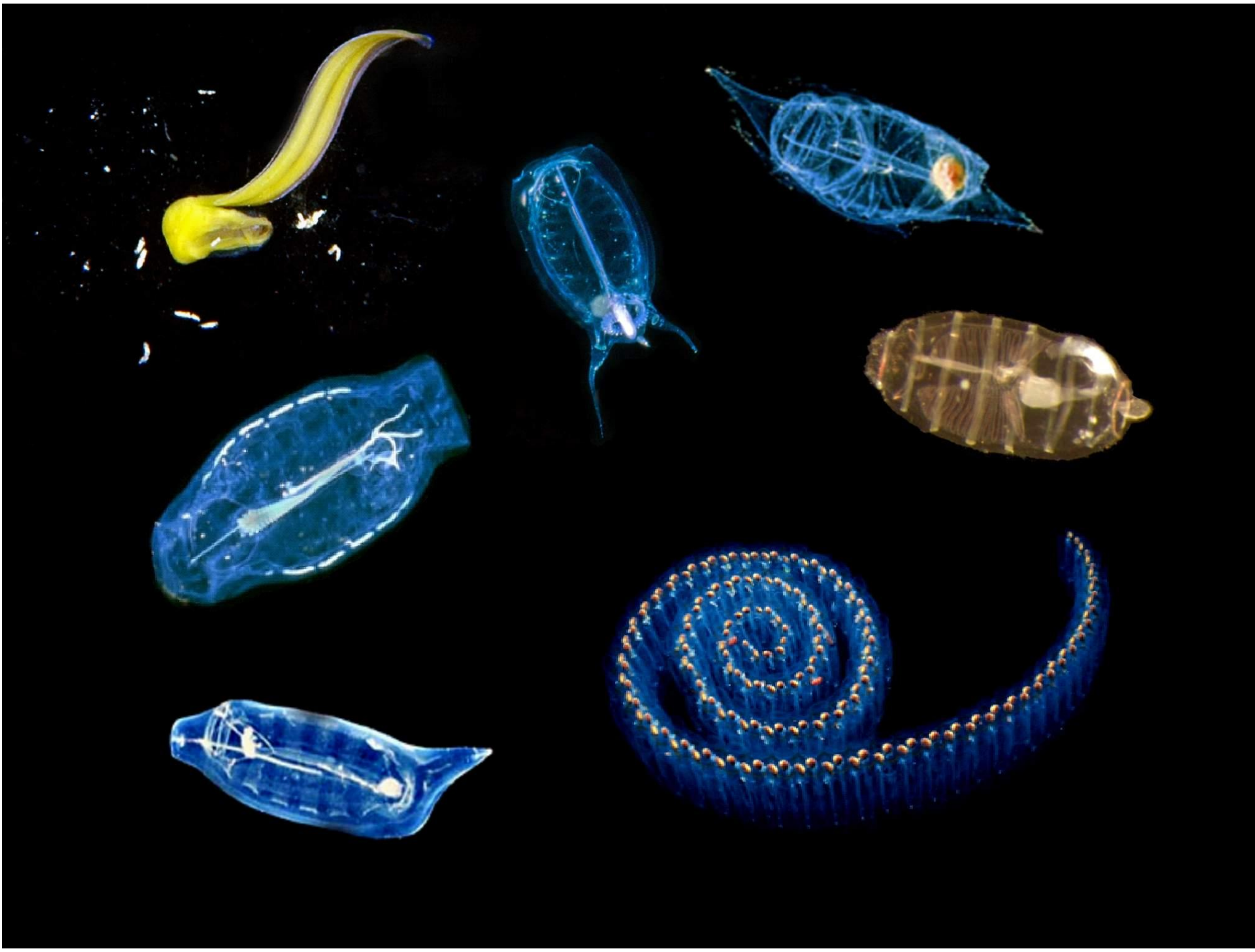

BOOK 13: THE PELAGIC TUNICATES

The intent of this report is to be used as a field guide for the identification of midwater invertebrates of South-eastern Australia. It is envisioned that this report will lead to further editions as a published field guide; comments toward improving the presentation and usability are appreciated. **This work was supported by CSIRO Wealth from Oceans Flagship.**

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http://zoobank.org/References/9A9676DD-F5AB-42D6-8349-3B1D93D7A47A

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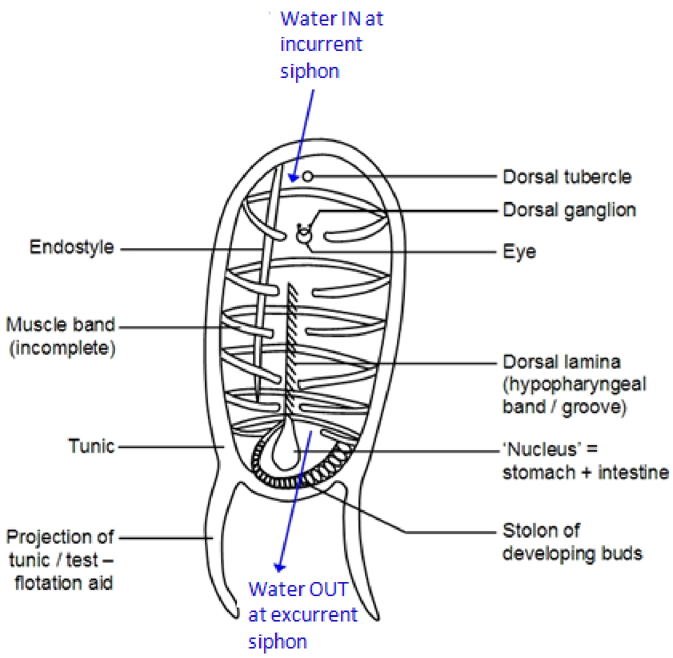
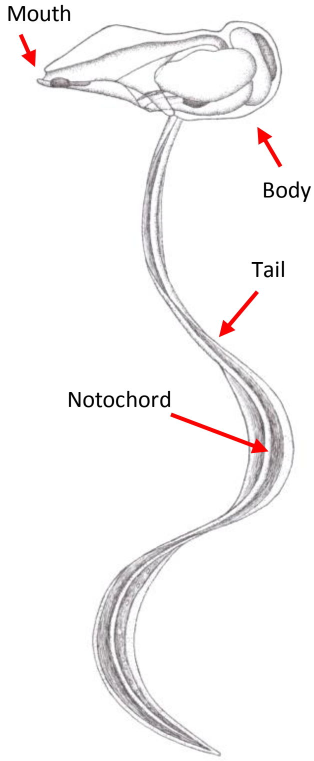
Cover montage

Clockwise, from upper left: *Oikopleura* sp. (copyright Guido & Philippe Poppe), *Thalia democratica* (copyright David Wrobel), *Salpa fusiformis* (copyright David Wrobel), *Doliolum denticulatum* (copyright L. Gershwin), *Pegea confoederata* (copyright Richard Herrmann), *Soestia zonaria* (copyright David Wrobel), *Cyclosalpa bakeri* (copyright David Wrobel).

GENERAL INFORMATION ABOUT THE PELAGIC TUNICATES



Salp anatomy – copyright http://cronodon.com/BioTech/Urochordates.html



Larvacean anatomy – redrawn from Alldredge, 1976

Tunicates as a group can be best described as pre-vertebrate in their grade of development. Their name, Tunicata, is derived from a unique cellulose-containing integumentary tissue (the 'tunic') that covers the epidermis. The tunicates are classified in the sub-phylum Urochordata; like all chordates they have a larval notochord. Even though they look like jellyfish, they are more closely related to us (humans) than to jellyfish. Most tunicates are benthic and resemble sponges; however, some are holopelagic, that is, they spend their entire life in the water column. These are the focus of this guide, the appendicularians, doliolids, pyrosomes, and salps.

The appendicularians (also called 'larvaceans') belong to the Class Appendicularia; these are tiny tadpole-shaped organisms that create a disposable mucous house for feeding. Their body consists of a short oval trunk and a broad, flat tail. Sitting in or under their house that is many times their own size, the animal undulates its tail to create a feeding current through the windows in the house. Discarded houses provide an important substrate and food source of planktonic debris known as 'marine snow'. Appendicularians are hermaphrodites.

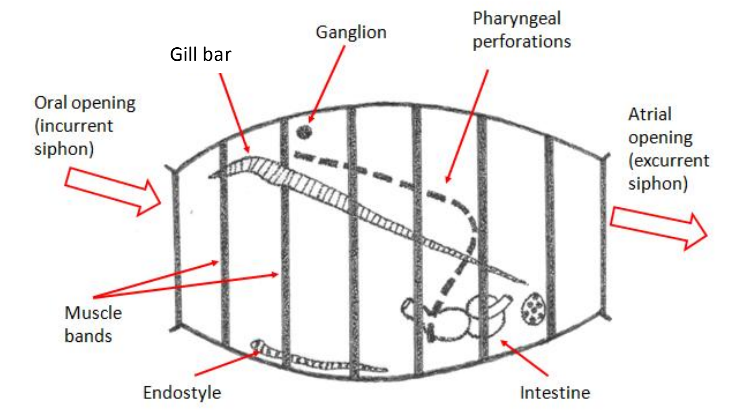
The salps belong to the Class Thaliacea and Order Salpida. In general, salps look like transparent gelatinous barrels encircled with numerous strong muscle bands: water is pumped in one end (the incurrent siphon) and out the other (the excurrent siphon), providing both a feeding current over a mucous net and jet propulsion. The internal body organs include a ciliated gill bar for driving the mucous net toward the oesophagus and a tight compact ‘nucleus’ near the posterior end of the body that contains the guts and gonads.

