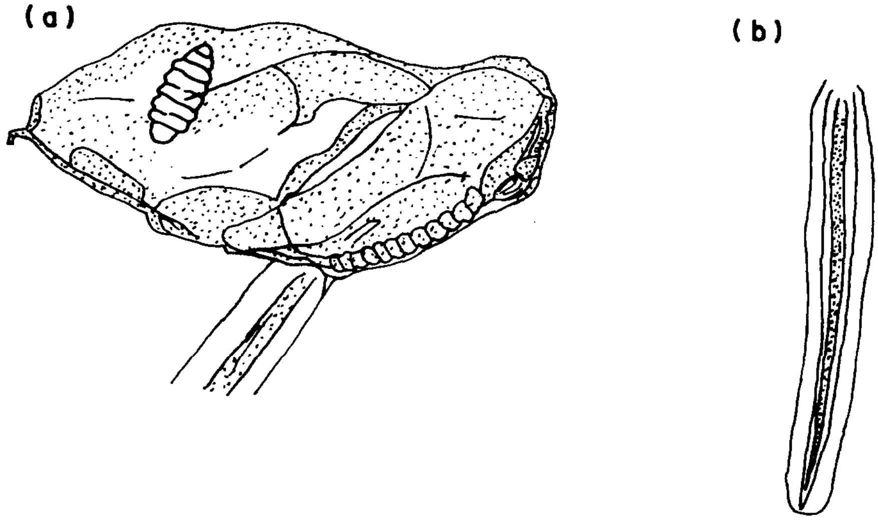
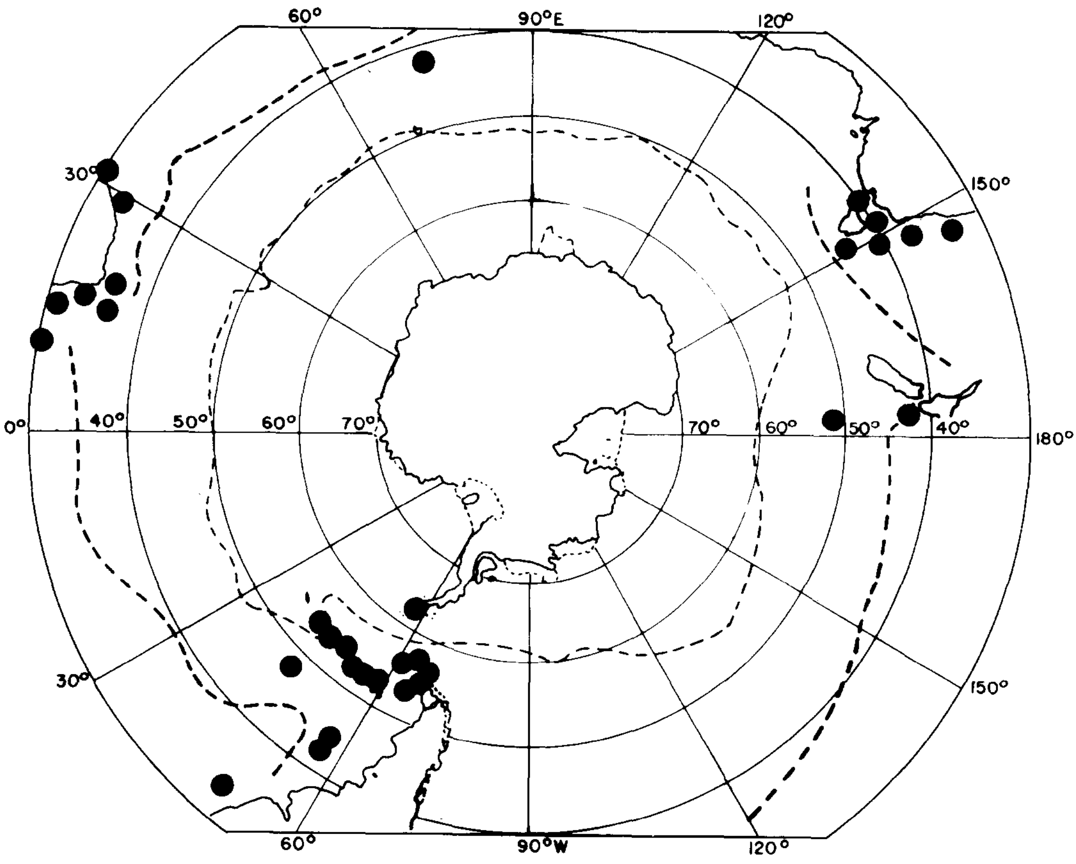


Figure 14. Oikopleura fusiformis (a) trunk, left side; (b) tail, dorsal view. Map of distribution.



This warm water species (Tokioka, 1961) has been found in the southern Atlantic and Antarctic by Lohmann and Buckmann (1926). Thompson (1948) found this species to be rare in the south-eastern Australian region, most of which were taken below 50 m.

Owing to the fact that it is so minute, and that it occurs only in small numbers and often at some depth, the species have probably been occasionally overlooked when collections have been examined (Thompson 1948).

Oikopleura fusiformis Fol 1872

(Figure 14)

(Oikopleura cornustogastra Buckmann, 1924; Lohmann and Buckmann, 1926; Lohmann, 1931)

Diagnostic characters:

Trunk: distinguished by its slender elongated spindle-shaped form, the dorsal contour is almost flat, the ventral is very slightly convex
Oikoplast epithelium: extends backwards over the anterior portion of intestinal tract
Oesophagus: opens into mid-portion of dorsal side of left stomach lobe almost without curvature
Stomach: with blindsac of large triangular left lobe very large, narrow, slightly curved, and directed upwards and backwards, right stomach lobe is small and continous with small anterior and upper part of left lobe, row of large glandular cells along base of left stomach
Intestine: long, of uniform diameter
Rectum: displaced by intestine anteriorly
Testes: paired, rectangular in front of ovary
Ovary: single, flat, lies in ventral part of genital cavity
Tail fin: long and narrow
Tail musculature: narrow
Subchordal cells: not present (Bary, 1961)
Length: body up to 1.5 mm, tail up to 5 mm.

The long stretched body clearly identifies this type (Lohmann and Buckmann, 1926). The species is almost universally distributed in warm oceanic waters, and is also carried by warm current, into cooler waters (Thompson, 1948). In the South Atlantic the edge of dense distribution is about 50°S (Tokioka 1961). This species is more tolerant to low water temperatures than O. longicauda (Vogt), another common warm water species, although it is very strange that O. longicauda has been found in the Antarctic Sea, reaching 72°30'S while O. fusiformis has never been collected in the Antarctic (Lohmann, 1928; Tokioka, 1960). Tokioka (1940, 1951) suggested that O. fusiformis and O. cornutogastra Aida may possibly be one species, but Thompson (1948) gave some points of difference.

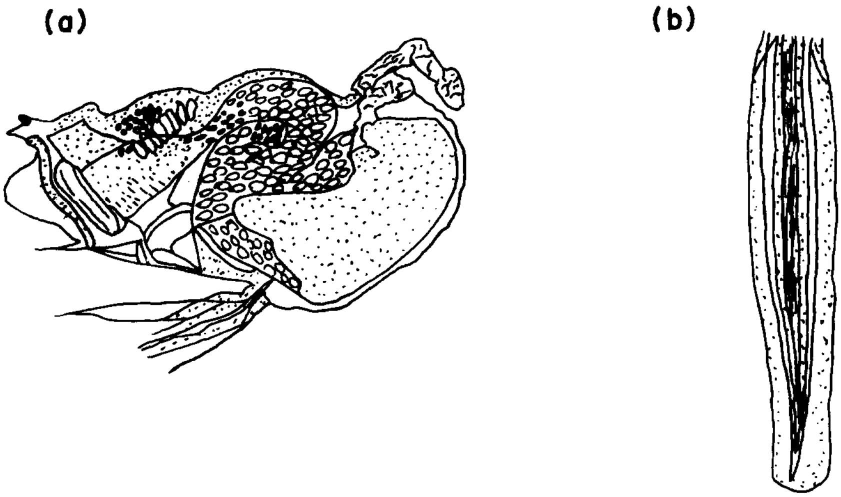
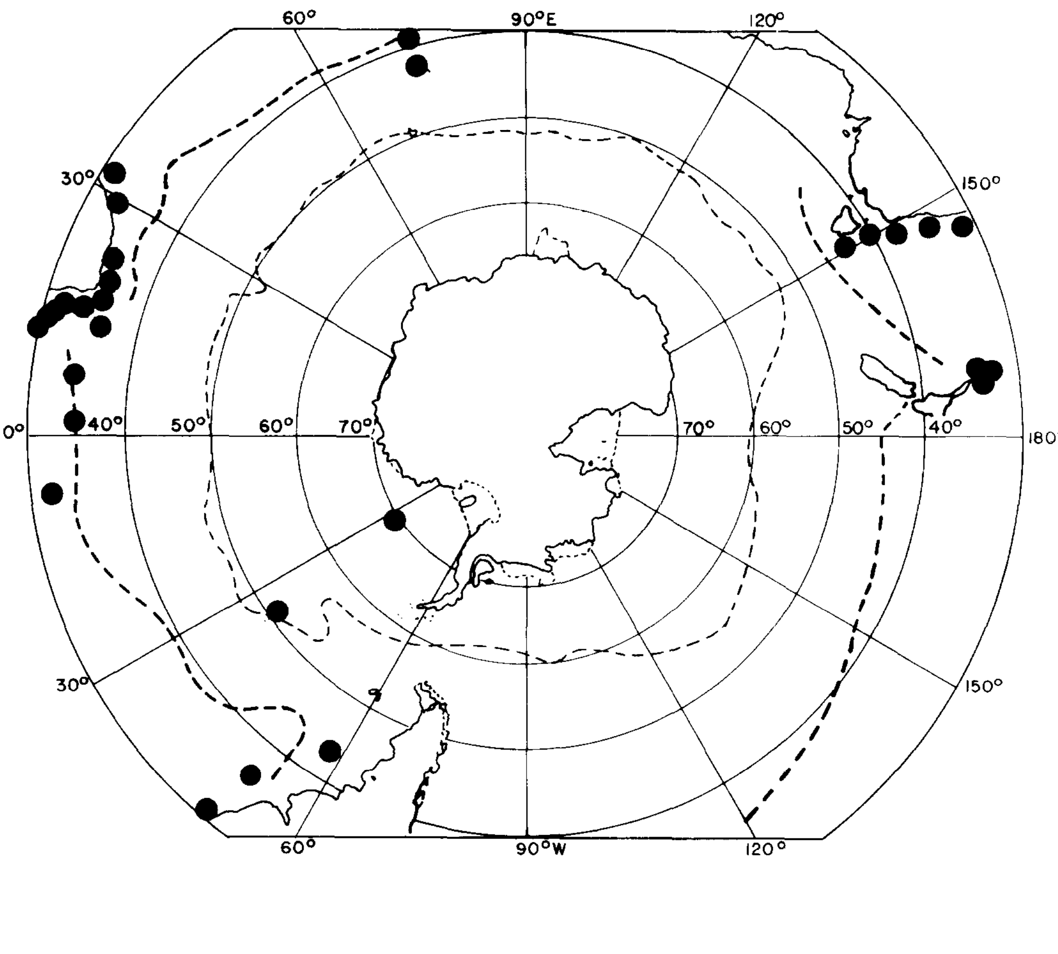


Figure 15. Oikopleura longicauda (a) trunk, left side; (b) tail, dorsal view. Map of distribution.



Oikopleura longicauda (Vogt 1854)

(Figure 15)

Diagnostic characters:

Trunk: usually short and stout, there is however considerable variation
Hood: present, arising from posterior edge of oikoplast epithelium (Buckmann, 1969)
Oikoplast epithelium: extends backwards over only a small portion of the alimentary tract
Buccal glands: absent
Eisen's oikoplast: absent
Fol's oikoplast: epithelial cells are small and of fairly uniform size
Endostyle: broad and long, its rear end lying close in front of the inner spiracles
Stomach: right and left lobes similar
Intestine: short
Rectum: short
Testes: paired, divide posteriorly into a great number of lobes, giving the animal a characteristic appearance, when mature cover the lateral aspect of the alimentary canal and form a very large roundish mass reaching well forward
Tail fin: round at its tip, broad
Tail musculature: strong
Subchordal cells: not present
Length: body up to 1.3 mm, tail up to 4.55 mm.

This eurythemic species (Udvardy, 1958) is by far the most common species of Appendicularia in most of the warmer oceanic regions (Fenaux, 1963), and next to Oikopleura dioica Fol it has the widest range of distribution (Thompson, 1948).

According to Thompson (1948) the species is found in regions where a certain degree of mixing of colder water occurs. It has been reported from the Southern Ocean by Lohmann and Buckmann (1926) and Lohmann (1928). The southern limit of dense occurrences of O. longicauda is along the 18°C isotherm and the distribution seems to be limited by the 15°C isotherm (Lohmann and Hentschel, 1939). Larzarus and Dowler (1979) found it to be most abundant at temperatures between 15 to 22°C.

Genus Folia Lohmann 1896

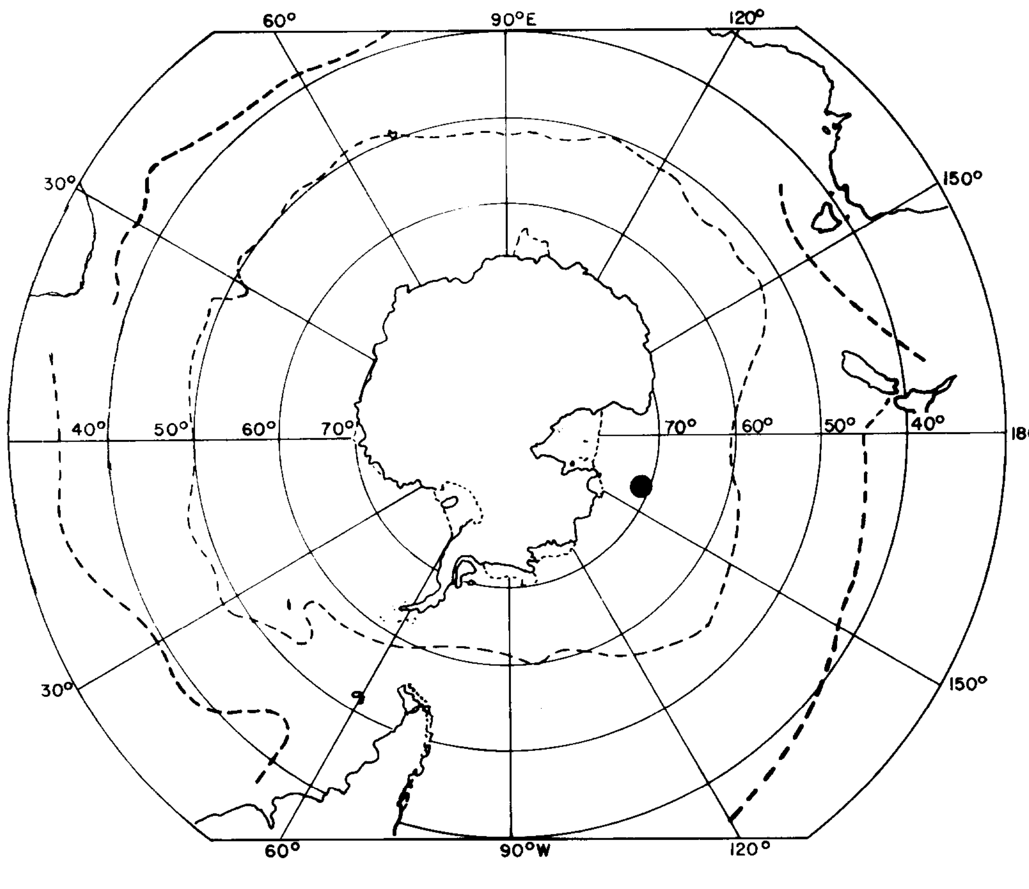
Alimentary canal incompletely developed through the absence of one or both lateral pouches; spiracles with a closed ciliated ring, stomach compact and roundish, with well-developed left lobe only; mouth opening small, with underlip as in Oikopleura; buccal glands and sub-chordal cells are present; two species.

Key to species:

Buccal glands large, oblong and conspicuous; oblique
peripharyngeal glands, large size (3 mm) .... F. gigas Garstang and Georgeson

Buccal glands small, no peripharyngeal glands, small size
(0.4 mm) .... F. gracilis Lohman

Figure 16. Folia gigas (a) trunk, dorsal view; (b) trunk, dorso-dextral view. Map of distribution.



Folia gigas Garstang and Georgeson 1935

(Figure 16)

Diagnostic characters (Garstang and Georgeson, 1935):

Trunk, oikoplast-epithelium, body wall, tail and most of gonads completely absent
Buccal glands: large, oblong and conspicuous
Peripharyngeal bands: oblique, extend from front of stomach to mouth of oesophagus
Endostyle: small, possibly injured
Stomach: asymmetrical ovoid bag set obliquely across the front of the oesophagus and compounded of a posterior left and an anterior right lobe imperfectly straightened out
Gonads: would fill space behind gut
Length: body probably greater than 3.25 mm.

This species was described from a single damaged specimen by Garstang and Georgeson (1935) who distinguished it from Folia gracilis Lohmann by its large oblong oral glands, its large size and the obliquity of its peripharyngeal bands which are independant structures from endostyle to oesophagus.

It was suggested that Folio gigas drifted down into the Antarctic from the Pacific Tropics (Garstang and Georgeson, 1935).

Folia gracilis Lohmann 1896

(Figure 17)

Diagnostic characters (Lohmann and Buckmann, 1926):

Fol's and Eisen's cell groups: exist
Buccal glands: small, next to endostyle
Oesophagus: raised in wide bow over upper edge of stomach, ends in upper corner of stomach whilst coming from the rear
Stomach: without right stomach lobe, left one well developed, without any postcardial connection
Testis and Ovary: are flat, shell-shaped and grow out in the form of a dorso-ventral directed small strip
Subchordal cells: small, roundish, lie randomly and in small numbers (about 6 to 18) in the rear section of the tail
Length: body up to 0.48 mm, tail up to 1.6 mm (Tokioka, 1958).

This is essentially a deep sea species of tropical regions (Lohmann, 1928) although Lohmann and Buckmann (1926) reported a single specimen from the Antarctic.

Genus Stegosoma Chun (1888)

The stomach is compressed sideways, and the anterior dorsal portion of the loop of the alimentary canal falls away vertically to the left; oesophagus opens into a short narrow duct connecting the round or triangular left stomach pouch with the elongated right stomach lobe; buccal glands and subchordal cells are present.

