

TAXONOMY AND ZOOGEOGRAPHY OF CERTAIN MEMBERS OF THE "SAGITTA SERRATODENTATA-GROUP" (CHAETOGNATHA)

by

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ABSTRACT

For the "*Sagitta serratodentata*-group", synonymy, morphology and biometrical data are given of *S. serratodentata*, *S. tasmanica* and *S. pacifica*. *S. serratodentata* is divided into two subspecies, *S. serratodentata serratodentata* and *S. serratodentata atlantica*. The zoogeography of all six taxa of the "*S. serratodentata*-group" is discussed.

INTRODUCTION

Before 1939 only one species of the "*Sagitta serratodentata*-group" was known, *Sagitta serratodentata* Krohn, 1853, which, however, was noted for its variability (Fowler, 1905; Michael, 1911; 1919; Burfield & Harvey, 1926; Burfield, 1930; Tokioka, 1939; 1940b).

In 1905 Cleve described a new species, *S. serrulata*, related to *S. serratodentata* but with more teeth than the latter, occurring off the east coast of South Africa. He gave no illustrations and only mentioned "seminal openings prominent" (Cleve, 1905: 127). Von Ritter-Zahony (1911a) treated *S. serrulata* as a synonym of *S. serratodentata* and so did subsequent authors (Germain & Joubin, 1916; Burfield & Harvey, 1926; Furnestin, 1953a; Tokioka, 1965a). There is reason to believe that *S. serrulata* is the same species as *S. pacifica* considering the number of posterior teeth and the locality.

In 1939 Tokioka described a new species closely related to *S. serratodentata*: *S. pseudoserratodentata*, and commented on the different teeth formulae and on the difference in shape of the seminal vesicles in the Japanese and European forms of the former species.

In 1940 Tokioka found two different forms of *S. serratodentata* in the waters off New South Wales, and distinguished a Pacific form and an

Atlantic-Mediterranean form (Tokioka, 1940b). In 1947 Thomson found a third form in East Australian waters and distinguished three subspecies, *S. serratodentata atlantica* Thomson, 1947, *S. serratodentata pacifica* Tokioka, 1940, and *S. serratodentata tasmanica* Thomson, 1947. The principal differences he gave are found in the armature formulae, the morphology of the seminal vesicle, the length of mature specimens, the geographic distribution, and the temperature range.

Furnestin (1953a) found two forms of *S. serratodentata* in the Morocco area of the Atlantic Ocean which she primarily named *S. serratodentata atlantica* and *S. serratodentata tasmanica*, but in the conclusion of the same paper these two taxa were raised to species rank, as was *S. pacifica*. For *S. serratodentata* and *S. tasmanica*, Furnestin (1957) pointed to fundamental differences in the total body length for specimens in the same maturity stages, in the musculature of the caudal segment and in the morphology of the seminal vesicle. Differences of secondary importance she noticed in the number of hooks and teeth. As ecological differences she found that *S. serratodentata* prefers a higher salinity and a higher temperature than *S. tasmanica*, the salinity being more important than the temperature in excluding *S. tasmanica* from certain water masses.

Fagetti (1958b) described *S. selkirkii* as a new species in the "*S. serratodentata*-group", but soon afterwards this species was synonymized with *S. tasmanica* by various authors (Alvarino, 1961; Tokioka, 1965a).

Alvarino (1961) described a species *S. bierii* new to science from Californian waters. The principal differences between this species and *S. tasmanica* are found in the relative length of the tail and in the morphology of the seminal vesicles. She de-

scribed differences between *S. serratodentata* and *S. tasmanica* in the total length of mature specimens, in the morphology of the seminal vesicles, and in the ovaries.

Tokioka (1965a) divided the Chaetognatha into 15 genera, the former genus *Sagitta* into 9 genera. The "*S. serratodentata*-group" got the generic name *Serratosagitta* with the species *Serratosagitta serratodentata*, *S. pseudoserratodentata*, *S. pacifica*, *S. tasmanica* and *S. bierii*. Tokioka commented: "*S. bierii* resembles very closely *S. tasmanica* differing from it only in the exact appearance of the seminal vesicle. As the main distributions of *S. tasmanica* and *S. bierii* are confined to the rather

cooler water of the southern hemisphere or to the northward flows, the Humboldt current and the effected area off the California coast and the Benguela current, both originating in the southern cool waters, it is not impossible that those two species are identical with each other." (Tokioka, 1965a: 346).

In the Atlantic Ocean (fig. 1) only two of the five species of the group are present, viz. *S. serratodentata* and *S. tasmanica*, which will be described here first (together with *S. pacifica* for sake of completeness) before discussing the infraspecific variation.

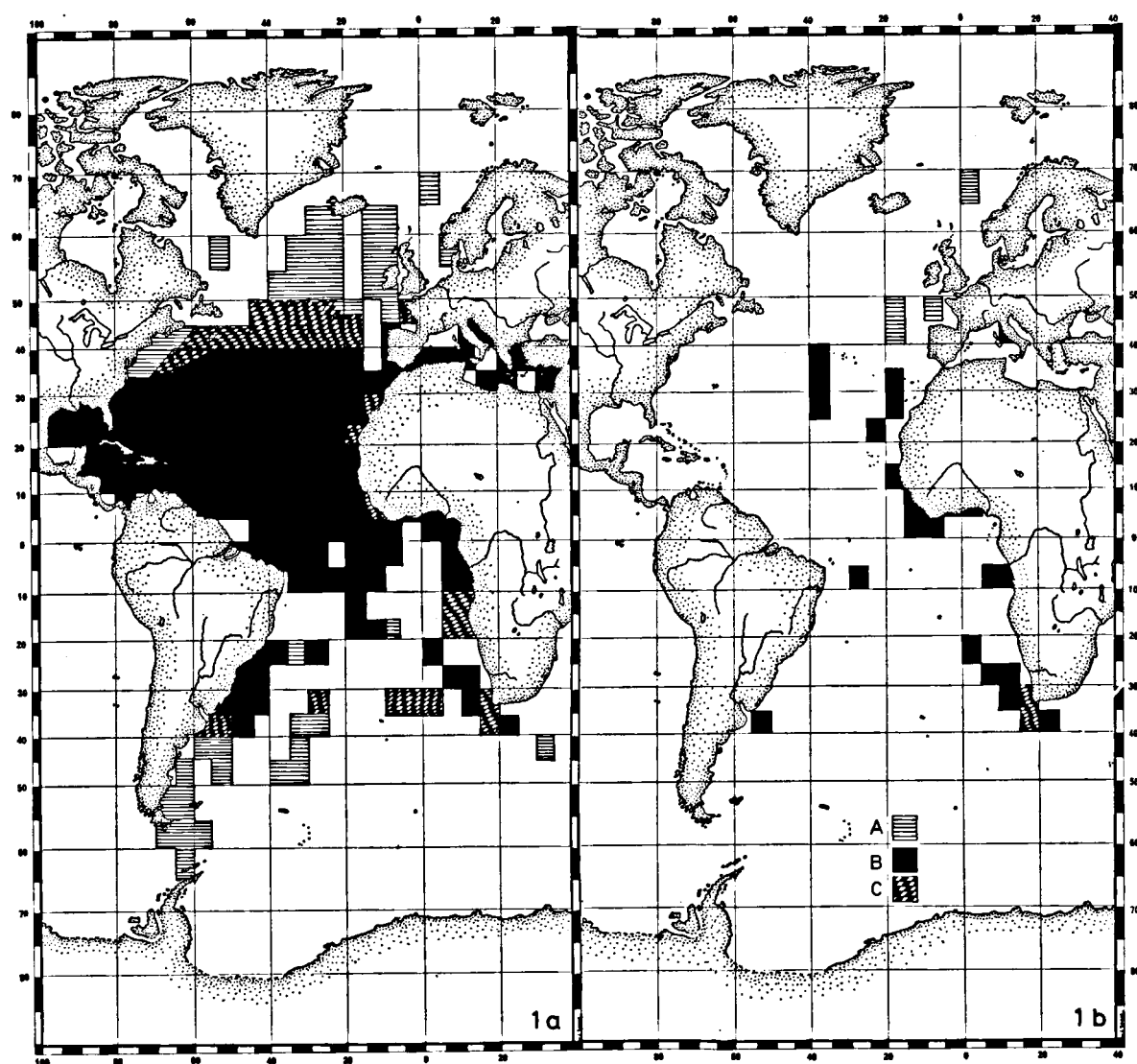


Fig. 1a. Localities based on literature references for *S. tasmanica* and *S. serratodentata serratodentata*.
1b. Localities from which specimens of *S. tasmanica* and *S. serratodentata serratodentata* were studied.
A. *S. tasmanica*, B. *S. serratodentata serratodentata*, C. overlap.