Salps feed with the aid of the mucous net to capture tiny particles. They are mostly herbivores, feeding on vast quantities of phytoplankton. Salps are easy prey for pelagic snails such as heteropods, jellyfish, sea turtles, sea birds, and many types of fish. They also provide travelling homes for hyperiid amphipods, pelagic octopus, and some species of fish.

Salps have a complex life cycle that alternates between solitary and aggregate generations. The solitary individual (or oozooid) develops a stolon that elongates with asexually developing aggregates. The aggregates (or blastozooids, which bear sexual gonozooids) are sequentially hermaphroditic: young females are fertilised by older males from other chains.

Thaliaceans get their name from their propensity to proliferate rapidly when environmental conditions are favourable (thalia means ‘blooming’ in Greek). Some salps are able to grow at the extraordinary rate of more than 10% of their body length per hour, and can complete an entire generation in a matter of hours (Heron, 1972a). These blooms exploit short-lived bursts of phytoplankton productivity, exerting tremendous pressure on the ecosystem. These massive aggregations may span hundreds of kilometres and interfere with human enterprise such as clogging up fishing nets and cooling water intake pipes of power plants.

Closely related to the salps the pyrosomes (Order Pyrosomatida) and doliolids (Order Doliolida). Doliolids look like tiny salps with a transparent, barrel-shaped body (see diagram). Pyrosomes are colonial forms, with the zooids encased in a tubular gelatinous matrix that is closed at one end: the zooids pump water in from the outside and funnel it into the common space inside the tube, providing jet propulsion for the whole colony. Pyrosomes are among the sea’s most brightly luminescent organisms: a point-source of stimulation will propagate through the colony in waves.



Doliolid anatomy

Pelagic tunicates are of great interest to marine biologists for two primary reasons. First, they are good indicators of different types of water masses and act as early warning systems for changing water chemistry. Second, they play an important role in carbon recycling and sequestration.

Only recently the phylogeny of the Thaliacea has been studied based on molecular sequences (Govindarajan, 2011). Most of the lineages interpreted through conventional taxonomy were mirrored in the molecular data, the notable exceptions being that the *Cyclosalpa* are nested within the Salpidae and that *Iasis* (*Weelia*) is distinct from the genus *Salpa*. The pyrosomes appear to be the sister group to the salps and doliolids. Currently at least 22 appendicularians and 26 species of thaliaceans and are known from Australian waters; most are cosmopolitan and none are endemic.

Species of appendicularians are distinguished based on body shape and characteristics of the endostyle, pharyngeal perforations, stomach wall, oikoplast epithelium, and tail. These characteristics are beyond the scope of this guide, so these species are treated at the family level.

Species recognition of thaliaceans is based on the number and arrangement of muscle bands that encircle the body: the muscle bands are counted starting at the oral opening (i.e., away from the visceral nucleus) and usually expressed as MI – MVII or as applicable. For the most part, salps are easy to tell apart and all are treated herein. Definitive identification of some species requires counts of the muscle fibres, which are beyond the scope of this guide.

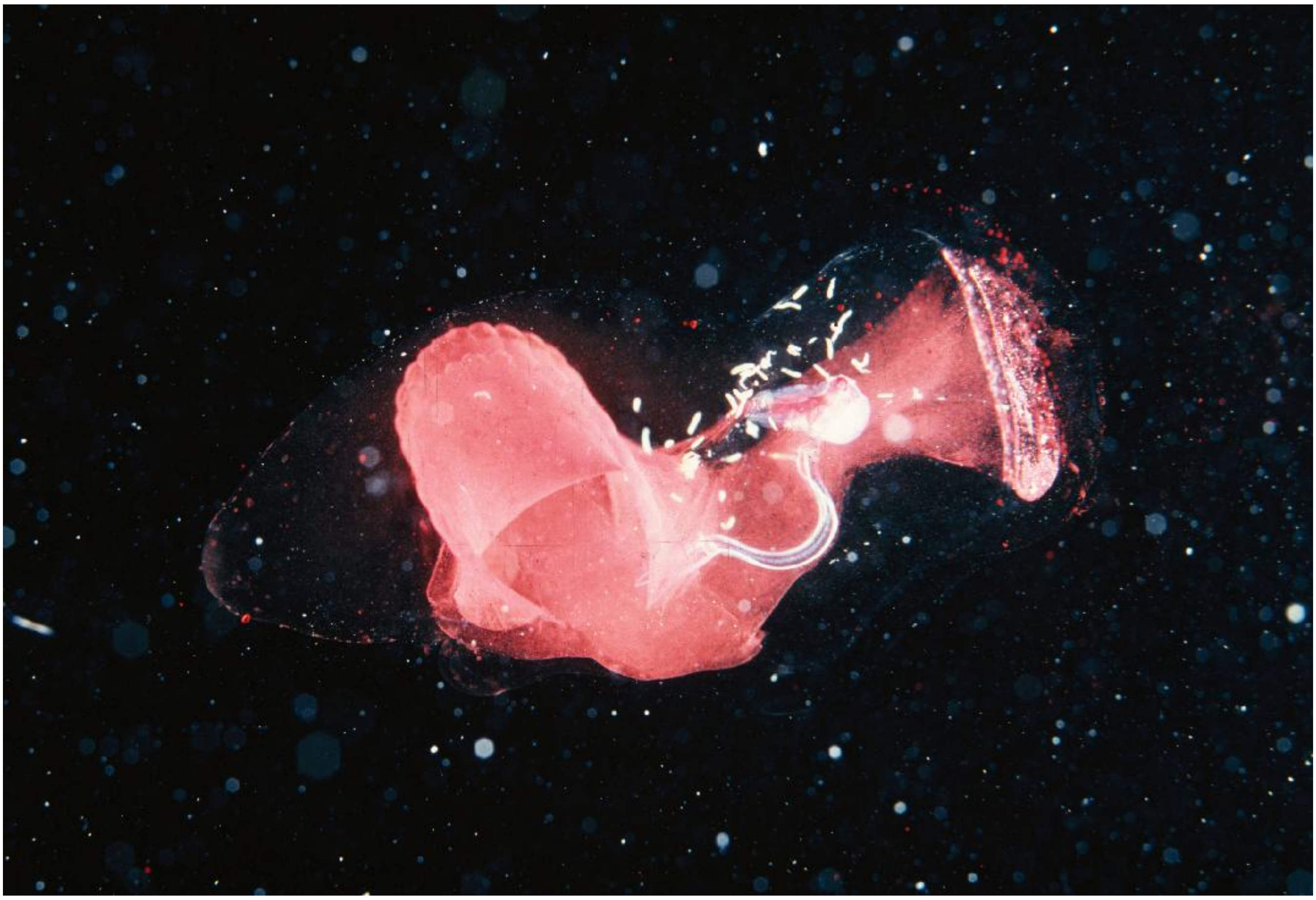
ANNOTATED CLASSIFICATION

PHYLUM CHORDATA: SUBPHYLUM TUNICATA

Traustedtia: body globular with numerous projections; 5 muscle bands lacking ventrally 22
Csirosalpa: body globular; 4 muscles; nucleus horizontal, with long ‘tentacle’ 23

The best identification resources for pelagic tunicates include the following:

- Bone, Q. 1998. The Biology of Pelagic Tunicates, Oxford University Press.
- Godeaux, J. E. A. 2003. History and revised classification of the order *Cyclomyaria* (Tunicata, Thaliacea, Doliolida). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 73: 191–222.
- Kim, S., J.-H. Won and C.-B. Kim. 2012. Taxonomic Study of Genus *Cyclosalpa* (Thaliacea: Salpida: Salpidae) from Korea. *Animal Systematics, Evolution and Diversity* 28(4): 261-268.
- O'Sullivan, D. 1983. A guide to the Pelagic Tunicates of the Southern Ocean and adjacent waters. Kingston, Tasmania, Antarctic Division.
- Thompson, H. 1948. Pelagic Tunicates of Australia. Melbourne, Council for Scientific and Industrial Research.
- Wrobel, D. Jellies Zone. http://jellieszone.com/

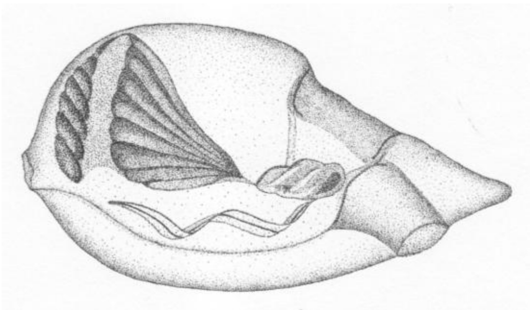


Megalocercus (the whitish tadpole-like creature in the centre) inside its mucous house. This photo was taken by using carmine dye. This particulate dye was filtered into the house as if it was phytoplankton to help make the house show up better. Image copyright Alice Alldredge.