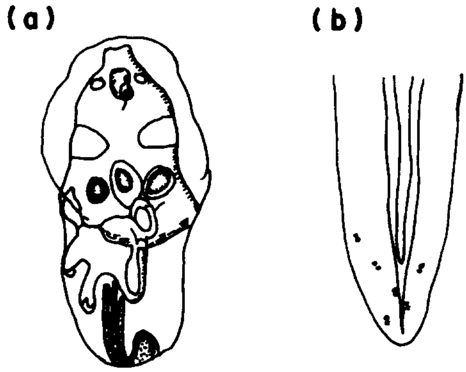
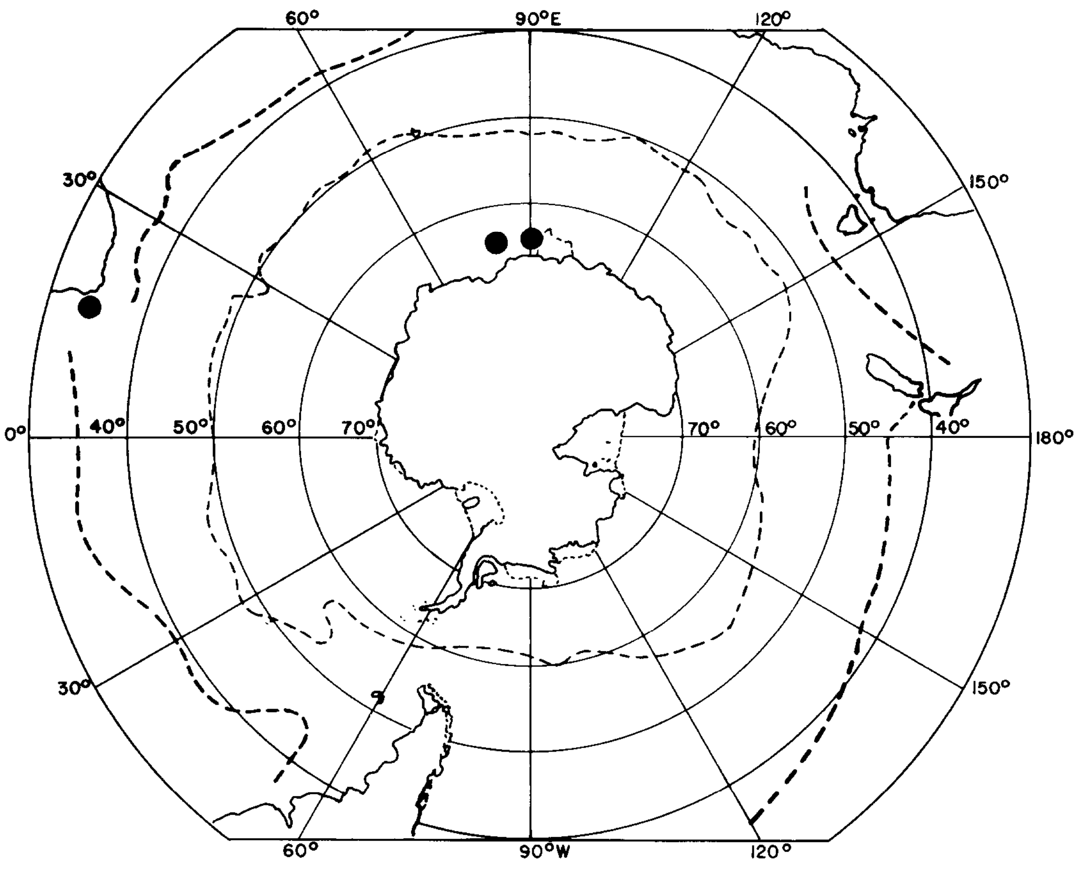


Figure 17. Folia gracilis (a) trunk, dorsal view; (b) tail, distal half. Map of distribution.



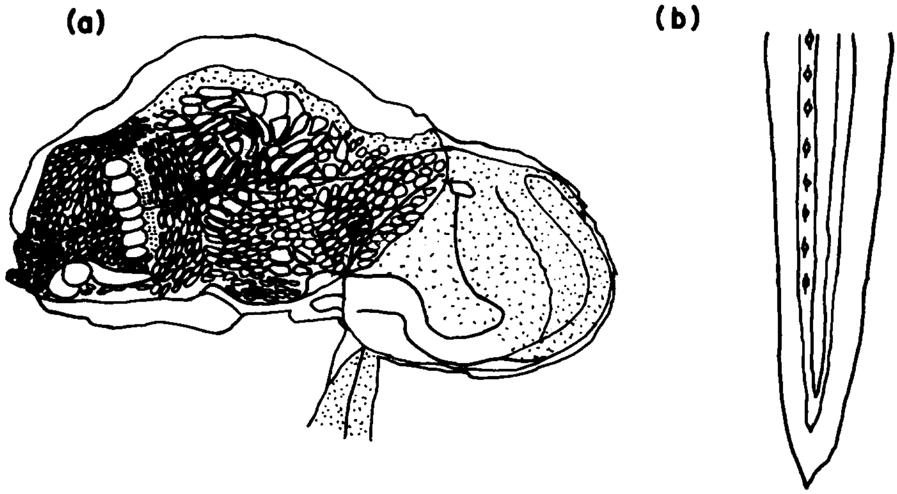
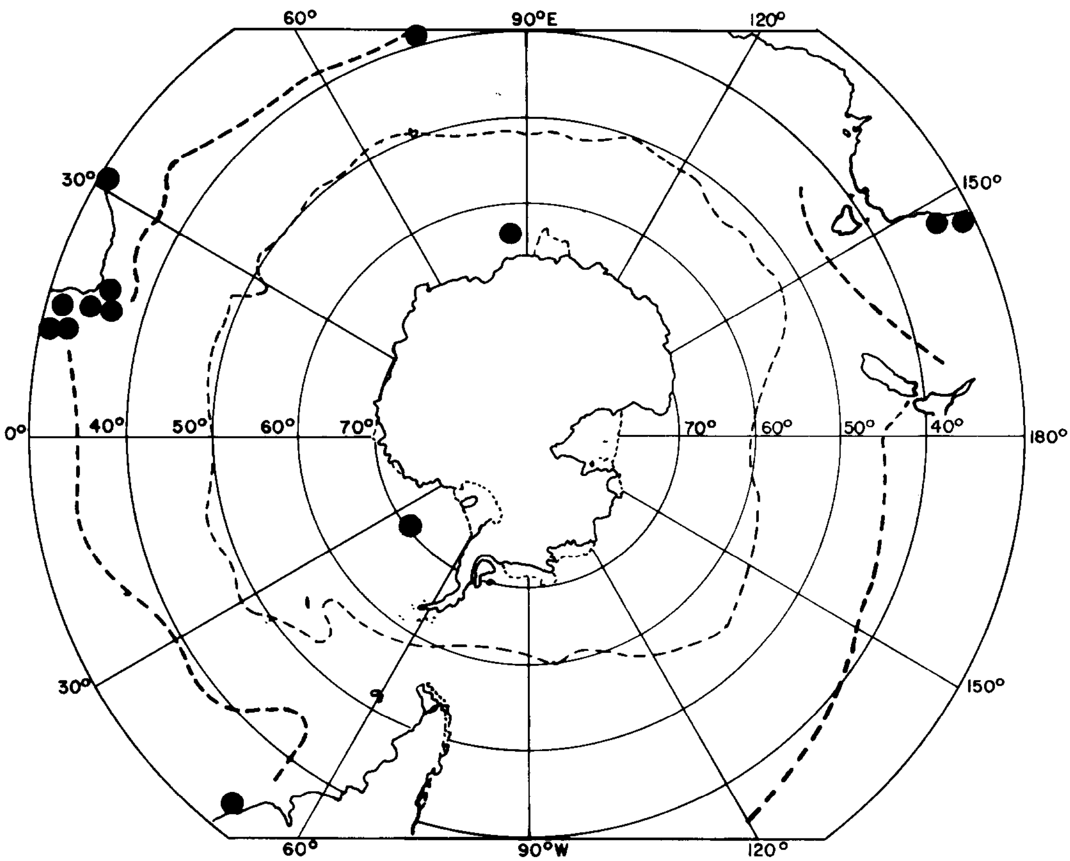


Figure 18. Stegosoma magnum (a) trunk, left side; (b) tail, distal half. Map of distribution.



Key to species:

Left stomach lobe produced into a blunty conical caecum (NZ) S. conogaster Garstang and Georgeson[1]

Stomach quadrangular, wallet-shaped .... S. magnum Langerhans

Stegosoma magnum Langerhans 1880

(Figure 18)

Diagnostic characters:

Trunk: laterally compressed, elongate, strongly arched in the dorsal line
Oikoplast epithelium: extends to just behind the anterior margin of the stomach, and is composed of variously shaped large cells
Eisen's oikoplast: well developed
Buccal glands: small, circular
Endostyle: short and slender, widely separated from spiracles
Spiracles: small
Stomach: compressed in older stages, left lobe is almost round in young specimens, but changes form in more adult stages, becoming flat and irregularly triangle-shaped, right lobe smaller and elongated
Intestine: long, forms nearly a right angle with the right stomach
Tail musculature: narrow.
Subchordal cells: arranged in rows, vary in number and appearance but usually about eight, flat or spindle or bladder-like
Length: body up to 4 mm, tail up to 10.4 mm.

Langerhans originally described this species as Stegosoma magna but I will follow the orthography of Lohmann (1928) and Thompson (1945). The specimen taken in the Antarctic is regarded as a "tropical guest" carried down by underflow from the Indian Ocean (Lohmann 1928). This epiplanktonous species (Garstang & Georgeson 1935) has also been taken from the southern Indian Ocean and off south-eastern Australia (Thompson 1948), South America (Udvardy, 1958) and South Africa (Lohmann & Buckmann, 1926; Lazarus & Dowler, 1979).

Genus Pelagopleura Lohmann 1926

The stomach has only a single lobe, from the anterior part of which both the oesophagus and intestine issue, the whole loop of the gut stands vertically along the sagittal axis of the body, but has no lateral pouch-shaped process; mid portion of the intestinal loop is modified to serve as stomach; amphichordal cells are present in the tail; there are sixteen giant cells in Fol's oikoplast; five species of which two are endemic to the Southern Ocean (Tokioka, 1961).

1. In view of the variation in shape of the stomach lobes found in Stegosoma with age, and that found in Oikopleura fusiformis Fol, Thompson (1948) suggests that the proposed species of Garstang and Georgeson (1935) requires further examination before being adopted. Nevertheless both species are included in this guide.

Key to species (Tokioka, 1964):

Endostyle short; stomach has distinct blind sac in posterio-ventral corner .... P. australis (Buckmann)

Endostyle long and slender, stomach roughly longate-oval in outline .... P. magna (Lohmann)

Pelagopleura magna Lohmann 1926

(Figure 19)

Diagnostic characters (Tokioka, 1964):

Trunk: elongate
Oikoplast-epithelium: covers anterior half of body, its posterior edge reached the level of oesophageal opening to the pharynx; provided with very prominent large dorsal cell group above Eisen's cell group, but is devoid of Martini's cell group; row of 16 elongate giant cells
Buccal gland cells: not present
Endostyle: large and very slender
Spiracles: characteristically large and elongated (Lohmann and Buckmann, 1926)
Stomach: laterally compressed, roughly oval in outline, slightly narrowed in anterior half
Intestine: thin and of considerable length
Testis: membranous, stretches along lateral and rear walls of posterior half of trunk covering both sides of ventral half of stomach, and becomes conspicuously narrower at the posterior bending point, deep ventral cleft near exterior end of both sides
Ovary: membranous, situated inside testis
Tail fin: anterior end rounded and does not show a ledge
Tail musculature: narrow, covers whole length of notochord
Amphichordal cells: six glandular patches
Length: body to 6 mm; tail to 18.3 mm.

Pelagopleura magna is an exclusively Antarctic species (Garstang & Georgeson, 1935; Tokioka, 1961). It may be safely said that this species and P. australis (incorrectly cited as P. antarctica) are distinct species (Tokioka, 1964).

Pelagopleura australis (Buckmann 1924)

(Figure 20)

(Althoffia australis Buckmann, 1924)
(Pelagopleura antarctica Tokioka, 1964)

Diagnostic characters (Lohmann and Buckmann 1926, Tokioka 1964):

Oikoplast-epithelium: has a large dorsal cell group comprising numerous cells
Buccal cells: not present
Endostyle: is short
Stomach: very stretched, very developed near the front and rear of the cardia, rear end is pushed down and ends in a wide tip, it has a distinct blind sac in the postero-ventral corner

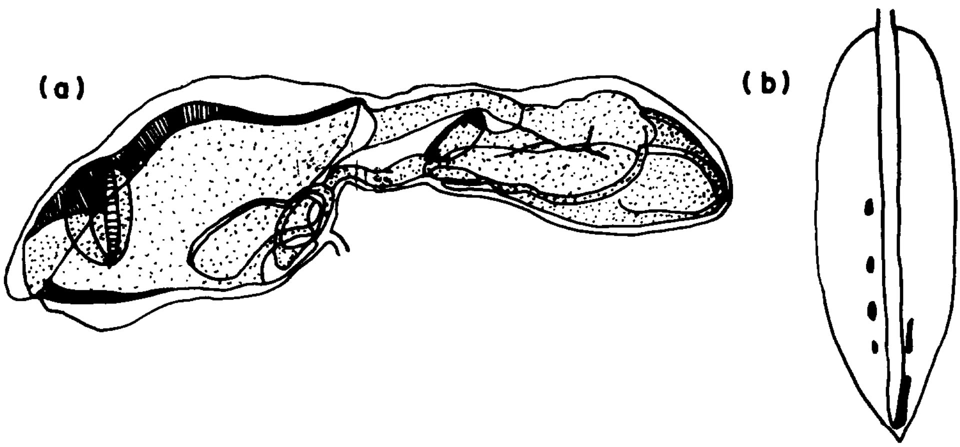
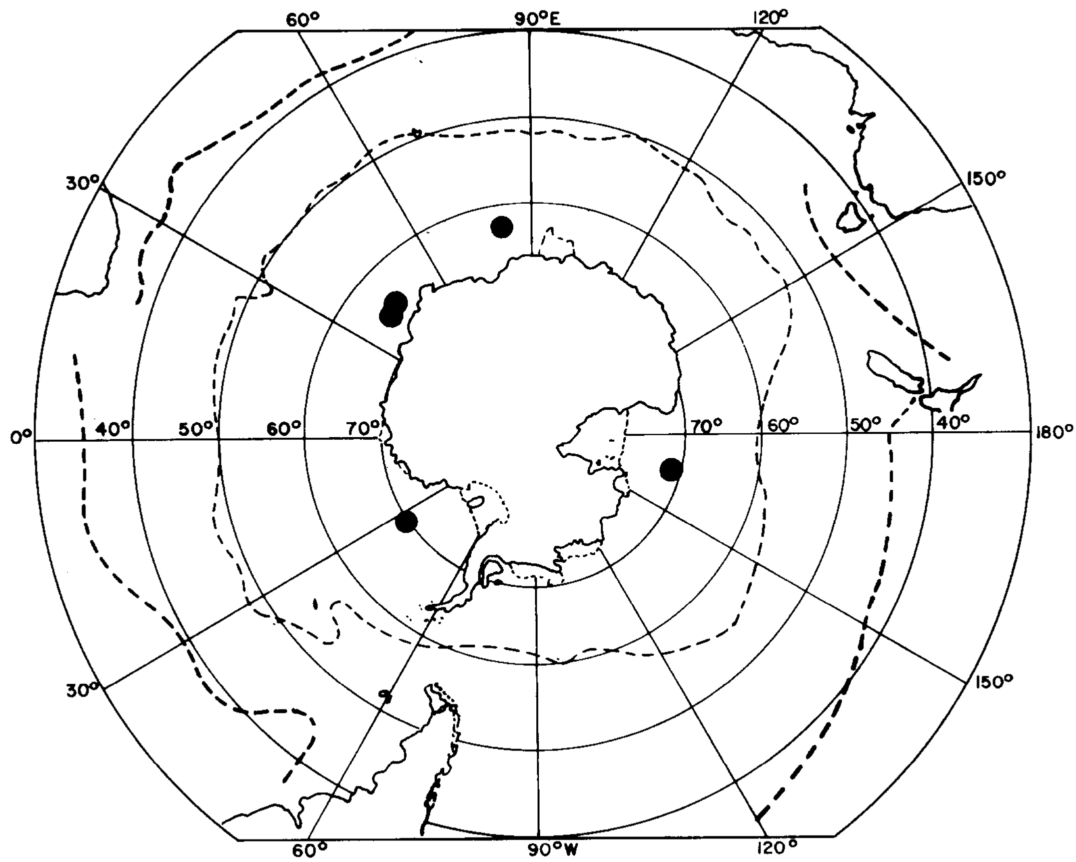


Figure 19. Pelagopleura magna (a) trunk, left side; (b) tail. Map of distribution.



