AUSTRALIAN NATIONAL ANTARCTIC RESEARCH EXPEDITIONS

ANARE RESEARCH NOTES 2

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

David O'Sullivan

INFORMATION SERVICES SECTION
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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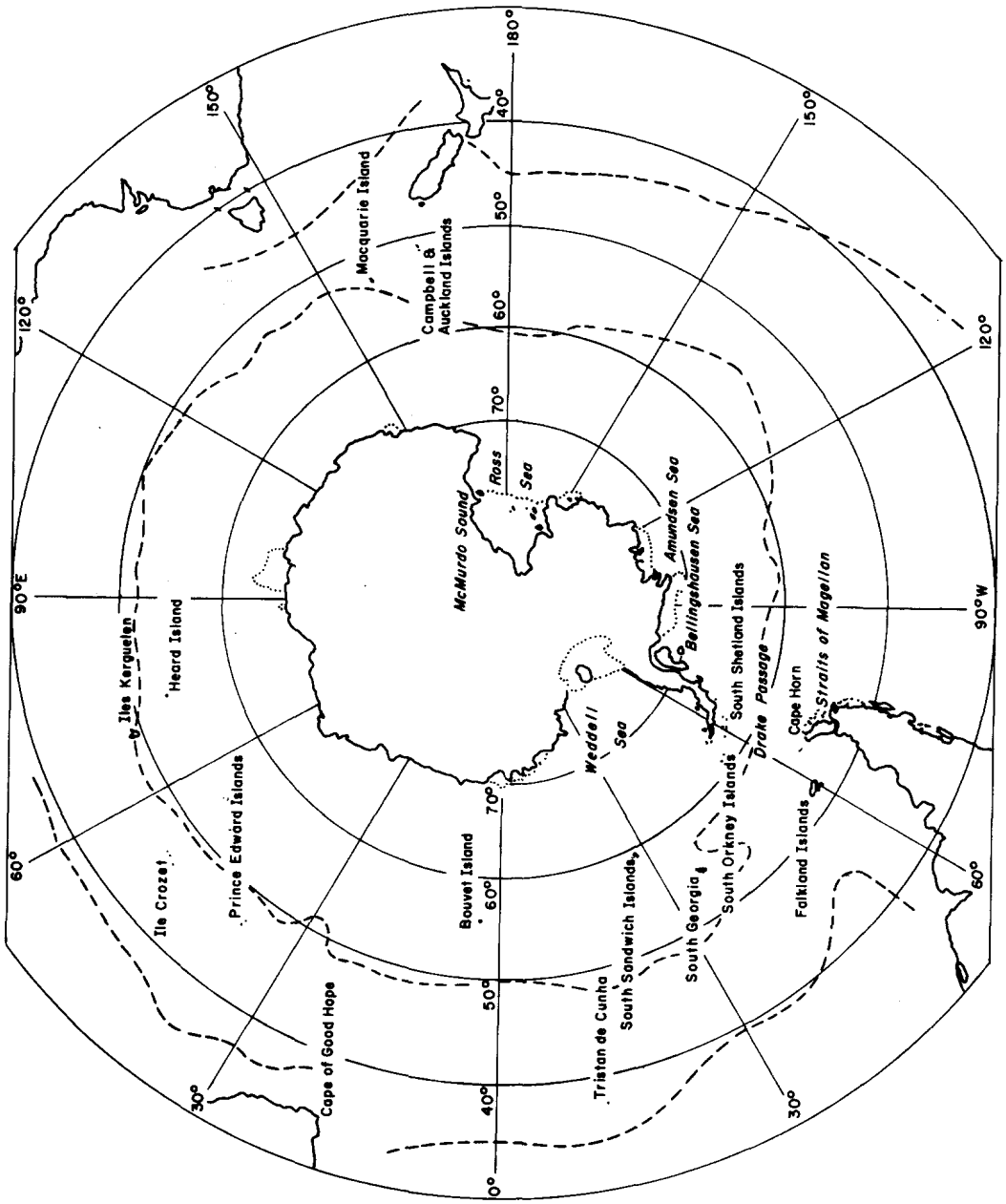
A GUIDE TO THE CHAETOGNATHS OF THE SOUTHERN OCEAN AND ADJACENT WATERS

by

David O'Sullivan
Antarctic Division, Department of Science and Technology,
Hobart, Tasmania, Australia

ABSTRACT

The Southern Ocean chaetognath fauna comprises Sagitta gazellae Ritter-Zahony, S. marri David and Eukrohnia bathyantarctica David which are endemic species; S. macrocephala Fowler, S. maxima (Conant), E. hamata (Mobius) and Heterokrohnia mirabilis Ritter-Zahony which are species common to other regions which maintain themselves in the area; and S. decipiens Fowler, S. hexaptera D'Orbigny, S. lyra Krohn, S. minima Grassi, S. planctonis Steinhaus, S. serratodentata Krohn, S. tasmanica Thomson, S. zetesios Fowler, Pterosagitta draco (Krohn), Krohnitta subtilis (Grassi), E. fowleri Ritter-Zahony and E. bathypelagica Alvarino which are exotic tropical or sub-tropical species, unable to reproduce in the area. The synonymy, diagnostic characters, geographical and bathymetric distribution of each species is given together with an illustration and a distribution map. Keys are provided for the identification of the genera and species from the Southern Ocean and adjacent waters.



Map of the Southern Ocean showing places mentioned in text.

1. INTRODUCTION

The phylum Chaetognatha is small, consisting of seventy to eighty species belonging to about eight genera (David, 1963). The chaetognaths, commonly known as arrow-worms, are frequently found in the plankton. The entire phylum is marine, and except for the benthic genus Spadella, all arrow-worms are adapted for a planktonic existance (Barnes, 1974). For a good account of the anatomy, embryology, ecology and physiology of the Chaetognaths see Hyman (1959).

The group has recieved a great deal of attention from plankton workers because some species have been shown to be characteristic of different water masses; there is therefore a substantial amount of published information available dealing with both the systematics and the distribution of the group (David, 1963).

This review is an attempt to summarise data on the chaetognaths of the Southern Ocean. The name Southern Ocean is used in the same context as in David (1958b). It describes all that ocean which lies between the Subtropical Convergence and the Antarctic Continent. This area is divided into two zones, the Subantarctic and the Antarctic which are separated by the Antarctic Convergence. On the distribution maps the positions of the Subtropical and Antarctic Convergences are from Lomakina (1960). Species which occur in adjacent waters (north of the Subtropical Convergence but south of 30°S) are included in the keys. The regions in which these animals have been found are given in brackets: (Au) for southern Australia; (NZ) for New Zealand; (Pa) for southern Pacific Ocean and (SAm) for South America; (At) for southern Atlantic Ocean; (SA) for southern Africa; (In) for southern Indian Ocean; and (Co) for cosmopolitan to all these areas.

The synonymy, diagnostic characters and bathymetric distribution is given for each of the Southern Ocean species, together with a distribution map and an illustration of its body, head and a seminal vesicle. The synonymy is from David (1958b) and Alvarino (1965). Only references with incorrect identifications from the Southern Ocean and adjacent waters are listed. For the baythymetric distribution the chaetognaths are classed as either epiplanktonic (found in the surface waters down to 200m), mesoplanktonic (200 to 1000m), or bathyplanktonic (below 1000m level) according to Alvarino (1964a). On the distribution maps a symbol may represent more than one sampling station. A symbol with a question-mark next to it means the identification was tentative or that subsequent workers have doubted its validity. Cross-hatchings have been used when a species has been found over a wide area.

Sund (1959) pointed out that the published keys (eg Ritter-Zahony, 1911; Michael, 1908, 1911, 1919; Johnston and Taylor, 1919; Thomson, 1947; Fraser, 1952) generally used characters that were often indistinguishable or whose determination was so time consuming that their use in general plankton surveys was impractical. For this reason a new key is given for use by non specialists that will allow rapid but accurate indentification using easily recognisable characters.

2. EXTERNAL STRUCTURE

Chaetognaths exhibit relatively little anatomical variation throughout the group (David, 1965). Their transparent, bilaterally symmetrical body is shaped like an arrow or a torpedo (see Fig. 1). The body comprises three regions: head, trunk, and tail.

On the ventral side of the head is a large chamber, the vestibule, that leads into the mouth. The alimentary canal is a straight simple tube. Long and curved chitinous hooks or spines project from each side of the head and these are used in seizing prey together with several rows of much shorter spines (anterior and posterior teeth) that are curved around the front of the head (Barnes, 1974). A pair of eyes is located anteriorly on the dorsal surface and behind this is the corona, an organ whose function could possibly be sensory. In the neck region is a fold of body wall (the hood) that can be pulled forward to enclose the entire head, presumably to protect the spines when they are not in use and to reduce water resistance whilst swimming (Barnes, 1974).

The remainder of the body is composed of an elongated trunk and tail, divided by a septum. A characteristic feature of the chaetognaths is the 1 or 2 pairs of lateral fins that border these regions of the body. Posteriorly, a large spatula-like fin encompasses the end of the tail. The tail and lateral fins all contain ray-like supports. The body can be covered with a layer of large cells called a collarette giving a foamy appearance. Chaetognaths are hermaphroditic with the ovaries anterior to the trunk-tail septum and the testes posterior to the trunk-tail septum. Sperm are released through the seminal vesicle. Mid way along the ventral side of the trunk is the subenteric ganglion from which a number of paired nerves serve the various sensory structures of the body and presumably the musculature (Laverack and Dando, 1974).

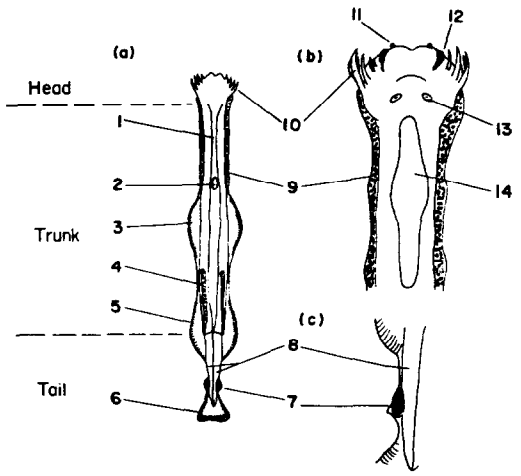


Figure 1. A chaetognath, Sagitta marri showing the major parts. (a) ventral view of adult; (b) head and anterior part of trunk, dorsal view ; (c) shape and position of seminal vesicle, dorsal view.

(1) intestine; (2) subenteric ganglion; (3) anterior lateral fin; (4) ovary; (5) posterior lateral fin; (6) tail fin; (7) seminal vesicle; (8) testes; (9) collarette; (10) hooks; (11) anterior teeth; (12) posterior teeth; (13) eyes; (14) corona.

3. IDENTIFICATION

Specific identification in the chaetognaths is based upon varying contributions of characters which differ in the ease with which they may be distinguished (Thomson, 1947). In well preserved mature specimens the shape and position of the seminal vesicles is characteristic (Tokioka, 1939; David, 1956), but unfortunately mature specimens are rarely caught, so immature or damaged specimens can only be determined by the combination of a number of features (Thomson, 1947).

Several authors, and in particular Fowler (1905), have stressed the desirability of recording the formula for the head armature (i.e. number of hooks or anterior or posterior teeth on one side of the head), while Ritter-Zahony (1911), Jameson (1914), and others recommended measurement of the length of the body, and the comparative length of the tail segment, excluding the tail fin (Thomson, 1947).

Measurements and counts of body length, tail length as a percentage of body length, number of hooks and number of anterior and posterior teeth are often tabulated and are sometimes referred to as the "formula" for that particular species (eg Michael, 1919; Burfield, 1930; Dakin & Colefax, 1940; Tokioka, 1940; Sund, 1959).

The species can therefore be identified, apart from the general form, by the number of teeth which occur in an anterior and posterior row on each side of the head (except for Krohnitta and Eukrohnia which only have 1 row); by the number of curved chitinous hooks or jaws, which are placed in a row on each side of the head; by the relative lengths of the body and tail segments and by the position of the fins (Dakin & Colefax, 1940).

Tokioka (1950) contends that the relationship between the eye pigment and the total area of the eye is specific as also is the shape of the pigment fleck. These can provide a means of separating imperfectly preserved specimens. Their use as an aid to identification should be unecessary except in specimens which have lost their normal form, although it must be remembered that there is considerable individual variation (Fraser, 1952).

Rigidity is a useful determining factor but it is one that is difficult to define because it is effected by size and state of preservation (Fraser, 1952). Fraser goes on to say that roughly speaking, a specimen which does not droop down on either side when picked up by the middle with a pair of forceps is "rigid", but if, however, the two sides hang down it is termed "flaccid".

To a large extent the Southern Ocean chaetognaths are all easily recognisable without recourse to features such as the corona and the fins, which are the most easily damaged (David, 1959). In this handbook, however, the formulae and of such characters as fin position and shape, seminal vesicle position and shape, ovary shape, presence or absence of a collarette and shape of corona, have all been listed for each species in a way similar to David (1956, 1958a).

4. BIOLOGY

Chaetognaths alternately swim and float but the fins play no role in propulsion and are only flotation devices (Barnes, 1974). When the body begins to sink, the longitudinal muscles contract rapidly and the animal darts forward, followed by an interval of gliding and floating. Typically, chaetognaths do not execute daily vertical migrations, but do change their depths seasonally (Timonin, 1968).

The chaetognaths are active, well armed, voracious animals feeding on Hydromedusae, crustaceans, other chaetognaths, and young fishes (Alvarino, 1965). The digestive tract is simple with the intestine extending from the mouth through the length of the trunk, and a pair of anterior lateral diverticula. Food is passed to the posterior part of the intestine where it is rotated and moved back and forth until it is broken down. Digestion is probably extracellular (Barnes, 1974).

They are hermaproditic but almost certainly not self-fertilising (David, 1965). A pair of elongated ovaries is located in the trunk coelom in front of the tail-trunk septum. A pair of elongated testes is located in the tail coelom behind the septum with a seminal vesicle on each side. A number of schemes exist for classifying the developmental stages of chaetognaths, notably those of Kramp (1917, 1939), Russell (1932), Thomson (1947), Faure (1953), David (1955), Coleman (1959), Alvarino (1965) and Pierrott-Bults (1974). Most species of Sagitta seem to die very soon after ovulation (Coleman, 1959). Alvarino (1968) gives a comparison of the breeding characteristics of the chaetognaths.

Chaetognaths can undergo an ontogenetic change in distribution (for example see Sagitta gazellae in David, 1955) with a movement of animals to deeper waters with the onset of maturity. This movement could be related to increase in weight of the individuals, associated with the ripening of the sexual products (Alvarino, 1964a) since the fully mature specimens are only found in deep waters, it can be assumed that the eggs are also laid in deep water and that they, or the newly hatched young, rise to the surface (David, 1955).

Michael (1913) pointed out that different species occuring at the same depth do not usually mature at the same time. Timonin (1968) added that differing times of the maturation cycles, observed in the case of the major part of populations of S. gazellae and Eukrohnia hamata, is the mechanism reducing the competitive relations between the species. David (1958b) likewise notes that, although the distribution areas of different chaetognaths species overlap, the areas of the maximum concentration of the species are not contiguous, possibly as a result of ecological competition. Some aspects of speciation in the chaetognaths are discussed by David (1963).