CHORDATA: TUNICATA: APPENDICULARIA: OIKOPLEURIDAE – The Larvaceans

Oikopleura Coecaria longicauda Vogt, 1854 CAAB 35 2030xx
O. Coecaria cornutogastra Aida, 1907
O. Coecaria fusiformis Fol, 1872
O. Coecaria intermedia Lohmann, 1896
O. Vexillaria albicans (Leuckart, 1853)
O. Vexillaria cophocerca (Gegenbaur, 1855)
O. Vexillaria doica Fol, 1872
O. Vexillaria parva Lohmann, 1896
O. Vexillaria rufescens Fol, 1872
Megalocercus huxleyi Ritter, 1905
Stegosoma magnum (Langerhans, 1880)
Althoffia tumida Lohmann, 1892
Bathochordeus charon Chun, 1900

Oikopleura sp. – Copyright David Wrobel



Oikopleura in house – redrawn from Emily Damstra

FIELD MORPHOLOGY: The oikopleurids are small, inconspicuous, tadpole-shaped organisms, with a 1mm oval-shaped trunk and tail that is 3 to 4 times the length of the body. The tail is thin and never indented at the tip. Overall, the animal resembles a sperm cell.

MAY BE CONFUSED WITH: Fritillariidae: see comparative notes therein.

NOTES: With the exception of *Bathochordeus*, which is huge (~7cm) in comparison to the others, the oikopleurids are unlikely to be recognised in a typical midwater sample because of their small size.

Appendicularians (also called larvaceans) secrete mucus from a special gland to make a feeding net (called a 'house'); the organism sits inside the house, producing water currents with undulations of the tail, thus filtering food particles. When the house becomes clogged with particles, it is discarded and a new one is built; more than 10 houses may be built in a day, depending upon feeding conditions.

Larvaceans develop rapidly and have a short generation time; these features make them able to quickly produce dense blooms. As discussed in the Introduction, discarded appendicularian houses slowly drift toward the seafloor as 'marine snow'. These houses serve as substrate for midwater microbes and as an important source of food for other zooplankton.

Keys to the species of Larvaceans may be found in: Fenaux, R. 1998. The classification of Appendicularia. The biology of pelagic tunicates. Q. Bone. Oxford, Oxford University Press: 295-306.

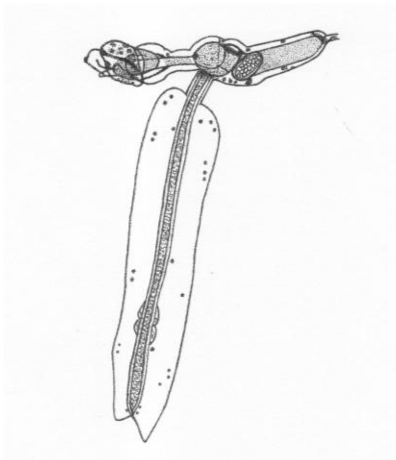
CHORDATA: TUNICATA: APPENDICULARIA: FRITILLARIDAE – The Larvaceans

Fritillaria bicornis Lohmann, 1896 (= *F. venusta*) CAAB 35 2010xx
Fritillaria borealis Lohmann, 1896
Fritillaria formica Fol, 1872
Fritillaria fraudax Lohmann, 1896
Fritillaria haplostoma Fol, 1872
Fritillaria megachile Fol, 1872
Fritillaria pellucida (Busch, 1851)
Tectillaria fertilis (Lohmann, 1896)
**Kowalevskaia tenuis* Fol, 1872

Fritillaria borealis -- Copyright Russ Hopcroft.

*Note that *Kowalevskia tenuis* is in the family Kowalevskiidae.

FIELD MORPHOLOGY: Less than 5mm total length, usually more on the order of 1-2mm. Body elongated or flattened dorso-ventrally; tail short and broad, indented in median part of front edge in some species.


Fritillaria sp. – redrawn from TAFI

MAY BE CONFUSED WITH: The three main groups of larvaceans look similar to each other, and in turn all look similar to the familiar tadpole (i.e., larval frog). The three main groups differ as follows:

- <u>Oikopleuriidae</u>: The body is oval and on the same axis as the tail.
- <u>Fritillariidae</u>: The body is dorsoventrally compressed or spindle-shaped, and the tail is orientated at a right angle to the body.
- <u>Kowalevskiidae</u>: The body is short and the tail is fusiform or spindle-shaped in outline.

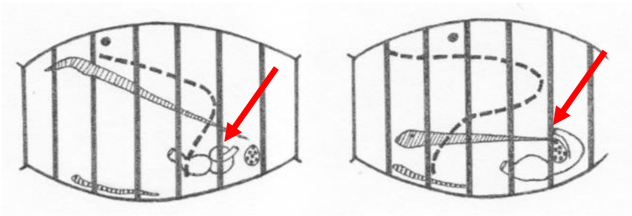
NOTES: As with most other appendicularians, the fritillarids are unlikely to be recognised in a standard midwater sample due to their small size (typically about 1mm). However, they can at times be extremely common and comprise an important part of the food web, both as living organisms and in their contribution to the marine snow by their discarded mucous houses.

In its normal undisturbed drifting mode, *Fritillaria* sits below the house, whereas *Oikopleura* sits within the house.

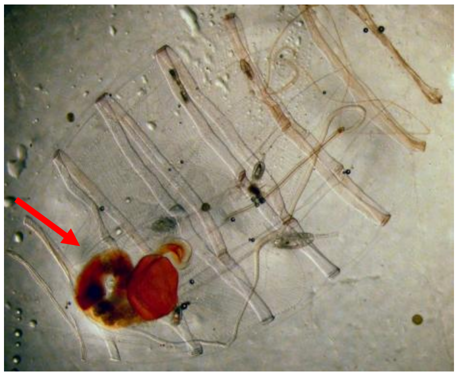
Fritillaria pellucida is by far the commonest fritillarid in SE Australian waters.

CHORDATA: TUNICATA: THALIACEA: DOLIOLIDAE – The Doliolids

Dolioletta gegenbauri (Uljanin, 1884) CAAB 35 102001
Doliolum denticulatum Quoy & Gaimard, 1834 CAAB 35 102002



Dolioletta gegenbauri *Doliolum denticulatum*
Redrawn from Fraser 1947



Dolioletta gegenbauri – Note coiled intestine. Copyright Moira Galbraith DFO Canada – Creative Commons: http://www. marinespecies.org/aphia.php?p=image&id=3

Doliolum dentaculatum – Copyright L. Gershwin. Note the arched intestine (arrow).

FIELD MORPHOLOGY: Doliolids are small (less than 2cm), transparent and inconspicuous, thin and delicate, free swimming organisms with a barrel-shaped body that is open at both ends. The body has 8 or 9 complete muscle rings encircling the body, which are parallel throughout. Several life stages look different, which can frustrate identification; the gonozooid is the most often found.

Dolioletta: Gonozooids: Intestine forming a close dextral coil; up to 12mm long.
Doliolum: Gonozooids: Intestine forms a dextral arch; up to 10mm long.

MAY BE CONFUSED WITH: Doliolids strongly resemble salps in their generally barrel-shaped body, but are distinguished in being generally much smaller and in the muscle bands being full rings and not converging.

NOTES: Doliolids are typically found in the euphotic zone of tropical and temperate shelf waters around the world. Both *Doliolum* and *Dolioletta* are common in SE Australian waters. They have the most complex life history of any thaliacean, with up to six distinct body forms among two life stages.

Like pyrosomes, doliolids move and feed by means of ciliary currents pumping water into the body, through a mucous feeding filter, and then passing out of the body. Unlike salps, which must contract the body wall to swim and feed, doliolids generally only contract the body wall for rapid escape.

When algal food is plentiful, a single oozooid can produce thousands of gonozooids within a few days; in these conditions, there may be up to 500 individuals per cubic metre of water.

CHORDATA: TUNICATA: THALIACEA: PYROSOMATIDAE – The Pyrosomes

Pyrosoma atlanticum Péron, 1804 CAAB 35 101001
Pyrostremma spinosum (Herdman, 1888) CAAB 35 101002

FIELD MORPHOLOGY: Free-swimming tubular colonies of hundreds to thousands of zooids embedded in a common gelatinous, semi-transparent, tube-shaped test, open at the posterior end, closed at the anterior. The zooids are arranged with their branchial apertures (incurrent siphons) to the outside of the tube, and their atrial apertures (excurrent siphons) to the inside, giving the colony outstanding jet propulsion via collective excurrent siphoning.

Two species are known in Australian waters: *Pyrosoma atlanticum* which has a firm cartilaginous test, and *Pyrostremma spinosum*, in which the test is soft and easily fragments.

MAY BE CONFUSED WITH: There is nothing that the pyrosomes could be confused with that naturally occurs in the pelagic realm.

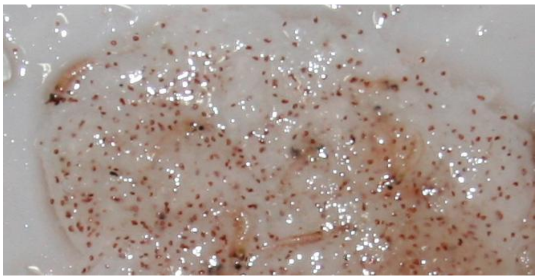
NOTES: Pyrosomes are generally associated with tropical and warm temperate waters, and are generally found in epipelagic or upper mesopelagic layers.