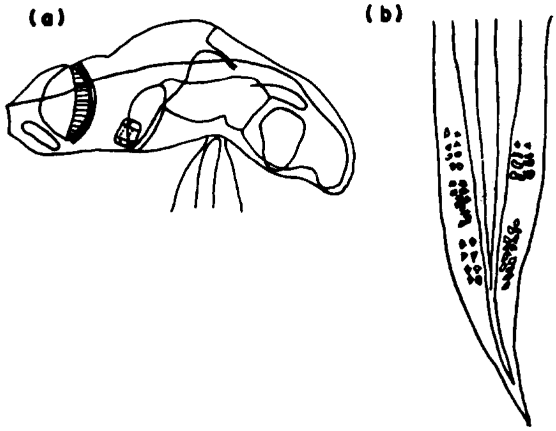
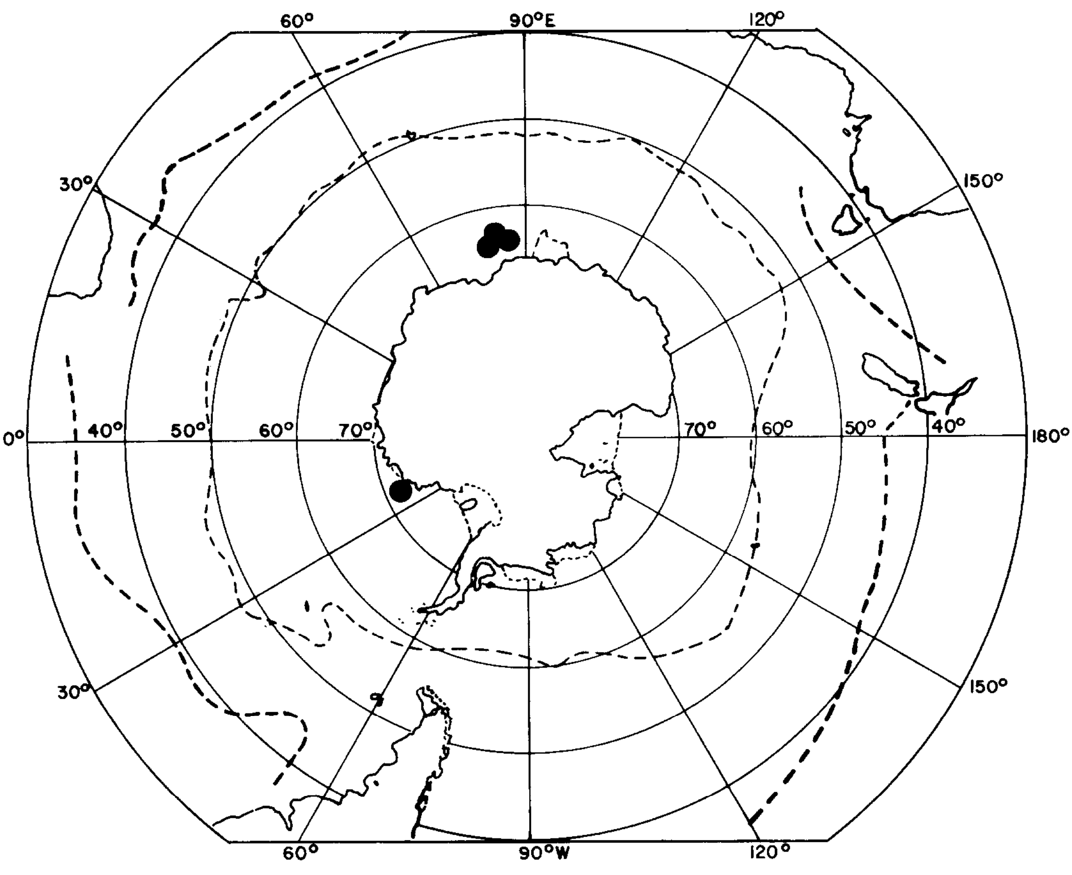


Figure 20. Pelagopleura australis (a) trunk, left side; (b) tail. Map of distribution.



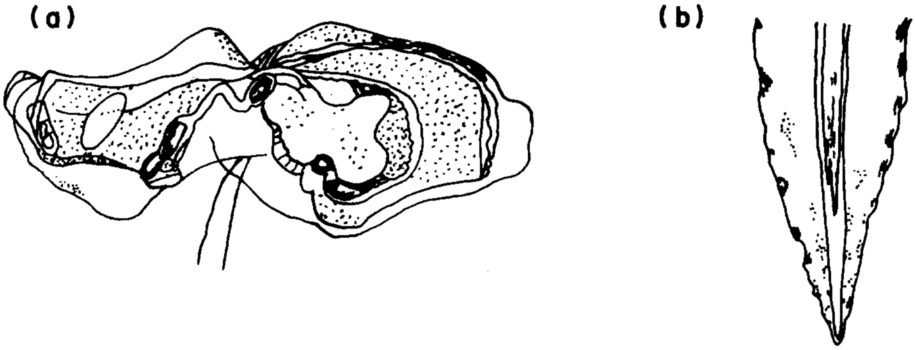
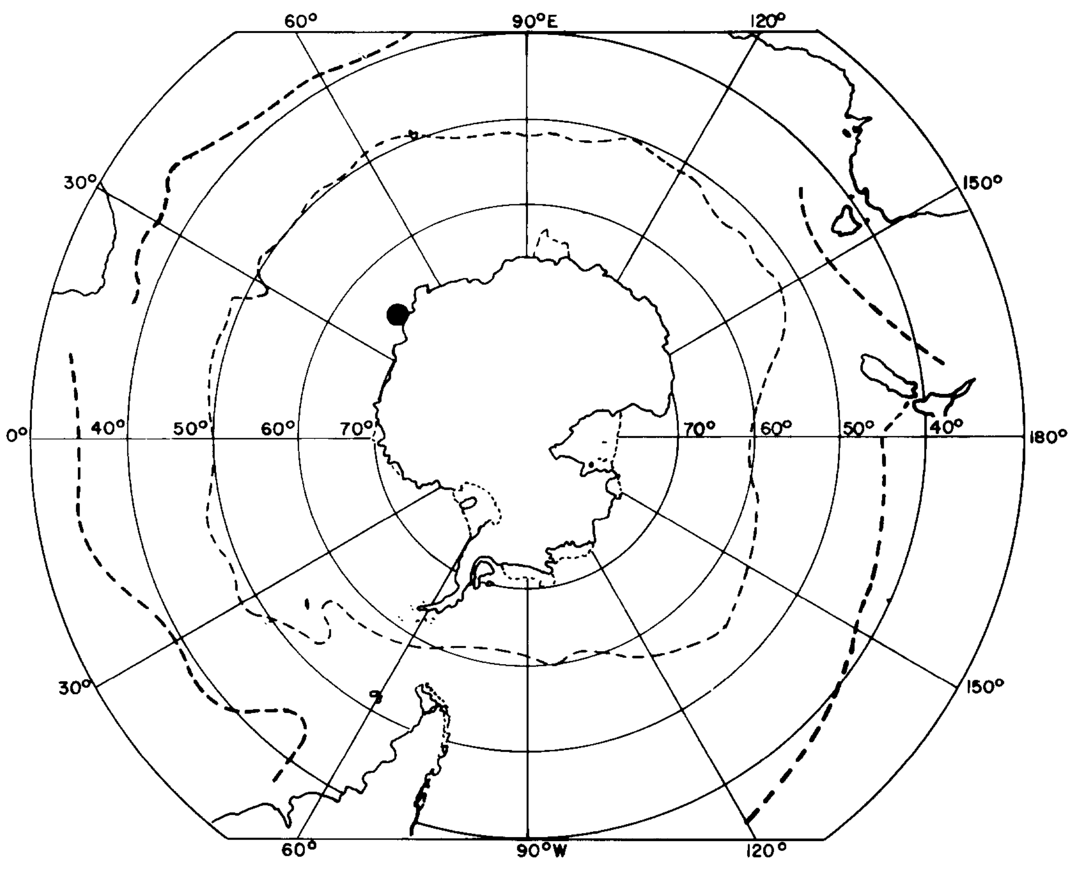


Figure 21. Sinisteroffia scrippsi (a) trunk, left side; (b) tail, posterior portion. Map of distribution.



Gonads: situated ventral to stomach in younger stages, grow towards the dorsal part of body
Amphichordal cells: arranged into long cell-rich groups
Length: body up to 1.5 mm, tail up to

This species is characterised by the shape of the stomach and details of the oikoplast-epithelium (Tokioka, 1964). It is endemic to the south polar seas (Tokioka, 1961) although Buckmann (1969) reported one specimen from the North Atlantic Ocean.

Genus Sinisteroffia Tokioka 1957

The endostyle and spiracles are present; the alimentary canal consists in part of a thin oesophagus, a single-lobed stomach and an elongate intestine; the stomach is situated vertically just along the left lateral body wall in the posterior half of the body; the gonad is hermaphroditic (Tokioka, 1957). This monotypic genus is related closely to Pelagopleura and Althoffia in that (1) the stomach has only a single lobe, from the anterior part of which both the oesophagus and the intestine issue, and (2) in the arrangement of the gland cells in the tail (Tokioka, 1957).

Sinisteroffia scrippsi Tokioka 1957

(Figure 21)

Diagnostic characters (Tokioka, 1957):

Trunk: considerably compressed dorso-ventrally, roughly elongate oval in dorsal view
Oikoplast-epithelium: covers anterior half of trunk, test is very soft, Eisen's cell group formed with a few elongate cells in the centre, Fol's cell groups present between endostyle and spiracles
Buccal glands: not present
Endostyle: short, situated near the mouth
Spiracles: oval, rather small, situated near anus
Oesophagus: narrow and comparatively long, opens into pharynx on the level of the tail insertion, opens into the stomach about one-third the stomach length from the cardiac end
Stomach: located vertically along left lateral wall of body in the anterior part of the posterior half of the body
Intestine: consists of a distinct pyloric division, the intestine proper and the rectum
Testis: thin, ribbon-like mass lying transversely on the inner surface of the ventral body wall of the posterior end of the body
Ovary: is a string-like tissue running along the whole margin of the testis
Tail fin: wide, long and pointed
Tail musculature: narrowed considerably in posterior part
Subchordal cells: small, 30-40 on respective sides, mostly spherical or spindle-shaped, but a few are elongate
Length: body up to 2 mm, tail up to 8.3 mm (Tokioka, 1964).

This species is unique to the Indo-Pacific (Tokioka, 1960) and has only been recorded three times: a sexually immature specimen from the Antarctic

(Tokioka, 1964), two specimens from the Humbold Current off Peru (Tokioka 1957) and another specimen from the North Pacific (Tokioka, 1957). It is uncertain whether this species is an Antarctic form (Tokioka, 1961).

Sub-family BATHOCHORDAEINAE

Spiracles open only through small apertures from the branchial sac, they widen out conically towards the outer openings; oesophagus swells in the mid portion to a wide crop-like sack; the oesophagus and anus lie medianly, but the stomach and intestine are united by a wide horizontal half-moon-shaped section; the oikoplast epithelium forms a flat shield dorsal to the branchial cavity, but its ventral development is restricted, as in Fritillaria, to a small anterior girdle; the subsidiary cells of Fol's oikoplast lie in front of the twelve giant cells, the gut is placed horizontally.

In this sub-family there is only one genus with a single species, Bathochordaeus charon Chun which has been found off South Africa (Lohmann, 1914) and south-eastern Australia (Thompson, 1948). It is yet to be reported from the Southern Ocean.

8.5 FAMILY FRITILLARIDAE

The forebody section is broad and shallow with a wide body cavity; branchial cavity is broadly developed to the rear as a separate body section; endostyle is curved; testis always, and the ovaries usually, lie behind the gut coil; tail fin is very broad and sharply indented in the median part of the fore edge, it is relatively shorter than in Oikopleuridae; in front of the mouth a snout is formed which often carries lobe-like lip-processes; body is elongated and more or less constricted in the middle; a dorsal hood is often present; stomach wall is beset with only a few large cells; small cells are absent; Fol's oikoplast group is absent - in its place there occur other specific oikoplast groups; obvious spiracles are absent; a water filtration apparatus lines the inner wall of a gelatinous vesicle, which either leaves the body free and projects in front of the mouth or surrounds the animal on all sides as a house, alternatively remaining latent in folded condition under the hood; 2 sub families.

Key to Sub-families:

Reproductive glands contiguous with alimentary canal, no branchial cavity .... Appendicularinae

Reproductive glands lie behind alimentary canal, branchial cavity present .... Fritillarinae

Sub-family FRITILLARINAE

Forebody broad and flat, with wide body cavity; branchial cavity developed to the rear as a separate body section; testis, and usually also the ovary, lying behind the elementary tract; tail fin very broad; in front of the mouth is a snout which often bears lobe-like processes; the ends of the endostyle are involute; 2 genera, of which Tectillaria Lohmann has no representatives in the Southern Ocean.

Genus Fritillaria Quoy and Gaimard (1835)

Body either elongated or sac-shaped; organs more or less free within the jelly of the body cavities; oikoplast epithelium covers dorsally only the branchial cavity and is ventrally restricted to a narrow zone below the endostyle, its posterior edge rises to form the hood, an epidermoidal duplicature bent orally; spiracles behind the endostyle, much in front of the stomach, which is spheroid and composed of only a few cells, intestine to the right of or behind the stomach; rectum small; (Buckmann, 1969); tail broad (Dakin and Colefax, 1960).

As in Oikopleura there are two subgenera in Fritillaria: Eurycereus Lohmann characterised by circular spiracles, broad tail fin with a notched end (Buckmann, 1969) and a pair of protuberances on the posterior margin of the trunk (Tokioka, 1960); and Acrocerus Lohmann with spiracles of various forms, pointed tail and no protuberances on trunk.

Key to species (after Lohmann & Buckmann, 1926):

1a) Spiracles round and small 2
 b) Spiracles are not round, they are extended and stretched but not split; tail is ending in a simple point; amphichordal cells and pharngeal cell packets are missing; mouth opening with lobe formation 13

2a) Spiracles touch in median line; tail fin terminates in a simple tip .... Frit. abjornseni Lohmann
 b) Spiracles stand far apart 3

3a) Tail fin terminating in a simple point; body bent upwards in mid-dorsal region .... Frit. formica Fol
 b) Tail fin widely notched at tip or squarely truncated 4

4a) Tail with amphichordal cells; pharyngeal cell packet present 5
 b) Tail without amphichordal cells 9

5a) One pair of amphichordal cells or cell groups with distinct glandular opening 6
 b) With 2 pairs of amphichordal cells, one behind the other 7

6a) Amphichordal cells short, formed like a jug; pharyngeal cells form a wide roundish pocket ..... Frit. tenella Lohmann
 b) Amphichordal cells long, tube-like; pharyngeal cells form a bean-shaped extension of the endostyle running along the median plane .... Frit. scillae Lohmann

7a) The pairs of amphichordal cells are separated by a gap, cells are flask-shaped with a short exit passage .... Frit. pellucida (Busch)
 b) The pairs of amphichordal cells are contiguous without obvious exit passage 8

8a) Ovary spherical, testis egg-shaped .... Frit. megachile Fol
b) Ovary forms a seam on the front of broad trapezoidal testis, the rear wall of which is indented and often develops horn-shaped lateral lobes (Au, SA) .... Frit. bicornis Lohmann

9a) A pharyngeal packet lies on the left of median line from rear end of the endostyle reaching towards the rear; pharyngeal cells absent; tail fin notched .... Frit. venusta Lohmann
b) No pharyngeal packet is formed but 3 pharyngeal cells lie between the endostyle and the spiracle; tail fun truncated (Frit. borealis group) 10

10a) With ovary lying to the left testis with asymmetrical proximal protuberance on the right side (Au, At) .... Frit. borealis f. sargassi Lohmann
b) With median ovary 11

11a) Ovary and testis cylindrical .... Frit. borealis f. allongata Lohmann
b) Ovary spherical, testis fusiform 12

12a) Tail musculature terminating in a point .... Frit. borealis f. typica Lohmann
b) Tail musculature cut squarely off at tip (Au) .... Frit. borealis f. intermedia Lohmann

13a) Spiracles extended and stretched but not split ... 14
b) Spiracles very small, often longer than wide, cleft; gonads lie behind each other; only 2 flat pocket-shaped pyloric glands .... Frit. aberrans Lohmann

14a) Spherical ovary lies in front of walnut-shaped testis; no pharyngeal cells; pyloric gland cells round; oikoplast epithelium with four small cells on rear edge (Frit. haplostoma group) 15
b) Ovary string-like, hemming the testis; pharyngeal cells situated between spiracles; pyloric gland cells large, often produced into a spit; oikoplast epithelim with 8 very large cells in rear 16

15a) Series of minute and 2 large gland cells mostly on right side of tail fin .... Frit. haplostoma f. glandularis Tokioka
b) Several pairs of fine gland cells in a row along fin margins on each side .... Frit. haplostoma Fol

16a) Intestinal coil situated transversely or lengthwise along body .... Frit. drygalski Lohmann
b) Intestinal coil lying across body 17

17a) Stomach spherical; pylorus and rectum close to it, making the cross diameter short; stomach with two comb like attachments (one horizontal and underneath, one vertical along the left wall), intestines with one attachment on the right hand side; testis forms a flat bow-shaped twisted band that lies across and proliferates to the front reaching the intestinal coil and unfolding in strong lobes; tail of a broad shape .... Frit. fraudax Lohmann

b) Stomach lying across, egg-shaped; pylorus and rectum developed far to the right which makes the lateral axis long, only 2 comb-like attachments (one on the left top of the stomach, one in the rear sitting vertically on the intestines); testis forms a flat bow-shaped twisted cord, lying lateral and standing alone without proliferating the bowel; the tail is small .... Frit. antarctica Lohmann

Subgenus Eurycercus Lohmann

Fritillaria borealis f. typica (Lohmann)

(Figure 22)

Diagnostic characters (Tokioka, 1964):

Trunk: pharyngeal region roundish in outline and covered with a large hood on the dorsal side, the ventral lip is deeply cut into two lateral lobes, while the dorsal lip is protruded anteriorly as a single lobe
Oikoplast-epithelium: has a pair of elongate elliptical cell groups and is bordered posteriorly by larger cells
Endostyle: short, broad, curved upwards at both ends (Thompson, 1948)
Spiracles: very small
Stomach: arranged obliquely antero-posteriorly with intestine
Intestine: furnished with 3 to 4 glandular appendages
Ovary: spherical, arranged anterior posteriorly with testis
Testis: elongate and median; symmetrical (Thompson, 1948); spindle-shaped (Buckmann, 1969)
Amphichordal cells: not present
Tail musculature: gradually narrowing towards the tip
Tail fin: not broadly notched (Thompson, 1948)
Length: body up to 1.3 mm (Lohmann, 1931); tail up to 1.8 mm.

A number of forms of Fritillaria borealis have been recognised (see Tokioka, 1940, 1960, Thompson, 1948; Buckmann, 1969 for discussion) of which the forms Frit intermedia, acuta and sargassi have been found off south-eastern Australia (Thompson, 1942, 1948). A cold-water form, typica has a bipolar distribution (Tokioka, 1964) and has been found in the Antarctic by Lohmann and Buckmann (1926) and Tokioka (1964).

Another form, Frit. borealis f. allongata Lohmann, a warm water species, was reported by Lohmann and Buckmann (1926) from the Antarctic. It can be differentiated from Frit. borealis f. typica by having a median cylindrical ovary and testis (Buckmann, 1969). Lazarus and Dowler (1979) reported Frit.