Each maturity stage of a species of chaetognath generally occurs at about the same level throughout the oceans, with the exception of Eukrohnia hamata (Mobius) which lives at great depths in the tropical and subtropical regions of the oceans, but in the Subarctic and Subantarctic regions it is found progressively nearer the surface towards the poles (Alvarino, 1964a). Thus the chaetognaths are a useful group of plankton indicators because many species are associated with a particular type of environment or water mass (Fraser, 1952). Nevertheless, salients of one water mass may from time to time be pinched off by another in boundary regions where water masses meet, and gradually absorbed so that the fauna carried in such a salient may be found outside its normal habitat. Such stray records should not be regarded as typical of the range of a species (David, 1958b).

5. PREVIOUS RECORDS FROM THE SOUTHERN OCEAN

Early workers on the chaetognaths of the Southern Ocean included Steinhaus, 1900 (Hamburg Magellens Expedition); Fowler, 1907 (Challenger and Discovery collections); Germain, 1913 (French Antarctic Expedition); Jameson, 1914 and 1920 (Scotia collection) and Johnstone & Taylor, 1921 (Aurora collection). Ritter-Zahony's (1911) "Revision der Chatognathen" was the first comprehensive monograph and his material was from the extensive Gauss collections. It provided data on the morphology and distribution of all the then known species (Alvarino, 1965) and stands as a milestone in the study of this group (David, 1965). The classification adopted by most workers, and that used here, is that published by Ritter-Zahony (1911).

Burfield (1930), working on the Terra Nova material, reported on the chaetognaths of both tropical and Antarctic regions. The chaetognaths of the Deutschland 1911-1912 expedition was published by Bollmann (1934). Hardy & Gunther (1935) and Mackintosh (1937) included chaetognaths in their works on Antarctic plankton. Thiel (1938), Ghirardelli (1953), Stadel (1958), Fagetti (1959), Timonin (1968), and Dinofrio (1973) all reported on Antarctic chaetognaths. David (1965) summed his previous work on the Discovery (1955, 1956, 1958a,b) and BANZARE (1959) material.

Work on chaetognaths in adjacent areas include South America (Baldasseroni, 1915; Fagetti, 1958, 1968; Kapp, 1980); South Africa and southern Indian Ocean (Steinhaus, 1896; Fowler, 1906; Ritter-Zahony, 1909, 1910, 1911; Gray, 1923; Heydorn, 1959; Alvarino, 1964c; Furnestin, 1966); New Zealand and southern Pacific (Kent, 1870; Parker, 1895; Fowler, 1908; Ritter-Zahony, 1909; Benham, 1912; Burfield, 1930; Alvarino, 1964a; Fagetti, 1972) and southern Australia (Whitelegge, 1889; Waite, 1899; Johnston, 1909; Ritter-Zahony, 1909, 1910, 1911; Johnston and Taylor, 1919, 1921; Tokioka, 1940; Thomson, 1944, 1947; Taw, 1978). Alvarino's (1965) review considered the problems arising in connection with the systematics of the chaetognaths as well as summarising the available knowledge on their biology and distribution.

6. SYSTEMATIC NOTES ON THE CHAETOGNATHS

It is generally accepted that there are six pelagic genera: Eukrohnia, Krohnitta, Pterosagitta, Sagitta, Heterokrohnia and Bathyspadella, of which the last two are sometimes considered doubtful (eg Alvarino, 1965). There are also 1 benthic genus (Spadella) and 1 fossil genus (Amiskwia).

Members of the genera Eukrohnia, Krohnitta, Pterosagitta, Sagitta and Heterokrohnia have all been reported from the Southern Ocean and diagnoses of these will be given in the following sections. Short systematic notes on the other genera are given below:

> Bathyspadella: B. edentata described by Tokioka (1939) from a single specimen off Japan; deep water.
>
> Spadella: Erected by Langerhans (1880); short body; one pair of lateral fins; 2 paired rows of teeth; large collarette; benthic; 3 species only. (A new species of Spadella from the Antarctic is presently being described by Dr. Hagen, Universitat Kiel, West Germany).
>
> Amiskwia: A. sagittiformis reported by Walcott (1914) from shales of the middle Cambrian in British Columbia; about 20mm long; a pair of well developed tentacles at the top of the head; a pair of short lateral fins at the midlength of the trunk; and a tail fin.

Tokioka (1965) proposed a new classification of Chaetognatha for the 65 taxa he considered valid. All of the above genera were kept except for Sagitta which was split into nine genera so that groups of similar species of Sagitta were now included in their own genera. This system of classification is yet to gain acceptance so that in this handbook the classification of Ritter-Zahony (1911) will be used.

David (1958b, 1965), working on material from the extensive Discovery collections, considered the chaetognath fauna of the Southern Ocean to be composed of three elements: (i) endemic species (Sagitta gazellae, S. marri, Eukrohnia bathyantarctica); (ii) species common to other regions which maintain themselves in the area (S. macrocephala, S. maxima, E. hamata, Heterokrohnia mirabilis); and (iii) exotic (subtropical or tropical) species which probably do not maintain themselves in the region but which are presumably carried in by water movements from other regions, (S. decipiens, S. hexaptera, S. lyra, S. minima, S. planctonis, S. serratodentata, S. tasmanica, S. zetesios, Pterosagitta draco, Krohnia subtilis, E. fowleri, E. bathypelagica). He points out that the chaetognaths of the Southern Ocean are well documented, but misidentification of poorly preserved specimens or mistakes in labelling has often lead to some confusion as to which species occur in the area.

6.1 KEY TO GENERA:

1a) Two pairs of lateral fins, the posterior on trunk and tail ..... *Sagitta* Quoy & Gaimard
b) Either one pair of lateral fins, or two of which the posterior fins lies on the tail segment only 2

2a) Two paired rows of teeth 3
b) No teeth or one paired row 5

3a) No collarette; lateral fins partly on trunk, partly on tail ..... *Heterokrohnia* Ritter-Zahony
b) Marked collarette; 1 pair of lateral fins on tail only, or two pairs of which posterior fin lies on tail only 4

4a) Collarette voluminous, foamy in appearance; one pair of lateral fins; without ventral transverse musculature; posterior teeth 8 to 18; oceanic ..... *Pterosagitta* Costa
b) Collarette present but not massive; ventral transverse musculature; posterior teeth less than 5; benthic (Au)..... *Spadella* Langerhans

5a) Lateral fins extend to or in front of ventral ganglion, do not reach seminal vesicle posteriorly ..... *Eukrohnia* Ritter-Zahony
b) Lateral fins do not reach ventral ganglion, reach seminal vesicles posteriorly ..... *Krohnitta* Ritter-Zahony

6.2 GENUS *Eukrohnia* Ritter-Zahony 1909

Chaetognaths characterised by a pair of lateral fins extending from the level of the ventral ganglion to the region of the seminal vesicles in the tail, 1 paired row of teeth, usually no collarette, mainly bathypelagic, 4 species all of which occur in the Southern Ocean.

Key to species (David, 1958a; Alvarino, 1962):

1a) More than 10 hooks; gut pigmented 2
b) Less than 10 hooks; gut not pigmented 3

2a) Eyes with pigment fleck; up to 30 teeth; collarette at ventral ganglion ..... *E. fowleri* Ritter-Zahony
b) Eyes with pigment fleck; up to 16 teeth; no collarette at ventral ganglion ..... *E. bathyantarctica* David

3a) Eyes without pigment fleck; up to 22 teeth; collarette begins at ventral ganglion, being broadest at the opening of the oviducts ... *E. bathypelagica* Alvarino
b) Eyes without pigment fleck; up to 25 teeth; no collarette ..... *E. hamata* (Mobius)

Character	Species			
	Eukrohnia hamata (Mobius 1875)	Eukrohnia fowleri Ritter-Zahony 1909	Eukrohnia bathyantarctica David 1958	Eukrohnia bathypelagica Alvarino 1963
Total length (mm)	43	40	31	23
Per cent tail	19-24	22-25	19.3-25	25.8-34
Head	Small	Larger than E. hamata	Like E. fowleri	Small, broader than long, attached to a very narrow neck
Hooks	8-9 (10) Straight, point end very curved	10-13 Gently curved	14	8-9 Gently curved, point end very much like E. hamata.
Teeth	Up to 23-25	30	16	17-22
Eyes	Without pigment	Pigmented	Without pigment	Without pigment, very close together
Collarette	Absent	At ventral ganglion and at the openings of the oviducts	Absent	Begins at the ventral ganglion, being broader at the opening of the oviducts.
Fins	Begin at the ventral ganglion, ending at the seminal vesicles, with rays at the posterior end only	Extending from the anterior part of the ventral ganglion to the seminal vesicles. With rays only at the posterior end, opposite to tail segment.	From ventral ganglion to about 1/3 of the tail segment.	From the ventral ganglion to the seminal vesicles. Very broad at the rayed posterior end.
Ovaries	Up to about half the length of the body	Short, with large ovulae in 2 rows. Opening of seminal receptacle as a sort of capsule.	Short; remnant of seminal receptacles project from the oviduct after fertilization.	Up to midway from neck to tail septum, filling body cavity. Large ovulae in two rows. Opening of seminal receptacle as a capsule.
Seminal vesicles	Elongated, ovoid	Ovoid, separated from tail fin	Probably ovoid	Separated from tail fin
Distribution	Inhabits all parts of water column, cosmopolitan.	Deep water form, below 750m, tropical and subtropical waters, cosmopolitan.	Deep water form, below 1000m, Antarctic and Subantarctic waters.	Deep water form, below 700 m, scattered distribution.

Table 1. Principal diagnostic characters of species of Eukrohnia (Alvarino, 1962).

The principal differential characters of the four species of Eukrohnia are given in Table 1. Three characters, the teeth, the eyes and the presence of a "collarette" like structure seem to be diagnostic (David, 1958a). The following discussion is from David (1958a) and Alvarino (1962): E. bathyantarctica has a smaller number of teeth (up to 16) than E. fowleri (up to 30), E. bathypelagica (up to 22) and E. hamata (up to 23). E. bathypelagica and E. fowleri have a 'collarette' in the region of the ventral ganglion which is not present in E. bathyantarctica or E. hamata. The gut of E. fowleri and E. bathyantarctica is brick red while the gut of the other two species is colourless though E. hamata can often have an oil globule in the gut (Fraser, 1957).

Eukrohnia bathyantarctica David 1958a.

(Figure 2, Map 1)

(E. fowleri Ritter-Zahony, 1911 part)
(Eukrohnia sp. David, 1958b)

Diagnostic characters (David, 1958a):

Fins commence at ventral ganglion and extend on to the tail segment for about one-third of its length
Tail broad, 19.3 to 25.0% of body length
Teeth up to 16
Hooks up to 14
Seminal vesicles shape is not known but is probably ovoid, situated close to lateral fins
Ovaries short, even when fully mature
Collarette absent
Corona shape is not known
Eyes have no pigment fleck
Length up to 31mm.

This species is very similar to Eukrohnia fowleri and often has been regarded as such. It is also, in some respects similar to the large form of E. hamata, and may possibly be equally related to both forms (David, 1958a).

This is an endemic bathyplanktonic Antarctic species living below 1000m, being most common below 1500m and possibly extending to more than 3000m (David, 1958a). The limits of the horizontal distribution of E. bathyantarctica are not yet known, although it is probably circumpolar (David, 1965). It has also been reported from the deep layers of the Gulf of Mexico and Caribbean Sea (Fagetti, 1968).

Eukrohnia bathypelagica Alvarino 1962

(Figure 3, Map 2)

Diagnostic Characters (Alvarino, 1962):

Lateral fins extend from region of seminal vesicle to near the ventral ganglion, broadest at tail region
Tail 27 to 34% of body length
Teeth 17 to 22

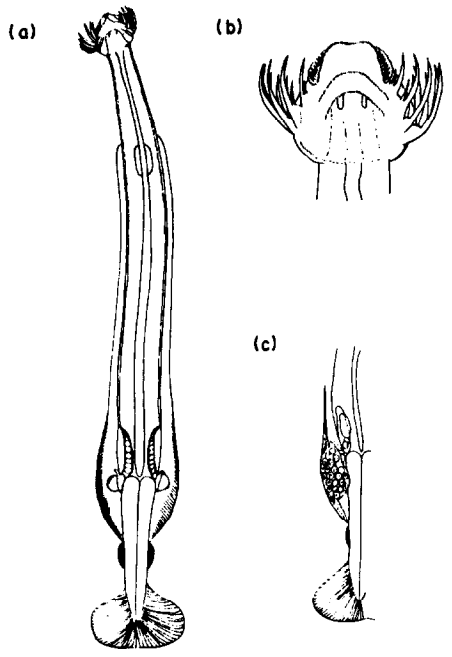
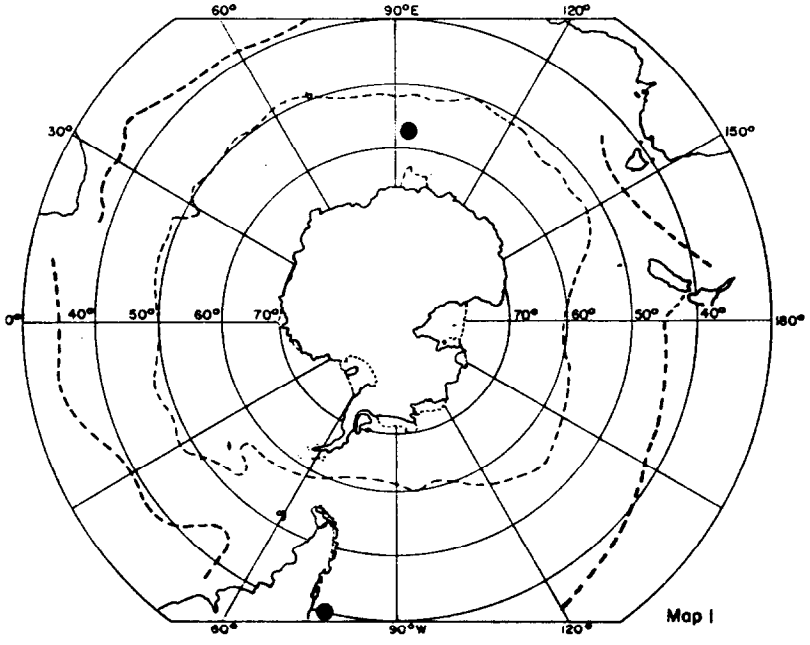


Figure 2. Eukrohnia bathyantarctica (a) adult, ventral view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 1. Distribution of E. bathyantarctica.