MATERIAL STUDIED

The material of *Sagitta* upon which the present study is based, is preserved in the following museums:

ZMUC Zoologiske Museum, Copenhagen;

BMNH British Museum (Natural History), London;

RMNH Rijksmuseum van Natuurlijke Historie, Leiden;

ZMA Zoologisch Museum, Amsterdam.

ZMUC Dana Expedition:

sta. 3971	35°49'S	23°09'E	29-01-1930	1 specimen
sta. 3975	35°42'S	18°37'E	31-01-1930	4 specimens
sta. 3976	34°01'S	18°10'E	01-02-1930	54 specimens
sta. 3978	30°15'S	13°15'E	13-02-1930	1 specimen
sta. 3979	27°10'S	08°59'E	15-02-1930	131 specimens
sta. 3980	23°26'S	03°56'E	17-02-1930	36 specimens

ZMUC Atlantide Expedition:

sta. 28	22°59'N	20°30'W	03-12-1945	98 specimens
sta. 31	18°57'N	23°28'W	06-12-1945	1 specimen
sta. 33	17°11'N	24°52'W	07-12-1945	6 specimens
sta. 50	07°16'N	13°29'W	30-12-1945	2 specimens
sta. 52	06°30'N	11°21'W	01-01-1946	10 specimens
sta. 62	04°16'N	08°18'W	10-01-1946	26 specimens
sta. 66	04°27'N	07°07'W	11-11-1946	9 specimens
sta. 67	04°29'N	06°41'W	11-01-1946	6 specimens
sta. 92	06°01'N	02°21'E	01-02-1946	10 specimens
sta. 134	07°35'S	12°46'E	16-03-1946	1 specimen
sta. 138	07°40'S	07°56'E	24-03-1946	23 specimens
sta. 139	01°30'N	10°10'W	02-04-1946	16 specimens
sta. 140	04°10'N	12°18'W	04-04-1946	54 specimens
sta. 150	10°22'N	16°34'W	15-04-1946	1 specimen
sta. 151	10°40'N	16°44'W	16-04-1946	96 specimens

ZMUC Galathea Expedition:

sta. 552	36°00'S	150°39'E	02-12-1951	41 specimens
sta. 665	35°30'S	177°48'W	19-02-1952	124 specimens
sta. 669	36°10'S	177°50'W	19-02-1952	19 specimens
sta. 670	34°07'S	179°20'W	01-03-1952	3 specimens

BMNH Terra Nova Expedition:

sta. 53	05°00'S	27°15'W	12-05-1913	11 specimens
sta. 86	± 33°S	± 171°E	$\frac{24}{25}$ -07-1911	14 specimens
sta. 87	ibid.		25-07-1911	8 specimens
sta. 127	ibid.		$\frac{24}{25}$ -08-1911	24 specimens
sta. 132	ibid.		29-08-1911	23 specimens
sta. 146	ibid.		18-09-1911	19 specimens
sta. 242	51°57'S	167°38'E	$\frac{27}{28}$ -03-1912	11 specimens
sta. 311	35°29'S	50°26'W	22-04-1913	100 specimens

BMNH Research Expedition:

	± 46°N	± 07°W	$\frac{7}{24}$ -07-1900	365 specimens
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BMNH Great Barrier Reef Expedition:

Low Isl. Great Barrier Reef	1929	110 specimens
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RMNH Stiasny coll. no. 5:

Bay of Naples	Jan./April 1914	96 specimens
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RMNH Snellius Expedition 1929/30:

sta. 185	05°51'S	119°22'E	13-02-1930	102 specimens
sta. 259	00°27'S	120°54'E	11-05-1930	194 specimens

ZMA Snellius Cruises:

33°52'N	19°20'W	11-04-1965	9 specimens
34°09'N	39°03'W	16-04-1965	6 specimens
37°26'N	38°46'W	20-05-1965	3 specimens
25°11'N	19°35'W	31-01-1965	30 specimens
22°02'N	20°35'W	05-12-1964	121 specimens

ZMA Cirrus Cruises:

65°59'N	02°00'E	31-07-1964	1 specimen
45°00'N	16°00'W	23-04-1964	3 specimens
ibid.		$\frac{01}{28}$ -05-1964	6 specimens
ibid.		03-06-1966	55 specimens
45°00'N	16°06'W	05-06-1966	26 specimens
45°06'N	15°55'W	28-05-1966	13 specimens
44°42'N	16°12'W	29-05-1966	16 specimens
44°48'N	16°18'W	30-05-1966	4 specimens

ZMA Cumulus Cruises:

44°54'N	15°56'W	07-03-1953	11 specimens
44°54'N	15°54'W	14-10-1963	1 specimen

METHODS

Because of the great number of specimens, about one third of the material was stained and mounted to make handling easier. Doing so, it rendered the structure of the seminal vesicles more clearly discernible and, if necessary, stronger magnifications could be used. At first, Carmine staining after Romeis (1948) was executed; contrary to the original recipe, however, Carmine in lactic acid was used (1 g carminium "Nacarath" C.M.V. dissolved in 30% lactic acid, by boiling the lactic acid till all the carminium is dissolved).

The Carmine gives the whole specimen a red stain, but nucleus-rich tissues stain deeper red, so the tissues of ovaries and testes show a deeper red than the muscles.

Part of the material was treated with a new stain with KOH-Alisarine-Cresyl, developed by Mr. A. F. de Fluiter, Institute of Taxonomic Zoology, Amsterdam, for intact planktonic animals like Chaetognaths, small worms and fish larvae. Integument and most appendages stain blue, muscles and sexual products stain reddish, jaws and teeth stain yellow. Transparency of animals is not lost by the staining. Animals preserved in formalin 4% or alcohol 70% can be used.

This new staining proceeds as follows¹⁾:

- I From preservative in aqua dest. (2 min.)
- II KOH-Alisarine Red S (7 min.)
- III Aqua dest. (1 min.)
- IV 2% phosphomolybdic acid (1 min.)

¹⁾ Times for staining are highly dependent on the species concerned and the size of the specimens; too long staining periods make the specimen less transparent.

- V Aqua dest. (1 min.)^{*)}
 - VI Lactic acid-Alisarine Red S (3 min.)
 - VII Aqua dest. (1 min.)
 - VIII Cresyl violet (10 min.)
 - IX Transfer immediately into alcohol 50%
 - X Alcohol 70%
 - XI Alcohol 96%
 - XII Alcohol 96%
 - XIII Toluol/Clove oil (5 min.)
 - XIV Best results with embedding in Rhenohistol
- Reagentia:
- KOH-Alisarine Red S: 35 g KOH and 0.3 g Alisarine Red S in 200 ml aqua dest.
- Phosphomolybdic acid: 2% solution in water.
- Lactic acid-Alisarine Red S: 0.3 g Alisarine Red S and 20 ml lactic acid in 200 ml aqua dest.
- Cresyl violet: 0.3 g Cresyl violet ($C_{17}H_{14}ClN_3O$) in 500 ml tap water. This solution should be prepared directly before use and filtered.
- Toluol-Clove oil: mixture of 60 ml toluol and 40 ml clove oil.

TAXONOMY

Sagitta serratodentata Krohn, 1853
subspecies *serratodentata* Krohn, 1853.

Sagitta serratodentata Krohn, 1853: 272, figs. 3—4; Hertwig, 1880: 64; Langerhans, 1880: 135; Strodtmann, 1892: 17, 39 (part); Steinhaus, 1896: 25 (part); Lo Bianco, 1904: 54, pl. 33 fig. 130; von Ritter-Zahony, 1909a: 15; 1911a: 22 (part); 1911b: 17 (part); 1911c: 22 (part); 1916: 137; Germain & Joubin, 1916: 41, pl. 3 fig. 12 (part); Burfield, 1930: 213 (part); Germain, 1932: 352; Bollmann, 1934: 258 (part); Thiel, 1938: 14 (part); Faure, 1952: 25 (part); Fraser, 1952: 8 (part); Vanucci & Hosoe, 1952: 18, pl. 3 figs. 1—4; Furnestin, 1953a: 31; Pierce, 1954: 327; Huré, 1955: 52; Bernard, 1955: 10; Furnestin, 1956a: 408, fig. 2; 1956b: 216; 1957: 170, fig. 53; Alvario, 1957: 16; Furnestin, 1958: 204; 1959: 223; Colman, 1959: 234; Heydorn, 1959: 12; Owre, 1960: 261; Furnestin, 1960a: 143; 1960b: 201; Suárez Caabro & Madrugo, 1960: 425, fig. 2e; de Almeida Prado, 1961: 27; Legaré & Zoppi, 1961: 159, pl. 3 figs. 3—6; Furnestin, 1962a: 364; Pierce, 1962: 150; Pierce & Wass, 1962: 411; Alvario, 1965: 178; Furnestin, 1965: 8; 1966: 119; Ducret, 1968: 116, fig. 19C.c; Alvario, 1968: 46; Lewis & Fish, 1969: 3; Alvario, 1969: 31, figs. 61, 62; Owre, 1972: 50; de Decker, 1973: 206.