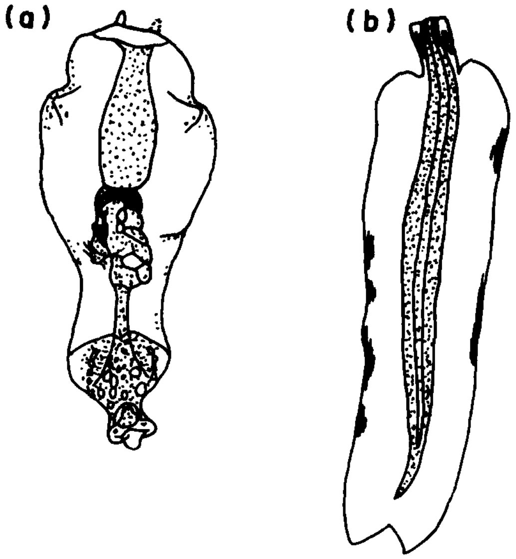
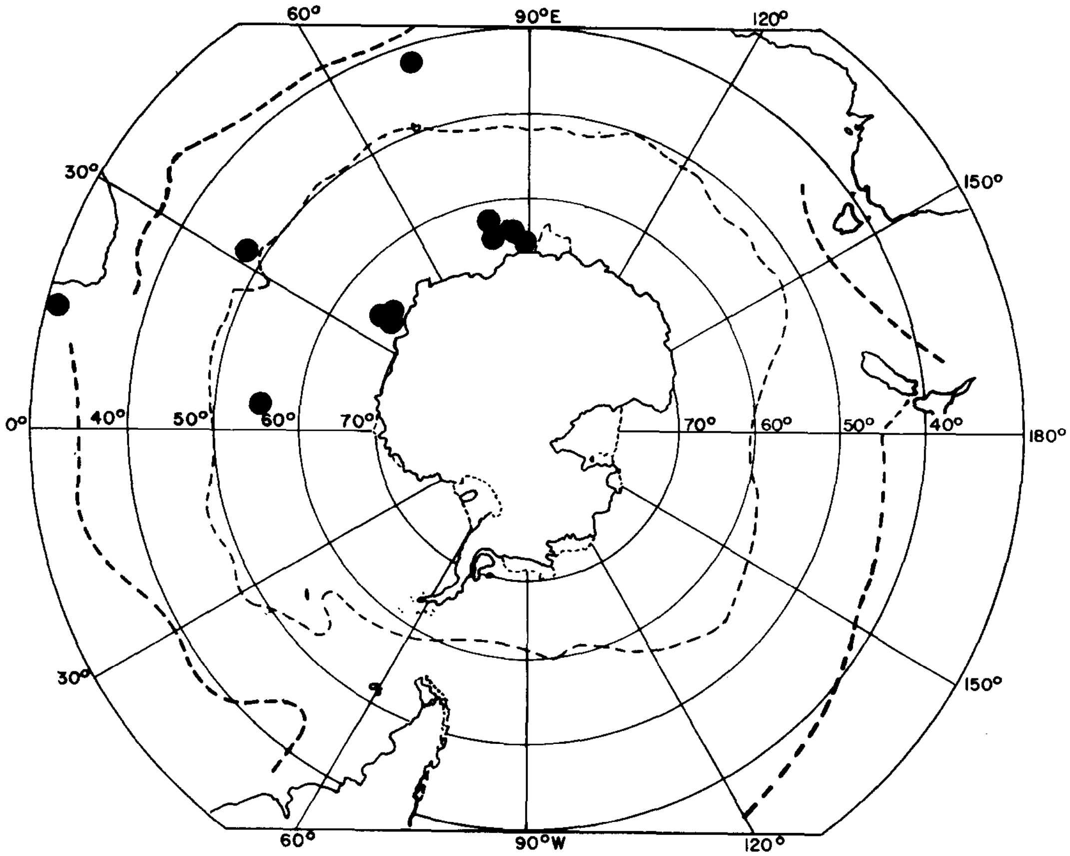


Figure 22. Fritillaria borealis f. typica (a) trunk, dorsal view; (b) tail. Map of distribution.



borealis from South Africa but specified no form. All forms have been included on the same distribution map (see Figure 22).

Fritillaria megachile Fol 1872

(Figure 23)

Diagnostic characters:

Trunk: elongated, extremely slim, profile is almost straight - not curved as in most other *Fritillaria* species
Hood: covers the whole pharyngeal portion except the anterior part of the dorsal lip, 2 short posterior processes are present; but are not always obvious in preserved specimens
Buccal gland: situated close to the left spiracle
Endostyle: slim and strongly curved
Spiracle: circular or oval
Stomach: prominent, without glandular appendages (Tokioka, 1960)
Intestine: without appendages, lies obliquely behind the stomach
Rectum: lies obliquely behind the stomach
Ovary: roundish, lies behind the stomach
Testis: behind ovary, long cylindrical
Tail fin: broad, sub-rectangular, rounded at the fore corners and is widely and clearly cut at distal end; tapers only slightly towards the rear
Tail musculature: narrow, being only slightly broader than notochord
Amphichordal cells: scattered at various points near edge of tail and near central musculature
Length: body up to 2.5 mm; tail up to 4 mm.

This is a rare species, usually found in warm oceanic waters (Tokioka, 1940; Thomspon, 1928). It has been reported from the Antarctic (Lohmann, 1928) and southeastern Australia (Thompson, 1948).

Some authors (eg. Thompson 1948) have suggested that this species may be identical with *Frit. tenella* but Tokioka (1960) points out the following differences: *Frit. megachile* has a more elongate trunk and a pair of amphichordal cells of quite different structure. The intestine of *Frit. tenella* is always provided with several glandular appendages or prominence, while that of *Frit. megachile* is clear.

Fritillaria pellucida (Busch 1851)

(Figure 24)

Diagnostic characters:

Trunk: depressed, stout and sack-shaped, anterior portion is broader than the posterior portion, two conical processes at posterior end
Hood: prominent
Pharyngeal cells: form packet which touches the left spiracle (Buckmann, 1969)
Endostyle: very slender and long, with both ends turned up dorsally, so it appears box-like in side view
Spiracle: circular and of medium size
Stomach: spherical, no appendages

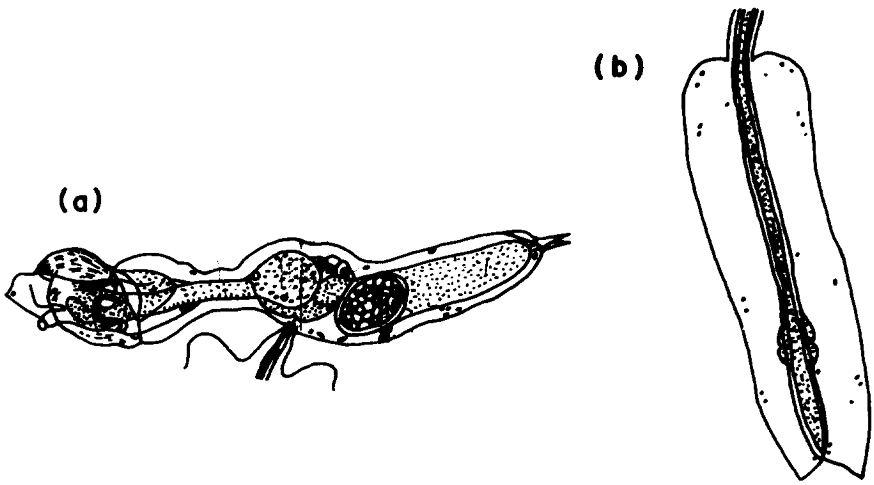
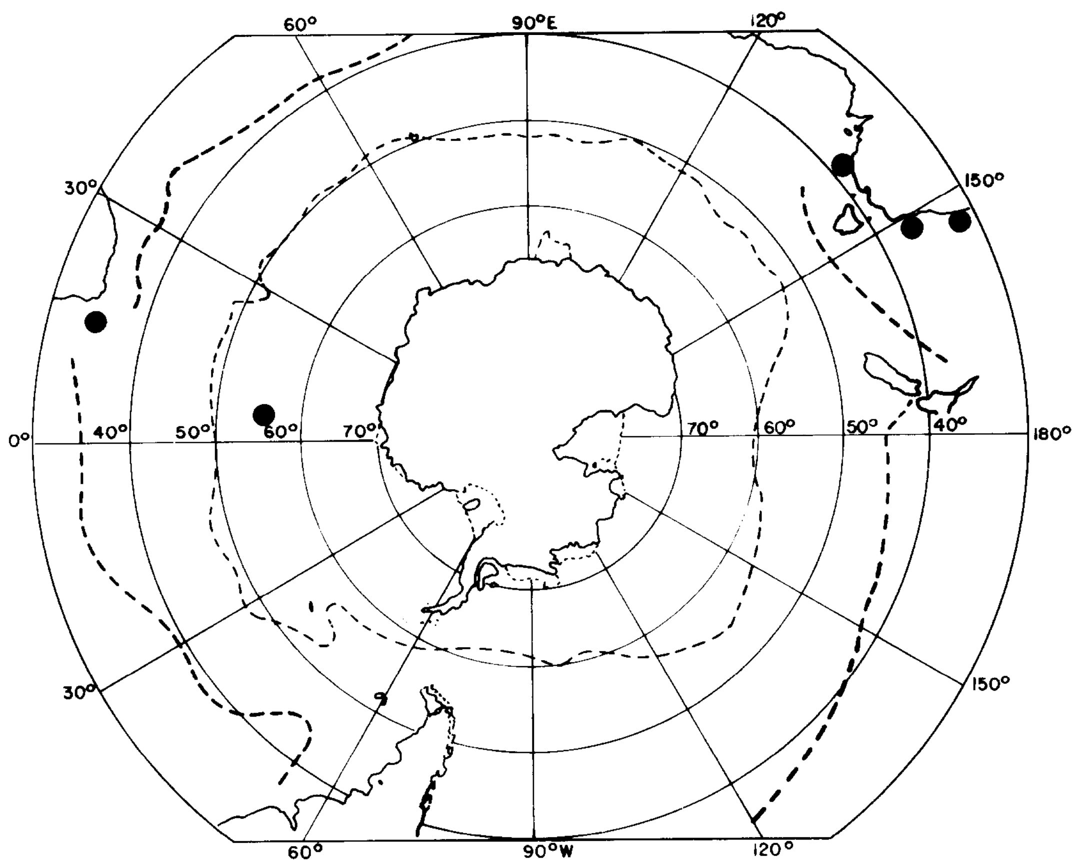


Figure 23. Fritillaria megachile (a) trunk, from left side; (b) tail, surface view. Map of distribution.



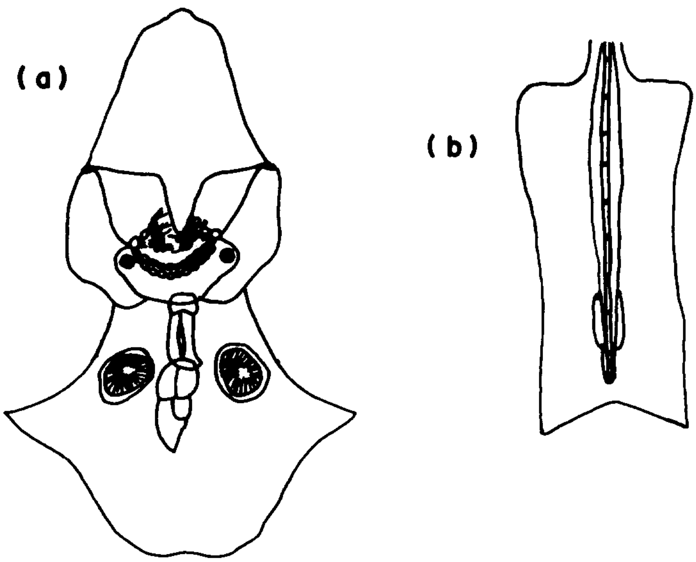
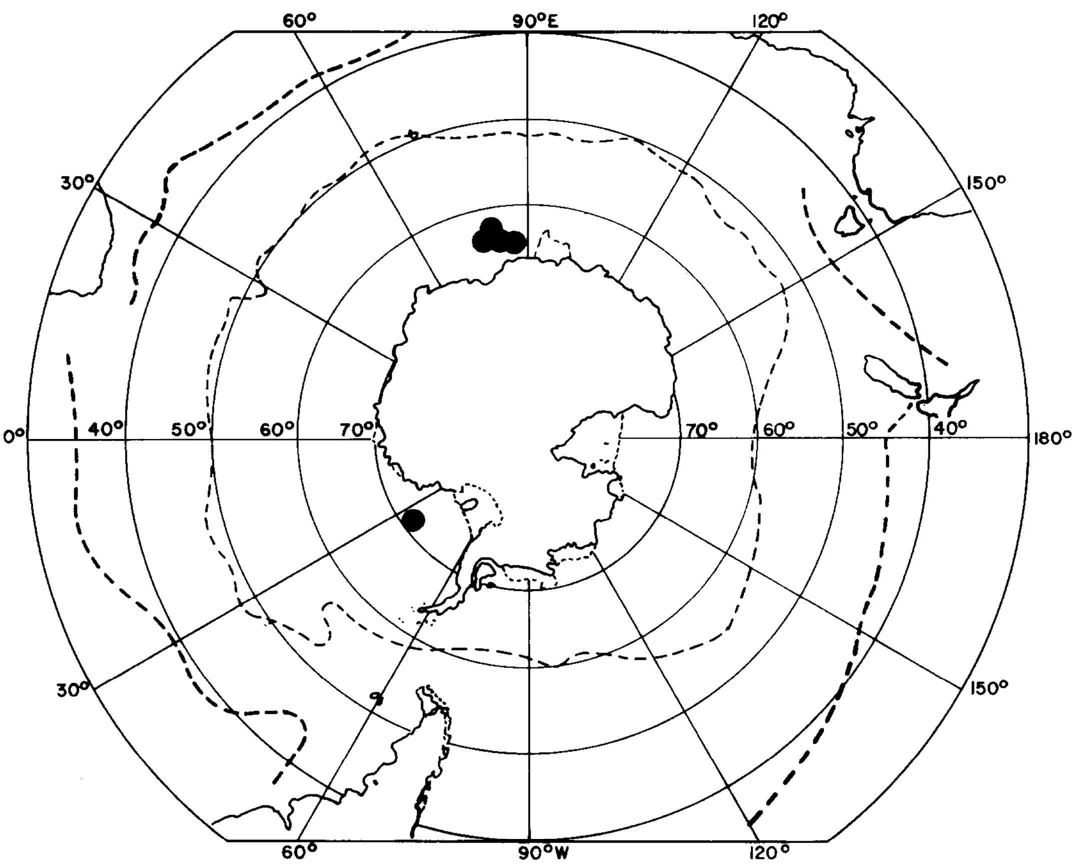


Figure 25. Fritillaria scillae (a) trunk, dorsal view; (b) tail. Map of distribution.



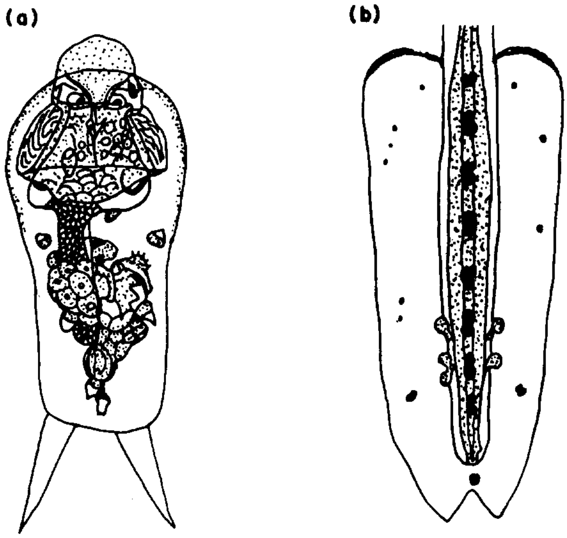
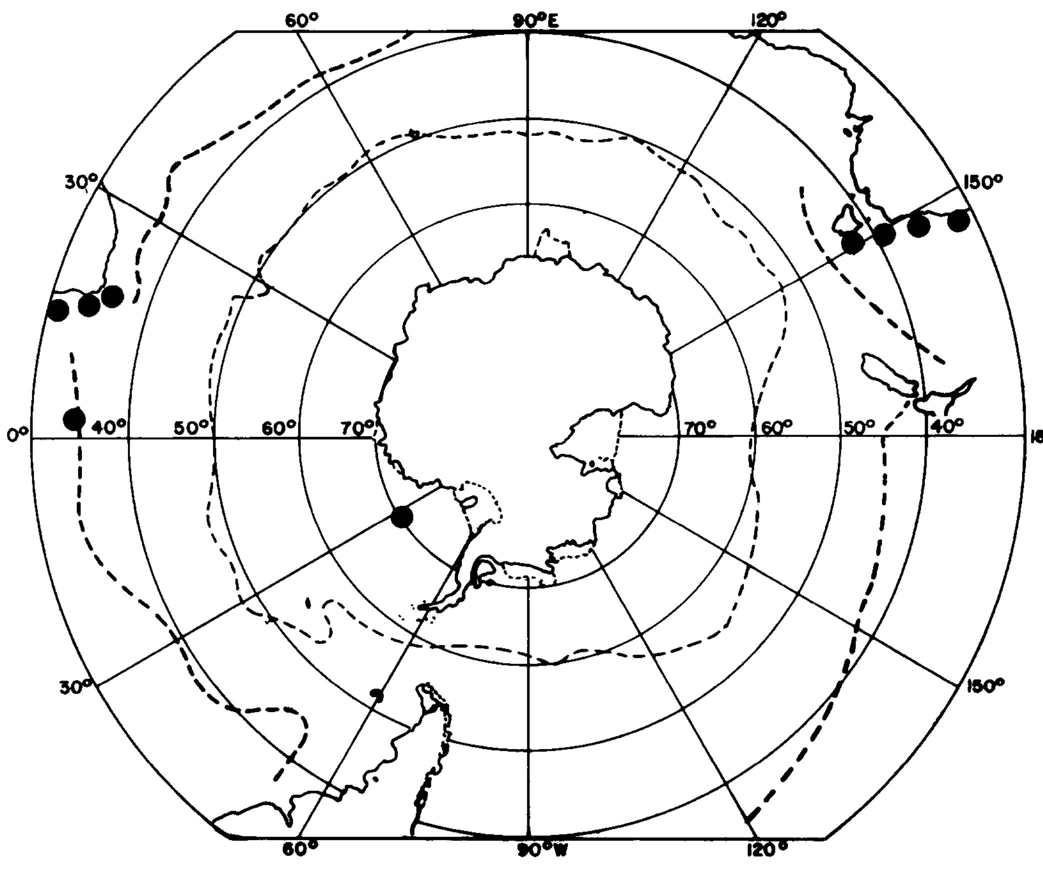


Figure 24. Fritillaria pellucida (a) trunk, dorsal view; (b) tail, surface view. Map of distribution.