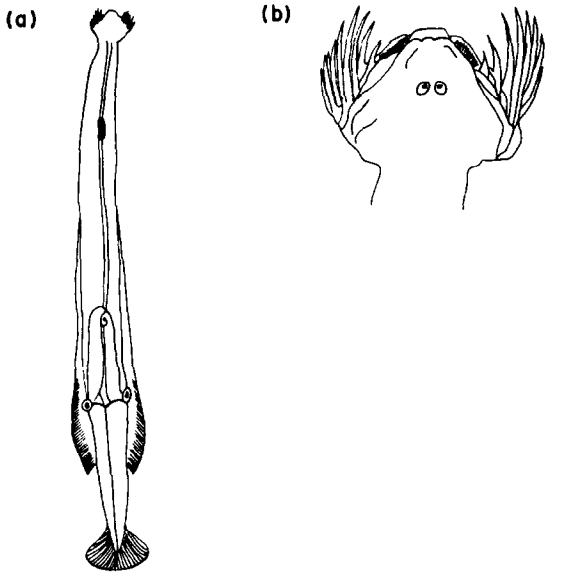
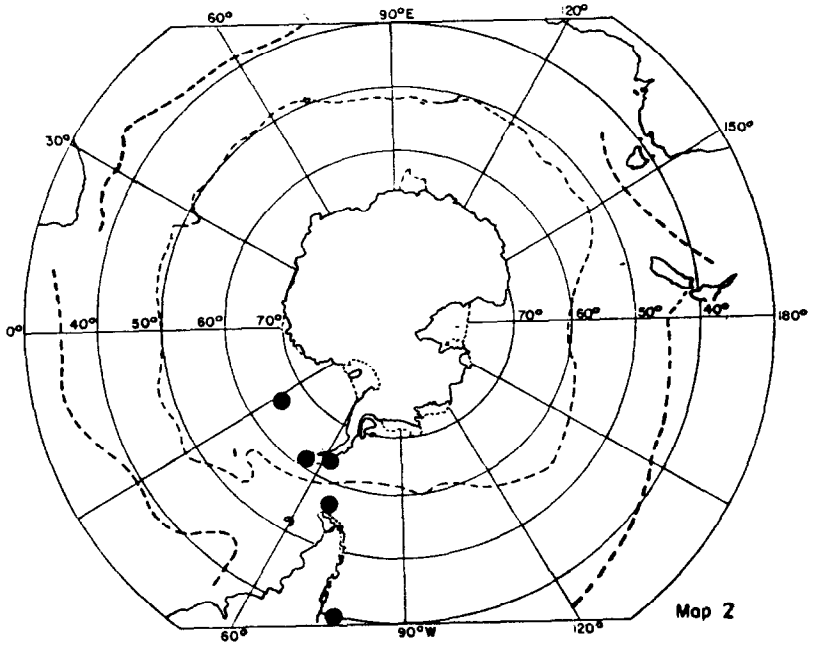


Figure 3. Eukrohnia bathypelagica (a) adult, dorsal view; (b) head, dorsal view.



Map 2. Distribution of E. bathypelagica.

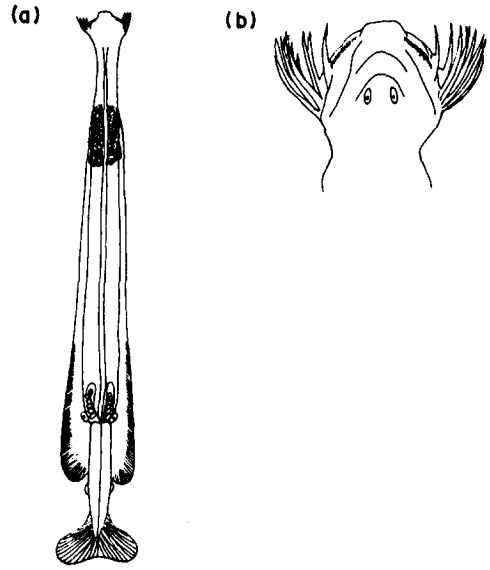
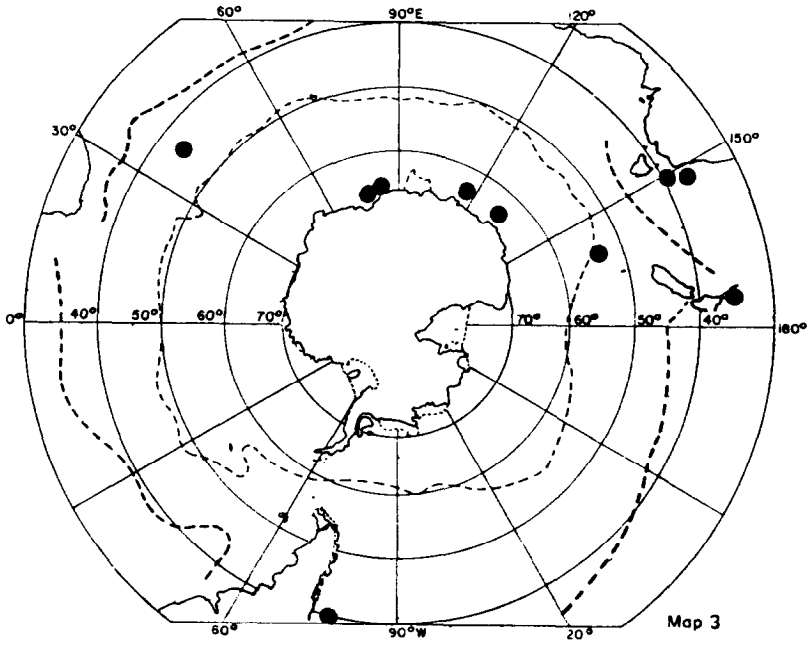


Figure 4. Eukrohnia fowleri (a) adult, dorsal view; (b) head, dorsal view.



Map 3. Distribution of E. fowleri.

Hooks 8 to 9
Seminal vesicles separated from both tail fin and lateral fins, appear only as damaged remains
Ovaries when mature completely fill body cavity
Collarette begins as a thin layer at anterior end of ventral ganglion, extends to base of tail fin and surrounds the end of tail segment
Corona yet to be described
Eyes have no pigment fleck, oval-shaped, close together
Length up to 23mm.

The records of Eukrohnia bathypelagica are so few and so scattered as to suggest that it inhabits deep waters and that the records are of occasional strays above its normal habitat (Alvarino, 1962a). It is mesobathypelagic and has been found in the Antarctic at Drake Passage (Dinofrio, 1973). Ducret (1968) believes that the distribution of this species corresponds to the cold water of the Antarctic Ocean though it is scattered throughout the sectors of this area.

In Subantarctic waters it has been found at depths below 600m (Alvarino, 1964a). Alvarino (1962) suggests that E. hamata var. antarctica Johnston & Taylor (1921) is possibly an immature E. bathypelagica.

Eukrohnia fowleri Ritter-Zahony 1909

(Figure 4, Map 3)

(E. hamata Thiel, 1938; Thomson, 1947 part)

Diagnostic Characters (David, 1958a):

Lateral fins extend from ventral ganglion to about one-third of tail segment
Tail 21 to 27% of body length
Teeth up to 30
Hooks up to 13
Seminal vesicles not yet described
Ovaries short and stumpy
Collarette-like structure at ventral ganglion
Corona pear-shaped
Eye has pigment fleck (Alvarino, 1962)
Length to 40mm.

David (1958a) points out that this species can be distinguished from Eukrohnia hamata and E. bathyantarctica by the presence of a pigment fleck in eye, and a foamy "collarette" at the ventral ganglion (see Table 1). The neck is very distinct and fragile (Fraser, 1957).

An oceanic, cosmopolitan species, E. fowleri is abundant at depths below 800m (Alvarino, 1965). It has been recorded from the Antarctic (Ritter-Zahony, 1911; Johnston & Taylor, 1921) and in the Subantarctic at depths below 600m (Alvarino, 1964a).

Eukrohnia hamata (Mobius 1875)

(Figure 5, Map 4)

(E. hamata var. antarctica Johnston & Taylor, 1921)

Diagnostic characters (David, 1958a):

Lateral fins from ventral ganglion to about one third of tail segment, seminal vesicles
Tail usually 19 to 24% of body length (to 31% Fraser, 1952)
Teeth up to 23 (to 25 Fraser, 1952)
Hooks up to 9 (to 12 Burfield, 1930)
Seminal vesicles elongated and ovoid
Ovaries extended to about half the length of the body segment at full maturity
Collarette not present
Corona pear-shaped
Eyes without pigment
Length up to 43mm.

The differences between this and the other species of this genus have already been discussed in the Eukrohnia bathyantarctica section (see Table 1). According to David (1958b) E. hamata var. antarctica, Johnston and Taylor (1921) is the spent form which seems able to live for a while after spawning. On the other hand, Alvarino (1962a) thinks it is possible that it is an immature E. bathypelagica.

This species is cosmopolitan in the deep sea, circumpolar, with the maximum abundance in the Southern Ocean in the vicinity of the Antarctic Convergence (David, 1958b). E. hamata is the commonest species in the Southern Ocean with concentrations in the top 50m, but it is common right to the surface (David, 1965). It is a classic example of bipolar distribution with a tropical submergence (David, 1958b), and is unique in that it covers the epi-, meso-, or bathyplanktonic categories in relation to latitude (Alvarino 1961). It is thought that in the winter E. hamata sink to deeper levels (Mackintosh, 1937). A number of investigators (Fowler, 1907; David, 1958b; Timonin, 1968) have recorded a transition from small to larger more mature individuals with increasing depth.

This species exhibits a great deal of variation in size. David (1958b, 1965) states that in the Southern Ocean there are two clearly defined races more or less separated by the Antarctic Convergence, but gives no details on the differences between them except to say that a large form is found in the cold Antarctic waters, while a smaller form is found in Subantarctic waters.

It appears that E. hamata does not extend northward from the boundary of the Subtropical Convergence in the Indian Ocean, or if it does the population is either scarce (and hence individuals are missed by the sampling) or it inhabits layers deeper than those sampled (Alvarino, 1965).

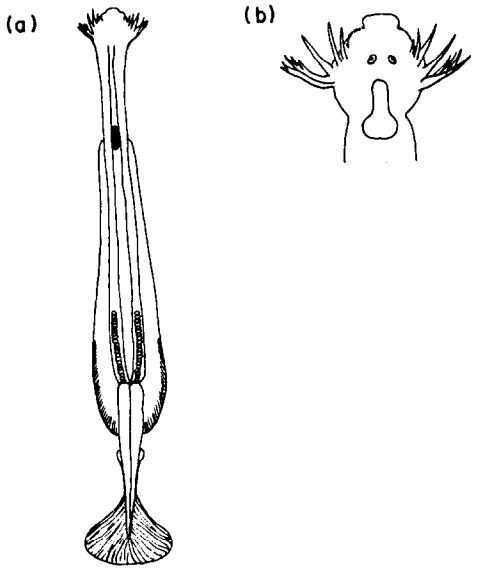
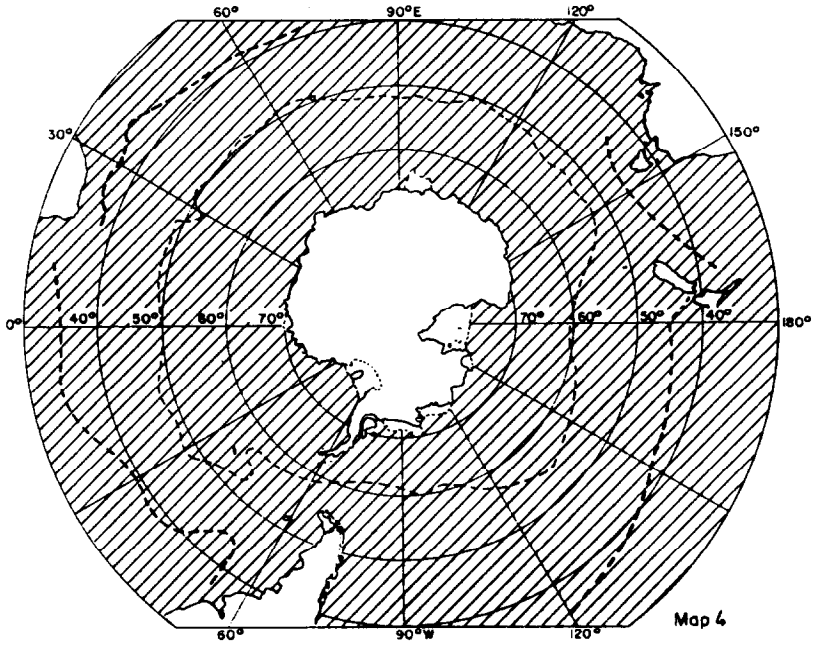


Figure 5. Eukrohnia hamata (a) adult, ventral view; (b) head, dorsal view.



Map 4. Distribution of E. hamata.

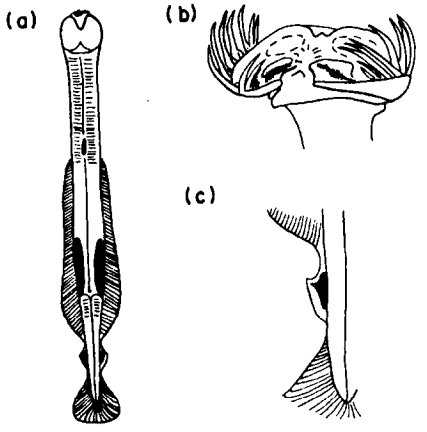
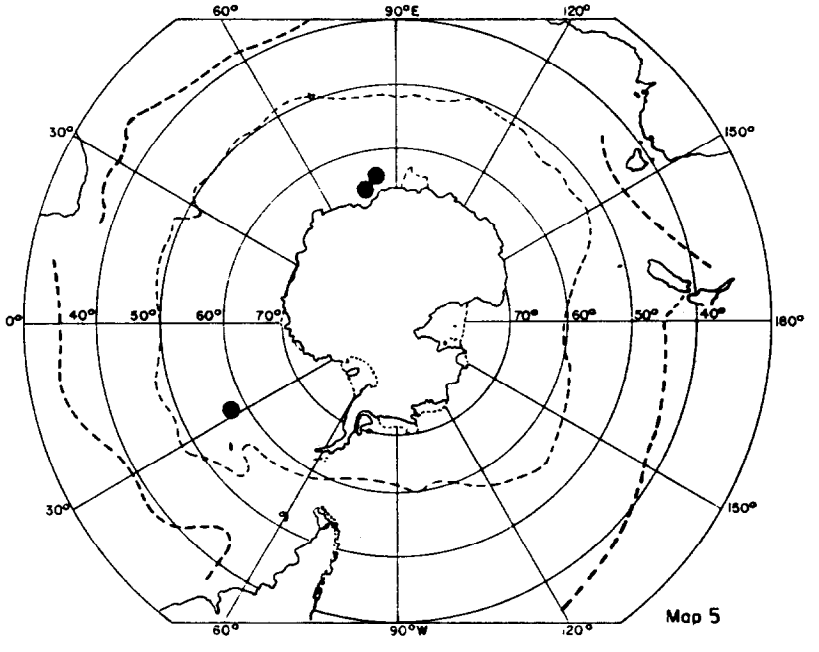


Figure 6. Heterokrohnia mirabilis (a) adult, dorsal view; (b) head, seen from anterior dorsal direction; (c) seminal vesicle, ventral view.



Map 5. Distribution of H. mirabilis.

6.3 GENUS Heterokrohnia Ritter-Zahony 1911

Chaetognaths with one pair of lateral fins lying partly on trunk and partly on tail, 2 paired rows of teeth, no collarette, inhabits waters below 1000 m, one species only.

Heterokrohnia mirabilis Ritter-Zahony 1911

(Figure 6, Map 5)

(Heterokrohnia sp. ? Jameson, 1914)

Diagnostic characters (see also David 1958b, p206-208 for discussion):

Lateral fins partly on trunk and partly on tail
Tail 32 to 44% body length
Anterior teeth 4 to 15
Posterior teeth 1 to 33
Hooks 8 to 14
Seminal vesicles, ovaries and corona yet to be described
Collarette not present
Length up to 36mm (Tchindonova, 1955).