Pyrostremma spinosum can reach truly gigantic dimensions, found periodically in the Tasman Sea in colonies up to 20m long and 2m wide, large enough for a diver to swim through (Griffin and Yaldwyn, 1970; Baker, 1971).

The bioluminescence of pyrosomes is among the most vivid and brilliant of any organism in the ocean, with waves of beautiful blue light undulating through the colony and visible from many metres underwater.

P. atlanticum - Copyright David Wrobel

Pyrosoma atlanticum – 2009 Rehua - Midoc 2, net 4



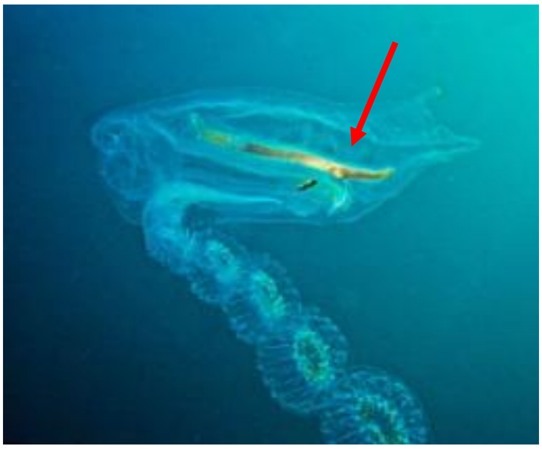
Pyrostremma spinosum – SS2011 TO2 OP47, MIDOC7

P. spinosum – Copyright Mick Baron, Eaglehawk Neck Dive Centre, available on YouTube

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: CYCLOSALPINAE – The Salps

Cyclosalpa affinis (Chamisso, 1819)	CAAB35 103001	*Cyclosalpa polae* Sigl, 1912	35 103004
Cyclosalpa bakeri Ritter, 1905	35 103002	*Helicosalpa virgula* (Vogt, 1854)	35 103006
Cyclosalpa floridana (Apstein, 1894)	35 103003		

Cyclosalpa sp. – ss2011_to2– Copyright Briony Hutton



C. affinis - Copyright David Wrobel

C. affinis - Copyright David Wrobel

Cyclosalpa sp. – ss2011 Copyright Mailie Gall

FIELD MORPHOLOGY: The test is soft, smooth, and lacking serrations or projections, except in the aggregates of *Helicosalpa*, which are firm and smooth, with a posterior-pointing projection. The taxonomy of *Cyclosalpa* was recently reviewed by Kim et al. (2012).

Solitary form: The gut mass is long and straight rather than coiled into a tight nucleus; the 7 body muscles form almost complete loops, with luminous organs on or between some of the bands. Body length: both genera to about 15cm, depending on species (e.g., *C. floridana* reaches 12mm).

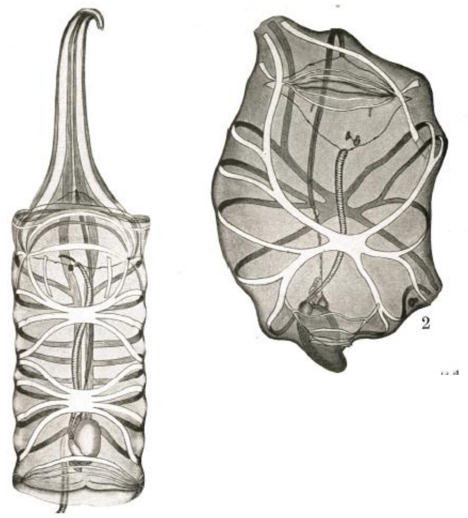
Aggregate form: The two genera differ in the form of the aggregates, with *Cyclosalpa* zooids are bilateral and arranged radially into whorls of up to 15 individuals (length to 10cm), and *Helicosalpa* zooids are asymmetrical and arranged in chains without an attachment peduncle (length to 3.5cm).

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Brooksia rostrata (Traustedt, 1893) CAAB 35 103007

FIELD MORPHOLOGY: The solitary form is immediately distinguishable from all other salps by the presence of a conspicuous anterior rostrum.

- Solitary form: Body elongate, cylindrical, with prominent anterior projection. Test soft. Muscles 7, joining mid-dorsally; arranged in two groups MI-MIII and MIV-MVII; MIII and MIV approach laterally; two ventral muscles run longitudinally to the tip of the rostrum. Length, including projection, up to 60mm.
- Aggregate form: Test thin and loose, often lost. Body oval to globular. Musculature strongly asymmetrical, separating zooids into dextral (four body muscles on the right and three on the left) and sinistral (vice versa) individuals. All body muscles are continuous dorsally and ventrally.



Brooksia rostrata – Copyright CSIRO 1948
Left, solitary form; right, aggregate form

MAY BE CONFUSED WITH: The solitary form is utterly distinctive with the long rostrum. The strongly asymmetrical aggregate zooid is similar to that of *Helicosalpa virgula*, but *Helocosalpa* has only 4 body muscles and they are hard to distinguish, whereas *Brooksia* has 7 that are easier to identify.

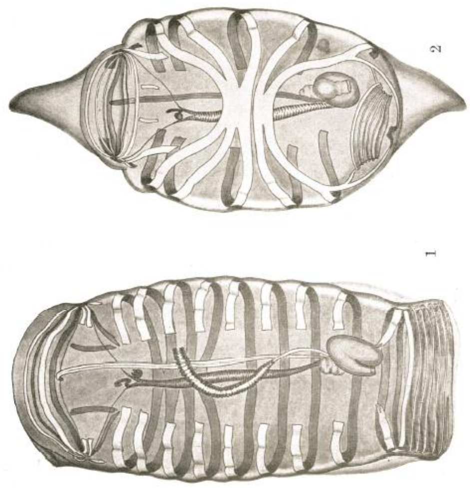
NOTES: *Brooksia rostrata* is a rare species about which little is known. It is easily overlooked, particularly the aggregate stage during dense salp blooms such as those seen with *Thalia democratica*. *Brooksia rostrata* is generally found in warm tropical waters along with its congener *B. berneri*, with which it is easily confused (note that *B. berneri* has not yet been reported from SE Australian waters). The morphology of *Brooksia* was reviewed by van Soest (1975a).

A distribution study during non-bloom conditions near Bermuda found that *Brooksia rostrata* was consistently present above 30m in relatively high numbers in the afternoon, compared to deeper net sampling and morning and nighttime dives where it was poorly represented, suggesting a strong vertical migration pattern (Madin et al., 1996). It was also considerably more common in the spring than in the autumn.

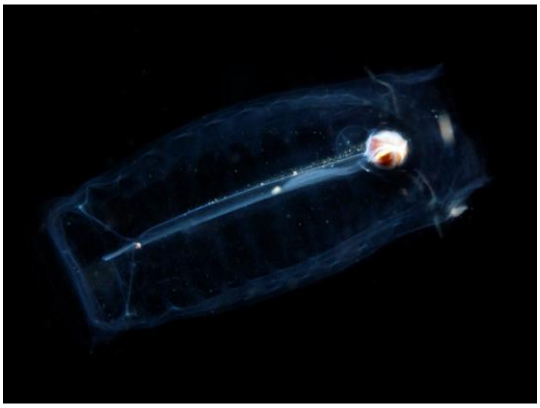
In SE Australian waters, *Brooksia* is strongly associated with offshore sub-tropical surface waters to the extent that its blooms actually track the seasonal southerly shift of sub-tropical conditions (Thompson, 1948). It peaks in abundance in tropical Queensland waters in December and May (Russell and Colman, 1935).

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Iasis cylindrica (Cuvier, 1804) CAAB 35 103008



Iasis cylindrica – Copyright CSIRO 1948
Top, aggregate form; bottom, solitary form



Iasis cylindrica, solitary form – ©2013 Guido & Philippe Poppe - www.poppe-images.com

FIELD MORPHOLOGY: Solitary form: Body elongate, cylindrical, soft, rounded in front, cut off squarely in back. Body muscles 9 dorsally, with MI – MIV fused mid-dorsally, all far apart ventrally. Small, spherical gut mass is at the posterior end. Length to 45mm.

Aggregate form: Body fusiform with short, conical anterior and posterior projections. Body muscles 5, all meeting mid-dorsally. Length to 17mm.

MAY BE CONFUSED WITH: Species in the genera *Ritteriella*, *Soestia* and *Iasis* were long grouped in the genus *Salpa*, and indeed, the life stages in these genera are similar. However, the genera *Iasis*, *Ritteriella*, *Salpa*, and *Soestia* have distinctive muscle banding patterns.

NOTES: *Iasis cylindrica* is the only species in the genus, and it is variously placed in its junior synonym *Weelia* or the closely related genus *Salpa*.

Iasis is widespread but not common. It is found in epipelagic waters of the three great oceans, as far north as the Bering Sea and as far south as the Cape of Good Hope.

