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Taxonomy of the subfamily Cyclosalpinae Yount, 1954 (Tunicata, Thaliacea), with descriptions of two new species

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#### ABSTRACT

The genera Cyclosalpa de Blainville, 1827 and Helicosalpa Todaro, 1902 are revised on the basis of material from all three oceans. Two new species, Cyclosalpa foxtoni and Cyclosalpa ihlei are described, and four taxa, formerly described as varieties or subspecies, are raised to specific rank. The existence of morphological groups of species within the genus Cyclosalpa is discussed.

#### Introduction

The subfamily Cyclosalpinae Yount, 1954 consists of two genera Cyclosalpa de Blainville, 1827 and Helicosalpa Todaro, 1902. Both genera differ from the salps of the subfamily Salpinae Yount, 1954 in a number of characters. All solitary generations (with the exception of one species) possess luminous organs, the body muscles form almost complete loops, the distal part of the intestine extends far anteriorly along the gill bar (the gut is not coiled into a tight nucleus); the aggregate generation bears only a single ventral attachment organ, which is mostly prominent and protruding strongly; in some species the aggregates also possess luminous organs.

The two genera of the subfamily differ in the arrangement of the sexual individuals into aggregates. In Cyclosalpa the sexual individuals are arranged in whorls i.e. all individuals are arranged radially and attached to each other in the center by their long peduncle; in Helicosalpa they are arranged in chains, just as in all other salps. Linked to this the aggregate individuals of the majority of the Cyclosalpa-species show bilateral symmetry (with the exception of C. strongylenteron, C. bakeri and the two new species to be described in this paper). In Helicosalpa, just as in all other salps, the aggre-

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gate individuals are not symmetrical and can be divided in left-sided (sinistral) and right-sided (dextral) individuals.

Up till now nine taxa have been distinguished in the genus Cyclosalpa and three in the genus Helicosalpa, viz. Cyclosalpa pinnata subsp. pinnata (Forskål, 1775), C. pinnata subsp. polae Sigl, 1912, C. pinnata subsp. sewelli Metcalf, 1927, C. pinnata subsp. quadriluminis Berner, 1955, C. pinnata subsp. parallela Kashkina, 1973, C. affinis (Chamisso, 1819), C. floridana (Apstein, 1894), C. bakeri Ritter, 1905, C. strongylenteron Berner, 1955, Helicosalpa virgula subsp. virgula (Vogt, 1854), H. virgula ssp. younti Kashkina, 1973 and H. komaii (Ihle & Ihle-Landenberg, 1935). In this paper two new taxa are added, a new species quite nearly related to C. bakeri, and one showing affinities to both genera. It is proposed here to treat the sympatric "subspecies" of C. pinnata and H. virgula as separate species. This proposal is made analogous to a similar proposal made in a previous paper on the genus Thalia Blumenbach, 1798 (van Soest, 1973a). There is not much point in treating the narrowly related sympatric forms as conspecific; a somewhat more detailed discussion of this subject will be given in a future paper. In the meantime an exception must be made for C. pinnata subsp. quadriluminis and C.p. parallela, which, as far as can be concluded from the material studied at present, are not sympatric. Both will be treated as formae of the same species C. quadriluminis.

Of the hitherto described taxa five are incompletely known in that only one of both generations has been described. Two of these unknown generations are described in the present paper. One of the new species described in the present paper is only known from the solitary generation, so in all still four species remain incompletely known.

Many of the taxa are only recently recognized, which is the cause for the insufficient information on their distribution and ecology. The literature data must be used with utmost reserve as most authors in the past did not give adequate descriptions or figures enabling the assignment of their specimens to the proper taxa now recognized. Most data on the distribution of the species of Cyclosalpinae are drawn form the present investigation.

#### MATERIAL.

The studied material is listed below. It consisted of samples collected by various oceanic expeditions and a number of incidental samples. Of the major expeditions (Dana Expeditions, Siboga Expedition) only the station numbers are given; for the data on these stations one is referred to the station lists of the expeditions. The ACRE-cruises were all held in the immediate vicinity of Bermuda. In addition, a chart showing the localities of all the studied samples, is given in fig. 1.

The author is indebted to Dr. E. Rasmussen and Dr. J. Knudsen of the Zoologisk Museum of Copenhagen (ZMUC) for their hospitality during his stay at the museum and for their cooperation in allowing him to select and study part of the extensive Dana-collections. Dr. C. F. E. Roper of the United

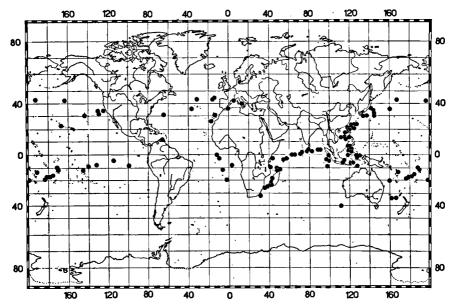


FIG. 1. Map showing the geographical positions from which the samples were taken.

States National Museum at Washington (USNM) is thanked for the loan of ACRE-material and Dr. R. H. Gibbs of the same museum for the loan of Mediterranean material (both collected with financial support from the U.S. Navy). Prof. Dr. W. Vervoort of the Rijksmuseum van Natuurlijke Historie at Leiden (RMNHL) kindly permitted the loan of some samples. The captains and crews of the HMS "Luymes", HMS "Snellius", RV "Tridens", OWS "Cirrus" and OWS "Cumulus" are thanked for their skill and cooperation in collecting the plankton samples from the Southern Caribbean (CICAR-cruises), the tropical Atlantic and the Northeastern Atlantic respectively.

## Atlantic Ocean (including the Mediterranean):

Dana Expeditions: Station 3980 IV, 3980 V, 3981 V, 3997 V, 3999 II, 3999 III, 4000 VI, 4000 XI, 4010 IV, 4018, 4762 (all ZMUC); US/SI-Med. cruises, station 1—4M, 37°04′ N, 00°51′ E (ZMA/USNM); Chazalie-expedition, 37° N, 36° W (ZMA); Snellius Expedition, station Mike 3, 45°58′ N, 32°12′ W (ZMA); Cirrus Expedition I, 45° N, 16° W (ZMA); Naples (ZMA/RMNHL); Tridens Expedition, station 11, 46°25′ N, 15°00′ W (ZMA); CICAR-cruise 13 (near Curaçao) (ZMA).

#### Indian Ocean:

Dana Expeditions: Station 3903 III, 3904 II, 3907 III, 3912 III, 3914 III, 3917 X, 3918 IV, 3918 V, 3919 II, 3921 VII, 3922 V, 3932 II, 3934 II+VII+IX, 3946 I, 3948 II, 3948 III, 3955 IV, 3957 II, 3958 II, 3961 I, 3962 III, 3964 II, 3969 IV, 3815 III, 3843 I, 3843 II, 3856 IV, 3893 IX, 4765 (all ZMUC).

Pacific Ocean (including the Indo-Australian Archipelago):

Dana Expeditions: Station 3558 VIII, 3561 X, 3563 II, 3563 V, 3567 II, 3569 III, 3579 IV, 3584 VI, 3587 XI, 3589 XI, 3591 IV, 3593 X, 3601 V, 3653 VIII, 3654 IV, 3686 III, 3720 I, 3722 III, 3722 IV, 3723 V, 3729 IV, 3732 V, 4722, 4761, 4768, 4771, 4772, 4773, 4775, 4777, 4779, 4785, 4789, 4790, 4791, 4793, 4797, 4798, 4802, 4809, 4813, 4815, 4818, 4820 (all ZMUC); Siboga Expedition, station 96, 106, 110, 144, 165, 177a, 215a, 220, 282 (all ZMA); Between Laysan and Honolulu, don. Schauinsland (ZMA).