Spadella serratodentata; Grassi, 1883: 14, pl. 1 fig. 8.
Sagitta serratodentata atlantica non Thomson, 1947; Furnestin, 1953a: 13, fig. 1; 1953b: 413; Hosoe, 1956: 1; Furnestin, 1957: fig. 3b; 1962b: 27; Ghirardelli, 1962: 380; Furnestin, 1963: 634; Bainbridge, 1964: 394; Ghirardelli, 1969: 30; Aurich, 1971: 8.

Sagitta serratodentata var. *atlantica*; Massuti, 1961: 239.
Sagitta pseudoserratodentata non Tokioka, 1939; Furnestin, 1963: 631, fig. 1.

Serratosagitta serratodentata; Tokioka, 1965a: 346 (part).

Type locality: Mediterranean off Messina. Location of type specimens unknown.

^{*)} Step V may be omitted in some species.

Description:

The original description by Krohn (1853) is not complete and therefore additions concerning the shape of the seminal vesicles are given.

The body shape is slender and rigid, preserved in formalin or alcohol it keeps its form well. The maximum length is about 13 mm; Krohn (1853) gives 4.5 mm. The head is small with small eyes. The eye pigment is elongated, shaped as shown in fig. 2. There is no gut diverticulum and only



Fig. 2. Diagram of the shape of the eye pigment in the "*S. serratodentata*-group".

the vestige of a collarete. The anterior fins reach to the level of the ventral ganglion and broaden at their posterior end having a small rayless zone. The posterior fins, beginning close behind the anterior fins, are broader than the latter and of about the same length, or slightly longer. Krohn (1853) stated that the posterior fins were considerably longer than the anterior fins, but in his figure there is only a small difference in length. The posterior fins have a small rayless zone and reach, or nearly reach, to the seminal vesicles. The tail fin reaches nearly to the seminal vesicles. The length of the tail is about 22—30% of the total length. There are 5 to 8 (sometimes 9) serrated hooks, 3 to 10 anterior teeth and 5 to 20 posterior teeth. Length of mature specimens varies between 7 and 13 mm. Mature ovaries may reach to about the ventral ganglion. The seminal vesicles are very conspicuous.

The seminal vesicle is basically a sac to contain mature spermatozooids which have developed in the tail segment. There are different forms of seminal vesicles in the Chaetognatha; those of the "*S. serratodentata*-group" are the most complexly built vesicles found. They consist of a posterior,

rather elongated part, the trunk, which contains the spermatozooids and an anterior part, the knob, which in the different species shows different structures. A more detailed study by the present author concerning the histology and the development of the seminal vesicles of the "*S. serratodentata*-group" is in preparation.

The trunk has a thin epithelium and is similar in all the species of the group.

The knob of the seminal vesicle of *S. serratodentata serratodentata* is broader than the trunk; the exact width of it depends on the stage of maturity and is variable within the species. Sometimes the vesicle is situated quite close to the tail as shown in fig. 3, but it can be much more pro-

basal in position, forming secretion granulae in the cells. This secretory product is filling the lumen of the knob and contacts with the spermatozooids.

When the vesicle opens, it ruptures at the place where there is, according to Tokioka (1939), an external opening, which is merely the point of initial burst. The spermatozooids are ejected with the secretion product.

The glandular area has at the outside of the seminal vesicle a layer of very large cells with large dark nuclei. This is clearly visible when the specimens are stained with KOH-Alisarine-Cresyl; in unstained specimens these nuclei appear as dark spots. Together these large cells form the two papillae at the anteriolateral corner which are so typical for this species. I did not observe small irregularities on the surface, as observed and shown by Furnestin (1953a: fig. 1) and I think the nuclei have been mistaken as such.

***Sagitta serratodentata* Krohn, 1853**
subspecies *atlantica* Thomson, 1947.

Sagitta serratodentata "Atlantic or Mediterranean form"; Tokioka, 1940b: 373, fig. 70.

Sagitta serratodentata atlantica Thomson, 1947: 15, figs. 1—2.

Sagitta serratodentata atlantica f. *typica*; Tokioka, 1952: 310.

Serratosagitta serratodentata; Tokioka, 1965a: 346 (part).

Sagitta serratodentata; Fagetti, 1958a: 40, fig. 4; 1972: 13.

Type locality: Western Australian waters. Location of type specimens unknown.

Nomenclature:

The correct author's name for this subspecies is Thomson, 1947, since Tokioka (1940) only called it the "Atlantic or Mediterranean form".

The indication "Atlantic or Mediterranean form" and the name *S. serratodentata atlantica* are first used for specimens of the isolated population of *S. serratodentata* in the South Pacific and seem not very proper for this population. It should nevertheless only be applied to these populations and the correct name for the subspecies from Mediterranean and Atlantic waters is *S. serratodentata serratodentata*, because the original description by Krohn (1853) was based on Mediterranean samples.

Description:

The morphology of this subspecies is the same as for *S. serratodentata serratodentata*, but there are fewer posterior teeth, viz. 6 up to 17 (see also p. 225).

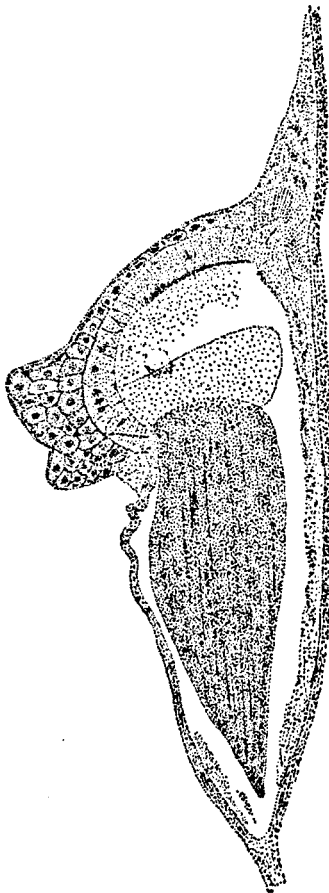


Fig. 3. Seminal vesicle of a specimen of *S. serratodentata serratodentata* from 25°N 19°W.

truding as shown by Vanucci & Hosoe (1952, pl. 3 fig. 1) and Alvarino (1969, figs. 61E, 62J). The knob of the vesicle of *S. serratodentata serratodentata* has a glandular area, consisting of a layer of longitudinal cells with the nuclei mostly

***Sagitta tasmanica* Thomson, 1947.**

Sagitta serratodentata; Strodman, 1892: 39 (part); Steinhaus, 1896: 25 (part); Fowler, 1904: 381; 1905: 58, pl. 4 figs. 1—6; 1907: 2; von Ritter-Zahony, 1909c: 792; 1910a: 2; 1911a: 22 (part); 1911b: 17 (part); 1911c: 22 (part); Apstein, 1911: 173; Bigelow, 1914: 121; 1915: 297; Germain & Joubin, 1916: 41 (part); Bigelow, 1917: 249; Johnston & Taylor, 1919: 29; Bigelow, 1926: 320, fig. 89; van Oye & de Waele, 1930: 38 (part); Bollmann, 1934: 258 (part); Russell, 1935: 15; Thiel, 1938: 14 (part); Furnest, 1938: 432; Bigelow & Sears, 1939: 356; Clarke, Pierce & Bumpus, 1943: 222, fig. 10; Fraser, 1949: 489; 1952: 8; Faure, 1952: 25 (part); Kielhorn, 1952: 238; David, 1958: 208; Deevey, 1960: 38; Fraser, 1961: 181; Grant, 1963a: 39; 1963b: 110; Shih, Figuera & Grainger, 1971: 80.

Sagitta serratodentata tasmanica Thomson, 1947: 15, figs. 1—3; Furnest, 1953a: 13, fig. 2; 1957: fig. 3c; Fraser, 1957: fig. 3a; Heydorn, 1959: 13; Furnest, 1962b: 27; Ghirardelli, 1962: 383; Furnest, 1963: 631; Fives, 1971: 123; Aurich, 1971: 8.

Sagitta tasmanica; Furnest, 1953a: 31; 1957: 170, fig. 54; Fagetti, 1958a: 46, fig. 7; 1959: 252; Alvarino, 1961: 70, fig. 6; 1964a: 66; 1964b: 336; 1964c: 53; Ducet, 1968: 116, fig. 19A.a; Fagetti, 1968: 123; Alvarino, 1969: 27, figs. 63, 64; Fagetti, 1972: 13; de Decker, 1973: 206.

Sagitta serratodentata atlantica f. *tasmanica* Tokioka, 1952: 310.

Sagitta selkirki Fagetti, 1958b: 125, figs. a-d.

Serratogagitta tasmanica Tokioka, 1965a: 346.

Sagitta tasmanica "f. meridional" Fagetti, 1968: 126, pl. 1 fig. 2, pl. 3 figs. c-d.

Sagitta tasmanica "f. septentrional" Fagetti, 1968: 126, pl. 1 fig. 1, pl. 3 figs. a-b.