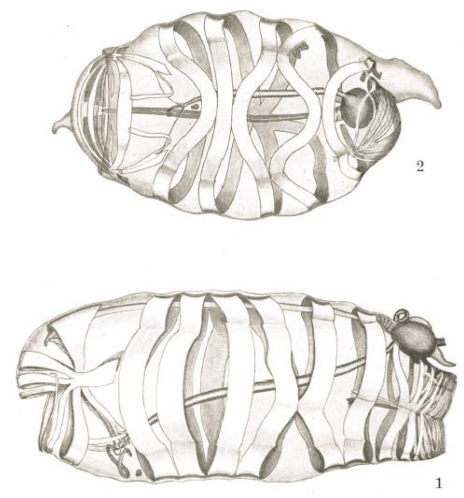
Off SE Australia, the *Warreen* expedition found it to be fairly common, with more than 1000 specimens taken at 19 stations. It is present in more or less equal quantities throughout the year, but tends to be commoner in southern Queensland and northern New South Wales than in colder, more southern waters.

Curiously, species of ctenophores in the genus *Lampea* depend on particular salps as their primary food source; for example, *L. lactea* is a highly specific parasite and predator on *I. cylindrica* (Harbison, 1998).

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Ihlea magalhanica (Apstein, 1894) CAAB 35 103009

FIELD MORPHOLOGY: Test thin and flabby. Aggregates arranged on opposite sides of the stolon are mirror images of each other with asymmetrical muscle banding.



Ihlea magalhanica – Copyright CSIRO 1948
Top, aggregate form; bottom, solitary form

Solitary form: Body elongate and cylindrical to barrel-shaped, inflated from muscles I-IV, noticeably reduced in diameter posterior to muscle IV. Body muscles 7, very broad, mostly continuous around body; MI-MIV pinched together at the dorsal midline; MV bends toward MVI; MIV-MV are interrupted ventrally and converge laterally. Length to 35mm.

Aggregate form: Body barrel-shaped like the doliolids, but with a gelatinous projection on one end and a slit-like opening on the other. Body muscles 5, continuous dorsally, interrupted ventrally; MIII-MIV continuous laterally on one side or the other depending on asymmetry; MII-MIII fused with MIV ventrally. Length to 15mm.

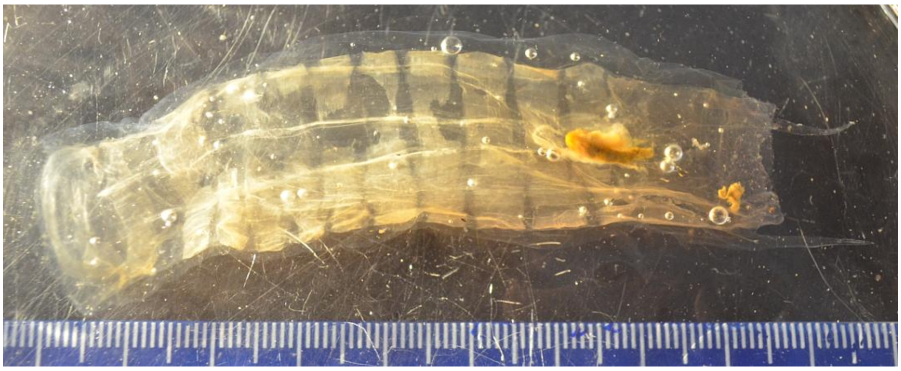
MAY BE CONFUSED WITH: The reduced posterior diameter and broad muscle bands make this species distinctive.

NOTES: Despite being typically regarded as rare, this was by far the commonest salp after *Thalia democratica* in south-eastern Australian samples from the *Warreen* survey, with over 130,000 specimens collected from 52 stations between 1938-1941 (Thompson, 1948). In fact, off Tasmania, *Ihlea* even surpassed *Thalia* in density, leading Thompson to conclude that it is a cold-water form and might be useful as an indicator of southern water masses. Here, *Ihlea* was found almost entirely in the top 50m of the water column, with its maximum numbers between October and February.

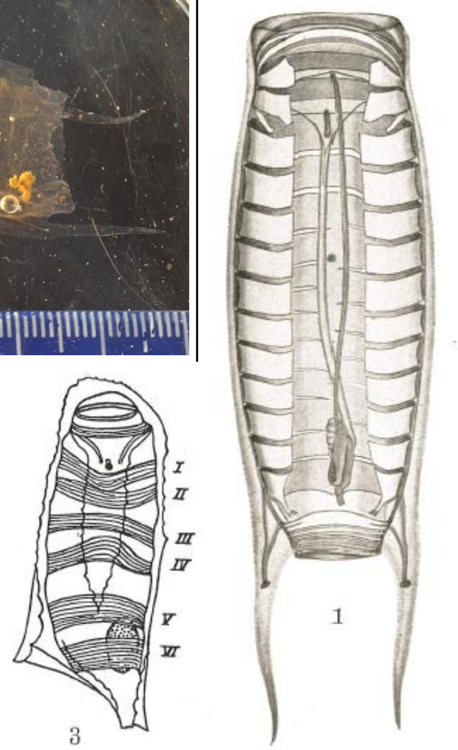
However, in contrast, New Zealand studies have demonstrated fairly conclusively that *Ihlea* is in fact a warm water species rather than a cold-water species (Bary, 1960). The salinity and temperature profiles coinciding with its occurrence led the author to conclude that *Ihlea* is associated with and indicative of water of subtropical origin. Foxton (1971), however, concluded that the species is circumpolar and generally associated with the subtropical convergence in a narrow range from 34-44°S in the Atlantic sector, from 39-49°S in the Australia-New Zealand sector, and as far north as Valparaiso, Chile in the Pacific sector. The closely related *I. racovitzai* is truly Antarctic and does not occur north of the Antarctic convergence.

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Metcalfina hexagona (Quoy & Gaimard, 1824) CAAB 35 103010



Metcalfina hexagona, solitary form – Copyright L. Gershwin/SPC



Metcalfina hexagona – Copyright CSIRO 1948
Left, aggregate form; right, solitary form

FIELD MORPHOLOGY: Solitary form: Body cylindrical and firm, somewhat wider in the middle, with finely denticulated longitudinal ridges; with a straight anterior edge and two long posterior processes. Muscle bands broad, variable in number (usually 9-12), widely interrupted ventrally. Body to 160mm, not including processes; more often to about 45mm.

Aggregate form: Body very firm, strongly asymmetrical, with an angular protuberance on one side of posterior end. Body muscles 6, broad and strong, widely interrupted ventrally. Length to about 30mm.

MAY BE CONFUSED WITH: The solitary stage might be confused with that of *Thetys*, as both grow very large and have two posterior 'tails'. However, the 9-12 broad muscle bands of *Metcalfina* compared to the 16-22 fine bands of *Thetys* should help to readily separate the two species.

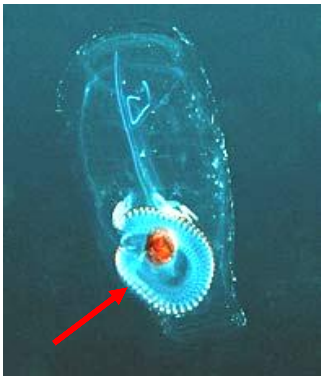
NOTES: While other salp genera are distributed over the warmer and temperate parts of the three great oceans, *Metcalfina* is exceptional in being confined to the warmer waters of the Indo-Pacific. Indeed, van Soest (1975b) described *Metcalfina* as an 'extremely stenothermous' species (i.e., capable of thriving only within a limited temperature range); its lowest temperature limit is 25°C. Paradoxically, it is typically found in deeper waters and was taken by the *Warreen* in the wintertime down to 200m.

Thompson (1948) reported that *Metcalfina* was one of the rarest forms of all in his extensive sampling from 1938-1941, and was only taken at times when other species were less abundant. However, Hereu et al. (2010) found that sometimes the abundance of *Metcalfina* (49%) surpassed even that of *Thalia democratica* in dominance in the Mexican Pacific.

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Pegea confoederata (Forskål, 1775) CAAB 35 103011

FIELD MORPHOLOGY: Test smooth, thick, not very firm. Both solitary and aggregate have only four body muscles which form into two X-shaped groups; the muscles only cover the dorsal surface of the body.

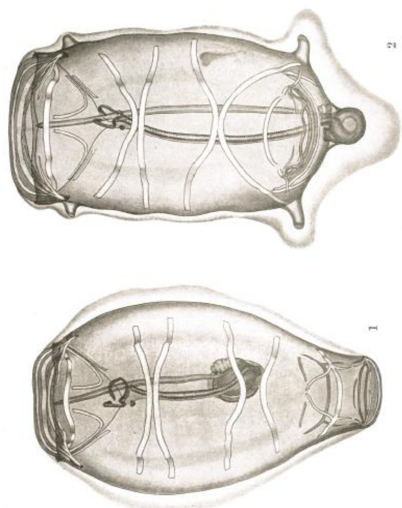


P. confoederata, solitary - ©2013 Guido & Philippe Poppe - www.poppe-images.com

P. confoederata, aggregate - Copyright David Wrobel

Solitary form: Highly distinctive with the developing stolon coiled flatly around the gut mass. Body barrel-shaped, to 14cm long.

Aggregate form: The chain forms in a tight spiral of two rows, with individuals at right angles to the main axis of the chain, like cans in a 6-pack of soda. Zooids are soft-bodied, cylindrical, to 12cm long.



Pegea confoederata – Copyright CSIRO 1948. Top, aggregate; bottom, solitary

MAY BE CONFUSED WITH: The flat coiled stolon of the solitary form and the spiral of the aggregate make *Pegea* unlikely to be mistaken for other species.