## Subfamily Cyclosalpinae Yount, 1954 Genus Cyclosalpa de Blainville, 1827

Type species: Salpa pinnata Forskål, 1775

Nomenclatorial note: Cyclosalpa de Blainville, 1827, seems to be a junior synonym of Thalia Blumenbach, 1798 (the type species T. lingulata is a cyclosalp), a name currently used for Salpa democratica (= Thalia democratica) Forskål, 1775, and its allies (see Van Soest, 1973). Waal (1966) proposed to the International Commission on Zoological Nomenclature to assign the genus name Thalia to Salpa democratica Forskål, 1775 and the name Cyclosalpa to Salpa pinnata Forskål, 1775, in order to avoid major confusion. It is assumed here that the Commission will eventually decide in favour of this proposition.

## Diagnosis of the genus:

Solitary zooids: Test soft, smooth, devoid of any serrations or projections; oral and atrial openings terminal. Musculature: 7 body muscles (M I - M VII), arranged symmetrically, variously continuous or interrupted along the dorsal median line; always interrupted on the ventral median line. In some species M VI has a forward longitudinal extension along the dorsal median line; these longitudinal muscles may be paired or fused into one. The oral musculature consists next to the intermediate muscle usually of four dorsal and two or three ventral oral sphincters. The atrial musculature consists of a varying number of complete hoops serving as sphincters, which often anastomose; there is one prominent atrial retractor on each side. Luminous organs: in all but one species pairs of luminous stripes are present, arranged laterally between or sometimes on the body muscles. The number of luminous stripes varies from 3-6 pairs in the various species. Dorsal tubercle: differing in the various species from a simple U-shape to a highly convoluted organ. Alimentary canal: oesophagus and stomach lying posteriorly accompanied by two caeca of equal or unequal length; anal part of the intestine extending forward dorsal to and along the gill bar; anus lying far anteriorly. Stolon extending forward on the mid ventral line; in one species it is coiled. In an advanced stage of development the stolon individuals are grouped into whorls of up to 15 specimens each.

Aggregate zooids: All individuals are arranged in whorls of up to

15 specimens each, Test soft, smooth, without serrations or dorsal projections; on the ventral side of the anterior half of the zooid one prominent attachment organ is present, the so called peduncle, by which the individuals are attached to each other. Oral opening terminal, atrial opening dorsal/terminal. Mus ulature: in general the body muscles are symmetrically arranged, with two exceptions. Four body muscles, all continuous dorsally, sometimes interrupted along the ventral median line. There may be a ventral longitudinal muscle. Usually M I and M II are continued into the peduncle; if a ventral longitudinal muscle is present, it is also continued into the peduncle. The body muscles may be fused into various patterns or completely free dorsally. The oral musculature consists of three to four upper sphincters and two to four basal sphincters. The intermediate muscle generally fuses with the first body muscle. The atrial musculature consists of 3—9 completely hooped sphincters. Peduncle: this attachment organ may be as long or even longer than the body, but it may also be quite short. Luminous organs are present in some species; if present they usually consist of one pair lying between M II and M III. Sometimes a second pair lies between M III and M IV. Dorsal tubercle: this varies from a simple, slightly arched stick to a convoluted structure. Alimentary canal: the intestine is generally loosely coiled in the posterior ventral region. The anal part may extend forward along the endostyl. In four species a real caecum is present and in three of these a distinct asymmetry is found in dextral and sinistral individuals with respect to the arrangement and the size of the caecum. In these three species also a blood forming organ is present, which protrudes posteriorly. In the remaining species a swelling of the gut serves as a caecum. Gonads: the testis may be positioned between endostyl and gut or protruding posteriorly beyond the gut, causing a pointed posterior part of the test. The ovary and the embryo lie between the third and fourth body muscles on the right side.

Ten species are recognized; one unnamed taxon will be described below, which may prove to be also a valid species of *Cyclosalpa*.

## Cyclosalpa pinnata (Forskål, 1775)

## Synonymy:

- ? Thalia no. 1, no. 2, no. 3 Browne, 1756 (after Metcalf, 1918: 9).
- ? Holothuria thalia Linnaeus, 1758: 657; Gmelin ir. Linnaeus, 1791: 3139.
- ? Holothuria caudata Linnaeus, 1758: 657; Gmelin in Linnaeus, 1791: 3139.
- Salpa pinnata Forskål, 1775: 113, pl. 35 (fig. Bb<sub>1</sub>-b<sub>2</sub>); Gmelin in Linnaeus, 1791: 3129; Lamarck, 1816: 116; Traustedt, 1885: 353, pl. 1 (fig. 1—5). (Non: Quoy & Gaimard, 1833: pl. 88 (fig. 12—15) and Quoy & Gaimard, 1834: 580, 582 (= Cyclosalpa affinis)).
- Salpa cristata Cuvier, 1804: 366, fig. 1—2; Lamarck, 1816: 118; Cuvier, 1817: 7, fig. 1—2.
- Salpa; Home, 1814: pl. 73 (fig. 2) (Non: Dagysa; Home, 1814: pl. 73 (fig. 1) (= Thetys vagina)).
- ? Salpa thalia; Lamarck, 1816: 119.
- ? Salpa caudata; Lamarck, 1816: 119.
- Salpa (Cyclosalpa) pinnata; de Blainville, 1827: 108; Brooks, 1908b: 81, pl. 2 (fig. 8); Streiff, 1908: 15, pl. 1 (fig. 1—4); Sigl, 1913: 223, fig. 8—9; Metcalf, 1918: 9, pl. 1

(fig. 1—4), pl. 2 (fig. 5—8), text fig. 3—12. (Non: Sewell, 1926: 68, fig. 1—3 (= Cyclosalpa sewelli)).

Salpa cyanea Della Chiaje, 1828: 59.

Salpa proboscidalis Reynaud in Lesson, 1830: 95, pl. 33.

Cyclosalpa pinnata; Apstein, 1906a: 160, fig. 1—2; Apstein, 1906b: 247 (in part); Stiasny, 1927: 414, pl. 1 (fig. 1—6), text fig. A; Apstein, 1929: 8, fig. 11—12; Ihle & Ihle-Landenberg, 1936a: 1; Belloc, 1938: 315, fig. 1—2; Thomson, 1948: 103, pl. 32, pl. 33 (fig. 1, 4A), pl. 34 (fig. 1); Godeaux & Goffinet 1968: 54. (Non: Ihle, 1910: 17 (= C. polae, C. sewelli, and C. quadriluminis forma parallela); nec: Tokioka, 1937: 219 (= C. quadriluminis forma parallela); nec: Yount, 1954: 283 (= C. sewelli, C. polae and C. quadriluminis forma parallela); nec: Fagetti, 1959: 210, fig. 1 (= C. polae); nec: Dossman, 1970: 69, fig. 2 (= C. polae)).

Type locality: Near Ibiza (Mediterranean).

## Diagnosis (fig. 15a):

Solitary zooids: Test quite thick and solid. Size up to 75 mm (Traustedt, 1885). Body muscles: all interrupted dorsally; M VI as other body muscles, not extending as a longitudinal muscle. Total number of muscle fibres in the studied specimen: 169. Luminous organs: 5 pairs between M I - M VI; strongly developed. Dorsal tubercle: moderately convoluted (fig. 19a). Intestine with two caeca of unequal length; anus lying just underneath the ganglion. No atrial palps; two ventral languets present near the intermediate muscle.