Sagitta serratodentata var. *tasmanica* Bradford, 1972: 70.

Type locality: Western Australian waters. Location of type specimens unknown.

Description:

The body is firm and rigid, the maximum length observed in the present study is about 20 mm, though Alvarino (1969) records 33 mm. The head is small with small eyes. The eye pigment is elongated as shown in fig. 2. There is no gut diverticulum and only the vestige of a collarette. The anterior fins are beginning at the level of, or slightly behind, the ventral ganglion and broaden at their posterior end. They have a small rayless zone. The posterior fins are slightly longer than the anterior fins and also provided with a small rayless zone, they reach not quite or just to the seminal vesicle. The length of the tail is about 20—30% of the total body length. There are 6 up to 8, sometimes 9 serrated hooks, 2 up to 9 anterior teeth and 3 up to 15 posterior teeth.

The species reaches maturity at a length of 9 up to 20 mm (Alvarino, 1969, records 28—33 mm). The ovaries reach to about the anterior end of the

anterior fins when mature. The seminal vesicles in this species are not as complex and as protruding as in *S. serratodentata*. The trunk of the seminal vesicles is much the same as in *S. serratodentata*, but the knob has a different structure. The knob of the seminal vesicle of *S. tasmanica* consists of a glandular area of cylindrical secretory cells, discharging their secretion product in the lumen of the knob. This secretion comes in contact with the spermatozoa in the lumen of the trunk of the seminal vesicle. In *S. tasmanica* the knob has no large cells with large dark nuclei, as is the

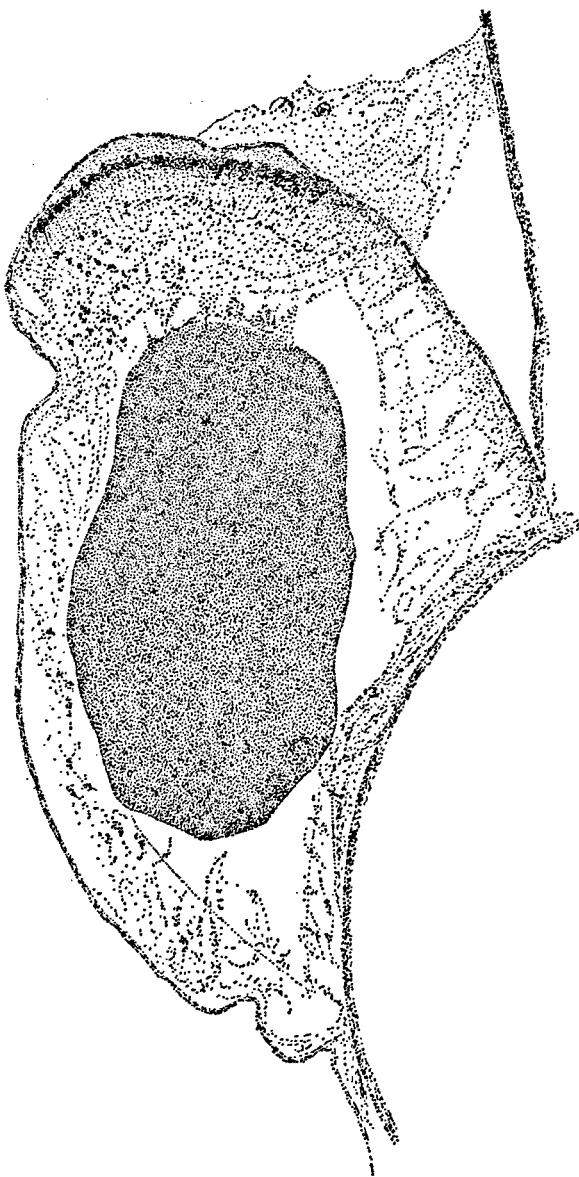


Fig. 4. Seminal vesicle of a specimen of *S. tasmanica* from 45°N 16°W.

case in *S. serratodentata*, but usually there is a layer of loose tissue covering the glandular area at the anterior part of the knob. It consists of cylindrically shaped cells without an epidermis and having the appearance of soft protuberances on the apical side of the seminal vesicle. This tissue is lost quite easily, as is represented for instance in fig. 4. In fig. 5 the seminal vesicle is shown of a *S. tasmanica* specimen from Juan Fernandez, originally described by Fagetti (1959) as *S. selkirkii*, which still shows the soft tissue on the anterior part of the knob. Figs. 4 and 5 are drawn to the same scale.

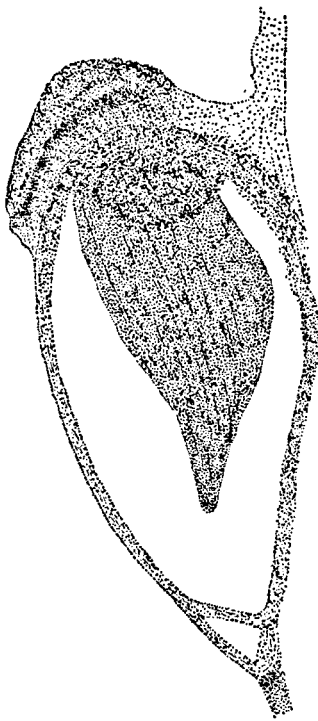


Fig. 5. Seminal vesicle of a specimen of *S. tasmanica* from Juan Fernandez.

Sagitta pacifica Tokioka, 1940.

?*Sagitta serrulata*; Cleve, 1905: 127.

Sagitta serratodentata; Béraneck, 1895: 152; Steinhaus, 1896: 46 (part); Aida, 1897: 14, pl. 3 fig. 2; Doncaster, 1902: 211; Fowler, 1906: 20, pl. 2 fig. 65; von Ritter-Zahony, 1909b: 50; 1910b: 126; 1911a: 22 (part); 1911c: 22 (part); Michael, 1911: 39, pl. 1 fig. 9; 1919: 249; van Oye & de Waele, 1930: 38 (part); John, 1937: 84; Tokioka, 1939: 129, fig. 53; 1940a: 4; Schilp, 1941: 35; Tokioka, 1942: 537; 1950: 129; Burfield, 1950: 464; Furuhashi, 1953: 65; Hida, 1957: 2 (part); Halim, 1969: 265.

Sagitta serratodentata forma *pacifica* Tokioka, 1940b: 375.

Sagitta serratodentata "pacific form" Tokioka, 1940b: 373, fig. 7.

Sagitta serratodentata pacifica; Thomson, 1947: 15, fig. 1a; Tokioka, 1952: 310; 1954a: 359; 1954b: 99; 1955a: 219; 1955b: 75; 1956a: 197; 1956b: 203; Hamon, 1956: 471; Yamazi, 1958: 141; Tokioka, 1958: 137; 1959: 364, fig. 10; Sund, 1959: 279, fig. 13; Furuhashi, 1961: 25; Ghirardelli, 1962: 383; Furnestin & Radiquet, 1964: 73; Motoda & Marumo, 1965: 156.

Sagitta pacifica; Furnestin, 1953a: 31; 1957: 171, fig. 66; Bieri, 1957: 260; Fagetti, 1958a: 44, fig. 6; Bieri, 1959: 9, fig. 9; Alvaríño, 1961: 70, fig. 7a-b; Tokioka, 1962: 9; Alvaríño, 1963: 121, figs. 18—19; 1964a: 66; 1964b: 336; 1964c: 53; 1967a: 275; 1967b: 36, figs. 22—23; Furnestin & Codaccioni, 1968: 153; Alvaríño, 1969: 31; Halim, 1969: 265; Fagetti, 1972: 13; de Decker, 1973: 206; Nair & Rao, 1973a: 306; Nair & Rao, 1973b: 322. *Serratosagitta pacifica*; Tokioka, 1965a: 346.

Type locality: off the coast of New South Wales. Location of type specimens: Australian Museum, Sydney.

Nomenclature:

Because of the rules of priority the name *S. serrulata*, Cleve, 1905, should be used, instead of *S. pacifica*, Tokioka, 1940. However, as the specimens used for the original description by Cleve (1905) could not be traced, it cannot be made absolutely certain that the specimens concerned belong to the taxon called here *S. pacifica*. In favour of the stability of nomenclature I therefore propose to use the name *S. pacifica* of Tokioka, 1940 and not of Thomson, 1947 as the term "form" or "forma" used before 1960 is not an express statement of either subspecific or infraspecific rank.

Description:

The body is firm and rigid, the maximum length observed is 11.7 mm (Alvaríño, 1969, records 12—14 mm). The head is rather small with small eyes. The eye pigment is elongated as shown in fig. 2. There is no gut diverticulum and only the vestige of a collarette. The anterior fins are beginning slightly behind of, or at the level of the posterior end of the ventral ganglion and broaden at their posterior end. They have a small rayless zone. The posterior fins are of about the same length as the anterior fins and have also a very small rayless zone; they reach to the seminal vesicles. The tail is about 21—26% of the total body length. There are 5 up to 8, sometimes 9 serrated hooks, 3 up to 12 anterior teeth and 8 up to 23 posterior teeth.