NOTES: This species is quite rare in SE Australian waters, whereas it can be quite common in the tropics.

Species of *Pegea*, including *P. confoederata*, are sometimes found with the octopod *Argonauta* (Paper Nautilus) living inside the body cavity (Harbison, 1998); this association is believed to be for feeding and shelter.

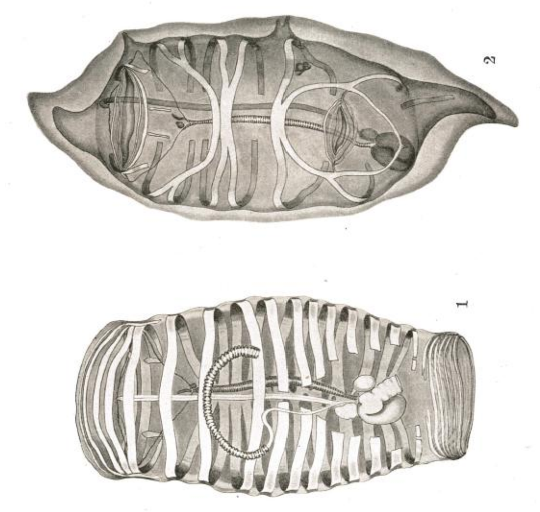
Copepods of the genus *Sapphirina* are often found in association with salps, particularly *Pegea* and *Thalia* (Harbison, 1998).

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Ritteriella amboinensis (Apstein, 1904) CAAB 35 103012
Ritteriella retracta (Ritter, 1906) CAAB 35 103013

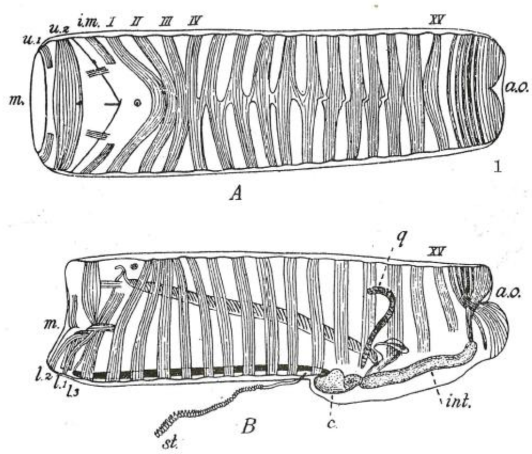
FIELD MORPHOLOGY: Solitary form: Body elongated, cylindrical or barrel-shaped, smooth, flabby and thin. Body muscles numerous and variable from 9 to 31, nearly parallel, and usually with ventral interruptions widening toward posterior end. Length to 35mm (*R. amboinensis*) or 60mm (*R. retracta*).

Aggregate form: Uncommonly encountered. Body soft, somewhat asymmetrical, cylindrical fusiform with anterior and posterior processes. Body muscles 6, asymmetrical, narrow, continuous dorsally but widely separated ventrally; 4 musclebands fused dorsally appear like 3. Length to about 40mm in both species.



Ritteriella amboinensis – Copyright CSIRO 1948
Top, aggregate form; bottom, solitary form

The two species differ as follows: SOL: *R. amboinensis* has 10-13 nearly parallel body muscles, usually 11, whereas *R. retracta* usually has 15-21 (even up to 26). AGG: of *R. amboinensis* resembles *Salpa maxima* (p. 17), whereas this stage of *R. retracta* resembles that of *Weelia cylindrica* (p. 22) but has much narrower muscle bands.



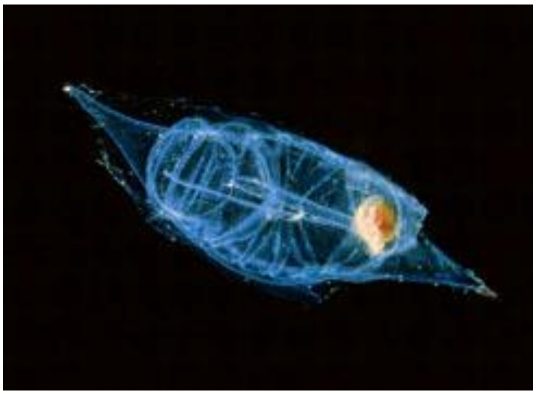
Ritteriella retracta – Copyright CSIRO 1948
Solitary form

MAY BE CONFUSED WITH: Species in the genera *Ritteriella* are quite similar to *Salpa*, *Soestia* and *Weelia*. The muscle banding patterns are distinctive among the four genera: the solitary form of *Ritteriella* has far more muscle bands than the others, and the aggregate form has the appearance of 3 dorsally fused muscle bands, whereas they are actually 4, as in *Salpa*.

NOTES: Three species are recognised in the genus, two of which are found in Australian waters. Both are relatively uncommon. Some authors have considered *R. retracta* to be a junior synonym of *R. picteti*, but van Soest (1974b) demonstrated sufficient morphological grounds for recognising *R. retracta* as a distinct species. Moreover, it appears from van Soest's same work that Indo-Pacific *R. retracta* may be further divided into two subspecies.

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

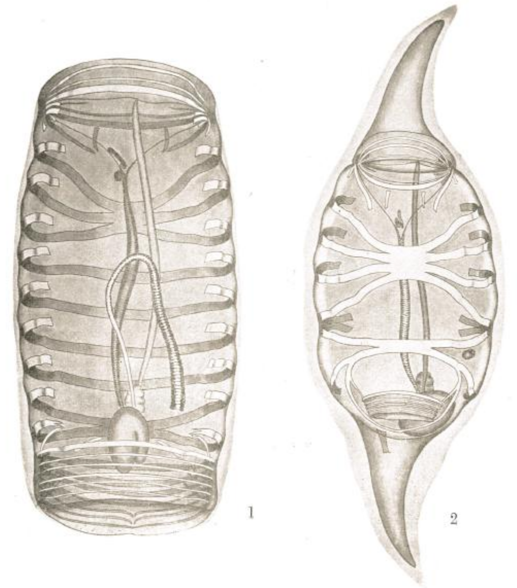
Salpa fusiformis Cuvier, 1804 CAAB 35 103014
Salpa maxima Forskål, 1775 CAAB 35 103015



Salpa fusiformis Copyright David Wrobel

FIELD MORPHOLOGY: Solitary form: The test is thick and firm, with longitudinal ridges. The body is elongated and cylindrical. Body muscles 9, only on the dorsal and lateral sides; ventral surface without muscles.

Aggregate form: Test thick and firm, with blunt or sharp ridges. Body fusiform with well developed anterior and posterior projections that taper to a narrow point. Body muscles 6, where MI-MIV and MV-MVI touch or fuse dorsally and MIV-MV approach or fuse laterally.



Salpa fusiformis – Copyright CSIRO 1948
Left, solitary form; right, aggregate form

***S. fusiformis**:* SOL: Test entirely smooth, of moderate thickness. Body muscles MI-MIII strongly fused, as are MVIII-MIX. Dorsal tubercle small and shallow, not causing swelling of the test. Length to 52mm. AGG: Anterior and posterior projections long and narrow; body muscles MI-MIV and MV-MVI strongly fused mid-dorsally, while MIV-MV between are fused laterally; length excluding projections to 52mm.
***S. maxima**:* SOL: Test extremely thick, smooth with shallow longitudinal depressions. All 9 body muscles parallel on dorsal side. Dorsal tubercle large, causing distinct ventral swelling of the test. Length to about 120mm. AGG: Anterior and posterior projections short and strongly abaxial; Body muscles MI-MII, MIII-MIV are fused dorsally, while MII-MIII and MV-MVI touch mid-dorsally and MIV-MV are widely separated laterally. Length excluding projections 90-150mm.

NOTES: *Salpa fusiformis* is among the most abundant salp species and has the widest distribution, from 70°N to 45°S worldwide. *S. maxima* is not uncommon in the tropical and subtropical world's oceans and seas.

Curiously, the sea urchin *Strongylocentrotus franciscanus* has been reported to switch its prey preference from macroalgae to *Salpa fusiformis* during times of salp blooms (Duggins, 1981).

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Soestia zonaria (Pallas, 1774) CAAB 35 103016

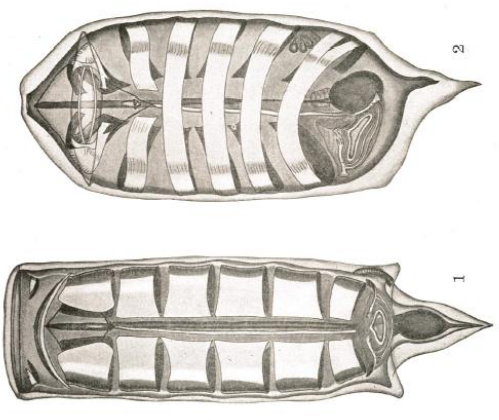

Soestia zonaria, solitary form, left; aggregate form, right - Copyright Mailie Gall

FIELD MORPHOLOGY: Characterised by wide muscle bands (6 in the solitary, 5 in the aggregate): <u>SOL</u>: all are interrupted both dorsally and ventrally; <u>AGG</u>: all but MI are continuous across the dorsal midline, and all are interrupted widely ventrally.