Aggregate zooids: Test quite thick and solid. Size up to 64 mm (n=20). Body muscles: M I and M II fused dorsally and lateroventrally before descending into the peduncle; M III and M IV approaching but not touching or fusing dorsally. Total number of muscle fibres 52—75 (m=66.8, n=16). A distinct medioventral visceral muscle is present. Luminous organs: one strongly developed pair lies between M II and M III. Dorsal tubercle: slightly convoluted (fig. 20a). Peduncle short compared to the body length (ratio about 1:4). Intestine with one "caecum" posteriorly; the last part extends anteriorly underneath the endostyl; anus lying at the root of the peduncle.

## Distribution (fig. 2):

Cyclosalpa pinnata seems to be restricted to the Atlantic. In fact the present author has found no specimens south of 30° N in the Atlantic. Literature data make it fairly certain, that it also occurs in the South Atlantic, e.g. along the coast of Angola (4°—17° S, 6°—10° E; Godeaux & Goffinet, 1968). Most literature data from the South Atlantic must, however, be referred to other taxa of Cyclosalpa. The present material originates from the Bermuda area, the Mediterranean and from various localities in the Northern Atlantic. Apstein (1929) states that this species may penetrate to 60° N. Farran (1906, after Apstein, 1929) has found it on the south coast of Ireland. All literature data on the occurrence of C. pinnata in Indo-Pacific waters must be referred to other species.

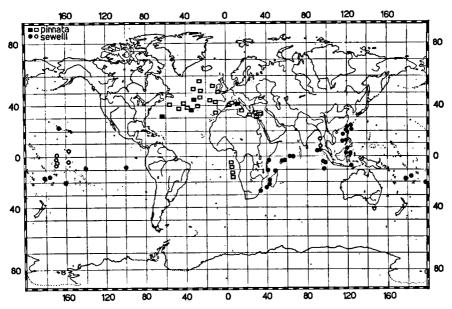


Fig. 2. Distribution of Cyclosalpa pinnata (black and open rectangles) and C. sewelli (black dots and open circles). Black symbols indicate studied samples, open symbols literature data.

#### Cyclosalpa sewelli Metcalf, 1927

#### Synonymy:

Cyclosalpa bakeri; Bomford, 1913: 242 (non: C. bakeri Ritter, 1905).

Salpa (Cyclosalpa) pinnata, Indian form; Sewell, 1926: 68, fig. 1—3.

Salpa (Cyclosalpa) pinnata subsp. polae; Sewell, 1926: 68, fig. 1—3.

Cyclosalpa pinnata subsp. sewelli Metcalf, 1927: 257; Thompson, 1948: 103, pl. 33

(fig. 2—4C), pl. 34 (fig. 3); Kashkina, 1973: 216.

Cyclosalpa pinnata var. sewelli; Sewell, 1953: 8.

Cyclosalpa pinnata; Yount, 1954: 283, fig. 3 (in part).

Type locality: Nankauri Harbour, Nicobar Islands.

## Diagnosis (fig. 15b):

Solitary zooids: Test soft, thin. Size up to 24 mm. Body muscles: all interrupted dorsally; M VI as other body muscles, not extended forward as longitudinal muscle. Total number of muscle fibres M I - M VII = 41-58 (m = 48.9, n = 37). Luminous organs: 4 pairs between M II - M VI. Dorsal tubercle: of a simple U-shape (fig. 19b). Intestine with two caeca of unequal length; anus lying underneath the ganglion. No atrial palps; no ventral languets have been found.

A g g r e g a t e z o o i d s: Up till now the aggregate zooid of C. sewelli has not been recognized, although Sewell (1926: 71—72) gave a description and figures of them, stating that they were indistinguishable from those of C.

polae. It is indeed understandable that the stolon individuals he studied caused him to confuse them with *C. polae*, as the differences between aggregate zooids of both species are only clear in mature individuals.

Description: Test soft, thin. Size up to 18 mm, usually much smaller. Body muscles arranged as in C. polae: M I and M II are fused over a considerable part of their length; M III and M IV are likewise strongly fused. Total number of muscle fibres of M I - M IV = 16.5 (range: 14-19; n = 104); normally there are four muscle fibres to each muscle. Atrial and oral musculature as in Cyclosalpa pinnata (cf. Sewell, 1926: fig. 4). Luminous organs: one pair lying between M II and M III; the length of the luminous stripes increases with the length increase of the body and normally is about 18% of the body length (m = 18.0%, range 11.9—30.0%, n = 48). This is somewhat shorter than the luminous organs of C. polae which measure about 24% (m = 23.6%, range = 15.3-32.1%, n = 50). Dorsal tubercle (fig. 20b): a very simple, slightly arched stick. Alimentary canal: as in C. pinnata. Peduncle: extremely long; as long as twice the body length is not unusual. Embryo: some well developed embryos have been found (still attached to the body wall of their parent) that conformed to the above described solitary zooid but for the luminous organs, which are only traceable in the very last stage of development. It could be established that they were definitely not C. polae.

## Distribution (fig. 2):

Literature data on *C. sewelli* are scarce. It is clear from Bomford's (1913) description of his "*C. bakeri*" that he had found *C. sewelli* at 15°25' N, 93°45' E (Gulf of Bengal). Sewell's (1926) specimens came also from that area. Yount's (1954) *Cyclosalpa pinnata* sol. is clearly *C. sewelli*; they originated from the area south of Hawaii. From the material presently studied it is clear that *C. sewelli* is confined to Indo-Pacific waters, roughly between 30° N and 30° S. No samples were available from the southeastern Indian Ocean and the southeastern Pacific Ocean, but it seems clear that *C. sewelli*, though not a true "Indian form" as Sewell (1926) stated, is most abundant in the Indian Ocean and the neighbouring tropical West Pacific.

## Cyclosalpa polae Sigl, 1912

## Synonymy:

Cyclosalpa pinnata; Ihle, 1910: 17 (in part); Fagetti, 1959: 210, fig. 1; Dossman, 1970: 69, fig. 2. (Non: Yount, 1954: 284 (= C. sewelli and C. quadriluminis forma parallela)).

Cyclosalpa polae Sigl, 1912: 68, fig. 1—7; Sigl, 1913: 225, pl. 1 (fig. 1—6), text fig. 2—6; Ihle & Ihle-Landenberg, 1936a: 1, fig. 1.

Salpa (Cyclosalpa) pinnata subsp. polae; Metcalf, 1918: 26, fig. 13—14. (Non: Sewell, 1926: 68, fig. 4 (= C. sewelli)).

Cyclosalpa pinnata subsp. polae; Tokioka, 1937: 220; Thomson, 1948: 103, pl. 33 (fig. 3, 4B), pl. 34 (fig. 2); Berner, 1955: 252; Godeaux & Goffinet, 1968: 54; Kashkina, 1973: 216.

Type locality: Eastern Mediterranean, 31°—39° N, 19°—34° E.

## Diagnosis (fig. 15c):

Solitary 200 ids: Test soft, thin. Size up to 36 mm (n = 21). Sigl (1912) found one specimen of 40 mm, the remaining specimens were smaller. Body muscles interrupted dorsally and ventrally with the exception of MVI, which are fused dorsally into one and extend longitudinally to the level of MII. The fusion of MVI is complete. Total number of muscle fibres of MI-MVII = 75 (m = 74.5, range 55—101, n = 21). Luminous organs: 5 pairs between MI-MVII, strongly developed. Dorsal tubercle: moderately convoluted, somewhat less so than in C. pinnata (fig. 19c). Intestine with two caeca of unequal length, anus lying posterior to the ganglion. No atrial palps or ventral languets have been found. Stolon: stolon individuals arranged in whorls of up to five specimens each (Sigl, 1912).