Intestine: short
Rectum: lies in transverse postion with stomach
Ovary: globular when mature, lying behind the stomach
Testis: becomes large, elongated and almost cylindrical being placed obliquely and extending from the rectum to near the posterior end of the body, (hammer-shaped, Buckmann, 1969)
Tail fin: has a V-shaped notch at rear end, broad; extends beyond the urochord (Dakin and Colefax, 1940)
Tail musculature: broad and strong (Buckmann, 1969); narrow (Thompson, 1948)
Amphichordal cells: characteristic, 2 symmetrical pairs about the mid portion of posterior half of tail, open on ventral surface; may be up to about 6 small cells on either side of tail fin, these occur singly or in groups of 2 or 3, near the edge of the fin
Length: body up to 2 mm (Sewell, 1953); tail up to 3 mm.

Fritillaria pellucida is a very common species with a wide range being taken in all the warmer oceanic regions (Thompson, 1948; Sewell, 1953). Lohmann (1928) reported it from the Southern Ocean stating that id did not occur at a greater depth than 200 metres. It has also been reported from south-eastern Australia (Dakin and Colefax, 1940; Thompson, 1948) and South Africa (Lazarus and Dowler, 1979).

Fritillaria scillae Lohmann

(Figure 25)

Diagnostic characters (Lohmann and Buckmann, 1926):

Trunk: small anterior section is separated, a slight narrowing from the wide flat abdomen which is identified on the rear edge by large horn-shaped extensions protruding on either side
Pharyngeal packet: near end of endostyle
Spiracles: small and roundish
Mouth: shows a large lip
Testis: long, stretched, cylindrical, rounded at tips and tapered at end, lies in median line in front of ovary
Ovary: egg-shaped, lies in median line
Tail fin: split in rear section into large parts
Subchordal cells: 2 tube-like multi-celled glands situated near rear of chorda to right and left, openings directed toward tail roots
Length: body up to 1.35 mm; tail up to

Fritillaria tenella Lohmann 1896

(Figure 26)

Diagnostic characters (Tokioka, 1951, 1964):

Trunk: dorso-ventrally compressed; anterior portion of trunk forms a remarkable hood, the posterior end is truncate and provided with a pair of large triangular protuberances
Spiracles: small
Pharyngeal gland cells: 3, found just behind endostyle between spiracles; form

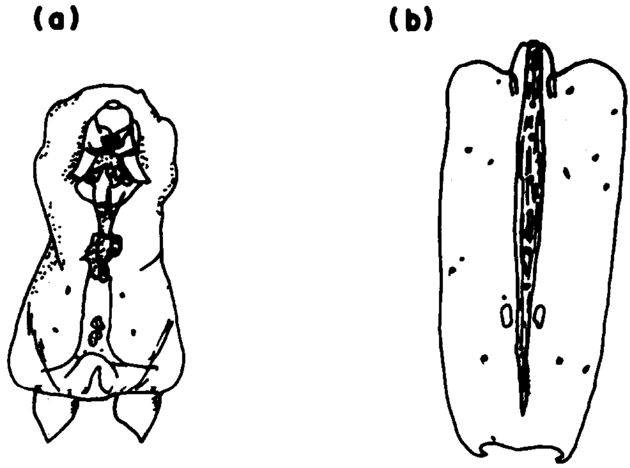
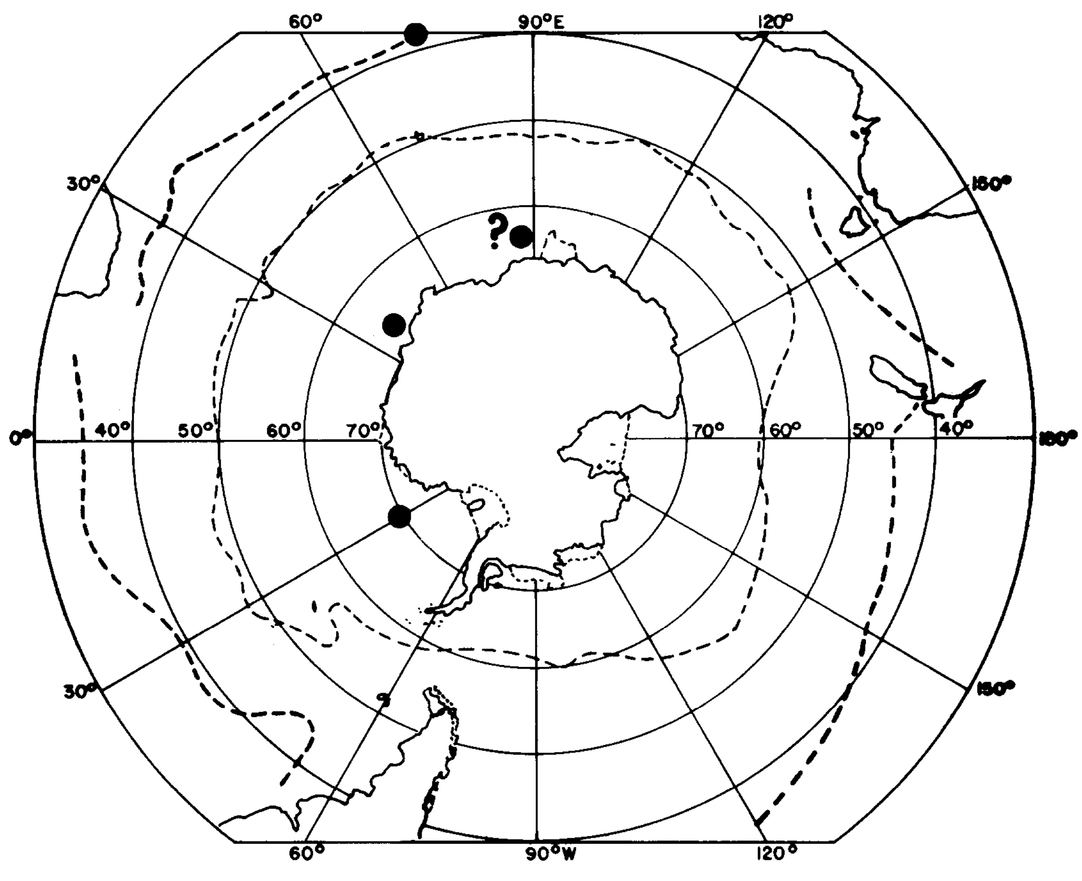


Figure 26. Fritillaria tenella (a) trunk, ventral view; (b) tail. Map of distribution.



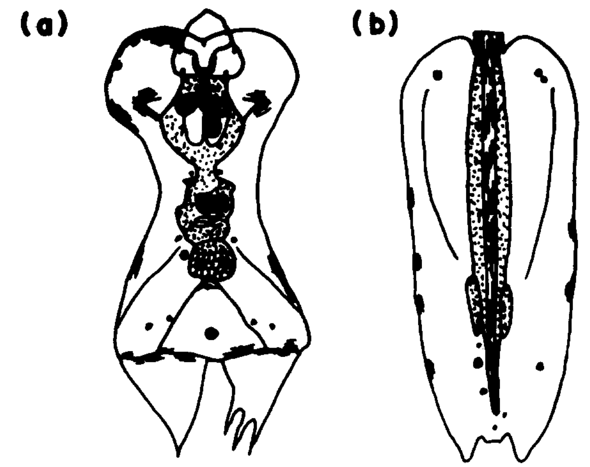
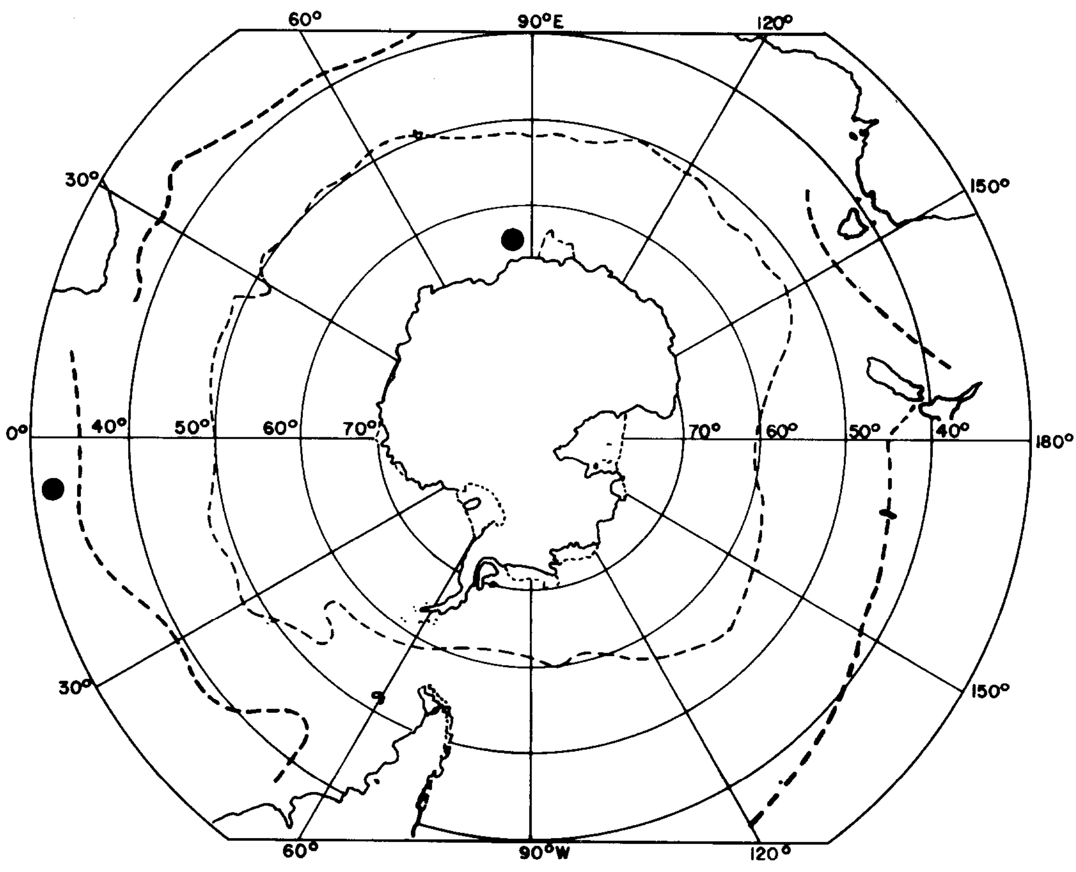


Figure 27. Fritillaria venusta (a) trunk, ventral view; (b) tail. Map of distribution.



packet (Buckmann, 1969)
Stomach: bears several protuberances
Intestine: configuration shows great variation (Tokioka, 1940)
Ovary: spheroid, in medium plane with testis (Buckmann, 1969)
Testis: coniform (Buckmann, 1969)
Tail fin: is very broad, widely cut at distal end; pair of glands embrances the musculature
Tail musculature: is narrow and delicate (Buckmann, 1969); scarcely wider than chorda
Amphichordal cells: jug-shaped, 1 pair (Buckmann, 1969)
Length: body up to 1.2 mm, tail up to 3.4 mm.

This type is closely related to Frit. scillae Lohmann (Tokioka, 1940) found in the Antarctic (Lohmann and Buckmann, 1926; Lohmann, 1928; Tokioka, 1964).

Fritillaria venusta Lohmann

(Figure 27)

(Fritillaria bicornis Thompson, 1948)

Diagnostic characters (Tokioka, 1951; Buckmann, 1969):

Trunk: posterior part of trunk varies considerably in shape from triangular to nearly truncate
Pharyngeal cells: form a packet, usually 4
Endostyle: large, displaced an appreciable distance towards the rear (Thompson, 1948)
Spiracles: small and round (Thompson, 1948)
Stomach: has no glandular appendages, globular
Intestine: occupies a median fore and aft position (Thompson, 1948)
Testis: when ripe develops horn-shaped lateral lobes
Ovary: forms a seam on the front of testis
Tail fin: broad and rectangular (Thomspon, 1948)
Tail musculature: broad but delicate, round nuclei arranged in a row, chorda does not reach end of musculature
Amphichordal cells: elongated but inconspicuous, one pair
Length: body up to 1.6 mm, tail up to 2.2 mm (Thompson, 1948).

Lohmann (1928) lists this warm water species as occurring in the Antarctic. Tokioka (1951) shows this species not to be specifically different from Fritillaria bicornis Lohmann.

Subgenus Acrocerus Lohmann

Fritillaria aberrans Lohmann 1896

(Figure 28)

Diagnostic characters (Tokioka, 1958):

Trunk: elongate, generally broadest at attachment of the hood and narrowest just posterior to the stomach; a distinct hood is present
Endostyle: is short and strongly curved upwards
Oikoplast epithelium: seems to cover the dorsal side of the distal half of the

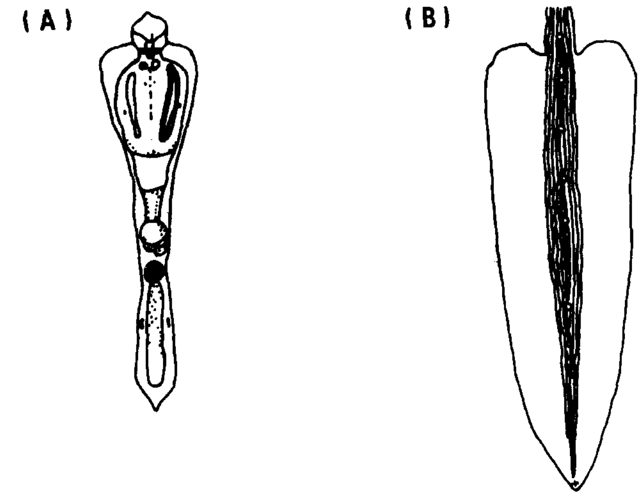
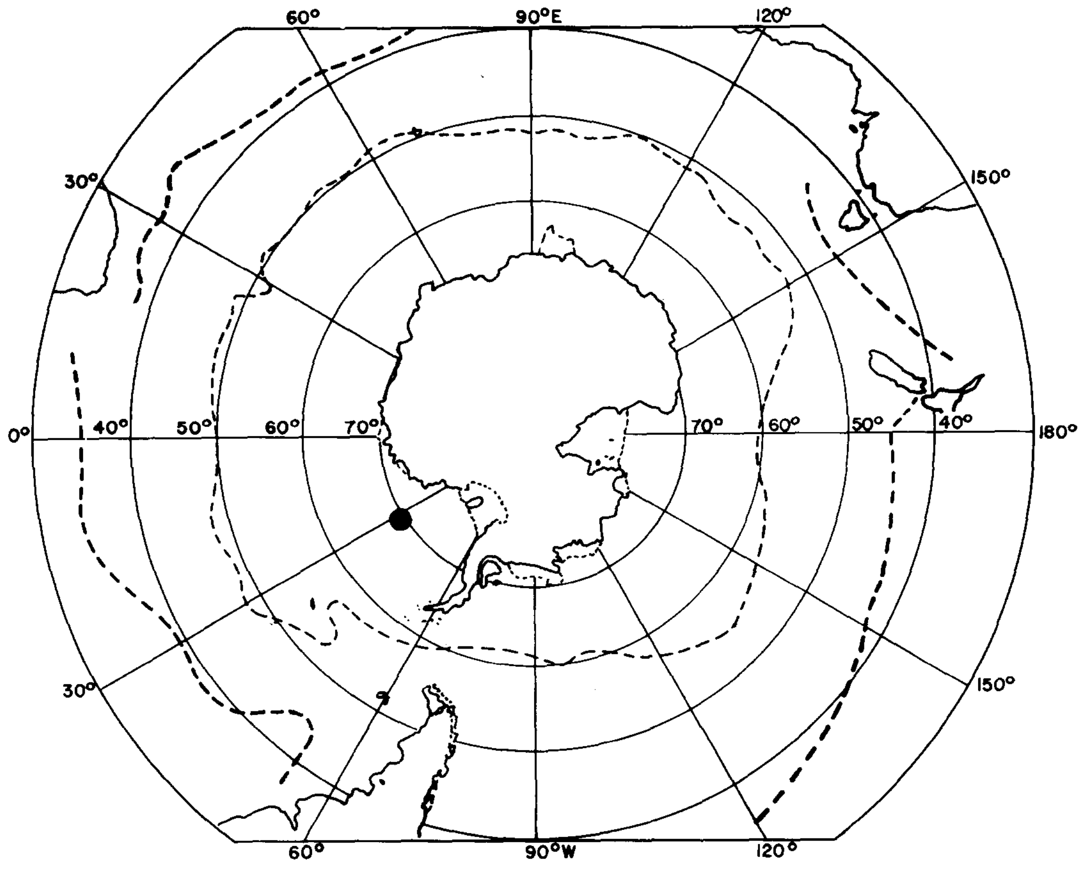


Figure 28. Fritillaria aberrans (a) trunk, ventral view; (b) tail. Map of distribution.