- <u>Solitary form</u>: The front of the body terminates squarely, the rear tapers to a point, with a small projection on each side near the base. Length to about 65mm.
- <u>Aggregate form</u>: General body shape elongate-oval with the back pressed flat; asymmetrical with a rear process lateral on the right side, and the front obliquely truncated. Length to 50mm.

MAY BE CONFUSED WITH: Species in the genera *Ritteriella*, *Soestia* and *Weelia* were long grouped in the genus *Salpa*, and indeed, the life stages in these genera are similar. However, the three other genera have front and back projections in the aggregate and no projections in the solitary form, and they have more and narrower muscle bands than *Soestia*.

Soestia zonaria, aggregate form above, solitary form below - Copyright L. Gershwin/SPC

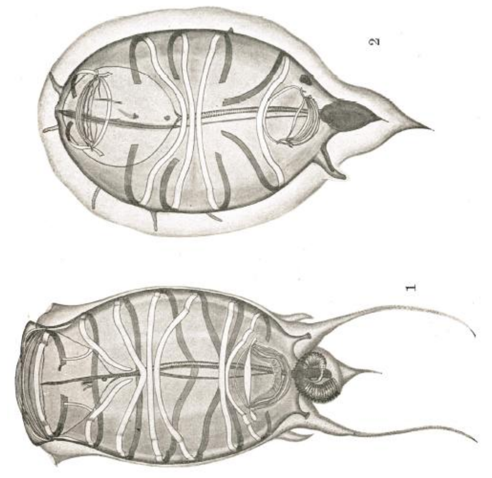


Soestia zonaria – copyright CSIRO 1948
Top, aggregate form; Bottom, solitary form

NOTES: The broad muscle bands serve to make this one of the most powerful swimmers amongst the salps.

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Thalia democratica (Forskål, 1775) CAAB 35 103018
Thalia longicauda (Quoy & Gaimard, 1824) CAAB 35 103019



Thalia democratica – copyright CSIRO 1948
Top, aggregate form; bottom, solitary form

FIELD MORPHOLOGY: *Thalia* is far and above the most abundant salp worldwide, and also one of the smallest.

Solitary form: Body barrel-shaped with a very thick test, with two long, slender tentacle-like processes on the posterior end and other pairs of smaller processes on the front and back. Five continuous body muscles converge into two groups in *T. democratica* (I-III and IV-V), or are dorsally parallel in *T. longicauda*. Length without processes to 12mm.

Aggregate form: Body oval, tapering to pointed or rounded posterior process. The test is thick, with both openings dorsal. Body muscles 4, continuous dorsally but broadly interrupted ventrally. Length to 12mm, more commonly 6mm.

Thalia democratica, solitary form – Copyright David Wrobel

MAY BE CONFUSED WITH: *Thalia* is fairly distinctive and generally occurs in vast swarms, making it difficult to overlook or confuse.

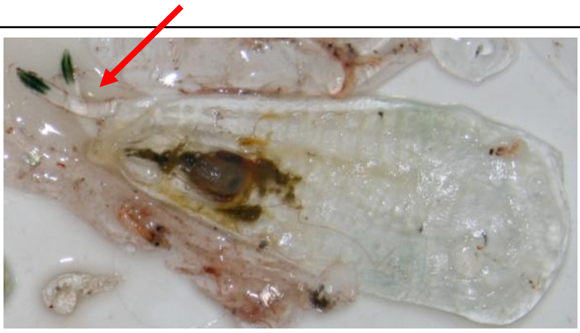
NOTES: *Thalia democratica* is very widely distributed in tropical and temperate seas, where it often occurs in enormous swarms. One such swarm off southern California extended over 9000km^2 and contained billions of individuals (Berner, 1967; Lavaniegos and Ohman, 2003). In 2008 off Sydney, *Thalia* bloomed so abundantly that it was measured with a mean abundance of more than 5000 individuals per cubic metre (Everett et al., 2011; Henschke et al., 2011).

Three other species in the genus, namely *Thalia cicar* Van Soest, 1973, *Thalia rhinoceros* Van Soest, 1975, and *Thalia rhomboides* (Quoy & Gaimard, 1824), also occur in Australia but have only been reported from Queensland and do not seem to have made it further south yet (Kott, 2009).

Copepods of the genus *Sapphirina* are often found in association with salps, particularly *Pegea* and *Thalia* (Harbison, 1998).

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Thetys vagina Tilesius, 1802 CAAB 35 103022



Thetys vagina, solitary -- MIDOC SS2011_T02 – OP31_MIDOC5. Note two posterior tails.

Thetys vagina, aggregate -- SS2011 TO2 – Copyright Mailie. Note thickened tuberculated region over gut.

Thetys vagina, solitary – Copyright Gregory Dallavalle

FIELD MORPHOLOGY: Mature *Thetys* are easily distinguished from other species by their large size and often greenish hue.

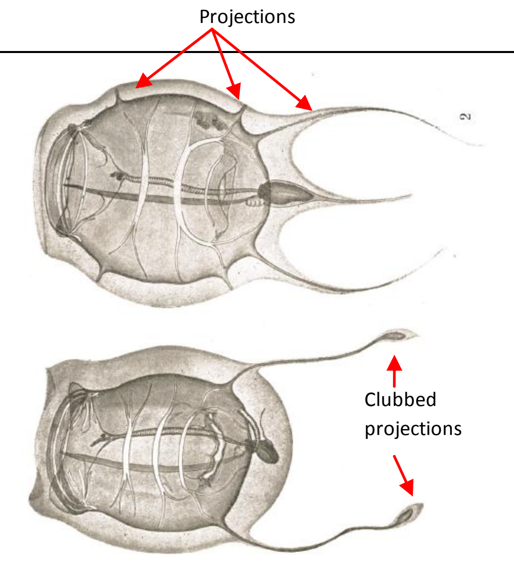
- Solitary form: 'Sole-shaped' with many (16-22) more or less parallel muscle bands and two conspicuous 'tails' that may be pigmented on the edges or the tip. The gut nucleus is large, darkly coloured, and positioned well toward the posterior of the animal. Length to 333mm, more commonly about 150mm.
- Aggregate form: Blob-shaped to pear-shaped, with a thickened, rigid region over the gut mass which bears tubercles. Five body muscles are interrupted dorsally and do not extend ventrally. Chains may reach several metres in length, with the individuals nearly at right angles to the axis of the chain in a double row. Length to 250mm.

MAY BE CONFUSED WITH: For most people familiar with salps, mention of a large salp brings to mind *Thetys*; however, several other species can also grow quite large. For example, species of *Cyclosalpa* and *Pegea* can reach 15cm in length. However, the numerous parallel muscles and two posterior projections make *Thetys* difficult to mistake.

NOTES: *Thetys* tolerates colder water than most other salps and is most often found in far southern waters, e.g., off the Tasmanian shelf; it is also known from California, Japan, and the Eastern Atlantic. Sometimes it occurs in large swarms off Tasmania and New South Wales.

CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Traustedtia multitentaculata (Quoy & Gaimard, 1834) CAAB 35 103023



Traustedtia multitentaculata – copyright CSIRO 1948
Top, aggregate form; bottom, solitary form.

FIELD MORPHOLOGY: Solitary form: Body globular-oval, voluminous, with two prominent posterior 'tentacle-like' projections, which may be clubbed; may have additional numerous, often paired, projections protruding from the body into the test and sometimes far beyond it; up to 23 processes have been reported. The test is soft with three prominent spiny crests (2 longitudinal dorsal, 1 transverse posterior). Body muscles 5, cover only the dorsal surface and part of the sides, in two groups: MI-MIII and MIV-MV. Length excluding tentacles to 36mm.

Aggregate form: Test soft and globular, with 3 long posterior projections, i.e., paired tentacles and a median projection from the nucleus. Body muscles 4 on dorsal and lateral surfaces, arranged in two groups of two. Length 16-20mm, excluding projections.

Traustedtia – ©2013 Guido & Philippe Poppe - www.poppe-images.com

MAY BE CONFUSED WITH: It may be possible to overlook *Traustedtia* in a dense *Thalia* bloom because the two species are small and bear a superficial resemblance. However, *Traustedtia* is more globular and tends to get larger than *Thalia*, and the projections are quite different in form.

NOTES: *Traustedtia multitentaculata* is the only species in the genus. Many authors have considered it to be 'very rare', while van Soest (1975a) believed that to be an exaggeration and indeed, Thompson (1948) found it in abundance in SE Australian waters, stating, "it is certainly not rare, being occasionally found in considerable numbers".

It is found in warm waters of the three great oceans from 40°N to 30°S. Thompson (1948) found its greatest abundance in the latitudes between Sydney and southern Queensland, with only a single specimen taken in the waters off Tasmania. No specimens were taken by the Great Barrier Reef Expedition (Russell and Colman, 1935). It is commonest in spring.