This rare species was first described from eight specimens from the Antarctic zone. Further records from the Antarctic include Jameson (1914) and David (1958b). Some other specimens have been found in the Pacific off Central America (Bieri, 1959) and in the Kurile-Kamchatka trench (Tchindonova, 1955).

The specimen reported as Heterokrohnia sp. by Jameson (1914) seems, from its head armature, to have been a damaged specimen of E. hamata (David, 1958b). Alvarino (1965) suggests that H. mirabilis could well be a mis-identification of S. maxima. David (1958b) points out that while his two specimens could be distorted examples of some better known form, he still considers H. mirabilis to be a valid species though he feels that really perfect specimens might show that it should belong to the genus Sagitta.

David (1958b) classed H. mirabilis as a species common to other regions but later (David, 1959), he considered it as endemic to the Antarctic. It is only found below 2000m and there is no evidence for a circumpolar distribution, but since the species has been found in other regions it is probable that it is widespread in very deep water (David, 1965).

6.4 GENUS Pterosagitta Costa 1869

Chaetognaths characterised by one pair of lateral fins which extend from the tail to the level of the posterior septum, 2 paired rows of teeth, and a massive collarette extending from the neck over the anterior part of the lateral fin, populates the upper strata, 1 species only.

Pterosagitta draco (Krohn 1853)

(Figure 7, Map 6)

Diagnostic Characters (Sund, 1959):

Lateral fins single pair restricted to tail segment; wide with rounded lateral borders; reaching seminal vesicles

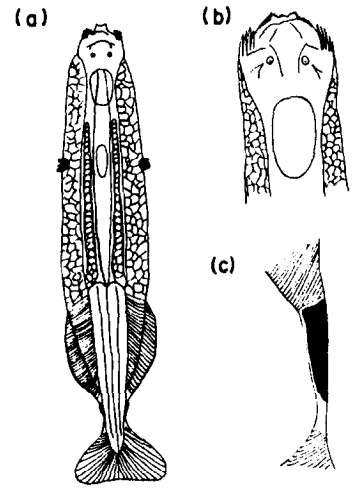
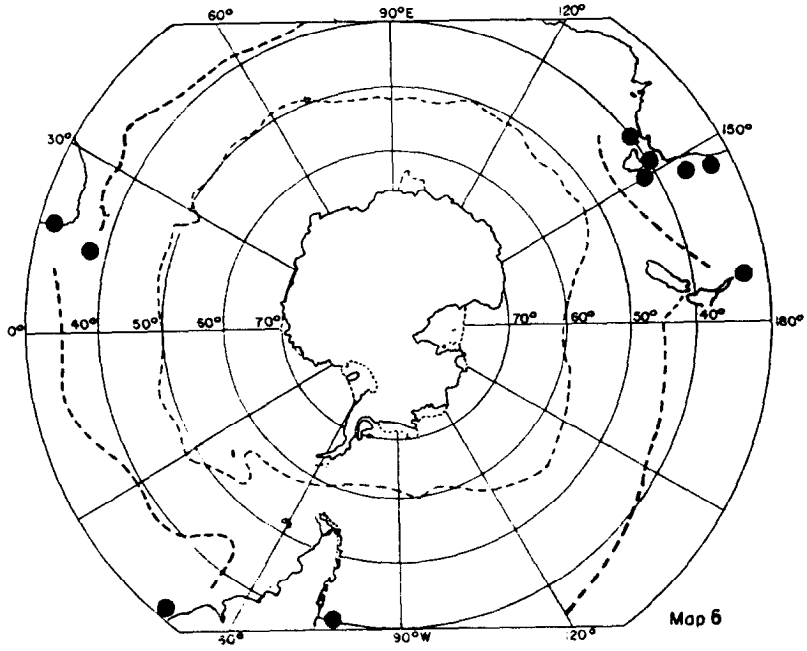


Figure 7. Pterosagitta draco (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 6. Distribution of P. draco.

Tail 32 to 38% of body length
Anterior teeth 4 to 9
Posterior teeth 8 to 17
Hooks 8 to 9
Seminal vesicles not touching tail fin
Ovaries when mature completely fill the body cavity, extending from tail septum to neck (Michael, 1919)
Collarette voluminous, all or part frequently missing, extending from head to anterior border of fins, confluent with fins
Corona oval behind head
Length up to 12mm (Thomson, 1947).

This cosmopolitan epiplanktonic species is found in warm and temperate oceanic regions (Alvarino, 1965). It has been reported from the Southern Ocean by Jameson (1914) and the south-eastern central Pacific (Alvarino, 1964a). Pterosagitta draco is not found south of the Antarctic Convergence (David, 1958b), and its southward extension in the Indian Ocean is limited by this oceanographic barrier (Alvarino, 1964c).

6.5 GENUS Krohnitta Ritter-Zahony 1910

Chaetognaths characterised by one pair of lateral fins reaching the seminal vesicles posteriorly but not the ventral ganglion anteriorly, one paired row of teeth, and no collarette, populates the upper strata, two species.

Key to species (Sund, 1959):

Body slender, transparent; fins very wide, rounded, widest at level of tail-septum; short ovary with rounded ova; collarette absent ..... K. subtilis (Grassi)

Body robust, opaque; fins not rounded, widest behind tail-septum; ovaries contain large cuboidal ova; collarette sometimes evident as a narow band of epidermal thickening extending from neck to anterior edge of fins (Au) ..... K. pacifica (Aida)

Krohnitta subtilis (Grassi 1883)

(Figure 8, Map 7)

Diagnostic Characters (Thomson, 1947):

Lateral fin does not reach ventral ganglion, reaches seminal vesicles posteriorly
Tail 29 to 40% of body length
Teeth 7 to 13
Hooks 7 to 10
Seminal vesicles relatively large, touching both tail and posterior fins (Fraser, 1952)
Ovaries are very short even in fully mature specimens
Collarette not present
Corona diamond-shaped, in the neck region (Fraser, 1952)
Length to 16.5mm (Fraser, 1952)

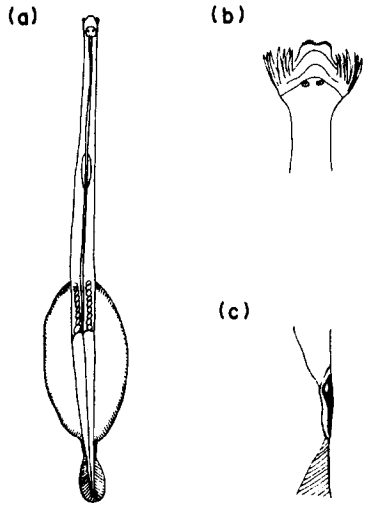
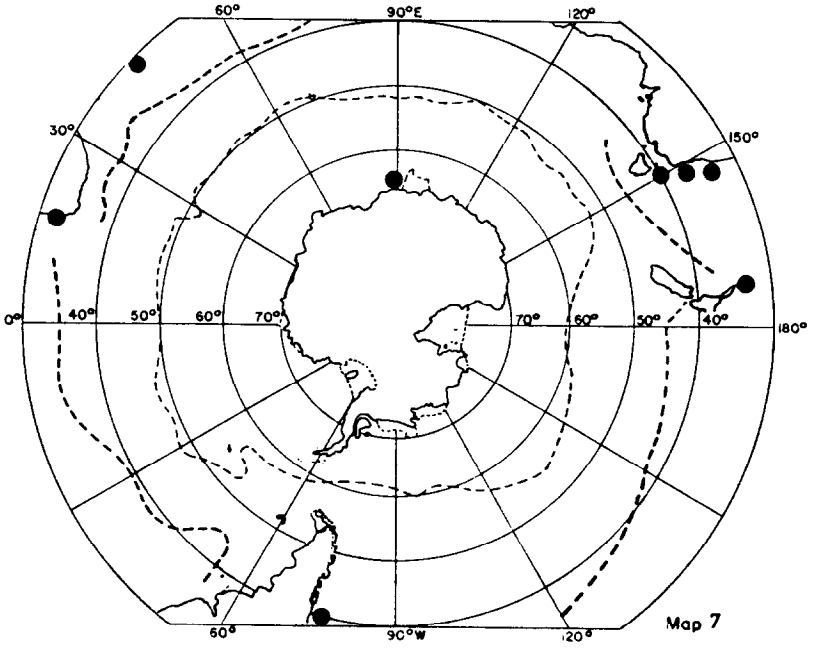


Figure 8. Krohnitta subtilis (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 7. Distribution of K. subtilis.

A cosmopolitan epiplanktonic species of warm and temperate oceanic regions (Alvarino, 1965), Krohnitta subtilis is uncommon in the Southern Ocean (David, 1965) being only reported from there by Ritter-Zahony (1911). It has also been found in the southeast central Pacific waters (Alvarino, 1964a), in the Indian Ocean (Alvarino, 1964c) and in the southern Atlantic Ocean (Thiel, 1938). It is usually in the 100 to 250m layer but is occassionally found in surface hauls (David, 1958b).

6.6 GENUS Sagitta Quoy & Gaimard 1827

Chaetognaths characterised by 2 pairs of lateral fins, the posterior on trunk and tail, 2 paired rows of teeth, no collarette. This is the most successful group as it appears to have the highest evolutionary level in the phylum, has the greatest number of species, and inhabits the greatest variety of environments throughout the ocean (Alvarino, 1964a). Sagitta neglecta Aida, a tropical species, was reported by Johnston & Taylor (1921) from 64°34'S, 117°1'E, and must be regarded as a case of mistaken identification (David 1958b). Taw (1975) described a new species S. guileri from Tasmanian waters and discussed its relation to S. neglecta.

Key to species:

1a) Hooks with serrated margins 2
b) Hooks without serrated margins 5

2a) Seminal vesicle with numerous short protruberances at anterior end 3
b) Seminal vesicle with one or two protruberances at anterior lateral end 4

3a) Ovaries long tubes extending to ventral ganglion; ovulae in two rows ..... S. tasmanica Thomson
b) Ovaries very fine tubes extending up to neck; ovulae in one row (Au,NZ,Pa,SAm) ..... S. pacifica Tokioka

4a) Seminal vesicle with one protruberance at anterior lateral end; ovaries extending to posterior end of anterior fins (Pa,SAm) ..... S. bierii Alvarino
b) Seminal vesicle with two protruberances at anterior lateral end; ovaries extending to anterior end of anterior fin ..... S. serratodentata Krohn

5a) Lateral fins joined by rayless crosspieces .. 6
b) Lateral fins separate 8

6a) Anterior fins reach ventral ganglion ..... S. maxima (Conant)
b) Anterior fins do not reach ventral ganglion . 7

7a) Both pairs of fins entirely rayless throughout at least their anterior thirds; tail usually exceeds 15 per cent of total length ..... S. lyra Krohn
b) Fins only rayless adjacent to body but not along outer margins, tail usually less than 15 per cent of total length ..... S. gazellae Ritter-Zahony

8a) Anterior fins entirely rayless ..... S. minima Grassi
b) Anterior fins not entirely rayless 9

9a) Anterior fins do not come within half of their own length of the ventral ganglion 10
b) Anterior fins extend almost or completely to ventral ganglion 12

10a) Tail more than 28 per cent of body length; head disproportionately large, much elongated anteriorly; numerous dark-brown teeth ..... S. macrocephala Fowler
b) Tail less than 28 per cent of body length; head proportionate, as wide as long 11

11a) Seminal vesicle touching tail fin; several anterior teeth, small and overlapping (Co) .. S. enflata Grassi
b) Seminal vesicle apart from both fins but nearer the posterior; anterior teeth few, large, dagger-shaped, spreading ..... S. hexaptera D'Orbigny

12a) Posterior fin reaches seminal vesicle..... 13
b) Posterior fin does not reach seminal vesicle 19

13a) Seminal vesicle in contact with tail fin 14
b) Seminal vesicle not in contact with tail fin 18

14a) Anterior of lateral fins rayless; no collarette (Au,NZ,Pa,SA,In) ..... S. bedoti Beraneck
b) Anterior of lateral fins completely rayless; collarette present 15

15a) Seminal vesicle with a distinct head (Au,Pa,SA,In) ..... S. ferox Doncaster
b) Seminal vesicle without a distinct head (Au,NZ,Pa,At,SA) ..... S. robusta Doncaster

16a) Collarette distinct; ovaries almost filling trunk cavity (Au,Pa,In) ..... S. ferox Doncaster
b) Collarette indistinct; ovaries short and club-shaped 17

17a) Pronounced constriction at tail-septum; sexually mature at a length of 5 to 6 mm (SAm) ..... S. tenuis Conant
b) No constriction at tail-septum; never sexually mature under 9 to 10 mm (SAm,At,SA) S. friderici Ritter-Zahony

18a) Collarette bulky, extends to anterior edge of head; posterior teeth less than 7 (Au,Pa,SA) S. regularis Aida
b) Collarette not extending to anterior edge of head; posterior teeth more than 10 (Au,SA,In) S. neglecta Aida

19a) Seminal vesicles in contact with tail fin ... 20
b) Seminal vesicles not in contact with tail fin 22

20a) Seminal vesicle is a low projection approaching close to posterior fin (Au,Pa) .. S. pulchra Doncaster
b) Seminal vesicle prominent, widely apart from posterior fin 21

21a) Fins completely rayed; collarette reaches seminal vesicles, thickening immediately in front of vesicle (Co) ..... S. bipunctata Quoy & Gaimard
b) Fins with anterior apices rayless; no thickening of collarette ..... S. decipiens Fowler

22a) Length of anterior fins less than 20% of total body length ..... S. marri David
b) Length of anterior fins more than 20% of total body length 23

23a) Posterior teeth usually more than 14; deep water form ..... S. zetesios Fowler
b)Posterior teeth usually less than 14; shallow water form ..... S. planctonis Steinhaus

Sagitta decipiens Fowler 1905

(Figure 9, Map 8)

Diagnostic Characters (Sund, 1959):

Anterior fins start just posterior to ventral ganglion
Posterior fins widest at level of tail septum, lying mostly on body segment, not reaching seminal vesicles
Tail 22 to 27% of body length
Anterior teeth 7 to 10 (5 to 10 Fowler, 1905) (8 to 11 Michael, 1919)
Posterior teeth 13 to 20 (12 to 18 Fowler, 1905) (19 to 22 Michael, 1919)
Hooks 5 to 7
Seminal vesicle prominent, widely apart from posterior fin, but touching tail fin, (wedge-shaped Fraser, 1957)
Ovaries short, not extending beyond anterior limit of posterior fins (Michael, 1919)
Collarette not extending to anterior edge of head, (very small Fraser, 1957)
Corona begins in the neck region (Fraser, 1952)
Length up to 12mm (Michael, 1919)

This mesoplanktonic, oceanic species is cosmopolitan in temperate and warm regions (Alvarino, 1965). It has been reported from the Subantarctic of the Atlantic (David, 1958b), Indian (David, 1958b; Alvarino, 1964c) and Pacific Oceans (Alvarino, 1964a). It is not found south of the Antarctic Convergence (David, 1958b) but is carried down by water movement into the northern part of the Subantarctic (David, 1965) where it lives at depths between 300 and 600m (Alvarino, 1964a).