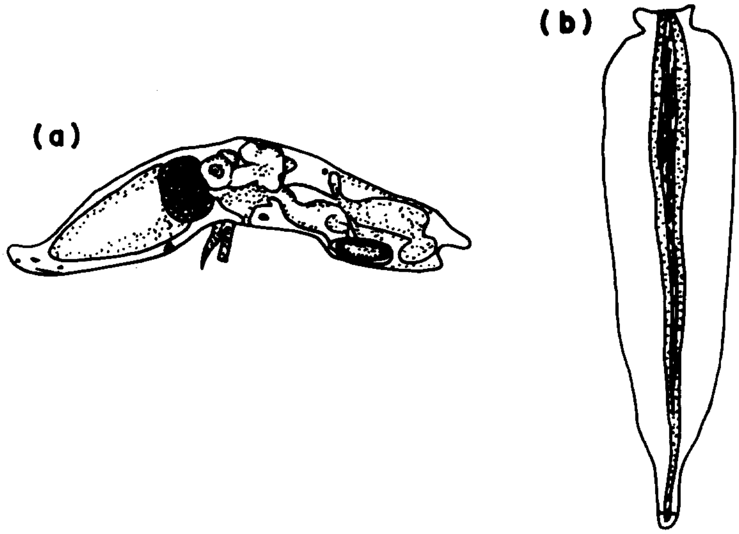
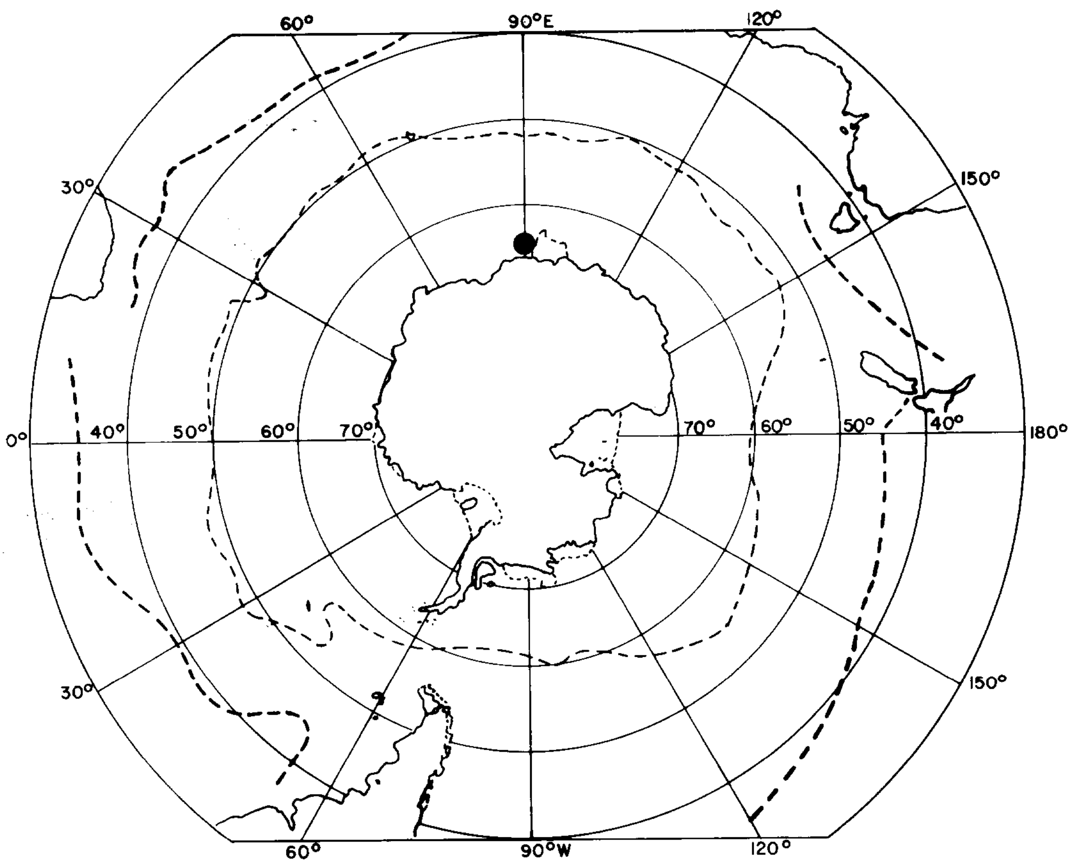


Figure 29. Fritillaria abjornseni (a) trunk, right side; (b) tail. Map of distribution.



anterior half of the anterior portion of the trunk
Spiracles: elongate, situated wholly beneath oikoplast epithelium
Pharyngeal gland cells: 3 pairs near spiracles, behind characteristic muscle-like structure encircling the pharynx over endostyle
Oesophagus: thick
Stomach: spherical, usually several protruded spherical cells over surface
Intestine: on right posterior side of stomach, with a pair of glandular appendages
Rectum: on right side
Ovary: an oval mass located behind stomach
Testis: seems to form an elongate mass, with an elongate gland cell on each side near the middle
Tail fin: rather wide, ending posteriorly in a single acute tip
Tail musculature: of moderate width, consisting of 10-12 muscle bands, provided with 11 roundish chordal nuclei, widest slightly anterior to the middle of the fin
Amphicordal cells: single pair, near posterior end of tail fin
Length: body up to 6.2 mm; tail up to 13 mm.

Tokioka (1958) reviewed the description of Fritillaria aberrans showing this species not to be specifically different from Frit. magna Lohmann and proposing that the name Frit. aberrans should be reserved according to the law of page priority. The characteristic feature of this species is the existence of a muscle-like structure encircling the pharynx at about the centre of the posterior half of the endostyle (Tokioka, 1958). Lohmann (1933) and Tokioka (1960) both suggest that this species might be a deep water form.

Fritillaria abjornseni Lohmann 1909

(Figure 29)

Diagnostic characters (Tokioka, 1955, 1956):

Trunk: small
Oikoplast epithelium: extends back towards stomach but not as far as in Frit. haplostoma
Spiracles: large and round, not separated but touch each other in the median line, with a gland cell at the postero-lateral corner
Oesophagus, Stomach, Intestine, Rectum, Ovary, Testis, Tail fin: like Frit. haplostoma
Tail musculature: narrow, approximately three times width of chorda at the broadest portion
Glandular cells: rear posterior end of tail fin, one small pair only
Length: body up to 2.7 mm; tail up to 1.2 mm.

A few specimens of this species have been collected in the Antarctic (Lohmann and Buckmann 1926) and off southwestern Australia (Lohmann, 1909). This coastal species (Tokioka, 1956) is considered a euryhaline and eurythermal form by Tokioka (1955) and is a member of the Fritillaria haplostoma complex.

Tokioka (1956) arranged the members of this complex systematically on size, position of spiracles in relation to each other, and relative widths of chorda and musculature in the tail. He placed the 10 forms into three sibling species Frit. abjornseni, Frit. haplostoma Fol and Frit. arafoera Tokioka adding that Frit. magna Lohmann and Frit. aberrans Lohmann may also be included when more

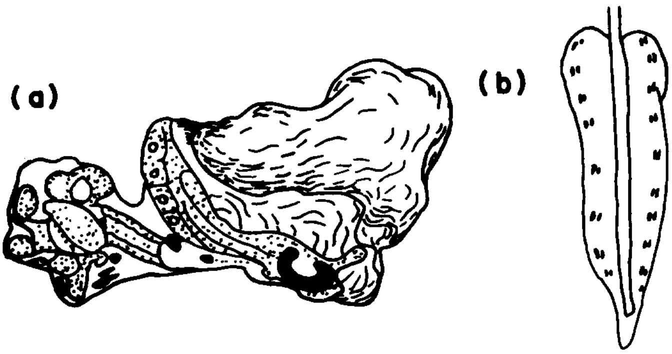
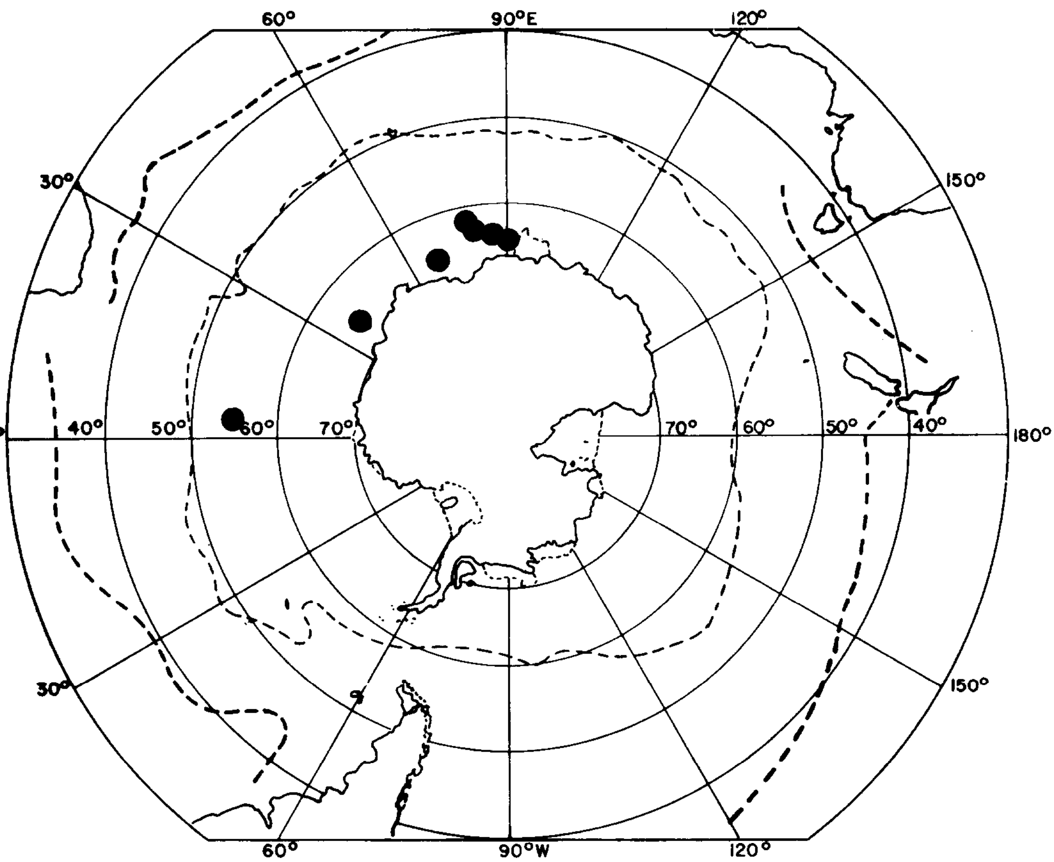


Figure 30. Fritillaria antarctica (a) trunk, right side; (b) tail. Map of distribution.



data concerning the feature of the alimentary canal are accumulated and considered carefully.
Frit. abjornseni can be identified by its very wide tail musculature and the spiracles touching each other on their inner size whereas the other Southern Ocean species, Frit. haplostoma has narrow tail musculature and the small spiracles are situated apart from each other.

Fritillaria antarctica Lohmann 1905

(Figure 30)

Diagnostic characters (Tokioka, 1964):

Trunk: roughly rectangular in outline, compressed dorso-ventrally, anterior half is occupied by pharynx covered dorsally with a prominent hood, dorsal lip protruded out in a single triangular lobe
Oikoplast-epithelium: furnished with 2 pairs of elongate elliptical groups of cells and bordered posteriorly with a transverse row of 8 large cells
Endostyle: narrow, strongly curved
Spiracles: vary large and round
Pharyngeal gland cells: no significant ones present
Stomach: arranged side by side to intestine on the transverse axis, has a prominent protuberance near the left posterior corner, with or without an additional glandular appendage
Intestine: bears 2 prominent glandular appendages:
Rectum: has prominent glandular prominence directed posteriorly, with 1 glandular appendage, and with or without a few small accessory appendages
Tail fin: long, very broad; posterior end remarkably narrow and bluntly pointed
Tail musculature: very narrow; distal end of chorda is not exposed
Amphichordal cells: minute, about 10 pairs, arranged in a row along each lateral margin of the tail fin
Length: body up to 0.4 mm; tail up to 1.4 mm.

Fritillaria antarctica has a very close affinity with Fritillaria fraudax Lohmann (Tokioka, 1964). Lohmann (1926) emphasized the difference in the appearance of the stomach between these two species, but Tokioka (1964) emphasized the rectum which is furnished with glandular appendages more complicatedly in antarctica than fraudax. Moreover, the narrowness of tail musculature in antarctica is noticeable; the musculature is much wider in fraudax (Tokioka, 1964). As Tokioka didn't have any mature specimens he couldn't comment on the validity of Frit. antarctica.

This cold water form (Tokioka, 1964) has only been found in the Antarctic (Thompson, 1954).

Fritillaria drygalski Lohmann

(Figure 31)

Diagnostic characters (Lohmann and Buckmann, 1926):

Stomach: large, spherical
Intestine: with two spherical or pear-shaped tapered appendices

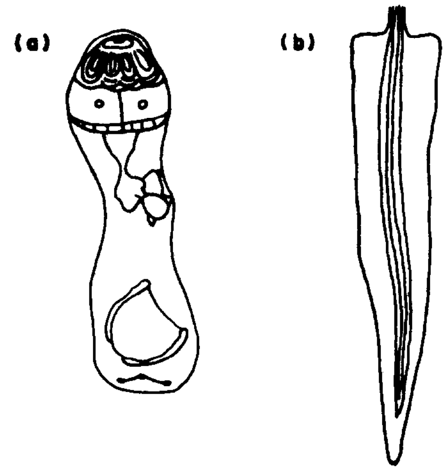
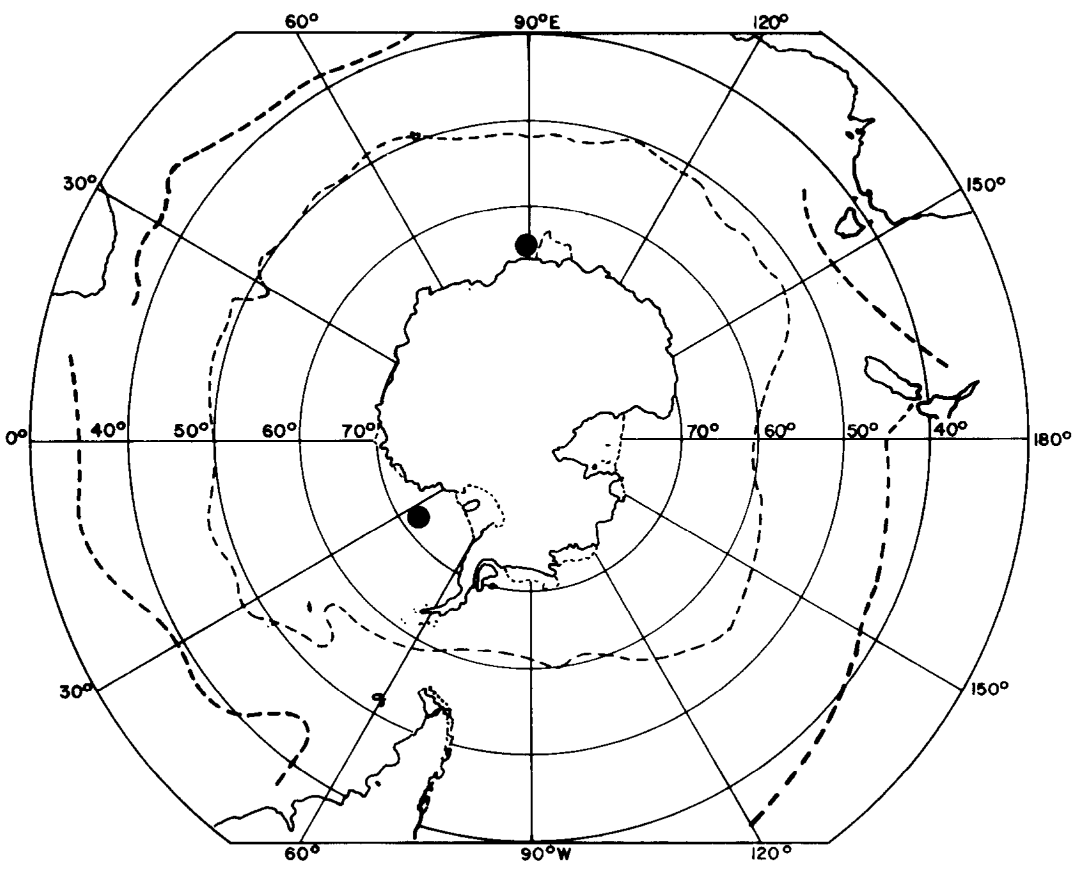


Figure 31. Fritillaria drygalski (a) trunk, dorsal view; (b) tail. Map of distribution.



Testis: forms a flat, roundish four-sided plate
Ovary: cord-like, frames the testis from the left and the right
Tail musculature: longer than chorda
Subchordal cells, very large and conspicuous, lie on one side of chorda
Length: body up to 1.4 mm; tail up to

This species has been reported from the Antarctic by (Lohmann and Buckmann, 1926). Some investigators consider Fritillaria drygalski to be synonymous with Frit. aequatorialis and if this is true, then it must be a warm-water form that penetrated into the Antarctic waters (Tokioka, 1961).

Fritillaria formica Fol 1872

(Figure 32)

Diagnostic characters:

Trunk: rather elongate; considerable space between the posterior end of the pharyngeal region and the anterior edge of the stomach; characteristically both dorsal and ventral lips are divided into lateral lobes (Tokioka, 1964)
Oikoplast epithelium: may or may not cover oesophagus
Endostyle: short and broad, both ends turned toward the dorsal aspect; characteristically exceedingly wide (Tokioka, 1964)
Spiracles: large and circular or slightly elliptical
Pharyngeal gland cells: 2, behind spiracles (Tokioka, 1964)
Stomach: variable in form; situated dorsally in front of rectum
Intestine: arises posterior ventrally to stomach; leads to large rectum
Ovary: spherical
Testis: spherical at first but becomes elongated to an oval or cylindrical form at a later stages
Tail fin: broadly lanceolate, anterior portion being broad and rounded at each shoulder, tip simply rounded
Tail musculature: broad and strong
Amphichordal cells: several paired sets, along fin margins, pair of large continuous cells at middle of fin
Length: body up to 2.0 mm; tail up to 4.1 mm (Tokioka, 1960).

Lohmann and Buckmann (1926) distinguished 2 forms: f. tuberculata and f. digitata with respect to structure of dorsal lips, tail length and musculature, and gonad shape but Thompson (1948) points out that allowing for normal variation with age the two forms cannot be separated..

This warm water species (Tokioka, 1961) has been found off southeastern Australia where it is very largely limited to the upper 200 metre water layer (Thompson, 1948). It can be carried south into the Southern Ocean by water currents (Sewell, 1953) where it has been reported by Tokioka (1964).

The specimens of Tokioka (1964) from the Antarctic may be a separate form as they had an enormously elongated trunk and unusually narrow tail musculature compared with the "typical" Fritillaria formica.