Aggregate zooids: Test soft, thin. Size up to 35 mm (n = 78). Body muscles arranged essentially as in *C. sewelli*, both M I/M II and M III/M IV are fused dorsally. Total number of muscle fibres M I - M IV = 24 (m = 23.4, range = 20—29, n = 78); normally there are 5 or 6 muscle fibres to each body muscle. Oral and atrial musculature as in *C. pinnata*. Peduncle: very long, often exceeding the body length. Luminous organs: one pair between M II and M III; luminous stripes longer than in *C. sewelli*. Dorsal tubercle: W-shaped (fig. 20c). Alimentary canal as in *C. pinnata*. Embryo: on several occasions an embryo in the body of its parent could be identified as *C. polae* sol., although the luminous organs were still undeveloped. One of them showed the forward extension of both M VI completely free from each other. The fusion of these into one longitudinal muscle probably takes place in an advanced stage of the development.

## Distribution (fig. 3):

C. polae is doubtless the most wide-spread of the near relatives of C. pinnata. It has been found in the eastern Mediterranean (Sigl, 1912), near Naples (e.g. present material), near Bermuda, in the southern Caribbean, in the tropical and southern South Atlantic (Godeaux & Goffinet, 1968), in the tropical and southern Indian Ocean, in the Arabian Sea, the Gulf of Bengal, the Indo-Australian Archipelago, east of Australia (Thompson, 1948), the China Sea, near Japan, near Hawaii (Metcalf, 1918), and in the western and eastern tropical Pacific (Fagetti, 1959; Berner, 1955; Dossman, 1970). The range of C. polae extends perhaps somewhat further into higher latitudes (40° N, 40° S) than that of C. sewelli.

Cyclosalpa quadriluminis forma quadriluminis Berner, 1955, comb. nov.

## Synonymy:

Cyclosalpa pinnata subsp. quadriluminis Berner, 1955: 251, fig. 6-7; Kashkina, 1973: 216.

Type locality: Eastern Pacific, 27°-33° N, 115°-125° E.

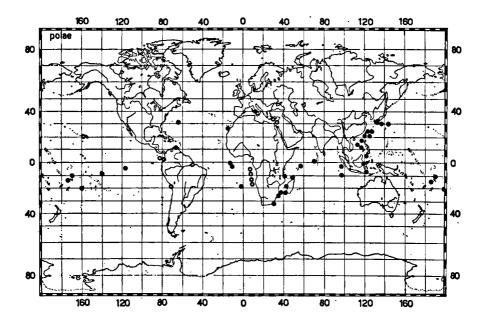


Fig. 3. Distribution of Cyclosalpa polae.

Note: As C. pinnata quadriluminis Berner, 1955 and C.p. parallela Kashkina, 1973 (both only known from aggregate zooids) are quite similar, differing only in the fusion or non-fusion of M III - M IV, and as they seem to be, judging from the present investigation, allopatric, it is proposed here to treat them as formae (sensu van der Spoel, 1971) of the same species Cyclosalpa quadriluminis. The forma-status of these two conspecific taxa seems the best way to explain the occurrence of intermediary characters.

## Diagnosis (fig. 15d):

Only aggregates are known. It seems probable that the solitary zooid will bear a strong resemblance to that of C.q. forma parallella, which will be newly described below.

Aggregate zooids: Test thick (not as thick as in C. pinnata, thicker than in C. polae). Size up to 29 mm (n = 20). Body muscles: MI - MII and MIII - MIV fused dorsally. Total number of muscle fibres of MI - MIV = 33 (m = 33.3, range = 29—38, n = 20). Peduncle: short, not exceeding one third of the body length, but mostly shorter than that. Luminous organs: 2 pairs lying between MII - MIII and MIII - MIV, the anterior pair roughly two times as long as the posterior one. Dorsal tubercle: of a slightly convoluted C-shape (fig. 20d). Intestine as in C. pinnata.

## Distribution (fig. 5):

This form is confined to the eastern part of the Pacific Ocean. It has been found in the area between 35° N—12° S and 145°—128° W. Berner's (1955) localities cover the area to the east of that.

Cyclosalpa quadriluminis forma parallela Kashkina, 1973, comb. nov.

#### Synonymy:

Cyclosalpa pinnata; Ihle, 1910: 17 (in part); Tokioka, 1937: 219; Yount, 1954: 283, fig. 3.

Cyclosalpa pinnata subsp. polae; Komai, 1932: 69, fig. 2.

Cyclosalpa pinnata subsp. parallela Kashkina, 1973: 215, fig. 1.

Type locality: Arabian Sea, 9°06′—9°29′ N, 63°37′—63°58′ E. Description of the solitary zooids (fig. 4):

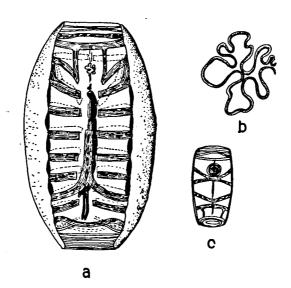


Fig. 4. a. Solitary zooid of Cyclosalpa quadriluminis f. parallela; b. Detail of the dorsal tubercle of the same specimen; c. Schematic representation of an individual from the stolon of the same specimen.

Only aggregate generations of this form (and this species) have been described up till now. From the appearance of embryos in some aggregate specimens it was clear, that an undescribed solitary zooid found in the present investigations belonged to this form. The stolon in some of these solitary specimens contained juvenile aggregate zooids conforming to this taxon but for the luminous organs which were still undeveloped. The solitary zooid resembles in all but a few small characters that of C. polae. Test moderately thick, transparent. Size up to 37 mm (n = 4). Body muscles: both M VI converge

into one in the mid dorsal line and extend forward as a longitudinal muscle; this fusion, however, is incomplete; both M VI are now and then separated by a narrow slit. Total number of muscle fibres of M I - M VII = 117 (range = 114—123, n = 3). Luminous organs: 5 strongly developed pairs lying between M I - M VI. Dorsal tubercle (fig. 4b, 19d): moderately convoluted, more than in *C. polae*. The two caeca of the intestine appear to be of equal length; however, when examined closely there is a very small difference in length. The anus lies underneath the ganglion. No atrial palps have been found. Two ventral languets are present.

The solitary zooid of *C. quadriluminis* forma *parallela* has been found in the same sample with that of *C. polae*; they can be readily separated by the slits in the longitudinal muscle and the higher number of muscle fibres.

## Diagnosis of the aggregate zooids (fig. 15e):

Test thick, but not solid. Size up to 43 mm (n = 53), up to 45 mm (Kashkina, 1973). Body muscles: M I and M II fused dorsally, M III and M IV approaching, sometimes touching but never fusing. Total number of muscle fibres of M I - M IV = 44 (m = 43.5, range = 37—50, n = 53). Luminous organs: 2 pairs lying between M II/M III and M III/M IV, the anterior one being roughly twice as long as the posterior one. Dorsal tubercle: as in C. quadriluminis forma quadriluminis (fig. 20d). Peduncle: short, not exceeding one third of the body length. Intestine as in C. pinnata. Embryo: one big embryo observed within the body of its parent showed a forward extension of M VI dorsally; both M VI, however, were not fused. The fusion, just as in C. polae probably takes place in the latest stage of development.