The species reaches maturity at lengths of 7.8 up to 11.7 mm. The ovaries reach to about the anterior end of the ventral ganglion when mature.

The seminal vesicles of this species are very complex and conspicuous. The trunk is much the

same as in *S. serratodentata* but the knob is different. The knob is about as wide as the length of the total seminal vesicle, it may be a little less. There is a glandular area consisting of cylindrical cells with basal nuclei which produce secrete

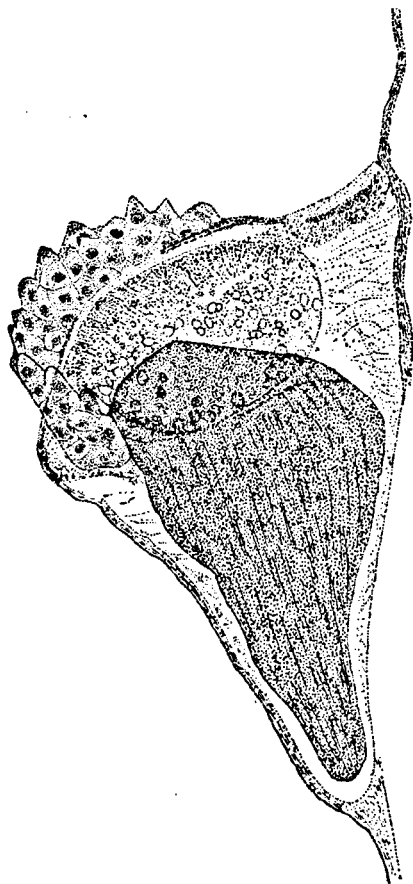


Fig. 6. Seminal vesicle of a specimen of *S. pacifica* from the Great Barrier Reef.

granulae. These cells fill the lumen of the knob with a secretory product which is in contact with the spermatozoa in the lumen of the trunk. In the anterior or anteriolateral area of the seminal vesicles a layer of large firm cells with large dark nuclei forms the outside, covering the glandular area. These cells look rather similar to the cells which form the papillae of the seminal vesicle of *S. serratodentata*, but in *S. pacifica* they form an irregular teethlike row, as shown in fig. 6. I did not observe the chitinous teeth as described by Tokioka (1939).

SEXUAL DEVELOPMENT

Chaetognatha are protandric hermaphrodites. The sexual stages distinguished in the "*S. serratodentata*-group" are based on the development of the seminal vesicles. It proved to be not practical, without histological examination, to distinguish more than three stages. Working with a large number of specimens, the sexual stage has to be recognized clearly at a low magnification in the intact animal and histological studies should be avoided as much as possible. The ovaries are sometimes difficult to see in damaged or badly preserved specimens, so the easiest way is to use the seminal vesicles in this species group. It must be admitted, however, that this does not necessarily work out in other species of Chaetognatha. It seems impossible to use the same division in sexual stages for all chaetognath species, because of the differences in sexual development. The protandric cycle shows telescoping in some species more than in others, and some species are hardly ever seen with mature seminal vesicles.

For comparison of the sexual stages distinguished by different authors one is referred to Alvarino (1965).

The following sexual stages are considered in this paper:

Stage I juveniles.

Stage II seminal vesicles are developing, but not yet filled with spermatozoa.

Stage III seminal vesicles full of spermatozoa or already burst, eggs developing or ripe. To distinguish a stage IV (seminal vesicles ruptured or disappeared, tail cavity empty, long ovaries with large eggs) is very difficult in this species group.

It looks as though the seminal vesicles are used more than once during the male stage; it is impossible that all the spermatozoa from the tail cavity could be stored at the same time in the two relatively small seminal vesicles. Sometimes the seminal vesicles have been burst already while the tail is still full of spermatozoa. Therefore the most reasonable explanation seems to be that the seminal vesicles are used more than once during the male phase. So one may observe specimens with the seminal vesicles filled with spermatozoa and still rather small eggs and other specimens with similar looking seminal vesicles but with large eggs.

However, this effect could also be due to telescoping; this is the shortening, under optimal con-

ditions, of the length of the male phase so that the succession of the stages occurs more rapidly (van der Spoel, 1971).

The presence of sperm in the tail cavity is sometimes difficult to see; on the other hand the development of the eggs in the ovaries is often not very

clear without staining, while even sectioning might be necessary. To discriminate a stage IV one has to be sure of the development of the eggs; therefore this stage has not been distinguished in the present study.

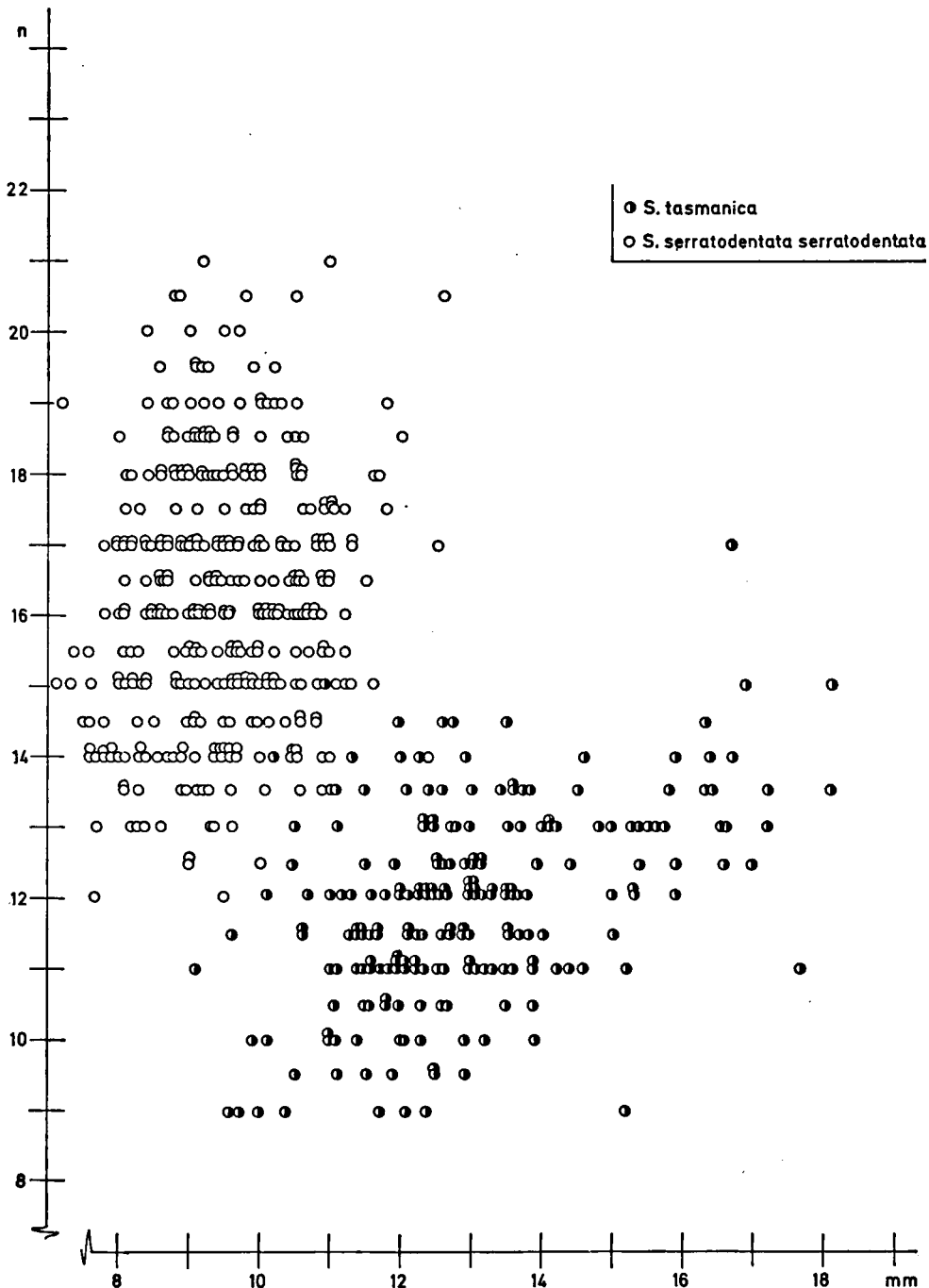


Fig. 7. Relation between total body length (x-axis) and number of posterior teeth (y-axis) for all samples from the Atlantic Ocean of *S. serratodentata serratodentata* and *S. tasmanica*, only mature specimens represented.

TAXONOMIC DIFFERENCES

S. serratodentata and *S. tasmanica* show considerable overlap in most of the discriminating characters, as there are the body length in mature specimens, the armature formulae, and the preference in temperature and salinity ranges. In the geographic distribution restricted overlap seems to be present in the Atlantic, and is rather pronounced in the Pacific.