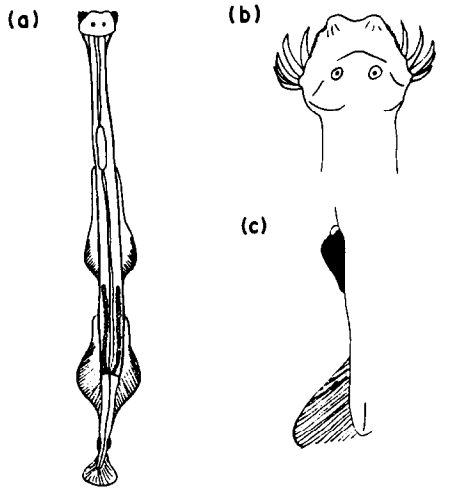
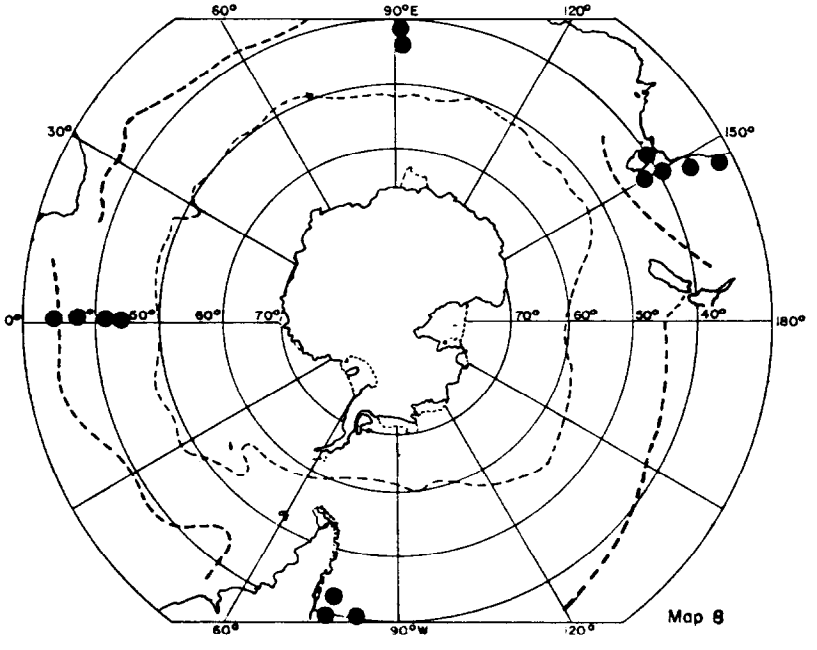


Figure 9. Sagitta decipiens (a) adult, dorsal view; (b) head, dorsal view ; (c) seminal vesicle, dorsal view.



Map 8. Distribution of S. decipiens.

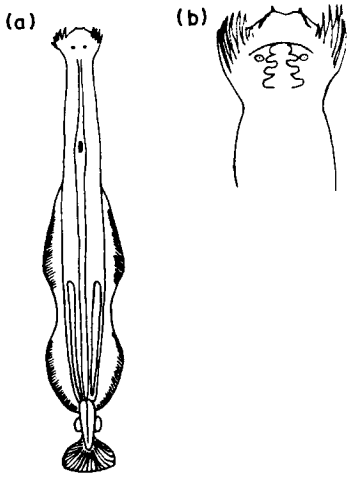
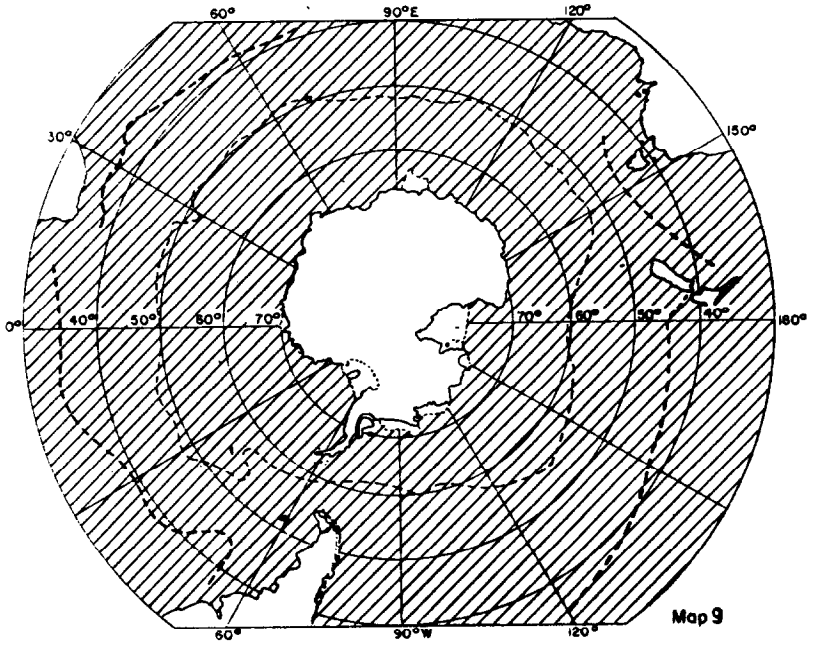


Figure 10. Sagitta gazellae (a) adult, ventral view; (b) head, dorsal view.



Map 9. Distribution of S. gazellae.

Sagitta gazellae Ritter-Zahony 1909

(Figure 10, Map 9)

(S. lyra Baldasseroni, 1915 part; Johnston & Taylor, 1921; Bollmann, 1934 part; Tokioka, 1940; Thomson, 1947 part; Fagetti, 1958; Bieri, 1959 part; David, 1959)
(Sagitta innom. Fowler, 1908)
(S. lyra "gazellae" type Tokioka, 1940)
(S. maxima group Thiel, 1938 part)
(S. hexaptera Steinhaus, 1900; Fowler, 1907; Germain, 1913)

Diagnostic Characters (David, 1955):

Anterior fins rayless adjacent to body but not along outer margins, do not reach ventral ganglion, joined to posterior fins by rayless crosspiece
Posterior fins rayless adjacent to body but not along outer margins, do not reach seminal vesicles posteriorly
Tail usually less than 15% of body length (Michael, 1919; Burfield, 1930)
Anterior teeth up to 7, usually 4 to 6
Posterior teeth up to 10
Hooks up to 14
Seminal vesicles midway between posterior and caudal fins
Ovaries extend up to 40% of body length
Collarette not present
Corona complex, near to eyes
Length up to 105 mm.

Sometimes Sagitta gazellae has been confused with other species. David (1955) completely redescribed S. gazellae and showed that it was separate from S. lyra. Alvarino (1962a) has given a descriptive account and pointed out the differences between it and S. maxima, S. lyra and S. scrippsae (see Table 2). These species can be separated by the tail length as a percentage of body length and by the number of posterior teeth. Because of their geographical localities, the S. lyra recorded by Johnston & Taylor (1921), Tokioka (1940) and David (1959) are probably S. gazellae (Alvarino, 1964c).

S. gazellae is found in the Antarctic and Subantarctic and extends into deep waters of the southern part of the Pacific, Atlantic and Indian Oceans (David 1955, 1958b; Alvarino 1964b, 1965). Its circumpolar distribution is restricted to the north by the region of the Subtropical Convergence and to the south by the Antarctic neritic zone with a maximum abundance in the Subantarctic (David, 1958b). It is much less numerous in the region of the Antarctic Convergence (David, 1965). S. gazellae is found in a fairly wide temperature range (from -1.5 to +10°C) and salinity range (33.6 to 34.7o/oo) but it is most frequently found in waters with temperatures from -1.5 to 14°C and salinities between 33.9 and 34.3o/oo (Timonin, 1968).

In the Southern Ocean S. gazellae exists in two races or forms which can be distinguished in all but the very young stages by small anatomical differences (David, 1955). The southern form is predominantly Antarctic and is larger at maturity than the predominantly Subantarctic northern form (David, 1955, 1958b, 1965).

It is epiplanktonic (Alvarino, 1964a) and is most numerous in the 50 to 100m layer and displays no diurnal vertical migration (David, 1965). The maturity stages are given by David (1955) who observed mature specimens only in deep waters. It may be assummed that the eggs are laid in deep waters and the newly

Character	Species			
	S. maxima Conant 1896	S. lyra Krohn 1853	S. gazellae Ritter-Zahony 1909	S. scrippsae Alvarino 1962
Total length when mature (mm)	>90	38	82	60
Per cent tail	19-25	>15	<15	<15
Anterior fins	Begin level with the middle of the ventral ganglion. Connected with posterior fins.	Close to the posterior end of the ventral ganglion. Connected with posterior fins by a wide bridge.	Separated from posterior end of ventral ganglion. Connected with posterior fins by a narrow bridge.	As in S. gazellae.
Posterior fins	Triangular in shape, a thick central rayless zone. Located more on the trunk than on the tail. The outer part is rayed.	As in S. maxima in shape but with rays in the outer part and posterior end. The anterior portion is rayless.	As in S. maxima but the rayed area extends forward.	As in S. gazellae.
Collarette	Absent	Absent	Absent	Present
Ovaries	Long and fine tubes.	Long tubes, broader than in maxima reaching the anterior end of anterior fins.	Long, but not filling completely body cavity. Reaching up to ventral ganglion.	As in S. gazellae. Reaching up to near the neck region.
Seminal vesicles	Ovoid, close to the posterior fins, separated from tail fin.	Separated from both posterior and tail fins, but closer to the posterior fins.	Halfway between posterior fins and tail fin, but closer to posterior fins. Slightly protandric.	At the middle of the tail segment, closer to the posterior fin. Protandric.
Eyes	Large oval. Pigmented region very small, fungiform peripherical cells round and larger than in S. lyra.	Ellipsoidal in shape. Pigment disposed in an X with two branches towards the centre smaller. Peripherical cells small.	Oval, with strong pigment disposed into a knob shape and extending diffusely around, giving to the whole a roundish shape.	Oval. Pigment in an arrow shape with the wing toward the side, but lighter wings appear also toward the center of the head.
Distribution	Cold waters. Deep layers beneath warmer areas.	Tropical, subtropical warm waters.	Antarctic, Subantarctic waters.	Subarctic and California waters.

Table 2. Principal diagnostic characters of the "maxima group" (Alvarino, 1962).

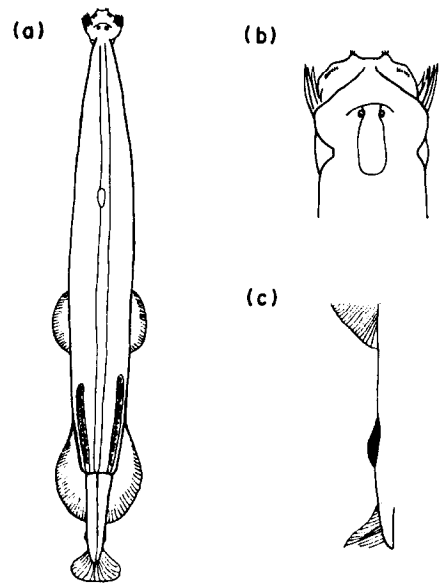
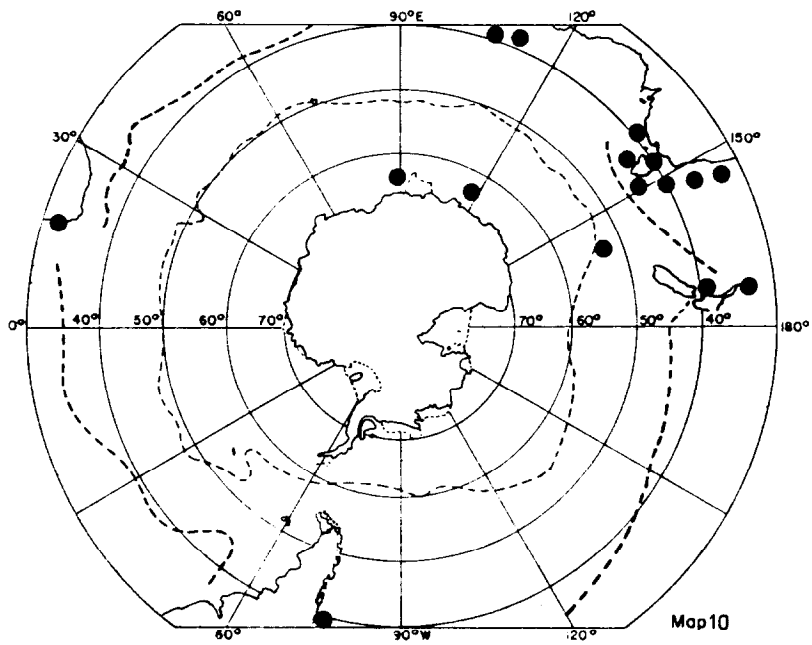


Figure 11. Sagitta hexaptera (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 10. Distribution of S. hexaptera.

hatched individuals rise to the surface (Alvarino, 1964a, 1965). This ontogenetic distribution was described in detail by David (1955). Details on racial characteristics, life history, growth rate and food are given by David (1955).

With the possible exception of S. maxima, S. gazellae is the largest known chaetognath (Burfield, 1930) reaching over 105mm in total length in Antarctic waters and 68mm in Subantarctic waters (David, 1955).

Sagitta hexaptera D'Orbigny 1843

(Figure 11, Map 10)

Diagnostic Characters (Sund, 1959):

Anterior fins widely separated from ventral ganglion, narrow and rounded
Posterior fins not joining seminal vesicle
Tail 15 to 22% of body length
Anterior teeth 1 to 4 (characteristically long and pointed, Burfield, 1930)
Posterior teeth 1 to 4
Hooks 4 to 8
Seminal vesicles rounded knobs near tail, well separated from posterior fins (Fraser, 1952)
Ovaries narrow, containing round ova, extending to posterior end of anterior fin when mature
Collarette absent (Fraser, 1952)
Corona pear-shaped, beginning beside the eyes and extending to the neck region (Fraser, 1952)
Length up to 63mm (Thomson, 1947).

David (1958b) points out that the reports of Sagitta hexaptera from the Antarctic by Fowler (1907), Germain (1913) and Johnston & Taylor (1921) may be explained by fin damage which confused the workers into incorrectly identifying specimens of S. gazellae with S. hexaptera. He suggests confusion caused by incorrect labelling in the case of Ritter-Zahony (1911).

This species is cosmopolitan, inhabiting the epiplanktonic zone of temperate and warm regions of the ocean (Alvarino, 1965). It is not usually found south of the Antarctic Convergence (David, 1958b), although David (1959) reported some specimens from the Antarctic. Alvarino (1964a) found it in the southern parts of the Pacific and Indian Oceans. It seems to have considerable tolerance for the colder parts of its range where it is mainly an inhabitant of the surface waters (David, 1958b) though in the Subantarctic it is found between 150 and 283m (Alvarino, 1964a).