Note: Several specimens have been observed in which M III and M IV had a few (up to three) muscle fibres in common in the mid dorsal line. These are thus intermediate between C.q. forma quadriluminis (M III - M IV completely fused) and C.q. forma parallela (M III - M IV completely free). The incidence of those specimens was perhaps somewhat greater in the bordering area of the distribution of both formae, but they also occurred in the Indian Ocean far from the distribution area of C.q. fo. quadriluminis. Furthermore there is a slight overlap in the number of muscle fibres of both forms. These observations lead to the conclusions that separation of both formae is not always possible.

## Distribution (fig. 5):

Originally described from the Arabian Sea (Kashkina, 1973) C.q. forma parallela has now been observed in the whole of the Indopacific with the exception of the northeastern part. Komai (1932) and Tokioka (1937) found it off the east coast of middle Japan, Ihle (1910) found some specimens in the Indo-Malayan area, and Yount (1954) records it from the area south of Hawaii. In the present investigations it occurred particularly numerous in the western part of the Indian Ocean; in fewer samples it has been found in the China Sea and the tropical Pacific.

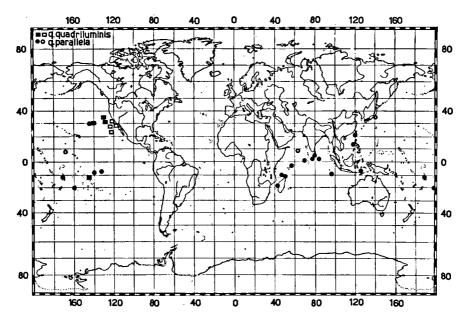


Fig. 5. Distribution of Cyclosalpa quadriluminis quadriluminis (rectangles) and C.q. parallela (circles).

#### Cyclosalpa affinis (Chamisso, 1819)

#### Synonymy:

Salpa affinis Chamisso, 1819: 11 (after Yount, 1954: 284); Traustedt, 1885: 357, pl. 1 (fig. 6-8).

Salpa (Cyclosalpa) affinis; de Blainville, 1827: 119; Apstein, 1894: 4; Metcalf, 1918: 27, pl. 3 (fig. 9—10), pl. 4 (fig. 11—12), textfig. 15; Sewell, 1926: 74; Komai, 1932: 70, fig. 3.

Salpa pinnata; Quoy & Gaimard, 1833: pl. 88 (fig. 12-15), 1834: 580, 582.

Cyclosalpa affinis; Traustedt, 1893: 5; Ritter, 1905: 59; Ritter & Byxbee, 1905: 196; Apstein, 1906a: 161, fig. 3—4; Apstein, 1906b: 247; Tokioka, 1937: 221; Thompson, 1948: 108, pl. 32, pl. 35 (fig. 1—3), pl. 41 (fig. 1); Yount, 1954: 285 (in part), fig. 4b; Godeaux & Goffinet, 1968: 56. (Non: Yount, 1954: 285 (in part), fig. 4a (= C. spec.)).

Type locality: Sandwich Islands.

## Diagnosis (fig. 16a):

Solitary zooids: Test thick and solid. Size up to 74 mm (n = 12). Body muscles normally continuous dorsally with the exception of M I and M II, which are interrupted in the mid dorsal line. However, one specimen has been observed having M III as well as M V interrupted dorsally next to M I and M II. Another specimen had M I, M II, M III and M VI interrupted in the mid dorsal line, so probably this character is variable. Total

number of muscle fibres of M I - M VII = 114 (m = 113.8, range = 93—135, n = 12). Luminous organs absent. Dorsal tubercle: strongly convoluted (fig. 19e). Intestine: two caeca, appearing as one, further details as in *C. pinnata*. For details of the stolon development see Ritter & Johnson (1910). No ventral languets; atrial palps minute.

Aggregate zooids: Test thin and soft, with a big posteroventral swelling. Size up to 46 mm (n=13). Body muscles all completely free dorsally. Total number of muscle fibres of M I - M IV = 49 (m=49.3, range = 41—57, n=14). Luminous organs: not present. Dorsal tubercle: moderately convoluted (fig. 20e). Peduncle: short, not exceeding 1/5 of the body length. Intestine lying posteriorly in a loose coil, protruding strongly posteriorly; no forward extension along the endostyl, the anus lying next to the oesophagus. There is a real caecum adhering closely to the gut loop, which causes it to appear as a mere thickening of the gut itself. Testis lying within the loop of the gut.

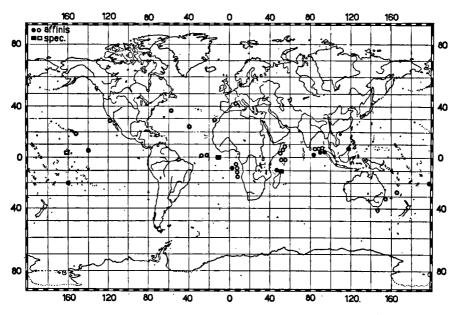


Fig. 6. Distribution of Cyclosalpa affinis (circles) and C. spec. (rectangles).

## Distribution (fig. 6):

Apart from the type locality (Sandwich Islands), *C. affinis* has been found in temperate and warm waters in all three oceans. Metcalf (1918) mentions specimens from the east coast of North America. Traustedt (1885) reports the species from the tropical East Atlantic, as did Apstein (1906a) and Godeaux & Goffinet (1968). Apstein (1894) found it in the North Atlantic up to 41° N. Sewell (1926) reports it from the Indian Ocean. Thompson (1948), Komai (1932), Tokioka (1937), Yount (1954) and Ritter & Byxbee

(1905) report this species from various localities in the Pacific Ocean. The present material conforms this wide-spread occurrence. C. affinis is one of the rarer salps.

#### Cyclosalpa spec. (aff. affinis)

Synonymy:

Cyclosalpa affinis; Yount, 1954: 285 (in part), fig. 4a.

Seven Cyclosalpa affinis-like aggregate zooids are dealt with separately, as they seemed to differ distinctly enough from C. affinis to suspect they may prove to be specifically different. They probably belong to solitary zooids of a type described by Yount (1954 as C. affinis). As no such solitary zooids have been found in the present material the diagnosis is based on Yount's description and figure. This aberrant solitary zooid differs from the typical C. affinis in at least two characters (fig. 7a). Firstly, it possesses one pair of

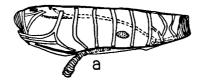




Fig. 7. a. Aberrant Cyclosalpa affinis-like solitary zooid referred to as C. spec. in the present study (copied from Yount, 1954: fig. 4a); b. Detail of the body of an aberrant C. affinis-like aggregate zooid also referred to as C. spec. in the present study. Note the peculiarly shaped luminous organs.

luminous organs of a somewhat aberrant type, as they are roundish rather than elongated, and of a very light colouring. The luminous organs are positioned between M IV and M V. A further discrepancy between typical C. affinis and Yount's specimen is the lateral anastomosing of M VI and M VII. The seventh body muscle divides into two branches of which the anterior one joins the sixth body muscle. Yount did not count the muscle fibres. In all other aspects the specimen conformed to the type.

The seven aggregate zooids found in the present investigation possess one pair of luminous organs (or structures resembling them) similar to the above mentioned luminous organs of Yount's solitary specimens. Their shape is peculiar (fig. 7b) and differs somewhat from that in the solitary specimen. There are some brown granules in the interior. They lie between M II and M III. No other differences from the typical C. affinis could be found in these specimens. The figure Yount gives of the aggregate zooid of C. affinis (1954: fig. 4b) apparently is that of the normal C. affinis, as no luminous organs are shown.