Only the morphology of the seminal vesicle is a clear distinguishing character, although this can be misinterpreted as well in badly preserved or damaged individuals. The specimens of *S. pseudoserratodentata* from the Mediterranean, described by Furnestin (1963), for instance, are in my opinion damaged specimens of *S. serratodentata serratodentata*. In the case of fully mature individuals it is sometimes difficult to decide to which species they belong on account of the seminal vesicles only. Sometimes the structures of the knob are completely lost leaving only the trunk filled with spermatozoa which looks much the same in different species.

Therefore, in this paper most attention is given to the other characters of the three species *S. serratodentata*, *S. pacifica* and *S. tasmanica*, in particular to meristic data. A correlation was made between body length, number of posterior teeth, and sexual stage. Comparing *S. serratodentata*, *S. pacifica* and *S. tasmanica* in the present study, mainly the numbers of posterior teeth were considered, as these showed the most pronounced differences.

When the body length and the number of posterior teeth found for stage III are plotted in a diagram, the differences between *S. serratodentata serratodentata* and *S. tasmanica* are easily seen for the Atlantic population (fig. 7). This holds also good for the Pacific Ocean where the values for *S. serratodentata atlantica* are intermediate between *S. pacifica* and *S. tasmanica* (fig. 8). The correlation for body length and posterior teeth is such that a linear regression proves to be present.

Fig. 9 shows the regression lines for stage III calculated for Atlantic samples of *S. serratodentata serratodentata* as well as for *S. tasmanica*. There exists a close correlation between length and number of teeth for specimens in the same sexual stage, indicating a clear-cut separation of the two species.

No difference was found between the northern and southern populations of *S. tasmanica* in the

Atlantic, neither in the calculated regression lines, nor in the morphology.

The dispersal of this species in the Atlantic (Alvariño, 1969, fig. 20) shows two separate or nearly separate distributional areas. Literature references record *S. tasmanica* in the Guinea Current (Ducret, 1968; Alvariño, 1969), although I did not find any in the Dana collections from that general area. Grant (1969) did not find *S. tasmanica* south of 18°N, but it should be borne in mind that it is sometimes difficult to identify a species on account of a few specimens. If these literature references reflect correctly the actual distribution, a narrow zone of contact between the two main distributional areas along the African coast would exist, allowing limited gene flow between the northern and southern populations.

Is the similarity between the northern and southern populations due to continuous gene flow, or are these populations isolated in fact and are their characters identical because the time elapsed since the isolation was too short to evolve along different paths? According to Mayr (1966) mere spatial isolation is not sufficient for genetic isolation mechanisms to develop, and as long as there is potential interbreeding only one species is involved. However, we could have here a case of genetically isolated populations showing very little difference in the phenotype, living both in almost the same type of environment. A buffering effect caused by homeostasis also cannot be excluded. The mechanisms effecting homeostasis in these species are unknown. Van der Spoel (1971) brought forward the hypothesis that homeostasis is weakened at higher temperatures, but it is not known how temperature can influence this mechanism.

As a consequence, the similarity between the northern and southern populations and the possibility of gene flow between those populations, prevent us, for the time being, from giving the northern populations in the Atlantic a separate taxonomic status.

Fig. 10 shows the regression lines for stage III calculated for Pacific samples of *S. serratodentata atlantica*, *S. pacifica* and *S. tasmanica*. The difference in the inclinations of the regression lines is difficult to explain. For most of the samples, data on the environmental conditions, which may be the cause of these differences, are lacking.

The separation of *S. serratodentata atlantica* and *S. tasmanica* (fig. 10) is less clear than that of *S. serratodentata serratodentata* and *S. tasmanica*. Specimens of *S. serratodentata* from the Pacific

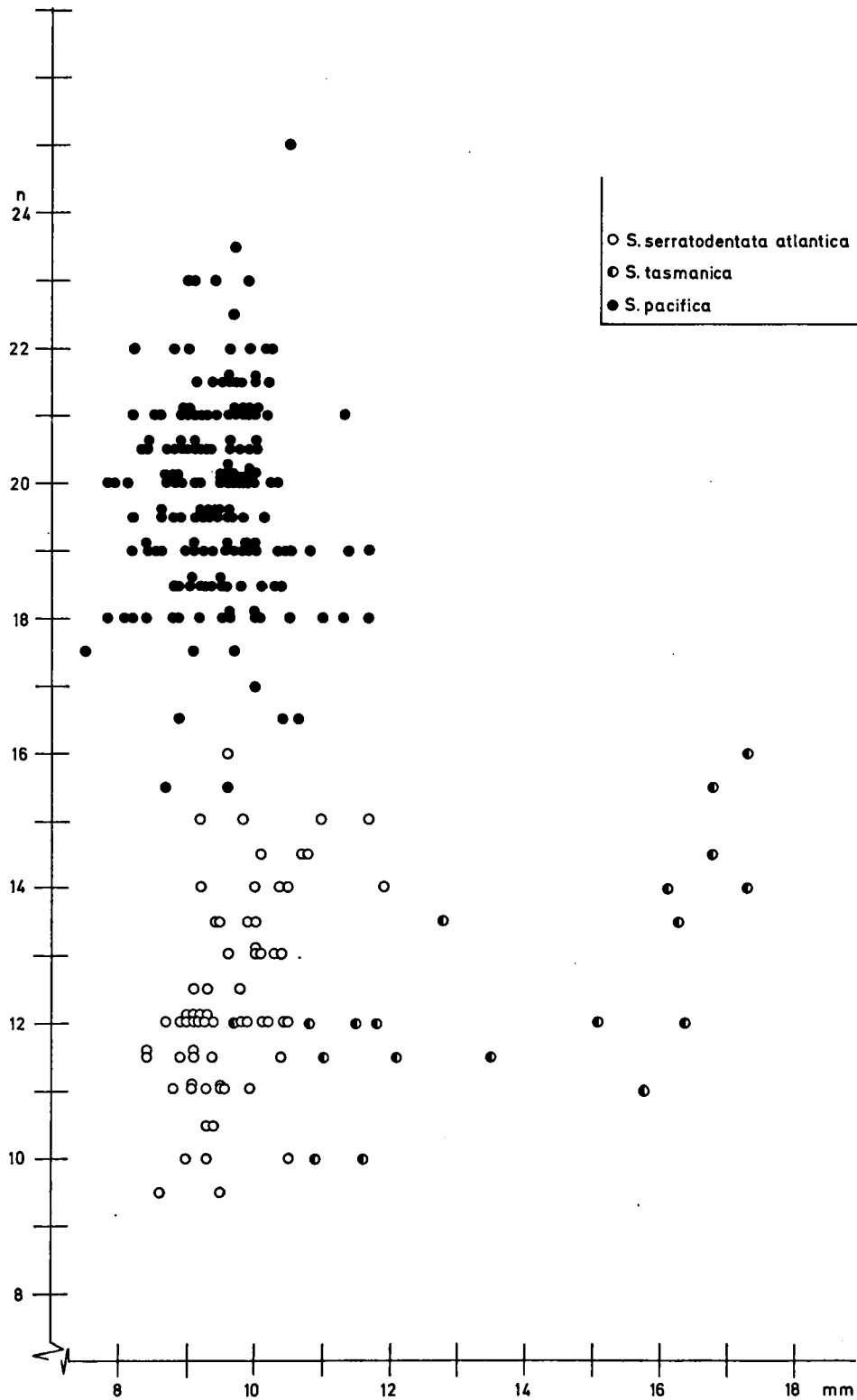


Fig. 8. Relation between total body length (x-axis) and number of posterior teeth (y-axis) for all samples from the Pacific Ocean of *S. serratodentata atlantica*, *S. pacifica* and *S. tasmanica*, only mature specimens represented.

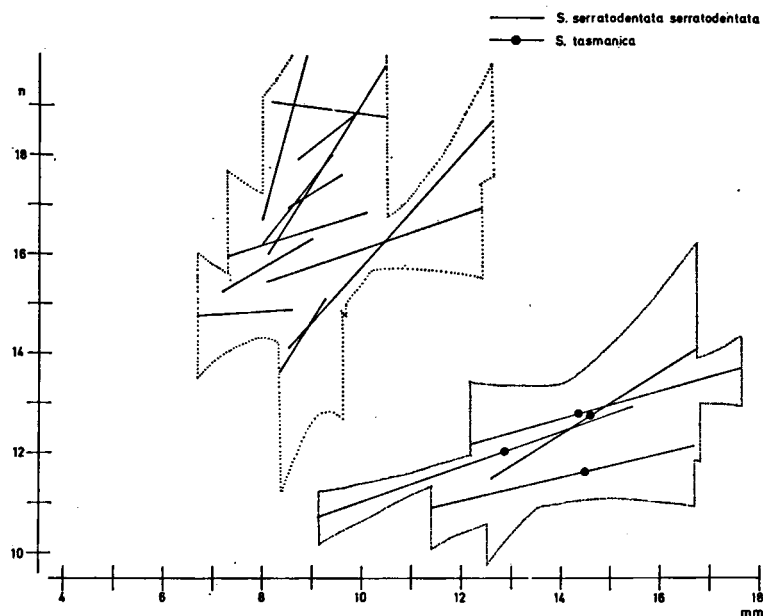


Fig. 9. Regression lines relating length (x-axis) and number of posterior teeth (y-axis) for stage III in *S. serratodentata serratodentata* and *S. tasmanica* from the Atlantic. Dotted lines include the area of the 95% confidence limits.