Sagitta lyra Krohn 1853

(Figure 12, Map 11)

(S. lyra var. gazellae Ghirardelli, 1959)
(S. maxima, Thiel, 1938 part)

Diagnostic Characters:

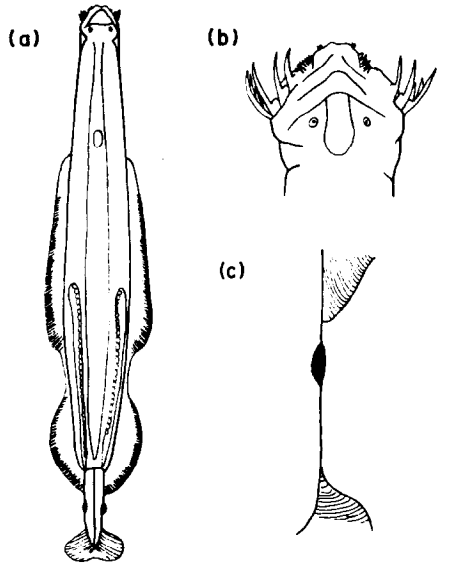
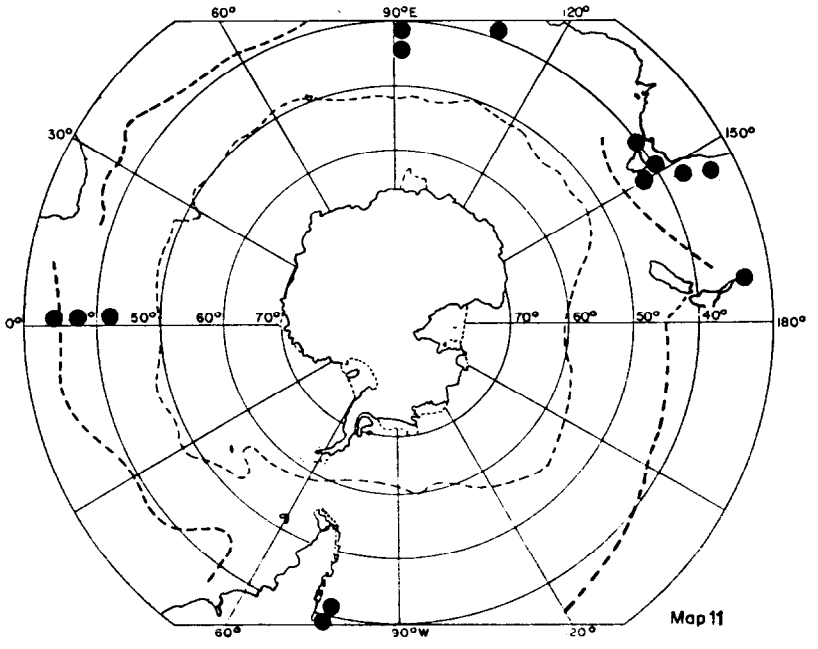


Figure 12. Sagitta lyra (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 11. Distribution of S. lyra.

Anterior fins are entirely rayless throughout at least their anterior third, do not reach ventral ganglion and are joined by a rayless crosspiece
Posterior fins are entirely rayless throughout at least their anterior third, close to, or touching seminal vesicles (Sund, 1959)
Tail usually more than 15% of body length (David, 1955)
Anterior teeth 4 to 5 (Sund, 1959)
Posterior teeth 3 to 9 (Sund, 1959)
Hooks up to 9 (Fraser, 1952)
Seminal vesicle ovate (Fraser, 1957), near to posterior fin, separate from caudal fin (David, 1955)
Ovaries long and thin (Fraser, 1952)
Collarette not present (Fraser, 1957)
Corona simple, pear-shaped, near to eyes (David, 1955)
Length up to 42mm (David, 1955)

The differences between Sagitta lyra and closely related species have already been discussed in the S. gazellae section (see Table 2). This oceanic species has a worldwide distribution in tropical and subtropical waters (David, 1955; Alvarino, 1965). It has been found in the Subantarctic (David, 1958b, 1959) and the southwestern waters of the Indian Ocean (Alvarino, 1964c). It does not usually occur south of the Antarctic Convergence (David, 1958b, 1959). It inhabits the water layers below 100m, though it is infrequent below 500m (David, 1958b)

Sagitta macrocephala Fowler 1905

(Figure 13, Map 12)

Diagnostic Characters (Fraser, 1952):

Anterior fins small, start well behind ventral ganglion
Posterior fins much bigger than anterior two, have inner rayless zone
Tail 30 to 34% of body length
Anterior teeth 6 to 10
Posterior teeth 20 to 38
Hooks 10 to 12
Seminal vesicles situated just behind the posterior fin, widely separated from tail fin (Tokioka, 1939), wedge-shaped (Fraser, 1957)
Ovaries long and thick
Corona yet to be described
Length up to 20mm.

This is an easily recognisable form due to its large head (Fraser 1952). It is a cosmopolitan deepwater mesoplanktonic oceanic species (Alvarino, 1965). The Antarctic specimens appear to be identical with those from other oceans (David, 1958b). It is not common in the Southern Ocean occurring sporadically at depths between 750 and 1500m (David 1965). This species has been reported from the Southern Ocean (Ritter-Zahony, 1911; David, 1958b, 1959; Alvarino 1964a) and the southern waters of the Pacific Ocean (Alvarino, 1964a). Johnston and Taylor (1921) recorded two specimens from a depth of about 200m but this must be regarded as a mistake in identification as no other specimens have been taken at such a shallow depth (David 1958b). On the other hand, Alvarino (1965) points out that upwelling occasionally brings specimens from deep layers to strata upper than those usually inhabited by the species. It is slightly more frequent in the Subantarctic than in Antarctic waters (David 1959, 1965) and is reported to have a red or orange gut when fresh (Fraser, 1957).

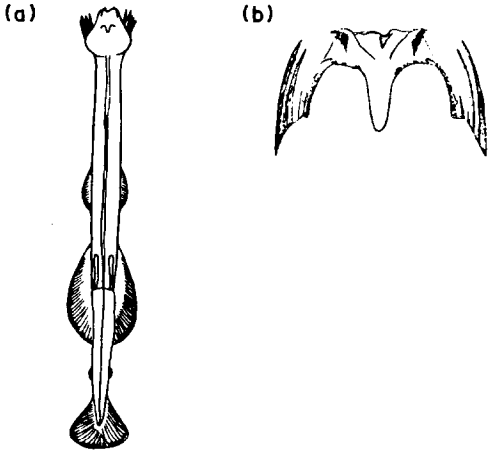
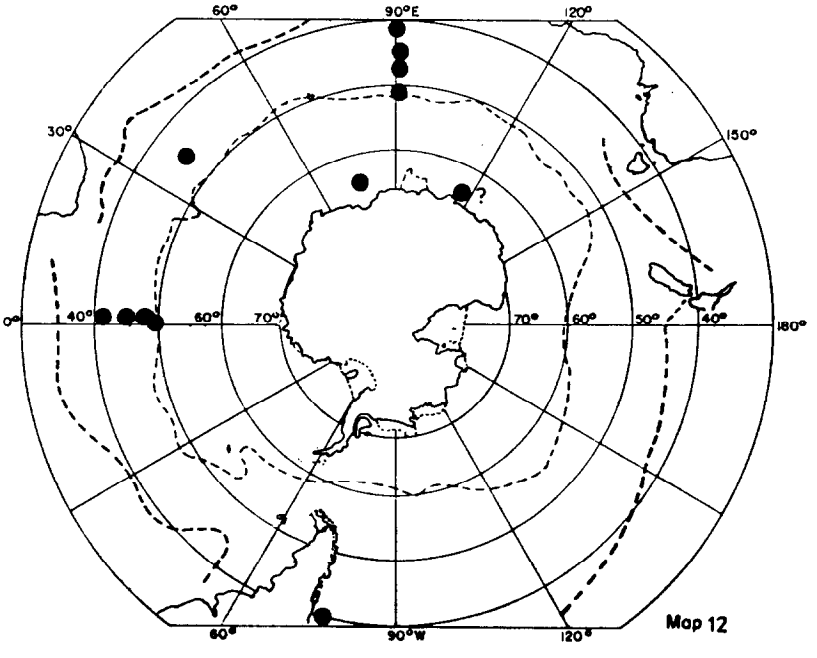


Figure 13. Sagitta macrocephala (a) adult, ventral view; (b) head, ventral view.



Map 12. Distribution of S. macrocephala.

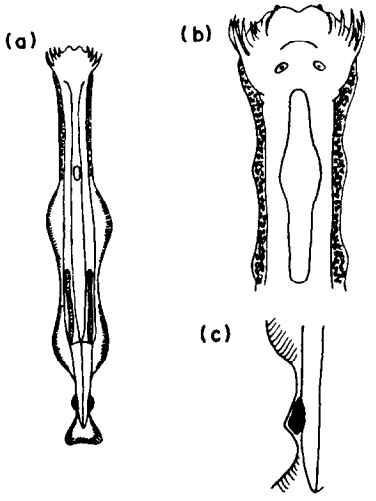
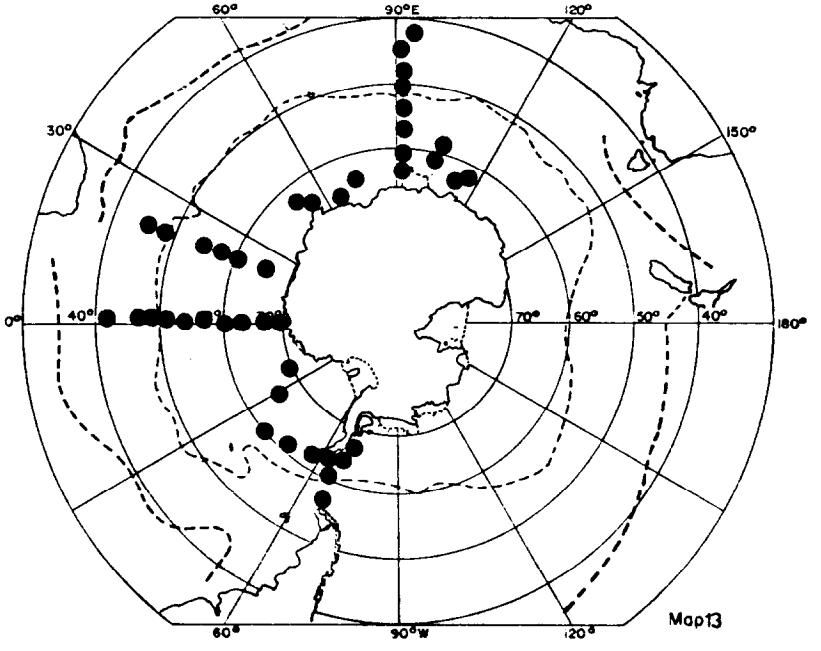


Figure 14. Sagitta marri. (a) adult, ventral view; (b) head, dorsal view ; (c) seminal vesicle, dorsal view.



Map 13. Distribution of S. marri.

Sagitta marri David 1956

(Figure 14, Map 13)

(Sagitta zetesios Fowler, 1907)
(Sagitta planctonis (non Steinhaus) Ritter-Zahony, 1911 part; Jameson, 1914;Johnstone & Taylor, 1921; Burfield, 1930 part; Bollmann, 1934 part; Mackintosh, 1937; Thiel, 1938 part)
(Sagitta planktonis Hardy & Gunther, 1936)

Diagnostic Characters (David, 1956):

Anterior fin completely rayed, rounded, begins slightly behind the ventral ganglion, length 10 to 19% of body length
Posterior fin rounded
Tail slender, 20 to 28% of body length
Anterior teeth up to 8, usually 6 to 7
Posterior teeth up to 17, usually 14 to 15
Hooks 7 to 11, usually 8 to 9
Seminal vesicles conical, very close to tail fin
Ovaries observed up to ventral ganglion
Collarette prominent between head and anterior fins, but very thin on remainder of the body
Corona commences at the posterior end of the head and reaches about 1/3 of the distance to the ventral ganglion
Length up to 28.5mm.

David (1956) described this species and separated it from synonomy with Sagitta planctonis, a surface living form of tropical and subtropical waters, and S. zetesios a deep water form also of warm latitudes (see Table 3). The following discussion is taken from this paper. "The group are all robust chaetognaths, usually opaque and white when preserved, having an extensive collarette which in well preserved specimens extends to the tail and in all specimens to the anterior fins. At all sizes above about 8mm S. marri can be distinguished by the shape and position of the seminal vesicles, the shape of the fins, the length of the anterior fins and the total length at maturity."

It is an endemic, mesobathyplanktonic Antarctic chaetognath with a circumpolar distribution (Alvarino, 1965). Sagitta marri has been reported from the Southern Ocean by David (1958b, 1959), Alvarino (1964a), Timonin (1968) and Dinofrio (1973). The main concentrations are found well south of the Antarctic Convergence at depths of about 250 to 500m and occasional specimens at 1000 to 1500m, with only small numbers in the uppermost 100m (David, 1959, 1965; Alvarino, 1965). The northern limit of the main concentrations of this species is south of the Antarctic Convergence but occasional specimens stray into deep water in the sub-Antarctic zone (David, 1959). Timonin (1968) found S. marri in waters with temperatures of -0.5 to +2.5°C and salinities ranging from 34.3 to 34.8o/oo with maximum numbers generally associated with salinities of 34.5 to 34.7o/oo.

Sagitta maxima (Conant 1896)

(Figure 15, Map 14)

Diagnostic Characters: (Sund, 1959):

Character	Species		
	S. planctonis Steinhaus 1896	S. zetesios Fowler 1905	S. marri David 1956
Total length when mature (mm)	37	40	28.5
Per cent tail	19-21	20-23	20-28
Anterior fins	Rayless at the anterior end and along the inner edge, begins at ventral ganglion.	Rayless or very sparsely rayed at the anterior end beginning at or about ventral ganglion.	Completely rayed, rounded, begins slightly behind the ventral ganglion.
Posterior fins	Sharply triangular, apex of fin level with or slightly behind tail septum.	Triangular, apex of fin level with tail septum.	Rounded
Anterior teeth	6-8 (9)	8-10 (12)	6-7 (8)
Posterior teeth	10-12 (14)	15-19 (22)	14-15 (17)
Hooks	8-11 (11)	8-10 (11)	8-9 (11)
Seminal vesicles	Elongate in contact with posterior fin.	As in S. planctonis	Conical, very close to tail fin.
Ovaries	Completely fill body cavity when fully mature.	Reach to half way between head and ventral ganglion.	Reach up to ventral ganglion.
Collarette	Very prominent, extending to tail in fully grown specimens.	As in S. planctonis	Prominent between head and anterior fins, but very thin on remainder of the body.
Distribution	A surface living form of tropical and sub-tropical waters.	A deep living form found in most deep oceans, but absent from the Antarctic.	Extends from surface down to about 1,500m, a purely Antarctic form.

Table 3. Principal diagnostic characters of the "planctonis group" (after David, 1956).