## Distribution of the aberrant specimens (fig. 6):

Yount's specimens originated from the area south of Hawaii. The aggregate zooids described above were captured at 11°24′ S, 50°05′ E (Indian Ocean) and at 0°31′ S, 11°02′ W (Atlantic Ocean), both by the Dana Expeditions.

## Cyclosalpa floridana (Apstein, 1894)

#### Synonymy:

Cyclosalpa dolicosoma-virgula; Traustedt, 1893: 5 (non: Salpa dolicosoma-virgula Todaro-Vogt, 1854).

Salpa (Cyclosalpa) floridana Apstein, 1894: 9, pl. 2 (fig. 1—6); Brooks, 1908a: 75, pl. 1 (fig. 1—6), pl. 2 (fig. 7, 9); Metcalf, 1918: 32, pl. 4 (fig. 13—14), pl. 5 (fig. 16), textfig. 16; Sewell, 1926: 72.

Cyclosalpa floridana; Ihle, 1910: 19, pl. 1 (fig. 1—2, 5); Ihle & Ihle-Landenberg, 1935: 21, fig. 1—2; Thompson, 1948: 111, pl. 37 (fig. 1—4), pl. 41 (fig. 3); Yount, 1954: 286, fig. 5; Godeaux, 1962: 21; Godeaux & Goffinet, 1968: 58. (Non: Apstein, 1906a: 162, pl. 8 (fig. 1—3), textfig. 7—8 (= C. bakeri); nec: Apstein, 1906b: 248, pl. 26 (fig. 3, 3a-d) (= C. bakeri); nec: Michaelsen, 1914: 505 (= C. bakeri)).

Type locality: 32°—41° N, 56°—63° W (western North Atlantic).

## Diagnosis (fig. 16c):

Solitary zooids: Test very thick, globular, transparent. Size up to 13 mm (n = 25). Body muscles: all interrupted dorsally; M I and M II fused dorsally into one together with the intermediate muscle. M I - M V fused ventrally into one mass of muscles, which is not interrupted in the mid ventral line. M VI interrupted ventrally, but M VII continuous ventrally. Total number of muscle fibres of M I - M VII = 43 (m = 42.7, range = 31—51, n = 20). Luminous organs: a weakly developed, more or less continuous, paired mass positioned between M I - M VI or M II - M VI. Dorsal tubercle: a simple C-shape (fig. 19f). Intestine: only one caecum present, anus' far anteriorly, but less so than in C. pinnata (not reaching the ganglion). Stolon: not in a straight line but spirally coiled in the midventral line. No ventral languets or atrial palps have been found.

A g g r e g a t e z o o i d s: Test thin, globular, voluminous. Size up to 9.5 mm (n = 12). Body muscles: apparently there are only three body muscles. Metcalf (1918) thinks that M II has merged into one of the other body muscles.

Yount (1954) takes the view that M I and the missing M II have fused completely. The intermediate muscle laterally joins M I (+ M II), M III and M IV are fused dorsally and touch ventrally. The fused M I (+ M II) and M III/M IV approach but do not touch in the mid dorsal line. M I (+ M II) touches M III lateroventrally before joining the intermediate muscle and descending into the peduncle. Total number of muscle fibres of M I (+ M II) — M III + M IV (counted in the mid dorsal line) = 14 (m = 13.6, range = 12—15, n = 14). Luminous organs: absent. Dorsal tubercle: of a simple C-shape (fig. 20f). Intestine: loosely coiled posteriorly, anus behind oesophagus. Testis sausage shaped, positioned posterior to the intestine and protruding completely beyond the body wall.

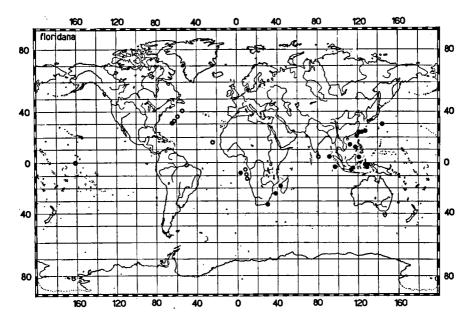


Fig. 8. Distribution of Cyclosalpa floridana.

## Distribution (fig. 8):

C. floridana has been reported from the western North Atlantic (Apstein, 1894; Brooks, 1908a; Metcalf, 1918), the tropical southeastern Atlantic (Godeaux & Goffinet, 1968), the northern Indian Ocean (Sewell, 1926), the Indo-Malayan Archipelago (Ihle, 1910; Ihle & Ihle-Landenberg, 1935), off eastern Australia (Thompson, 1948) and south of Hawaii (Yount, 1954). The present material reflects this wide spread distribution all over the warmer parts of the three oceans; particularly in the China Sea many samples contained C. floridana, although almost invariably only one or a few specimens were found.

#### Cyclosalpa strongylenteron Berner, 1955

#### Synonymy:

Cyclosalpa strongylenteron Berner, 1955: 247, fig. 1—5; Tokioka & Berner, 1958: 323, fig. 6—7.

Type locality: 0°01.5′ S, 99°08.5′ W.

As no specimens of this species have been found during the present study, the data given below have been derived from Berner (1955) and Tokioka & Berner (1958).

## Diagnosis (fig. 17c):

Solitary zooids: The solitary generation is only known from embryos, thus the structure of this generation is incompletely known. According to Berner (1955) the arrangement of the body muscles is more complicated than in other species of *Cyclosalpa*. All are ventrally interrupted and appear to form "two bundles dorsally". The oral musculature consists of five sphincters. The dorsal tubercle is a highly convoluted organ. It is unknown whether there are luminous organs. The last part of the gut extends forward for only a short distance, the anus lying halfway between the oesophagus and the ganglion. Two prominent ventral languets are present, but no atrial palps.

Aggregate zooids: Test soft and thick, with a distinct posteroventral swelling. Size up to 100 mm. Body muscles: M I and M II fused dorsally, M III and M IV run parallel dorsally. M I joins M II lateroventrally before descending into the peduncle. There is a strongly developed visceral muscle. Number of muscle fibres unknown. Luminous organs: absent. Dorsal tubercle: a strongly convoluted organ (equal to that of the solitary generation) (fig. 20i). Intestine loosely coiled posteriorly, rather like that of *C. affinis*. There are distinct asymmetries in dextral and sinistral individuals with respect to the shape and the position of the left caecum and the last part of the gut. Testis projecting posteriorly much as that of *Helicosalpa virgula*. Peduncle moderately long.

Note: It is not clear from Berner's (1955) description whether the aggregate zooids are arranged in whorls or in chains. Tokioka & Berner (1958) refer to dextral and sinistral individuals as derived from the right, viz. the left side of the stolon. Furthermore they state that C. strongylenteron is intermediate between Cyclosalpa bakeri and Helicosalpa virgula.

## Distribution (fig. 9):

Cyclosalpa strongylenteron has been found exclusively in the most eastern part of the Pacific Ocean between 32° N and 10° S.

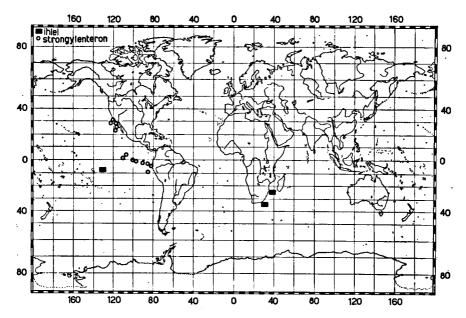


Fig. 9. Distribution of Cyclosalpa strongylenteron (circles) and C. ihlei nov. spec (rectangles).