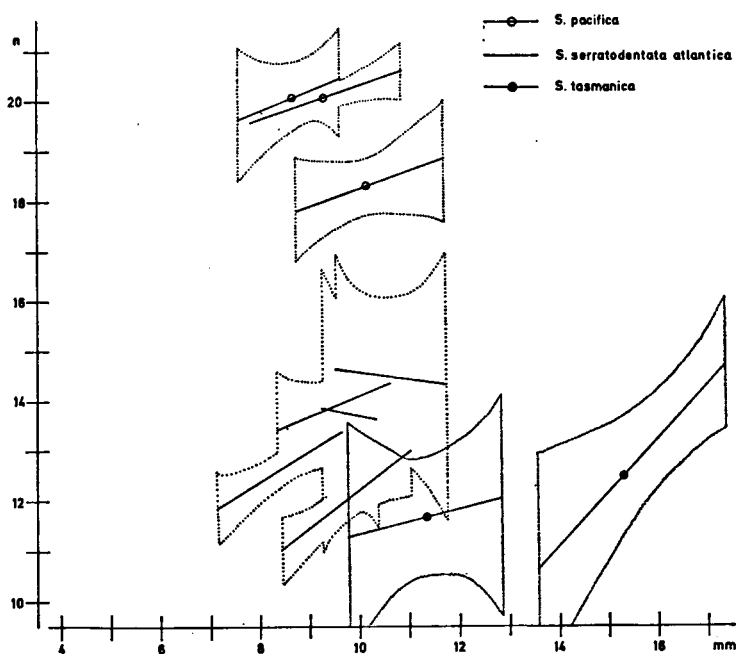


Fig. 10. Regression lines relating length (x-axis) and number of posterior teeth (y-axis) for stage III in *S. serratodentata atlantica*, *S. tasmanica* and *S. pacifica* from the Pacific. Dotted lines include the area of the 95% confidence limits.

reach maturity at about the same length as the Atlantic specimens, but they show a considerably lower number of posterior teeth. Thomson (1947) found a lower number of posterior teeth for *S. serratodentata atlantica* than for *S. tasmanica*, which demonstrated the difference between the two subspecies of *S. serratodentata* as the nominal subspecies shows a higher number of posterior teeth than *S. tasmanica* does.

There proved to be no references in literature recording *S. serratodentata* from the Indian Ocean. David (1963) gives on the 90°E meridian two abundancy areas: for *S. serratodentata* one between 0°S and 12°S and another between 30°S and 43°S; showing, in my opinion, however, the abundancy areas for respectively *S. pacifica* and *S. tasmanica* in the Indian Ocean.

East of South Africa I found specimens of *S. serratodentata serratodentata* together with *S. pacifica*, viz. at Dana sta. 3969 (31° 33'S 30°07'E) but the former are regarded as originating from the Atlantic and they reach their easternmost extension near South Africa. This is confirmed by the studies of de Decker (1973) who found *S. serratodentata serratodentata* one of the species useful for indicating Atlantic influence in the Agulhas Bank region. Fagetti (1958a; 1972) records *S. serratodentata atlantica* from the East Pacific at about 30°S 80°W and these samples also show a low number of posterior teeth. There seems to be no contact around the southern part of the South American continent because *S. serratodentata atlantica* does not extend farther south than 55°S along the western coast of South America. Consequently the *S. serratodentata* populations from the Pacific seem to be isolated from those in the Atlantic.

According to Mayr (1966: 554) "geographic isolation is a purely extrinsic and completely reversible factor that does not in itself lead to the formation of species".

Neither difference in the structure of the seminal vesicles, nor in any of the other morphological characters of these isolated populations of *S. serratodentata* could be found. Real proof that the taxonomic status proposed is correct could only be reached experimentally. In absence of such cross-breeding experiments, the Atlantic as well as the Pacific populations are given the rank of subspecies because of their isolated areas; their morphology, including the seminal vesicles, is identical, except for one biometrical difference, viz. the number of posterior teeth of mature specimens.

The pacific populations are named *S. serratodentata atlantica* Thomson, 1947, the Atlantic and Mediterranean populations *S. serratodentata serratodentata* Krohn, 1853.

The use of the number of teeth in taxonomy meets a lot of opposition because of the variation and overlap in these numbers. However, I cannot think of many numerical characters in animals without measurable variation and I would like to point to what Mayr (1966: 349) stated about subspecies: "Although it is usually possible to assign populations to subspecies, it is often impossible to do this for individuals because of the individual variability of each population and the overlap of the curves of variation of adjacent populations" and this is not necessarily restricted to subspecies, but it also may be applied to many problems in delimitation of species in Chaetognatha.

ZOOGEOGRAPHY

The geographic distribution of the five species of the "*S. serratodentata-group*" is shown in fig. 11. The distribution of *S. tasmanica* is subantarctic in the Pacific, Indian and Atlantic Ocean, from 35° to 65°S, it is recorded also from the area of the Benguela Current. The species is present in the North Atlantic from about 35° up to 65°N and off Morocco. There are records of a more southern extension of the North Atlantic populations, but Grant (1969) could not confirm these. The occurrence near Morocco can be due to the Canary Current which transports organisms at least as far south as Dakar. There seems to be no connection between the northern and southern populations of *S. tasmanica* in the Atlantic (see p. 224). *S. tasmanica* is not found in the North Pacific.

A somewhat similar biboreal distribution pattern is found in the pteropod *Limacina helicina* (Phipps, 1774) (cf. van der Spoel, 1967) although this species developed distinct so-called formae in the different regions and is also found in the North Pacific. Of the "*S. serratodentata-group*" *S. pseudoserratodentata* is endemic in the North Pacific. It was Brinton (1959) who gave an explanation for this distribution pattern. He based his theory of the distribution of the euphausiids on the supposition that during the Pleistocene a shifting of the populations took place. In a cool period the populations were concentrated in the equatorial region, in a warmer period the populations spread

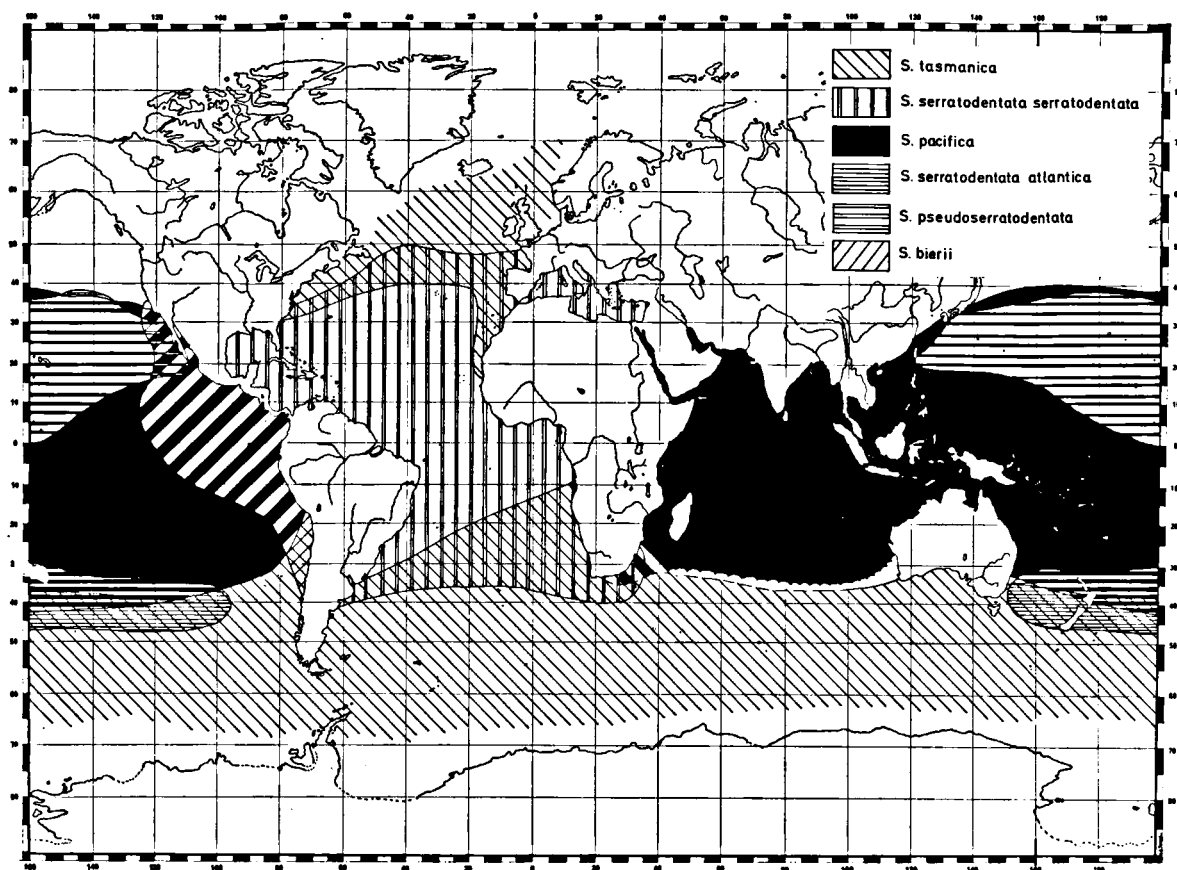


Fig. 11. Distribution map of the "*S. serratodentata*-group" based on literature references, viz. *S. serratodentata serratodentata*, *S. serratodentata atlantica*, *S. tasmanica*, *S. pacifica*, *S. pseudoserratodentata* and *S. bierii*.

into northern and southern zones. Geographic isolation might then have led to speciation, but of course not necessarily so.