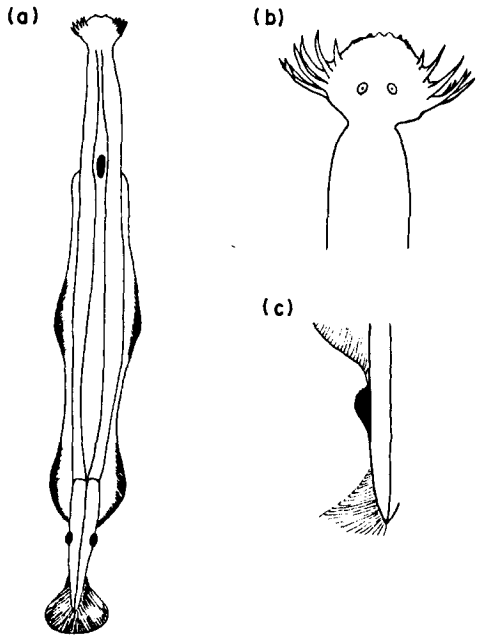
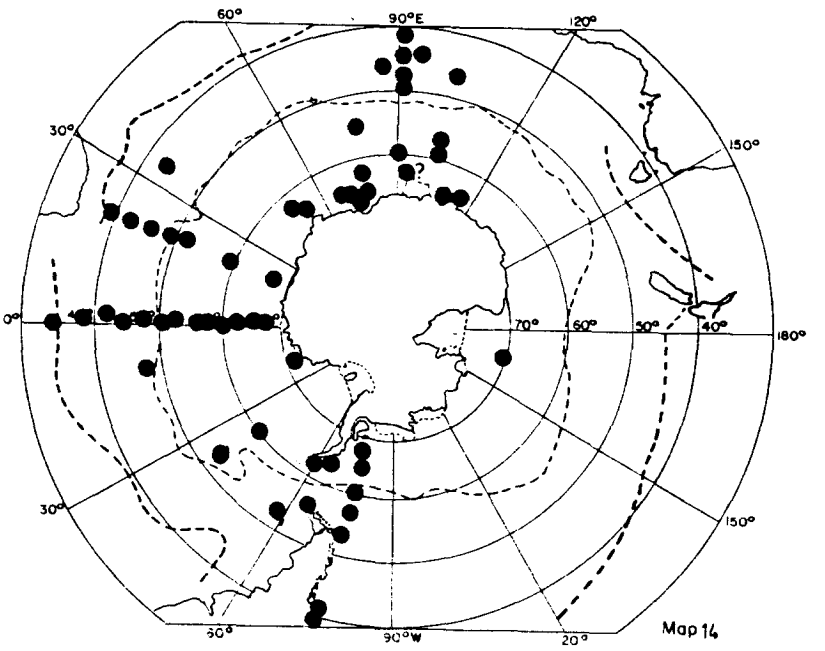


Figure 15. Sagitta maxima (a) adult, ventral view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 14. Distribution of S. maxima.

Anterior fins reach ventral ganglion, joined to posterior fins by rayless crosspiece
Posterior fins broadest behind the tail septum (Fraser, 1952)
Tail over 20% of body length (Burfield, 1930)
Anterior teeth up to 6, usually 4 to 5 (David, 1958b)
Posterior teeth do not exceed 8 in number on each side (Burfield, 1930)
Hooks up to 7, usually 5 to 6 (David, 1958b)
Seminal vesicles ovoid, close to posterior fin (Fraser, 1952)
Ovaries long and thread-like when mature (Fraser, 1952)
Collarette absent (Fraser, 1952)
Corona short and pear-shaped, beginning beside the eyes and scarcely extending on to the body (Fraser, 1952)
Length up to 55 mm in Antarctic (David, 1958b).

Confusion between this species and its close relatives Sagitta lyra and S. gazellae has lead to some mistakes in identification but S. maxima can be differentiated by its greater tail segment percentage, the position of commencement of the anterior fins, and the position of the seminal vesicles (see Table 2). S. maxima has sometimes been called the Subantarctic counterpart of S. marri (David, 1965).

This species is one of the largest chaetognaths (Burfield, 1930), but the Southern Ocean form of this species is considerably smaller than its Arctic counterparts, the latter being reported at more than 90mm in length (Fraser, 1952), whereas 55mm appears to be the maximum length of the southern form (David 1958b, 1959).

S. maxima is a cosmpolitan meso- or bathypelagic form (Alvarino, 1965) which changes its depth distribution with latitude in a way similar to E. hamata (Alvarino, 1964a). It has been taken in surface hauls on isolated occasions at Heard Island where it has presumably been carried up from deeper waters (Ealey & Chittleborough, 1956). David (1958b, 1965) gives the northern limit as usually just north of the Subtropical Convergence and the southern limit as not usually far south of the Antarctic Convergence, but it does frequently occur in Antarctic waters. It has been found in the south-east central waters of the Pacific (Alvarino, 1964a). It is most numerous between 150 and 500m but it is found in small numbers to 1500m as it breeds at depth around 1000m in the Southern Ocean (David, 1965). David (1958b) suggests that its typical habitat is in Antarctic intermediate waters and this is supported by Timonin (1968) who found S. maxima in waters with salinities of from 34.0 to 34.9o/oo and temperatures ranging from +1 to +8°C.

Sagitta minima Grassi 1881

(Figure 16, Map 15)

Diagnostic Characters (Sund, 1959):

Anterior fins entirely rayless, narrow, tapered but rounded, removed from ventral ganglion
Posterior fins not reaching seminal vesicles, of greatest width behind tail-septum (Michael, 1919)
Tail 16 to 24% of body length (to 27%, Thomson, 1947)
Anterior teeth 2 to 5
Posterior teeth 3 to 11

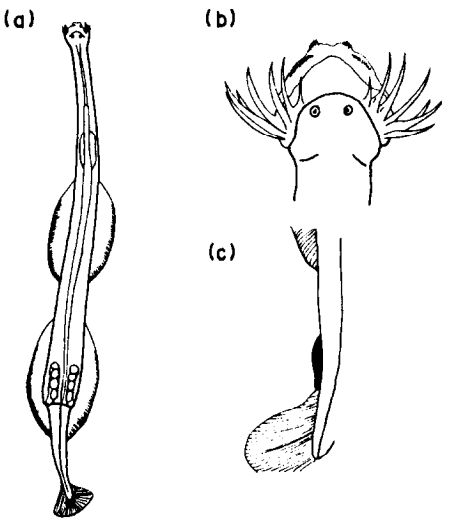
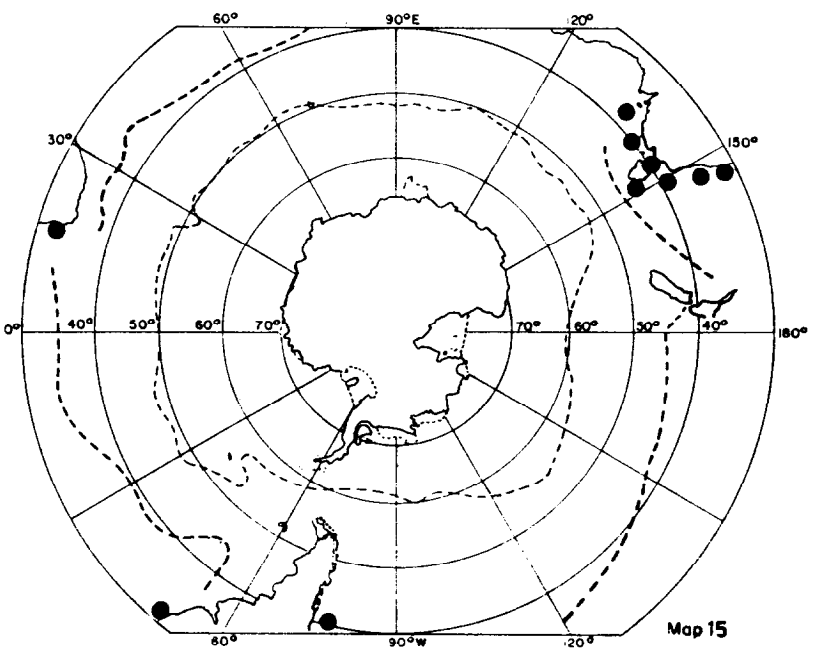


Figure 16. Sagitta minima (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 15. Distribution of S. minima.

Tail 16 to 24% of body length (to 27%, Thomson, 1947)
Anterior teeth 2 to 5
Posterior teeth 3 to 11
Hooks 5 to 8
Seminal vesicles connected to tail fins
Ovaries short, when mature they appear to contain 3 to 5 large, round ova
Collarette absent (Michael, 1919)
Corona yet to be described
Length to 9.5 mm (Michael, 1919).

Another cosmopolitan oceanic epiplanktonic species (Alvarino, 1965). It is not usually found south of the Antarctic Convergence though it is common in the subtropics of the Southern Hemisphere (David, 1958b).

Sagitta planctonis Steinhaus 1896

(Figure 17, Map 16)

(S. zetesios David, 1959 part)

Diagnostic Characters (David, 1956):

Anterior fin rayless at the anterior end and along the inner edge, begins at the ventral ganglion, length 24 to 32% of body length
Posterior fin sharply triangular, apex of fin level with or slightly behind tail septum
Tail stout, 19.2 to 21.4% of body length
Anterior teeth up to 9, usually 6 to 8
Posterior teeth up to 14, usually 10 to 12
Hooks up to 11, usually 8 to 11
Seminal vesicles elongate, in contact with posterior fins, simple
Ovaries completely filling body cavity when fully mature
Collarette very prominent, extending to the tail in fully grown specimens
Corona commences at the posterior end of the head and extends to about half way between the head and the ventral ganglion
Length up to 37 mm.

David (1956) added a revision of this species when describing Sagitta marri. He also pointed out the first published orthography, planctonis with a "c" must stand over planktonis with a "k". S. planctonis can be differentiated from S. zetesios in the number of posterior teeth (David, 1956), the length of the tail segment, the position of commencement the anterior fins, and the shape of the posterior fins (Alvarino, 1964a) (see Table 3).

This mesoplanktonic species extends along the southernmost parts of the Indian, Pacific and Atlantic Oceans (Alvarino, 1964a,c, 1965). In this area it has often been confused with Sagitta zetesios. It is found in the Subantarctic usually below 250m (David, 1955), but upwellings may take it higher (Alvarino, 1965).

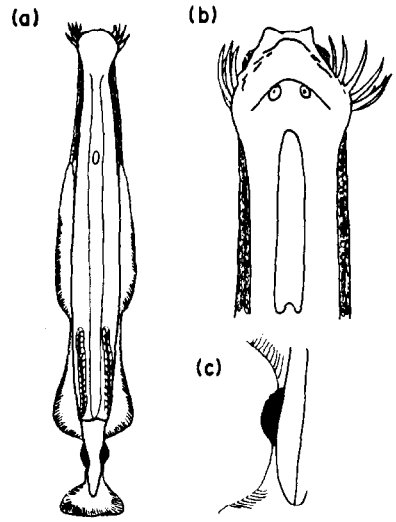
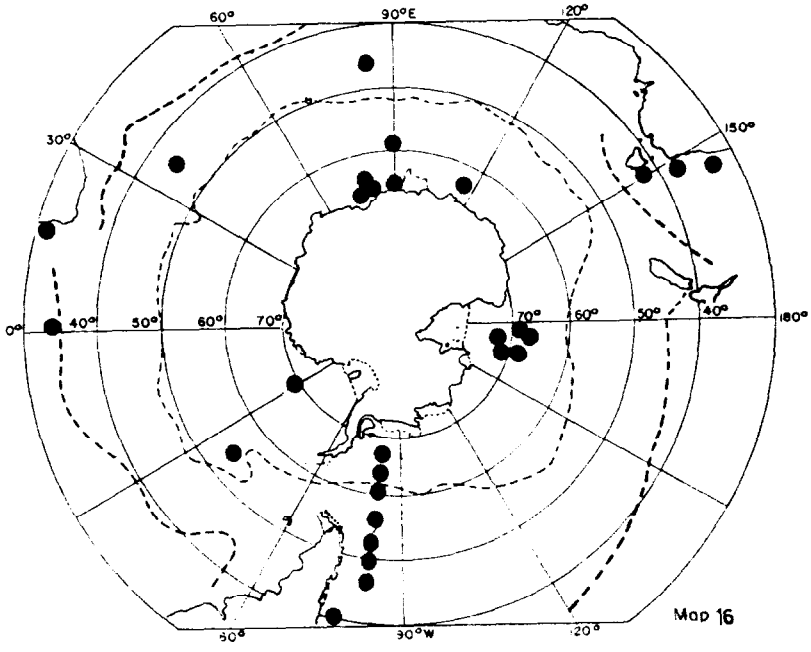


Figure 17. Sagitta planktonis (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, dorsal view.



Map 16. Distribution of S. planktonis.

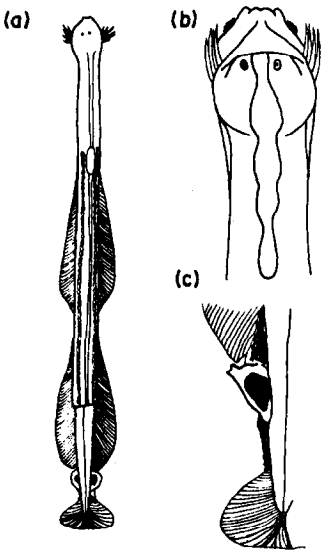
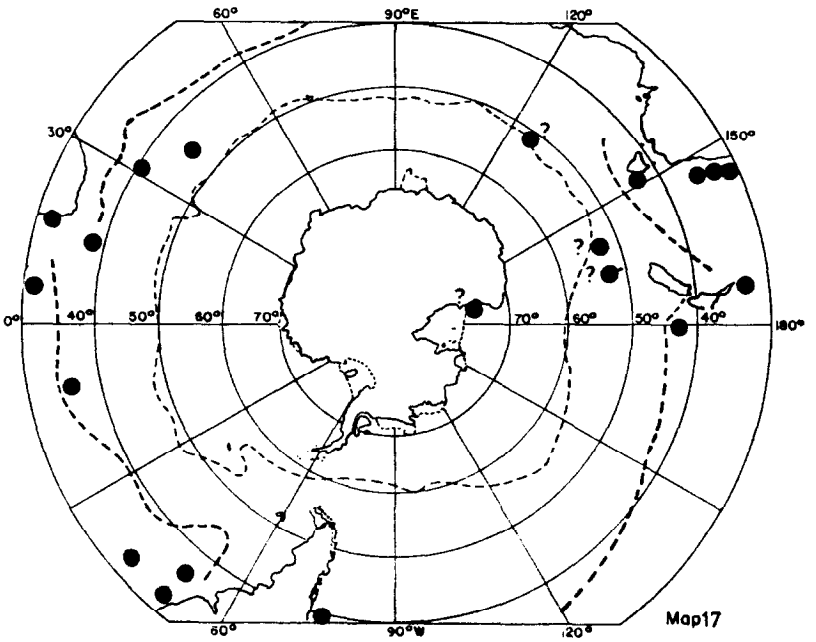


Figure 18. Sagitta serratodentata (a) adult, dorsal view; (b) head, dorsal view; (c) seminal vesicle, ventral view.



Map 17. Distribution of S. serratodentata.