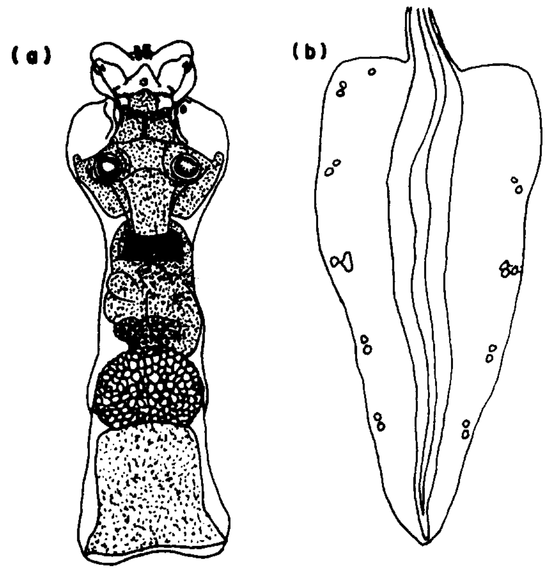
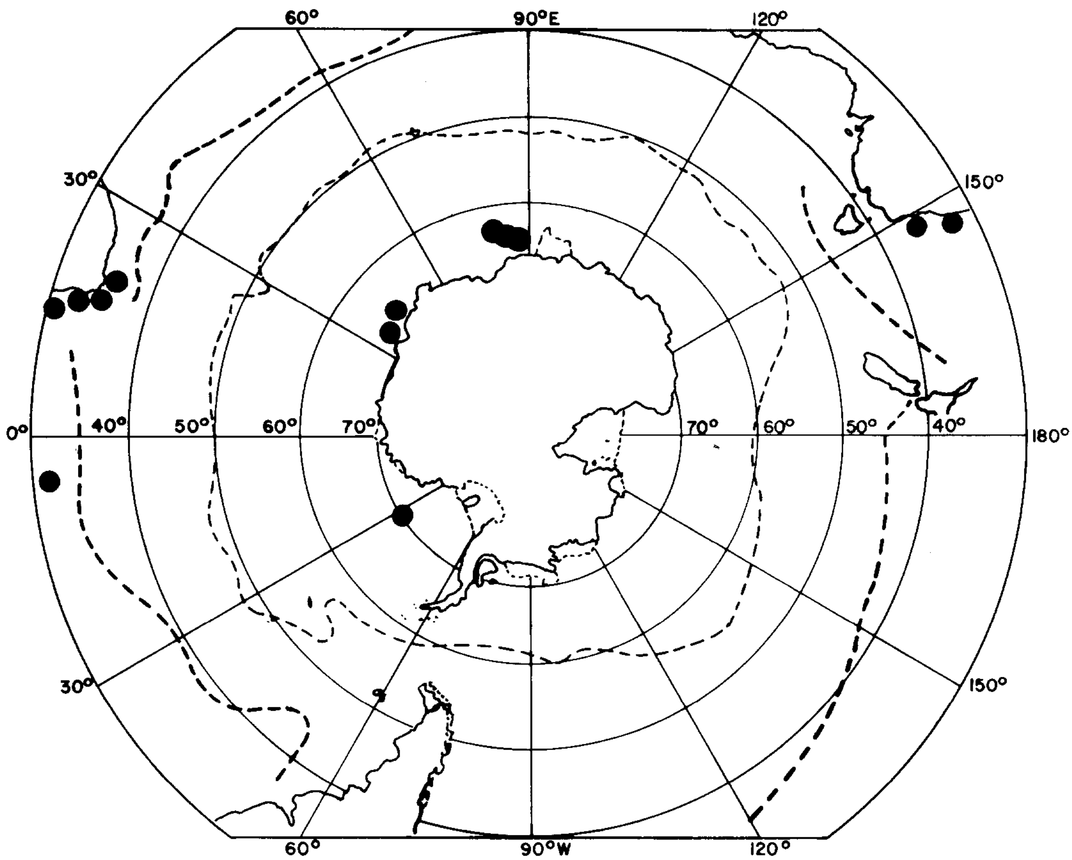


Figure 32. Fritillaria formica (a) trunk, ventral view; (b) tail, surface view. Map of distribution.



Fritillaria fraudax Lohmann 1896

(Figure 33)

Diagnostic characters:

Trunk: very plump, compressed sac-like form, rounded behind, no obvious hood structure
Endostyle: close to mouth, strongly curved
Spiracles: elongated elipitical form, may collapse to irregularly shaped narrow slits in preserved material
Alimentary canal: lies transversely
Stomach: has prominent triangular glandular projection on left side with 2 minute gland cells (Tokioka, 1960)
Rectum: large, directed steeply towards the ventral surface
Gonads: form semi-circular band running parallel to rear wall of body
Tail fin: is very broad, fore edge being at right angles to longitudinal axis, the shoulders slightly rounded; narrows very gradually towards the tip, which is somewhat pinched off in finger-shaped fashion
Tail musculature: fairly broad
Glandular cells: 3 at tip, 1 or more near margin of tail fin
Length: body up to 1.8 mm; tail up to 4.5 mm.

This species is scarce, though occurring down to a depth of 200 metres, and possibly still deeper (Thompson, 1948). Lohmann (1928) lists this warm water species as occurring in the Antarctic.

Fritillaria haplostoma Fol 1872

(Figure 34)

Diagnostic characters:

Trunk: long and slender
Hood: strongly developed and is drawn out sideways into a process which curves down ventrally and partly covers the spiracles
Oikoplast epithelium: proportionally very small
Endostyle: curved, very short and broad
Spiracles: large, and vary from elongate to round shape (Tokioka, 1956)
Pharyngeal gland cells: scattered
Stomach: spherical, anterior to rectum
Intestine: curves round stomach ventrally and towards the left side
Rectum: small
Ovary: spherical, may lie just behind the rectum
Testis: large, cylindrical or elliptical may be separated from ovary
Tail fin: very broad but narrowing to a more or less elongated tip
Tail musculature: is very narrow, ending some distance in front of the rear end of the notochord
Glandular cells: several pairs, fine, arranged in a row along the fin margin on each side (Tokioka, 1964)
Length: body up to 1.5 mm (Russell and Coleman, 1935); tail up to 2.5 mm (Thompson, 1948).

Fritillaria haplostoma is broadly distributed in all warm oceanic regions, though small specimens may be met more frequently in coastal waters (Tokioka,

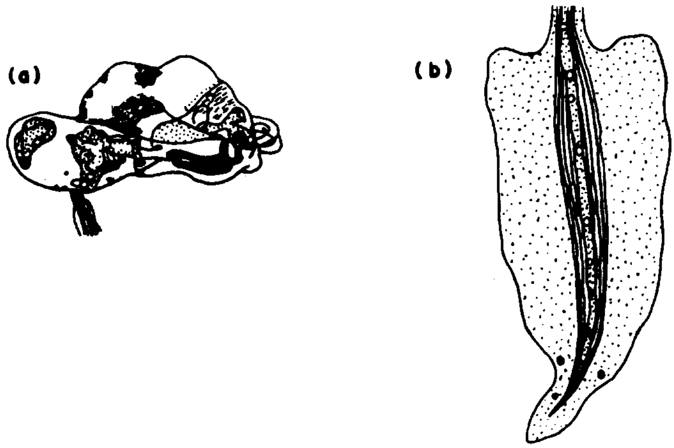
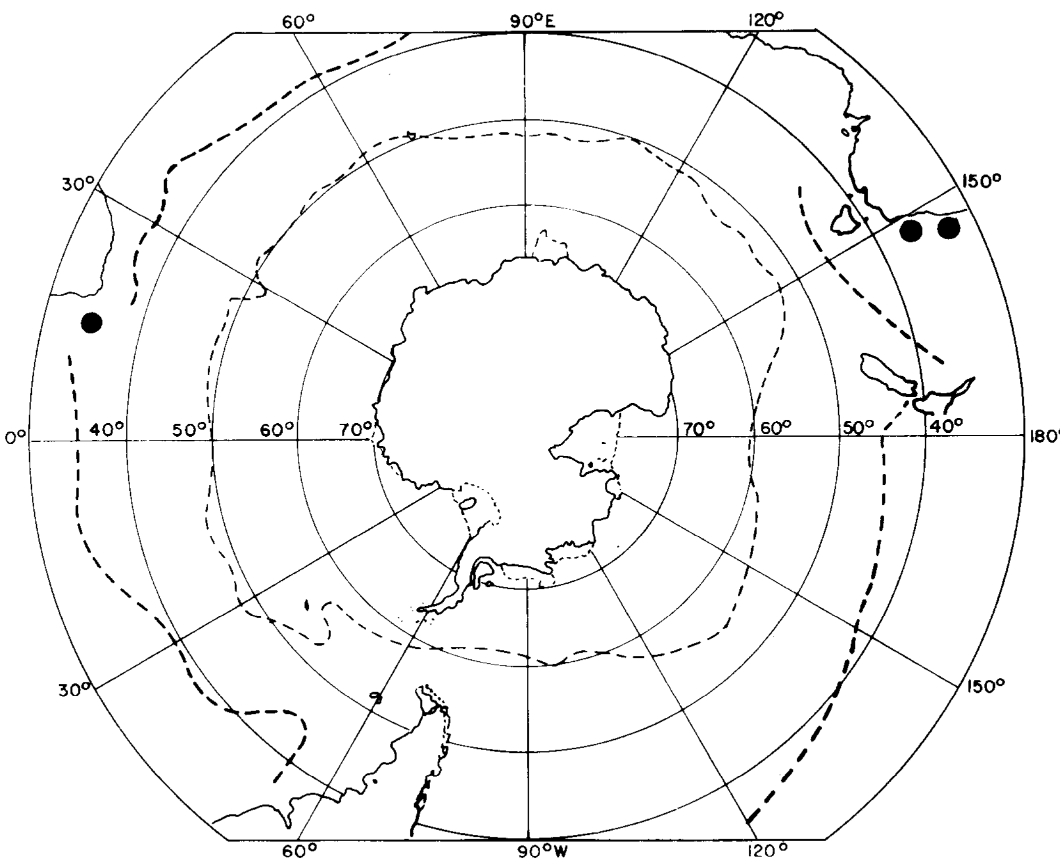


Figure 33. Fritillaria fraudax (a) trunk, right side; (b) tail, surface view. Map of distribution.



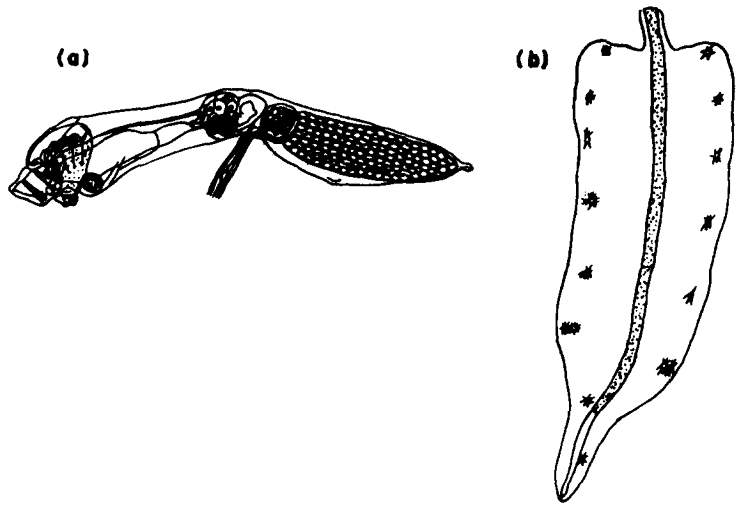
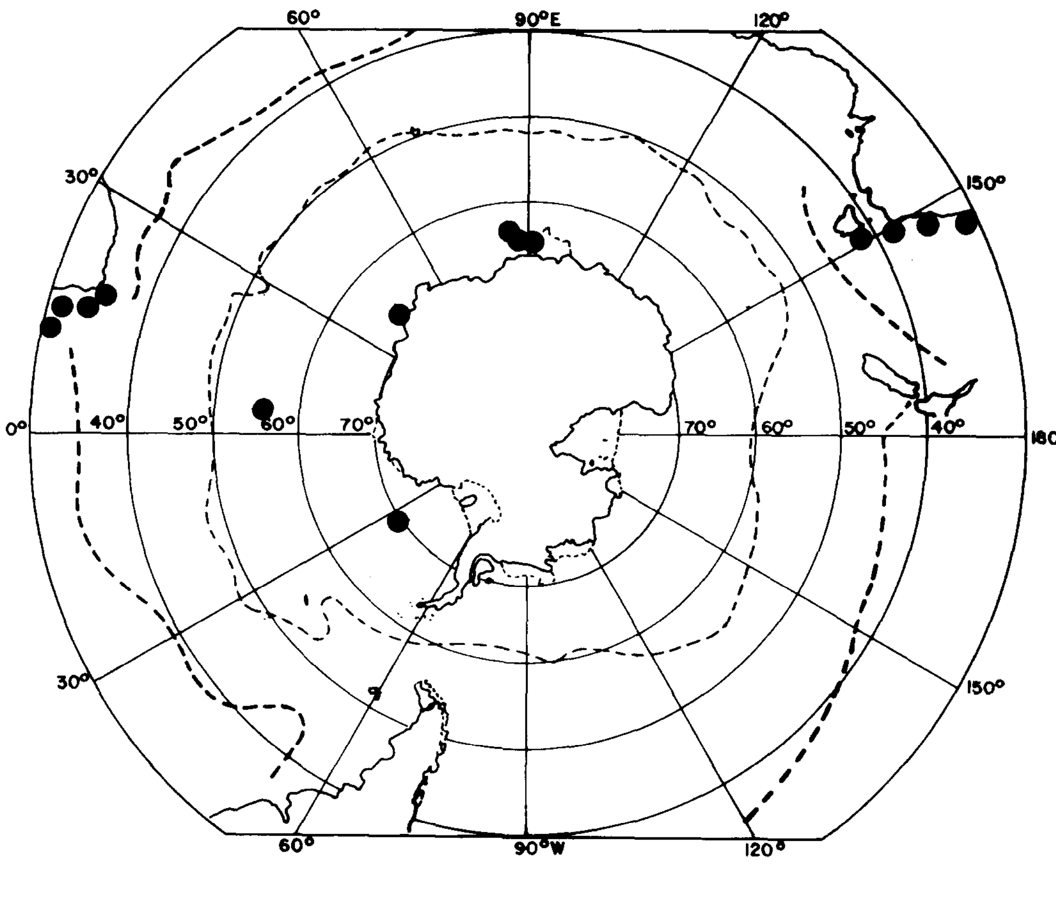


Figure 34. Fritillaria haplostoma (a) trunk, left side; (b) tail, surface view. Map of distribution.



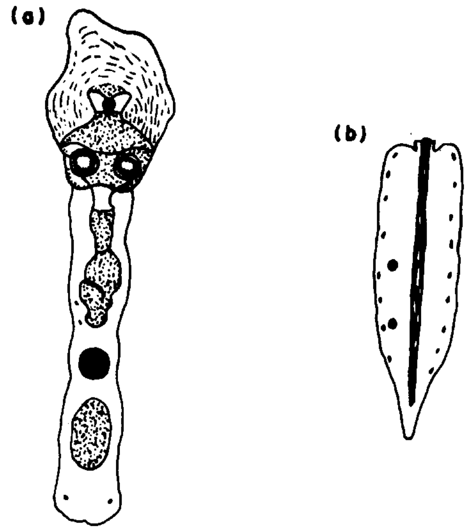
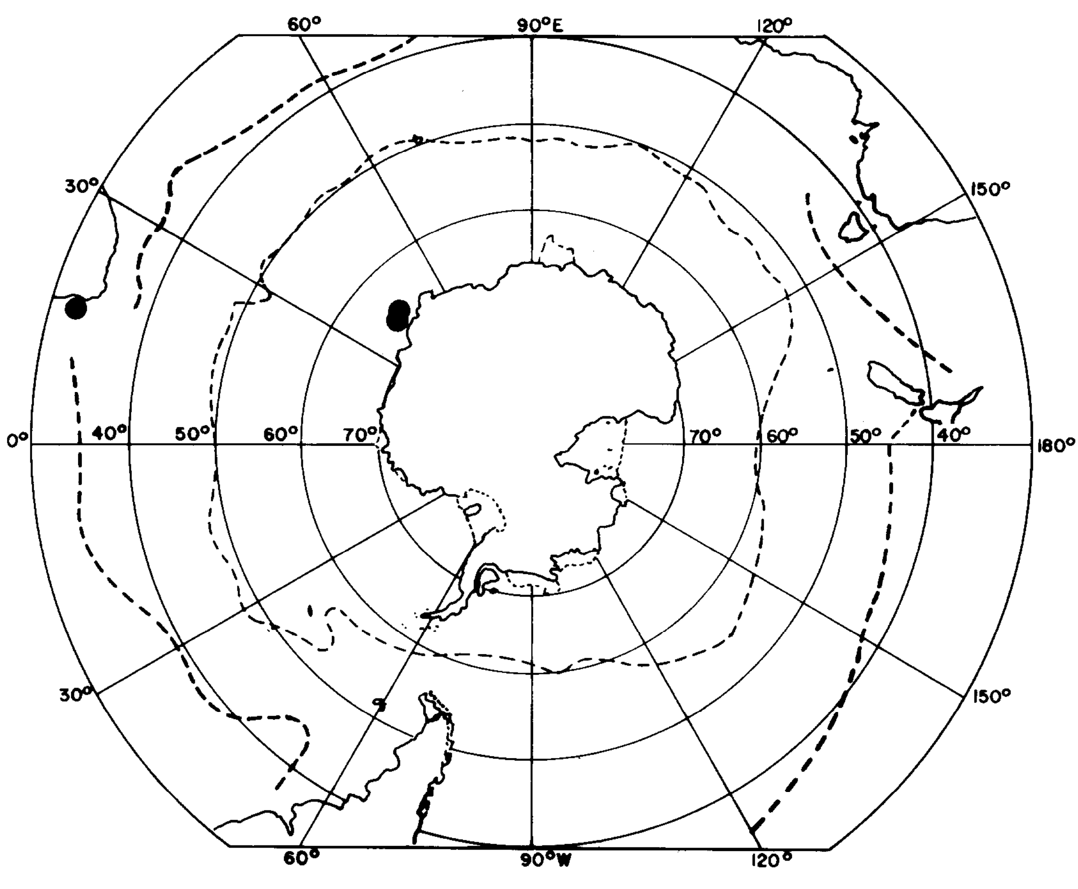


Figure 35. Fritillaria haplostoma f. glandularis (a) trunk, ventral view; (b) tail. Map of distribution.



1956). Tokioka (1960) points to the possibility that the main propogating area of Fritillaria haplostoma is in the neritic waters and the individuals which are found in the far offshore oceanic waters may be drift forms, and if this is true then Frit. haplostoma should be treated as a neritic water inhabitant. It has been found in the Antarctic by Lohmann and Buckmann (1926), Lohmann (1928) and Tokioka (1964) and off southeastern Australia (Thompson, 1948).

This species shows a considerable range of variation in body length (Tokioka 1951). Tokioka (1956) found Frit. haplostoma to have a number of allied forms and two sibling species (see Frit. abjornseni for discussion).

Tokioka (1961) tentatively identified some Antarctic specimens as Fritillaria spp. Saying that they closely resembled Frit. haplostoma but were unique in having two very remarkable gland cells only on the right side of the tail fin. He pointed out that is is very possible that this is a distinct form of haplostoma characteristic in the Antarctic and later described it as a new form Frit. haplostoma f. glandularis (Tokioka, 1964).