S. bierii seems to be restricted to the Pacific Ocean off California and Peru (Bieri, 1959). It does not breed in the bridging zone of the tropical regions but only in the two subtropical areas (Alvariño, 1965) which indicates its temperate origin. Furnestin (1962b; 1966) and Ducret (1968) recorded this species from east African waters and I did find one specimen, looking like *S. bierii*, at Atlantide sta. 62 (4°16'N 8°18'W). The material however, is too scarce to reach a final conclusion as to the taxonomic status of this specimen. Careful examination of more abundant samples may reveal differences between *S. bierii*-like specimens from the East Atlantic and *S. bierii* from the Pacific. At any rate they are geographically isolated.

S. serratodentata serratodentata is found in the Mediterranean and Atlantic, generally between

40°N and 25°S. However, the Gulf Stream may carry specimens of *S. serratodentata serratodentata* further north to about 50°N in the warmer season, sharp areal limits being generally rare in the North Atlantic. In the South Atlantic the southernmost limit of the subspecies is more definitely restricted at about 35°S. There were specimens of *S. serratodentata serratodentata* at Dana sta. 3969 (31°33'S 30°07'E) and 3966 (29°25'S 32°00'E) in the Indian Ocean mixed with *S. pacifica*, but they seem to be restricted to the African region and not extending further eastwards, which is confirmed by de Decker (1973).

S. serratodentata atlantica is found near Australia and New Zealand and more eastward (Tokioka, 1940b; Thomson, 1947; Fagetti, 1959) in temperate waters in the southern part of the south transitional area, east of Australia. The ranges of the two subspecies of *S. serratodentata* do look similar to that of the pteropod *Limacina helicoides* (Jeffreys, 1877) (cf. van der Spoel, 1967) which has an

atlantic distribution with isolated populations in the Australian and New Zealand waters.

S. pacifica is restricted to the Pacific and the Indian Oceans and is found between 40°N and 40°S. This is a range comparable to that occupied by *S. serratodentata serratodentata* in the Atlantic.

S. pseudoserratodentata in the North Pacific is restricted to the northwestern and northeastern areas and to the central north equatorial area.

The distribution of the six taxa of the "*S. serratodentata*-group" and of the polymorphic pteropod species *Clio pyramidata* (Linnaeus, 1767) (cf. van der Spoel, 1967), which is divided into seven formae, have more or less the same pattern. The *Clio pyramidata* forma *lanceolata* is found in the entire Atlantic and Indo-Pacific, covering the same area as *S. serratodentata serratodentata* and *S. pacifica*, respectively. The formae *antarctica* and *sulcata* of *Clio pyramidata* both occur in the South Atlantic as well as in the South Pacific in about the same area as *S. tasmanica*, and *Clio pyramidata* forma *pyramidata* is found in the North Atlantic, but there is no forma in the North Pacific. Dunbar (1954) gives a discontinuous subarctic distribution for some pelagic amphipod species as well. Speciation in the "*S. serratodentata*-group" seems to have reached a more advanced level than in *Clio pyramidata*, as there is no evidence of hybridization between the species.

In the Atlantic there is not much overlap in the distribution of *S. tasmanica* and *S. serratodentata serratodentata* which may be an indication that these species have reached their species rank not very long ago (Mayr, 1966), but in the Pacific Ocean there is considerable overlap in the distribution of *S. pacifica*, *S. pseudoserratodentata*, and *S. bierii*. There also seems to be more frequently overlap in distribution of *S. tasmanica* and *S. serratodentata atlantica* than in that of *S. tasmanica* and *S. serratodentata serratodentata*, which might indicate that the speciation process has already been effective for a longer period in the Pacific Ocean. This supports the theory advanced by Tokioka (1965b) that the Chaetognatha have their origin somewhere in the Pacific Ocean.

In tracing the evolutionary relations of the "*S. serratodentata*-group" the seminal vesicles may have a guiding value. They are the most complexly built of all Chaetognatha.

The seminal vesicle in *S. tasmanica* looks like the most primitive of the group, and also *S. bierii* does not possess the anteriolateral structures of the vesicles whose presence makes this structure con-

spicuous in the other three species. The seminal vesicles in *S. serratodentata*, *S. pacifica*, and *S. pseudoserratodentata* are very similar in this respect (figs. 3-6). A more detailed histological study of the structure of the seminal vesicle will be dealt with in a forthcoming paper.

In the "*S. serratodentata*-group", the primitive *S. tasmanica* is a Circum-Subantarctic and Boreal Atlantic element, while *S. bierii* occurs in the East Pacific, and *S. bierii*-like specimens are found in the East Atlantic. Of the more advanced species, *S. pacifica* lives in the tropical and subtropical Pacific, *S. pseudoserratodentata* in the temperate North Pacific and the subspecies *S. serratodentata atlantica* in temperate South Pacific waters, whereas the subspecies *S. serratodentata serratodentata* is found in the tropical and subtropical Atlantic.

The connections between tropical Atlantic and Pacific waters, through the channels present in central America up to the lower Pliocene, were rather shallow (Ekman, 1953: 368) and important for migration of shallow-water species only. The cold-water connection between the South Pacific and the South Atlantic around the south coast of South America was never very important for the dispersal of tropical and subtropical species.

The isolation of the Atlantic and Indian Oceans took place in the Miocene when the Tethys Sea broke up (Fell, 1967). The fact that only *S. pacifica* occurs in the Red Sea indicates that the Indian Ocean was populated after the Miocene. So one may conclude that the present distribution is influenced greatly by the Pleistocene ice age causing the biboreal distribution of *S. tasmanica* in the Atlantic and giving opportunity for the development of *S. serratodentata serratodentata* in that ocean.

In the Pacific the climatological circumstances need not necessarily have been the same as in the Atlantic. Speciation and distribution of the group did perhaps already start before the Pleistocene so that the ice age may have included the development of different species in the Pacific. *S. pacifica* occurs in the whole Indo-Pacific, *S. pseudoserratodentata* related to *S. pacifica* in the North Pacific, *S. serratodentata atlantica* related to *S. pacifica* is found in the South Pacific, and *S. bierii* related to *S. tasmanica* in the East Pacific. The results were less pronounced in the Atlantic where only *S. serratodentata serratodentata* in the central parts and *S. tasmanica* in the cooler parts are present.

SUMMARY

The description and synonymy are given of *Sagitta serratodentata* Krohn, 1853, subdivided into two subspecies (*S. serratodentata serratodentata* Krohn, 1853, and *S. serratodentata atlantica* Thomson, 1947), of *Sagitta tasmanica* Thomson, 1947, and of *Sagitta pacifica* Tokioka, 1940. The distinguishing characters: shape and structure of the seminal vesicles, total body length in mature specimens and number of posterior teeth, are compared. The regression lines relating total body length and number of posterior teeth for mature specimens are calculated for all samples and compared with each other, showing two distinct groups in the Atlantic, one for *S. serratodentata serratodentata* and one for *S. tasmanica*, and three groups in the Pacific, one for *S. pacifica*, one for *S. serratodentata atlantica* and one for *S. tasmanica*. The regression line for *S. serratodentata atlantica* shows less posterior teeth than that for *S. serratodentata serratodentata*.

Distribution patterns of all species of the "*S. serratodentata*-group" viz. *S. serratodentata*, *S. tasmanica*, *S. pacifica*, *S. pseudoserratodentata* and *S. bierii* are analyzed, as well as taxonomic relations deduced from the structure of their seminal vesicles.

S. tasmanica and *S. bierii* seem to form one group, and *S. serratodentata*, *S. pacifica* and *S. pseudoserratodentata* another group of closely related species.

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