Sagitta serratodentata Krohn 1853

(Figure 18, Map 17)

(S. serratodentata var atlantica Baldessoroni, 1915; Tokioka, 1940; Thomson, 1947)

Diagnostic Characters (Alvarino, 1961):

Anterior fins begin just behind the ventral ganglion, incompletely rayed at the front end and inner edges (Fraser, 1952)
Posterior fins long, rounded, about same length on tail as on trunk
Tail 23 to 26% of body length, (22 to 30%, Pierott-Bults, 1974)
Anterior Teeth 7 to 10 (Fraser, 1952), (3 to 10, Pierrott-Bults, 1974)
Posterior Teeth 22, usually 10 to 19 (Fraser, 1952), (5 to 20, (Pierrott-Bults, 1974)
Hooks serrated, 6 to 7 (Fraser, 1952), (5 to 9, Pierrott-Bults, 1974)
Seminal vesicles separated from tail fin, close to posterior fins, two prominences at anterior lateral corner, thickening of collarette tissue in front of anterior end
Ovaries long tubes extending to anterior end of anterior fins, ovulae small and in one row
Collarette small (Fraser, 1952)
Corona long and sinuous, beginning between the eyes (Fraser, 1952)
Length 10-13mm.

There has been much confusion between Sagitta serratodentata and its close relatives S. pacifica, S. pseudoserratodentata, S. bierii and S. tasmanica. Table 4 gives the principal differential characteristics of this "Serratodentata" group. This group is characterised by having hooks with serrated margins but each species can be differentiated by length at maturity, head armature and position and shape of the seminal vesicles. Pierrot-Bults (1974) discusses the taxonomy and zoogeography of certain members of this group and subdivided S. serratodentata into two subspecies (S. serratodentata serratodentata Krohn, 1853 and S. serratodentata atlantica Thomson, 1947). The atlantica form is found near Australia and New Zealand and more eastward in temperate waters of the Pacific, while the serratodentata form is found in the Mediterrean and Atlantic, generally between 40°N and 25°S.

S. serratodentata is an oceanic epiplanktonic chaetognath, typical of temperate and warm waters (Alvarino, 1965). It normally inhabits the surface water and is not found south of the Antarctic Convergence (David, 1958b). Burfield (1930) reported S. serratodentata from the Antarctica but this record was probably due to contamination from a more northerly sample (David, 1958b). The Antarctic records of S. serratodentata by David (1958b, 1959) are actually S. tasmanica (Alvarino, 1965).

Sagitta tasmanica Thomson 1947

(Figure 19, Map 18)

(S. serratodentata tasmanica type Thomson, 1947)
(S. serratodentata var. tasmanica Heydorn 1959)
(S. serratodentata Ritter-Zahony, 1911 part; Jameson, 1914 part; Johnston & Taylor, 1919 part; Burfield, 1930 part; Bollman, 1934 part; David, 1958b, 1959)
(S. selkirki Fagetti, 1958)

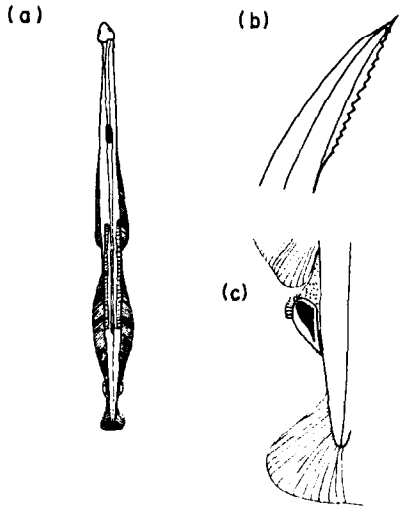
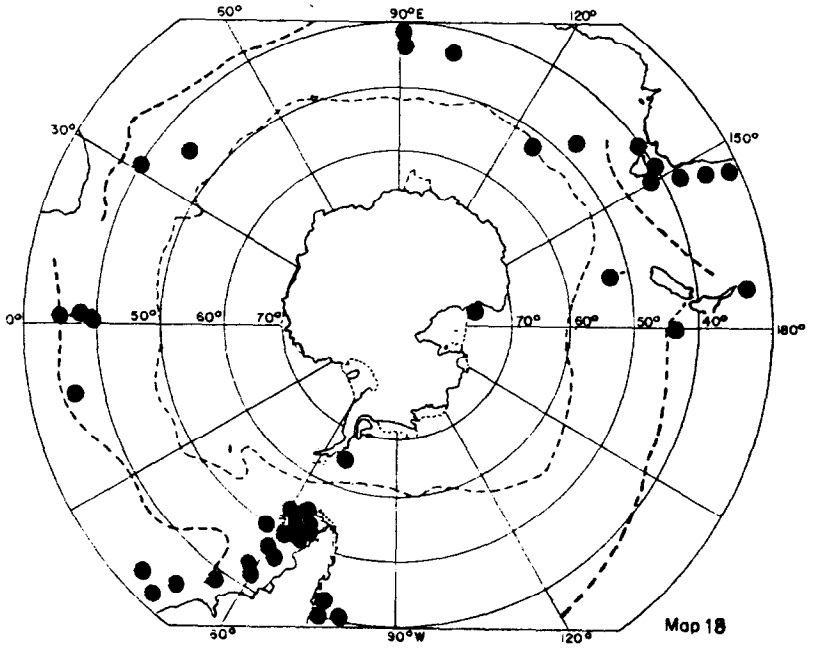


Figure 19. Sagitta tasmanica (a) body, ventral view; (b) hook; (c) seminal vesicle, ventral view.



Map 18. Distribution of S. tasmanica.

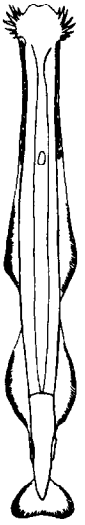
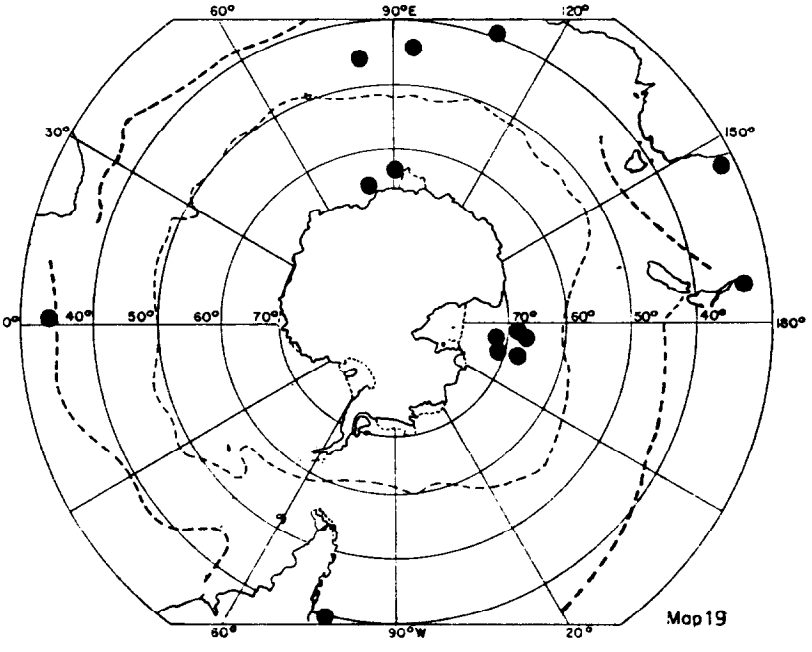


Figure 20. Sagitta zetesios adult, dorsal view.



Map 19. Distribution of S. zetesios.

Diagnostic Characters (Alvarino, 1961):

Anterior fins begin just behind the ventral ganglion
Posterior fins continuous with anterior fins by extremely narrow connection, not visible under low power magnification, and in badly preserved specimens more on tail than trunk
Tail 22 to 26% of body length, (20 to 30%, Pierrott-Bults, 1974)
Anterior teeth 7 to 9 (Thomson, 1947), (2 to 9, Pierrot-Bults, 1974)
Posterior teeth 13 to 19 (Thomson, 1947), (3 to 15, Pierrot-Bults, 1974)
Hooks with serrated margins, 6 to 9 but usually 6 to 8 (Thomson, 1947)
Seminal vesicles close to posterior fins, separated from tail fin, numerous short protruberances
Ovaries long tubes extending to ventral ganglion, ovulae in two rows
Collarette well apparent
Corona yet to be described
Length 15 to 20mm (Alvarino, 1969 records 28 to 33mm).

The similarity of this species with Sagitta serratodentata has already been discussed (see Table 4). It is an oceanic epiplanktonic species typical of Subantarctic waters and the southernmost parts of the Indian and Pacific Oceans (Alvarino, 1964a,c). It is also found in the high latitudes of the North and South Atlantic but there seems to be no connection between these two populations of S. tasmanica (Pierrot-Bults, 1974). The Subtropical Convergence acts as a barrier to the northward extension of the species (Alvarino, 1965).

Sagitta zetesios Fowler 1905

(Figure 20, Map 19)

(S. planctonis Ritter-Zahony, 1911 part; Burfield, 1930; Bollmann, 1934 part; Thiel, 1938 part; Tokioka, 1940 part, Thomson, 1947 part; Fagetti, 1958; Sund,1961)

Diagnostic Characters (David, 1956):

Anterior fin rayless or very sparsely rayed at the anterior end, beginning at or about the ventral ganglion, length 20 to 26% of body length
Posterior fin triangular, apex of fin level with tail septum, not extending back to seminal vesicles
Tail stout, 20 to 23% of body length
Anterior teeth up to 12, usually 8 to 10
Posterior teeth up to 22, usually 15 to 19
Hooks up to 11, usually 8 to 10
Seminal vesicles shape not known, but remnants of vesicles indicate that it is in contact with the posterior fin, elongate and of similar dimensions to that of S. planctonis
Ovaries longest observed reach to half way between head and ventral ganglion
Collarette very prominent, extending on to the tail in large specimens
Corona similar to S. planktonis
Length up to 40mm.

This cosmopolitan mesoplanktonic species found in temperate and warm oceanic regions is often included under the Sagitta planctonis synonym (Alvarino, 1965). Table 3 gives the differences between these 2 species. It is found in deep water, usually below 750m, and is not found south of the Antarctic Convergence (David, 1958b, 1959, 1965).

Character	Species				
	S. serratodentata Krohn 1853	S. pseudoserratodentata Tokioka 1939	S. pacifica Tokioka 1940	S. tasmanica Thomson 1947	S. bierii Alvarino 1961
length when mature (mm)	10-13	7-10	12-14	15-20	11-17
Per cent tail	23-26	26-29	23-26	22-26	20.5-23.3
Body shape	Same width from head to tail septum.	Same	Same	Same	Neck region long, thin. Body widest at ovary region.
Collarette	Well apparent	Smaller than in S. serratodentata	As in S. pseudoserratodentata	As in S. serratodentata	Very small, if present.
Posterior fins	Long, rounded. About same length on tail as on trunk. At level of tail, septum begins rayless zone which extends over anterior part of fin.	Long, rounded, more on tail than trunk. Very close to posterior fins. Internal portion of fins on trunk is rayless.	As in S. pseudoserratodentata. very close to anterior fins. No rayless zone.	Continuous with anterior fins by extremely narrow connexion, not visible with low power 10X and in badly preserved specimens. More on tail than trunk. Rayless zone begins at level of first third of tail extending over anterior part of fins as S. serratodentata.	Triangular, rounded, more on trunk than tail. No rayless zone.
Seminal vesicles	Separated from tail fin, close to posterior fins. Two prominences at anterior latera corner. Thickening of collarette tissue in front of anterior end. Markedly protandric	Close to posterior end of posterior fins and at longer distance from tail fin. One prominence at lateral anterior corner and small teeth at anterior end. Protandric.	Oval with thickening frothy tissue. 5-10 chitinous teeth at anterior end. Protandric.	Close to posterior fins, separated from tail fin. Numerous short protuberances at anterior end. Notable thickening in front and behind vesicle. Markedly protandric.	Pear shape. One prominence and no soft proturberances as in S. tasmanica.
Ovaries	Long tubes extending to anterior end of anterior fins. Ovulae small and in one row.	Fine tubes extending to anterior end of ventral ganglion. Ovulae large for size of specimens, arranged in one row.	Very fine tubes, extending up to neck. Ovulae in one row.	Long tubes extending to ventral ganglion. Ovulae in two rows.	Fine tubes extending to posterior end of anterior fins. Ovulae in two rows.
Distribution	Mediterranean and Atlantic generally between 40°N and 25°S. In Southern Pacific between 30°S and 45°S.	Restricted to North Pacific Ocean.	Restricted to Pacific and Indian Oceans between 40°N and 40° S.	Southern parts of the Indian Pacific and Atlantic Oceans and North Atlantic.	Restricted to Pacific Ocean off California and Peru.

Table 4. Principal diagnostic characters of the "serratodentata group" (after Alvarino, 1961).

7. SOURCES OF FIGURES AND MAPS

Sources	Figures
Ritter-Zahony (1911)	5, 8(a),(c)
Johnston & Taylor (1921)	7(b)
Tokioka (1940)	10, 11, 13, 14, 16, 17(a),(c)
David (1955)	2
David (1956)	1, 3, 13, 15, 18(a)
David (1958a)	4(b), 18(b)
David (1958b)	8(b)
Alvarino (1961)	4(c),(d),(e)
Newell & Newell (1963)	5
Alvarino (1962)	7(a), 18(b), 19(a),(b)
Alvarino (1963b)	9(a),(b),(c), 12, 17(b)
Dinofrio (1973)	2, 4(a),(b); 6(a),(b), 7(a),(b)

Sources	Maps
Steinhaus (1896)	16
Fowler (1907)	17, 18, 19
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Hardy & Gunther (1936)	14, 16
Mackintosh (1937)	14, 16
Dakin & Colefax (1940)	6, 7, 10, 11, 16, 17, 19
Tokioka (1940)	6, 7, 10, 11, 16, 17, 19
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David (1959)	4, 9, 10, 11, 12, 13 14, 16, 18, 19
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Almeida Prado (1961)	15
Furnestin (1962)	17
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Kapp (1980)	4, 9, 14, 18

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APPENDIX I

PRESERVATION AND STAINING

The appearance of chaetognaths varies considerably according to the medium in which they are kept (Johnston & Taylor, 1921): specimens retain shape well and remain more or less opaque according to their nature when in formalin; but in alcohol normally firm and turgid species become rather flaccid and quite transparent while normally flaccid species become very difficult to measure correctly. Therefore specimens should be preserved in neutral sea water formalin instead of alcohol. The early confusion of S. hexaptera and S. gazellae was due to the use of alcohol as a preservative which made characteristic fin differences unrecognisable (David, 1965).

Staining can be used to show the corona (Thomson, 1947) and the eyes and fins (David, 1959). Fowler's (1907) method of immersing the animal in a weak solution (c. 1 percent) of methylene blue for about one minute is both simple and productive of good results. Staining is sometimes necessary to make out the gonads of the more opaque species so that immersion in 5 percent methylene blue for five minutes will bring the gonads of opaque specimens into a sharp relief while in the most strongly muscled species borax-carmine followed by methylene blue gives better results (Thomson, 1947). A new stain with KOH-Alisarine-Gresyl is described by Pierrot-Bults (1974): integument and most appendages stain blue, muscles and sexual products stain reddish, jaw and teeth stain yellow. Transparency of animals is not lost by the staining. Animals preserved in formalin 4% or alcohol 70% can be used. The methylene-blue stain is preferable because the colour soon fades and leaves the specimen unaffected while on storing the other stains react on the specimens so as to obscure the internal structure (Thomson, 1947).

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1. John M. Kirkwood (1982). A guide to the Euphausiacea of the Southern Ocean.

2. David O'Sullivan (1982). A guide to the Chaetognaths of the Southern Ocean and adjacent waters.

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