## Cyclosalpa bakeri Ritter, 1905

#### Synonymy:

Cyclosalpa bakeri Ritter, 1905: 54, pl. 2 (fig. 1—6), pl. 3 (fig. 7—8); Ihle, 1910: 23, pl. 1 (fig. 3—4); Thompson, 1948: 114, pl. 32, pl. 36 (fig. 3—4), pl. 38 (fig. 1—4), pl. 42; ? Tokioka, 1951: 183; Tokioka & Berner, 1958: 323; Godeaux & Goffinet, 1968: 59. (Non: Bomford, 1913: 242 (= C. sewelli); nec: Yount, 1954: 286, fig. 6 (= C. foxtoni)).

Cyclosalpa floridana; Apstein, 1906a: 162, pl. 8 (fig. 1—3), textfig. 7—8. Salpa (Cyclosalpa) bakeri; Metcalf, 1918: 37, pl. 7 (fig. 19—20), pl. 8 (fig. 21—22), pl. 9 (fig. 23—24), pl. 10 (fig. 25), textfig. 17.

## Diagnosis (fig. 17a):

Solitary zooids: Test globular, voluminous, not particularly transparent. Size up to 47 mm (n = 26). Body muscles: All interrupted ventrally and dorsally, except for M VII which may be continuous dorsally. M VI extends forward to the level of M III; both M VI are completely free in the mid dorsal line, which means that there are two parallel longitudinal muscles. M I is often joined by the intermediate muscle just before its dorsal interruption. Total number of muscle fibres of M I - M VII = 115 (m = 115.2, range = 90—145, n = 31). Luminous organs: five strongly developed pairs between M I - M VI and one small pair between the intermediate muscle and M I. The light organs are often broken or indented halfway between the body muscles, which gives the appearance as if the specimen has 11 pairs of

light organs (the first small pair is never broken) in stead of 6. Dorsal tubercle: of a distinct G-shape, often slightly indented (fig. 19g); it is somewhat more elaborate than that of the next species. Intestine: in all aspects similar to that of *C. pinnata*; only the two caeca are of equal length. Two ventral languets, but no atrial palps are present. Stolon: extending anteriorly in the mid ventral line. Stolon individuals arranged in round whorls of up to nine specimens.

Aggregate zooids: Test soft and thin, distinctly bifid posteriorly. Size up to 26 mm (n = 31). Body muscles: distinctly asymmetrical; on the basis of the asymmetry the aggregate zooids can be divided in dextral and sinistral individuals. In dextral individuals M I and M II are fused dorsally, free on the right side and fused lateroventrally before descending into the peduncle; this situation is the same as in C. pinnata. On the left side M II is absent; many authors consider a lateral connecting muscle between M I and M III (which is absent on the right side) as the missing M II. This consideration seems very acceptable as it simplifies the difference in musculature between C. pinnata and C. bakeri. For if one considers this lateral connecting muscle turned upwards to join M I in stead of its real course, then a normal C. pinnata-like pattern has been achieved. There is no asymmetry in M III and M IV, which are fused dorsally. In the mid ventral line a ventral longitudinal muscle extends forward from M IV to the peduncle into which it descends. M IV also gives off a prominent visceral muscle that extends posteriorly into the intestinal loop. Sinistral individuals are quite like dextral individuals, but for the pattern of M I and M II, which is the reverse of that in dextral individuals: a normal C. pinnata-like pattern on the left side and absence of a normal M II on the right side. Dextral and sinistral individuals oppose each other in the same whorl; neighbouring specimens are either dextral or sinistral (not alternated), which means that the whorl, though appearing radially symmetrical, is in fact bilateral symmetrical, comparable to Helicosalpa-chains. Total number of muscle fibres of M I - M IV = 29 (m = 29.2, range = 22-39, n = 31). Luminous organs: in all investigated specimens there are no luminous organs; however, Tokioka & Berner (1958) found some specimens with one pair of them situated between M II and M III. Dorsal tubercle: C-shaped, more concave than in the next species (fig. 20g). Peduncle: moderately long, roughly one third of the body length. Intestine: loosely coiled posteriorly, protruding beyond the body wall; there is one caecum lying on the right ventral side; posteriorly to the caecum an elongated blood forming organ protrudes into one of the posterior test proiections. Testis long and narrow, lying posteriorly to the intestine on the left dorsal side and protruding into a second posterior projection of the test.

## Distribution (fig. 10):

As previous authors did not discriminate between the present species and the next, many literature data referring to *C. bakeri* cannot be used to assess its distribution. It is clear, however, from the little data that can be used and

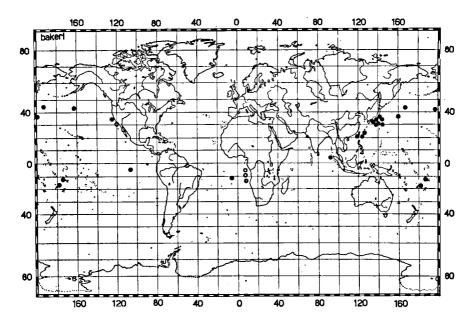


Fig. 10. Distribution of Cyclosalpa bakeri.

the present investigations, that *C. bakeri* has a wide distribution in all three oceans from at least 45° N to 40° S. It is not uncommon in certain parts of the Pacific, e.g. the north-eastern part. In the Indian Ocean it seems quite rare.

## Cyclosalpa foxtoni nov. spec.

#### Synonymy:

Cyclosalpa bakeri; Yount, 1954: 286, fig. 6.

Type locality: Dana Expeditions, st. 4779, 30°44′ N, 145°55′ E, collected by ss "Falstria", 19-IV-1933; 20.00 h; 183 m wire out.

Type material: Holotype: a solitary specimen, paratypes: six solitary specimens and 4 whorls of 6—9 aggregate zooids each, incorporated in the Zoologisk Museum at Copenhagen. One paratype (solitary specimen) has been donated to the Zoological Museum of Amsterdam, reg. no. TU. 1367.

#### Description (fig. 11):

Solitary zooids: Test very thick, globular, voluminous, perfectly transparent. Size of the holotype: 35.1 mm, range of all investigated specimens: up to 37 mm (n = 19). Body muscles: arranged exactly like those of *C. bakeri*. Total number of muscle fibres of M I - M VI in the holotype =

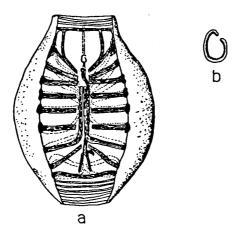


Fig. 11. a. Holotype (solitary zooid) of Cyclosalpa foxtoni nov. spec.; b. Detail of the dorsal tubercle of the holotype.

73; the mean number in all the investigated specimens = 70 (m = 69.6, range = 61-83, n = 22). The muscles are notably narrower than in C. bakeri. Luminous organs: there are three to four pairs of weakly developed dots of luminous material, situated in contrast to all known cyclosalpas on the body muscles M II - M V, instead of between them. Dorsal tubercle: of a smooth, simple G-shape (fig. 11b, 19h). Alimentary canal: agreeing in all details with that of C. bakeri. Stolon as in C. bakeri. Two ventral languets, but no atrial palps present.

The very globular transparent test and the small luminous organs situated on the body muscles make the solitary zooid easily recognizable.