Fritillaria haplostoma f. glandularis Tokioka 1964

(Figure 35)

Diagnostic characters (Tokioka, 1964):

Trunk: slender, pharyngeal region is very short, covered by a large hood on the dorsal side; the lower lip is divided into two lateral lobes, while the dorsal lip seems to protrude anteriorly as a single lobe
Endostyle: is a narrow to moderately wide, curved dorsally strongly
Spiracles: round and situated close to each other
Pharyngeal gland cells: one, may be found between spiracles, plus one or two minute glandular cells between the spiracles and the oesophageal opening
Stomach: ovoid, furnished with a few gland cells on surface, far apart from posterior edge of pharynx
Intestine: bears two, (dorsal and ventral), very distinct glandular appendages
Ovary: anterior and spherical
Testis: posterior and elongate
Tail fin: wide, becoming narrower in distal portion ending in a bluntly pointed tip
Tail musculature: is narrow, covers whole lenth of notochord
Glandular cells: minute series, along each lateral margin of the fin, two much larger and more compact gland cells found on right side of fin
Length: body 1 mm; tail 2.1 mm.

The absolute absence of the exposed distal portion of notochord and the presence of two remarkable gland cells mostly on the right side of the fin of some Antarctic specimens led Tokioka (1964) to erect a form glandularis but as he pointed out Fritillaria haplostoma is well known by its great range of variation, it is highly possible that the new form merely represents an ecological form of haplostoma and bears no specific significance. Its distribution is considered to be limited to Antarctic seas. (Tokioka, 1964).

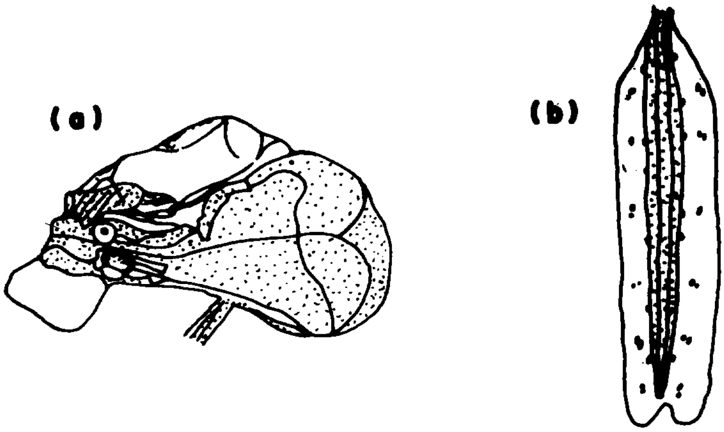
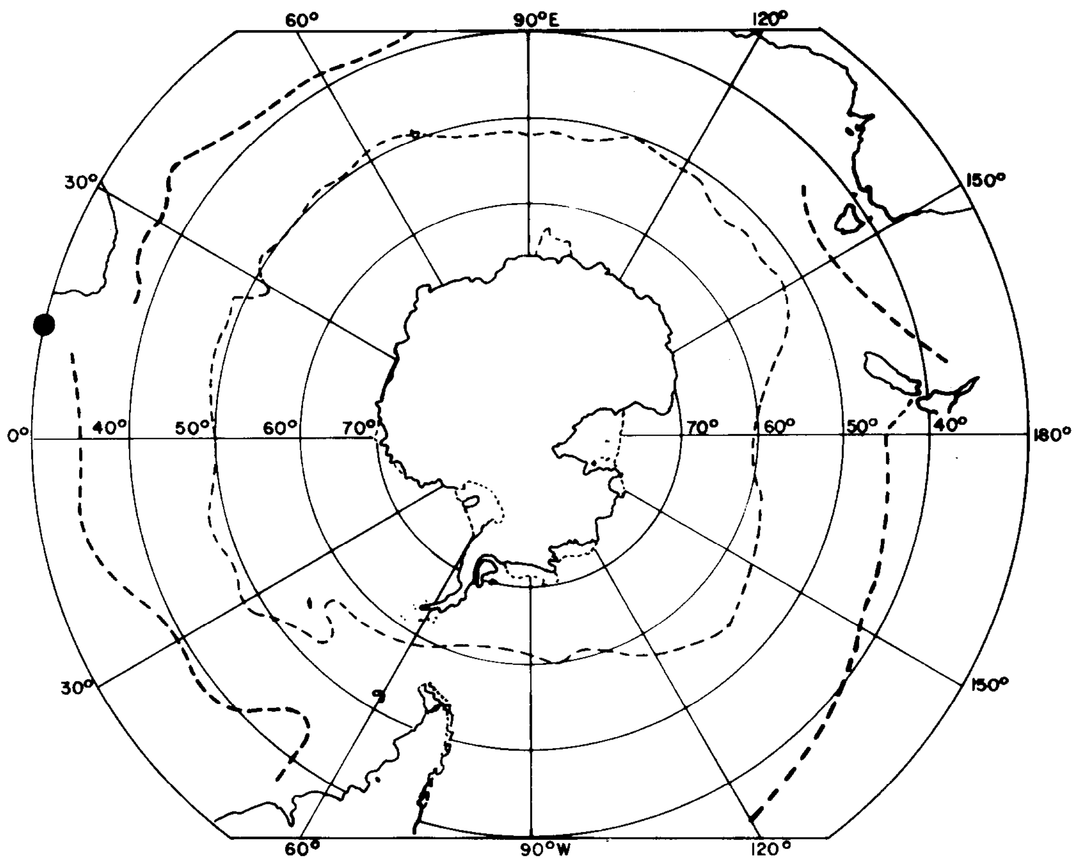


Figure 36. Appendicularia sicula (a) trunk, left side; (b) tail. Map of distribution.



Sub-family APPENDICULARINAE

The reproductive glands are contiguous with the alimentary canal, but a special rear section of the body containing the branchial cavity is absent; the whole fore section of the body is short and compact; the mouth section is without snout prolongation; the tail fin narrows gradually towards its root, not being broad and indented in this region as in Fritillarinae; monogeneric.

Genus Appendicularia Fol

Endostyle present, spiracles with a simple strip of bristles, without finger-like extensions; dorsal oikoplast epithelium bilaterally arranged, without back pin; tail fin wide, narrowing toward the tail roots slowly, not cut off at any stage; body hunched without sectioning in front, middle or end of body; monotypic for Appendicularia sicula Fol.

Appendicularia sicula Fol

(Figure 36)

Diagnostic characters (Buckmann, 1969):

Oikoplast epithelium: extends dorsally above stomach, but ends ventrally just behind the endostyle
Spiracles: much in front of anus
Oesophagus: opens into front wall of stomach
Stomach: spherical, composed of only a few cells
Intestine: forms three coils, to right of stomach, spherical glandular appendage behind the pyloris
Rectum: large, pear-shaped
Testis: touches posterior wall of gut
Ovary: disciform, rests upon testis
Tail fin: with a broad notch at the end, proximally tapering towards end
Length: body up to 0.5 mm

This is a neretic water inhabitant (Tokioka, 1960).

8.6 FAMILY KOWALEVSKIIDAE

Endostyle missing; spiracles absent; elongated branchial appertures; heart missing; tail elongated; body ovoid, monogeneric.

Genus Kowalevskia

The body is ovoid and truncated in front; the branchial cavity has ciliated grooves, which bear finger-shaped processes, forming a sieve; endostyle and heart are absent; the rectum is of simple form; the oikoplast cells are arranged radially round a great central giant cell; the large lanceolate tail fin runs out behind into a simple point; three species of which K. tenuis

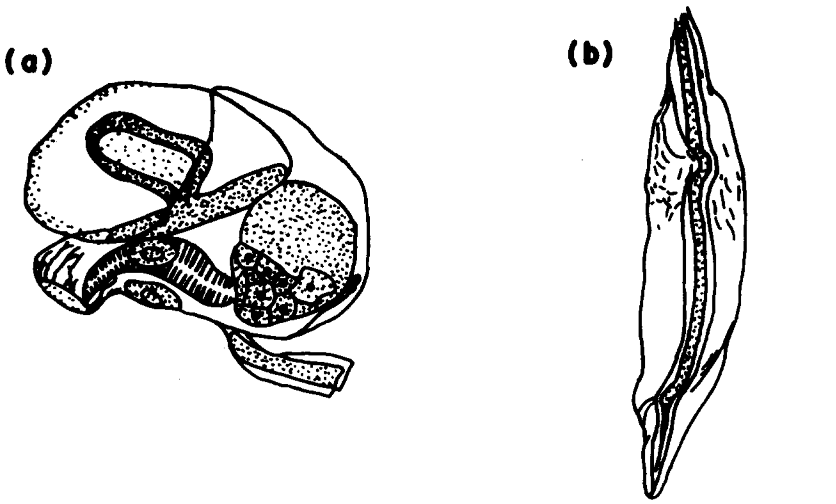
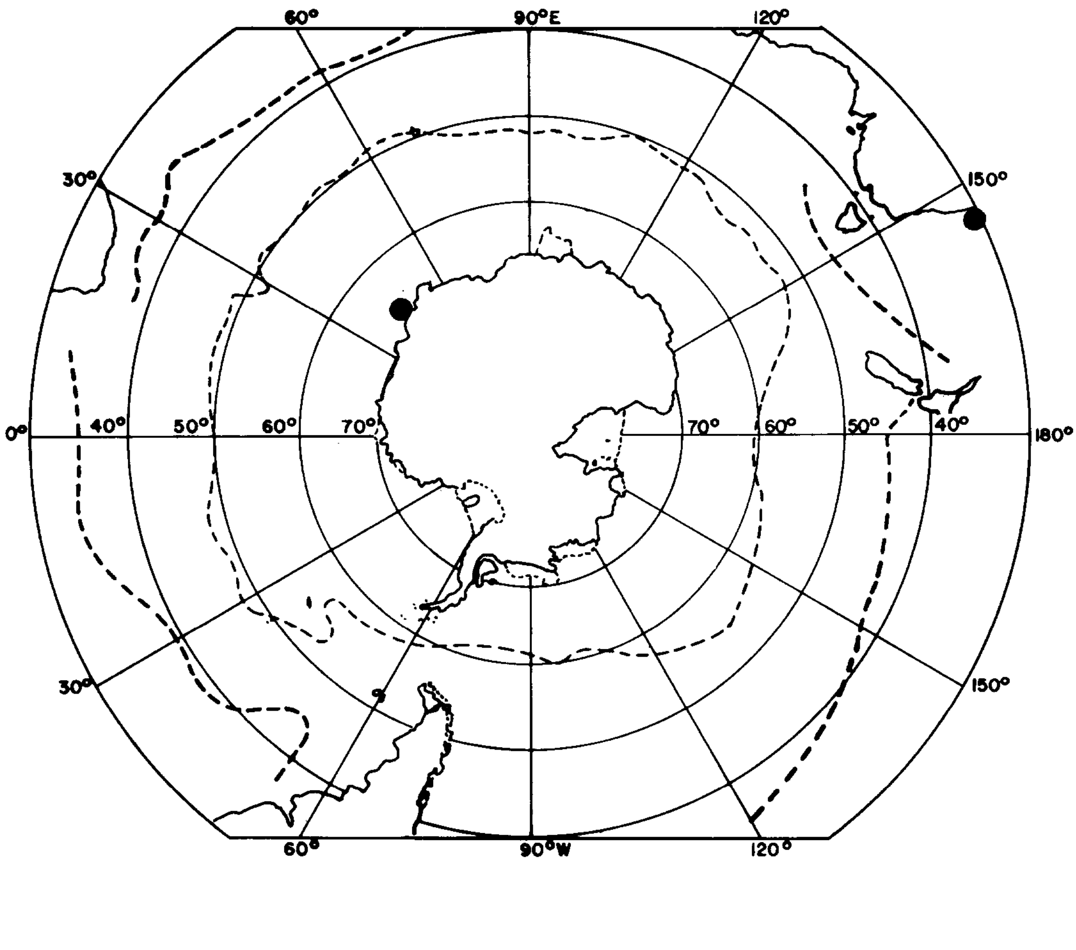


Figure 37. Kowalevskia tenuis (a) trunk, left side; (b) tail, surface view. Map of distribution.



occurs in the Southern Ocean. Lazarus and Dowler (1979) tentatively identified three specimens from South Africa as K. oceanica.

Kowalevskia tenuis Fol 1872

(Figure 37)

Diagnostic characters:

Trunk: ovoid, truncated at the buccal extremity; walls very thin and transparent; branchial portion strongly compressed dorsoventrally and sharply distinguishable from the swollen gastro-genital region, large hood
Oikoplast epithelium: covers dorsal side of branchial and front side of gastro-genital region, forms at lateral and ventral sides of body and narrow zone along lip
Endostyle: not present
Stomach: situated antero-ventrally on left side; almost spherical when full, ovoid when empty; walls composes of large cells
Intestine not obvious, pyloric end of stomach employing directly into rectum
Rectum: postero-dorsal, adjacent to stomach, ovoid
Ovary: large, spherical, more ventral than testis
Testis: elongated, reniform when mature
Tail fin: characteristically lanceolate and undulating in appearance
Tail musculature: is weak
Length: body 1.1 mm; tail 8.0 mm (Fol 1872).

This warm water species (Lohmann, 1896) has been found off southeastern Australia (Thompson, 1948). Tokioka (1964) tentatively identified a specimen of Kowalevskia from Antarctica as K. tenuis.

9. SOURCES OF FIGURES AND MAPS

Source	Figure
Lohmann (1896)	13b
Herdman (1910b)	11c
Neumann (1913b)	1d, 10
Lohmann & Buckmann (1926)	18b, 20, 25, 31
Garstang & Georgeson (1935)	16
Tokioka (1940)	22, 26, 27, 33a, 36
Thompson (1948)	1a, 4, 8, 11b, 13a, 14, 15, 18a, 23, 24, 32, 33b, 34, 37
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Tokioka (1958)	17, 28, 29
Foxton (1961)	6
Tokioka (1964)	12, 19, 30, 35
Foxton (1966)	1c, 3, 5
Foxton (1971)	7
Barnes (1974)	1b, 2, 9, 11a

Source	Map
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Lohmann (1905)	8, 26
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van Beneden & de Selys-Longchamps (1913)	4, 5
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Buckmann (1924)	16, 21, 27
Lohmann (1924)	8, 18, 19, 30
Lohmann & Buckmann (1926)	8, 9, 10, 11, 13, 14, 15, 16, 18, 20, 21, 22, 23, 25, 26, 27, 28, 30, 32
Lohmann (1928)	8, 11, 14, 15, 20, 22, 24, 28, 30
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Kruger (1939)	6
Dakin & Colefax (1940)	1, 2, 11, 20
Thompson (1948)	1, 2, 6, 9, 10, 11, 14, 19, 20, 28, 29, 30, 33
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Ealey & Chittleborough (1956)	6
Stadel (1958)	3, 5
Udvardy (1958)	8, 10, 11, 14

Fagetti (1959)	5, 6
van Zyl (1960)	6
Bary (1961)	1, 2, 6, 10
Foxton (1961)	3, 4
Tokioka (1964)	8, 10, 11, 15, 17, 18, 22, 26, 28, 30, 31, 33
Caldwell (1966)	2, 3, 4, 5
Ensal (1970)	3, 4
Foxton (1971)	5, 6
Lazarus & Dowler (1976)	1, 2, 6, 9, 10, 11, 13, 14, 18, 19, 20, 28, 29, 30, 31
Taw (1978)	2, 6

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APPENDIX I   AIDS FOR THE DETAILED EXAMINATION OF PELAGIC TUNICATES

Pelagic tunicates often are very delicate and fragile animals and are prone to damage during capture and subsequent preservation. For this reason some aids are given for the detailed examination of salps and appendicularians.

1. SALPS

The importance of salp musculature as a taxonomic character was confirmed by Streiff (1908). Various authors have remarked upon the caution that must be exercised in distinguishing between natural variation in muscle arrangement and artifacts due to preservation and damage (Sewell, 1926; Thompson, 1948; Foxton, 1961) as salps are notorious for the vagaries that preservation plays with their morphology and this applies particularly to the arrangement of the oral, body and atrial musculature (Foxton, 1971).

In specimens such as Ihlea racovitzai and I. magalhanica, where the body structure are unsupported by a firm well-developed test, damaged muscle are the rule rather than the exception and this no doubt contributed to the numerous discrepancies with regard to muscle arrangement that occurs in the literature (Foxton, 1971).

Foxton (1965) describes a method for staining the musculature of preserved salps and reforming their natural shape by injecting the body cavity with molten agar: The salp is first stained using the method of Berner (1954) to differentiate the musculature. A 0.1% solution of Rose Bengale is added to the water into which the specimen has been removed from formalin. Stain is introduced into the body cavity of the salp via the oral aperture, using a glass pipette. Staining is allowed to proceed until the musculature assumes a strong pink colour, at which point the specimen is transferred, using a perforated spoon, to clean water in a glass dish some 50 mm deep and any excess stain is flushed out of the salp. Molten agar, previously prepared, is then quickly injected into the body cavity of the salp via the oral aperture, using a warmed glass pipette. As the molten agar comes into contact with the colder water it sets, forming a plug that seals off the atrial aperture. More molten agar is then introduced, gradually inflating the animal until the body cavity becomes filled with solidified agar. Any excess agar protruding from the oral and atrial apertures is removed with a sharp scalpel and the stained reconstituted salp is transferred to neutral 5% formalin which in addition to acting as a preservative, prevents the growth of bacteria on the agar. Methylene Blue (Yount, 1954) can be used to differentiate details of the test (Foxton, 1961).

Individuals treated in this way provide a three-dimensional representation of the animal as in life (Foxton, 1971), so that in this stage the musculature is revealed in detail and the arrangement of oral and atrial muscles can be traced with ease (Foxton, 1965).

A low power steromicroscope is adequate to see the structure of individual bands, and except in very small specimens it is possible to count the number of constituent fibres in each muscle (Foxton, 1971).

2. APPENDICULARIANS (Fenaux, 1976b)

Formaldehyde (2 per cent) is a good fixative when diluted with sea-water. With Appendicularians it seems to make little difference whether the formaldehyde has been neutralized or not. Generally, determination of the species may be completed with specimens fixed in formaldehyde, but where the specimens are in poor condition or where advanced sexual maturity hides an important part of the digestive tract, staining with borax carmine followed by dehydration and clearing in methyl salicylate, will improve the clarity of the specimen.

The following technique (Fenaux, 1971) gives good results for the study of the oikoplastic epithelium. Fix the animals in 2 per cent formaldehyde in seawater or Carnoy's fluid. Treat in toto by the Feulgen method. After dehydration transfer to and keep in methyl salicytate. The hardening which follows this permits dissection of areas or cells, using tungsten needles. Parts to be studied may be mounted under a cover slip after direct passage from the methyl salicylate to Canada balsm.

Photography of living animals is made more readily with the aid of a microcompressor which keeps the animal still. Photographs of fixed material are greatly improved if the animals are stained for several minutes in Janus Green solution at 1:10,000. The cuticle becomes blue-gree and the internal organs and the muscles become red, improving the contrast of black and white photographs, and the subject is also suitable for colour photography (Fenaux, 1967).

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