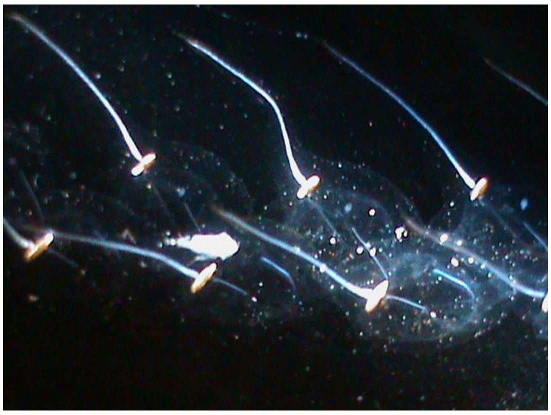
CHORDATA: TUNICATA: THALIACEA: SALPIDAE: SALPINAE – The Salps

Csirosalpa caudata, new genus, new species

FIELD MORPHOLOGY: Solitary form: Currently unknown.

Aggregate form: Test soft and globular, with a small, cigar-shaped nucleus orientated perpendicular to the main body axis across the posterior end of the zooid (or distal, when zooids are attached to each other), and with a long white solid filament emanating from this nucleus. Numerous long transparent gelatinous projections arise around the body. The projections and the filament are contained within the tunic. Body muscles 4, ventrally all four united at the midline, and dorsally the middle two are united a short distance before the midline. Zooid length to about 10mm, excluding filament and projections.

Csirosalpa caudata, single zooid of aggregate stage, holotype SAMA E3846 – image by L. Gershwin/CSIRO.



Csirosalpa caudata, aggregate form, holotype SAMA E3846 – image by L. Gershwin/CSIRO.

MAY BE CONFUSED WITH: The small, soft, somewhat spiky body is reminiscent of *Traustedtia*. However, in *Traustedtia* the nucleus is orientated with the main body axis (rather than across), the conspicuous flexible filament of this species is lacking, and *Traustedtia* has paired posterior projections not associated with the nucleus.

NOTES: This species is new to science and will be more thoroughly described in an upcoming publication. It was found in very large numbers at the surface in a dense multi-species salp swarm during an upwelling event off the coast of eastern Tasmania.

The curious long posterior filament is worthy of discussion. In life, it flows with colony movement as if it were a fine thread. However, as it is encased within a thick gelatinous extension of the tunic, it is not a filament as such. Its function is unknown.

GLOSSARY TO THE PELAGIC TUNICATES

Aboral – literally, 'away from the mouth', or in salps, the end closest to the nucleus; the term is used for orientation. See also 'oral'.

Aboral processes – finger-like extensions of the body on the aboral end, particularly obvious in *Metcalfina*, *Thalia* and *Thetys*.

Aggregate stage – the sexual stage of salps, developed asexually; compare with 'solitary stage'.

Appendicularian – mucous-house-building, tadpole-shaped pelagic tunicate resembling the larvae of other tunicates.

Dorsal tubercle – in the cyclosalps, a raised gelatinous design on the outer surface over the gill bar, near the oral opening; the pattern of the dorsal tubercle is highly diagnostic.

Excurrent siphon – the opening where water is expelled; in salps, used for jet propulsion.

Gill bar – a ciliated internal structure in salps and doliolids; the cilia drive the mucous net to the oesophageal opening.

Hermaphrodite – an individual that is both male and female; hermaphroditic organisms may be either simultaneous hermaphrodites (male and female at the same time), or sequential hermaphrodites (male first, then female, or vice versa).

Holopelagic – spending one's entire life drifting in the open ocean.

Incurrent siphon – the opening where water is taken in; this current of water passes through a mucous net, which filters out food particles.

Marine snow – small, sinking organic particles that concentrate carbon, acting both as an important food source for organisms in the deep sea, and also to help transport and sequester carbon

Muscle bands – prominent bands of muscle tissue that encircle the salp body and are used in locomotion and feeding; the number and arrangement of the muscle bands are highly diagnostic.

Nucleus – the gut mass; globular in most salps, but linear in the cyclosalps.

Notochord – a flexible, rod-like body found in the embryo stage of all chordates, including tunicates; notochords served as the first 'backbone' support structures in early chordates.

Nurse – see 'solitary stage'.

Oral – the mouth-end of the animal, in salps, the opening farthest away from the gut mass; see also 'aboral'.

Pelagic – drifting.

Salps – barrel-shaped pelagic tunicates floating singly or in chain-like colonies; the incurrent and excurrent siphons for feeding and locomotion are located at opposite ends.

Solitary stage – also called the 'nurse' stage of salps, the solitary individual develops a stolon of asexually developing aggregates; compare with 'aggregate stage'.

Tunic – a layer of cellulose integumentary tissue that covers the epidermis, found in benthic and pelagic tunicates and unique to this group; the tunic of salps is often lost during collection.

Tunicate – invertebrates in the subphylum Urochordata.

A dense bloom of *Thalia democratica* in the Derwent River, Tasmania.

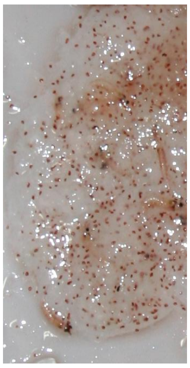
CHECKLIST FOR THE PELAGIC TUNICATES

Oikopleura

Fritillaria

Doliolids

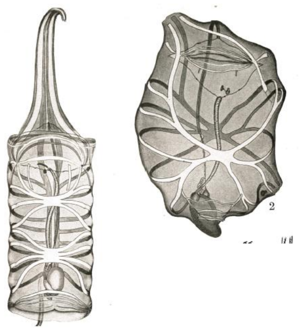
Pyrosoma



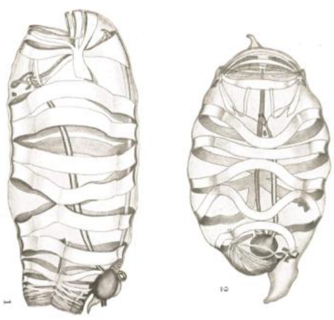
Pyrostremma

Cyclosalpa (SOL)

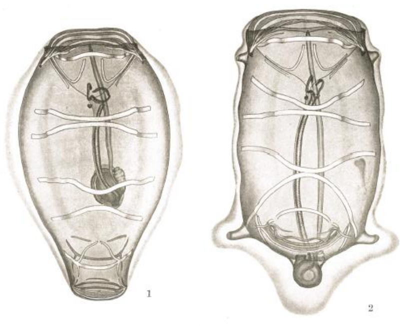
Cyclosalpa (AGG)



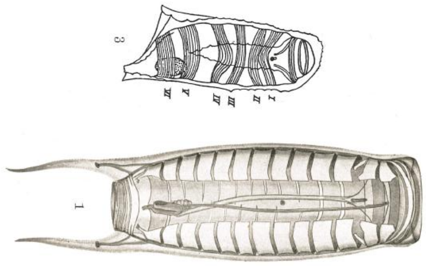
Brooksia



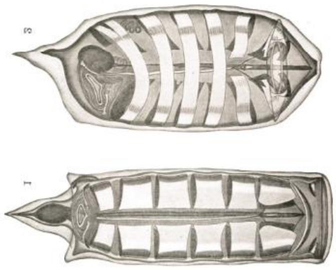
Ihlea



Pegea

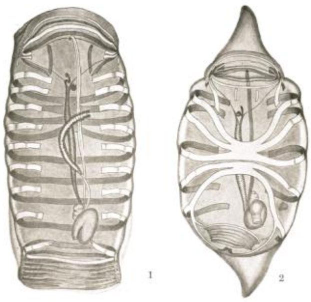


Metcalfina

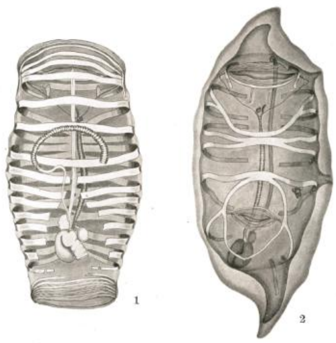


Soestia

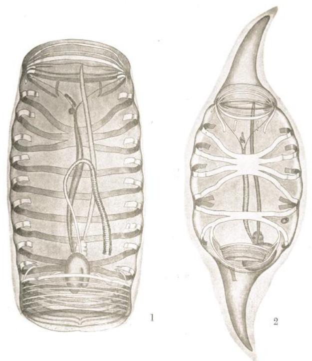
Thetys



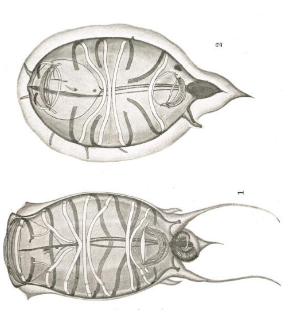
Iasis



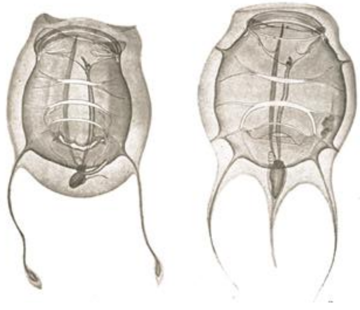
Ritteriella



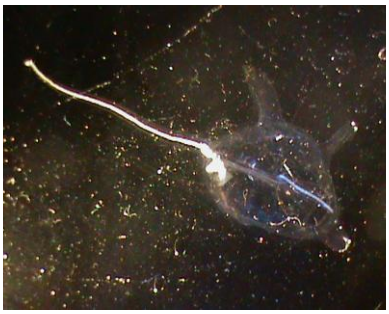
Salpa



Thalia



Traustedtia



Csirosalpa caudata

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