A g g r e g a t e z o o i d s: The identity of the aggregate zooids has not been completely ascertained. On the basis of the dorsal tubercle Cyclosalpa bakerilike aggregate zooids could be divided into two groups, one with a deeply concave C-shaped dorsal tubercle and one with a shallow, less concave C-shaped dorsal tubercle (fig. 20h). The latter appeared to have a lower number of muscle fibres than the former, although some overlap exists. The specimens with a shallow C-shaped tubercle are supposed to belong to C. foxtoni, those with a deeply concave tubercle are considered C. bakeri. The total number of muscle fibres of M I · M IV in C. foxtoni is thus 21 (m = 21.3, range = 18—26, n = 25). Individuals from the stolon of the solitary specimens were too small to study the shape of the dorsal tubercle or to count the number of muscle fibres. They were in all further details similar to aggregate zooids of C. bakeri.

## Distribution (fig. 12):

Yount (1954) found this species south of Hawaii. Present investigations reveal the species to have a distribution almost as wide as that of *C. bakeri*.

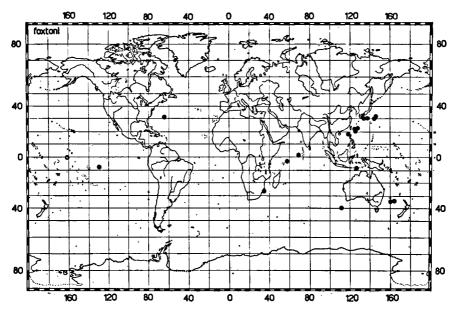


Fig. 12. Distribution of Cyclosalpa foxtoni nov. spec.

It has been found in the north western part, the tropical eastern part and the south western part of the Pacific Ocean. In the Indian Ocean it has been found in the north, but also far south (40° S). There is one record from the Atlantic Ocean (near Bermuda). Only in the North Pacific it seems to be somewhat more restricted to warm waters than *C. bakeri*.

#### Etymology:

The species has been named after Dr. P. Foxton (Institute of Ozeanographic Sciences, Great Britain), the first biologist to properly estimate the value of such characters, as the number of muscle fibres, shape and serrations of the test and minor differences in the arrangement of the body muscles, for salp taxonomy.

## Cyclosalpa ihlei nov. spec.

Type locality: 31°33′ S, 30°07′ E, Dana Exp., st. 3969 IV, 27-I-1930; 02.20 h; 100 m wire out.

Type material: Holotype and three paratypes, Zoologisk Museum, Copenhagen. One paratype has been donated to the Zoological Museum of Amsterdam, reg. no. TU. 1368. All specimens are of the solitary generation.

## Description (fig. 13):

Test thin, flabby, closely adhering to the body. Size of the holotype: 20 mm, size of all investigated specimens up to 51 mm (n = 9). Body muscles

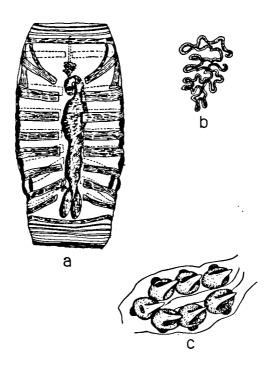


Fig. 13. a. Holotype (solitary zooid) of Cyclosalpa ihlei nov. spec.; b. Detail of the dorsal tubercle of the holotype; c. Caudal view of the terminal part of the stolon of the holotype, demonstrating the asymmetry of the stolon individuals with respect to the direction the posterior projection (containing the gut) is pointing.

arranged as in Cyclosalpa pinnata: all interrupted dorsally and ventrally, no longitudinal muscles. Total number of muscle fibres of M I - M VII in the holotype is 150, mean number in all investigated specimens is 136 (m = 135.9, range = 112—159, n = 10). Luminous organs: 5 pairs of strongly developed stripes between M I - M VI; in addition to these an extra pair is present between M V and M VI parallel to the normal pair; in one specimen the pair of luminous organs between M IV and M V is double as well. This condition has never been reported before. Dorsal tubercle: of an intricately convoluted shape comparable to that of C. affinis (fig. 13b, 19i).

Alimentary canal: oesophagus lying posteriorly; two caeca of equal or almost equal length; the last part of the gut extends far anteriorly beyond the ganglion, but a distinct loop brings the anus in the normal position just underneath the ganglion, a condition reminding of that found in *Helicosalpa*. The anal part of the gut is grossly swollen, more so than in any other cyclosalp. Only in the holotype the attached stolon is sufficiently developed to ascertain at least some details of the structure of the aggregate zooid, but the stolon individuals were too small to enable a full description of the aggregates. The gut of stolon individuals is looped posteriorly and protrudes sideways beyond

the contours of the body in a way reminding of the condition found in *C. affinis*; however, in that species all protrusions are on the left side. In the present species the gut loop protrudes either to the left or to the right in individuals lying opposite to each other in the stolon, so that one can speak of dextral and sinistral individuals; this condition reminds of that found in the genus *Helicosalpa*. The musculature could not be studied properly, due to the smallness of the specimens (largest: 0.6 mm). In one dextral individual the musculature on the right side seemed to be exactly that of the *C. pinnata*-type as it is found in many species: M I and M II fused dorsally and lateroventrally before descending into the peduncle, and M III and M IV fused dorsally and free lateroventrally. Further details could not be seen. The terminal stolon individuals were arranged in a whorl of seven.

## Distribution (fig. 9):

Apart from the type locality *C. ihlei* has been found in a locality slightly to the north (24°33′ S, 38°26′ E, one solitary specimen), and in one widely separated locality in the Pacific: 07°45′ S, 131°22′ W (Dana Exp., st. 3563 V, five solitary specimens).

## Etymology:

The species is named after the late Prof. Dr. J. E. W. Ihle (1879-1956), distinguished Amsterdam scientist and specialist of pelagic tunicates.

#### Remark:

At first the view was taken that the present solitary zooids could perhaps be the unknown solitary generation of *C. strongylenteron*; however, the details given by Berner (1955) of the embryos of that species differ strongly from the structure found in the present specimens. According to Berner (1955) the embryos at least possess a pair of dorsal longitudinal muscles and their anus lies about halfway between the ganglion and the oesophagus. Furthermore the distinctly asymmetric protrusion of the gut loop is not found in *C. strongylenteron*. Together these differences are strong enough to conclude that the present material is not identical to *C. strongylenteron*.

#### Genus Helicosalpa Todaro, 1902

Type species: Salpa virgula Vogt, 1854

Diagnosis of the genus:

Solitary zooids: Test soft, smooth, devoid of any serrations or projections; oral and atrial openings terminal. Musculature: seven body muscles, arranged symmetrical, dorsally and ventrally interrupted. One or two dorsal longitudinal muscles, linking M I and M VI or M I and M VII; M I and M II may be fused near the middorsal line, in which case the dorsal longitudinal muscle links both with M VI or M VII. Two ventral longitudinal

muscles, either interrupted on the level of M III or continuous, linking (if the interruption is disregarded) M I and M V or the intermediate muscle and M VII. Ventral longitudinal muscles either free or fused with the body muscles. Oral musculature: four dorsal and three ventral sphincters; atrial musculature: a large number of completely hooped sphincters and a prominent atrial retractor on each side. The intermediate muscle may be either continuous or interrupted ventrally. Luminous organs: a continuous lateral stripe extending from M I - M VI (sometimes extending slightly in front of M I), or composed of interrupted stripes between the intermediate muscle and M VI, thus forming six pairs. Dorsal tubercle: extremely convoluted. Alimentary canal; oesophagus and two caeca of equal length lying posteriorly, the forward extending part (dorsal to the gill bar) passes beyond the ganglion but turns back to it with a distinct loop; anus lying just underneath the ganglion. Stolon: extending forward in the mid ventral line to the level of M I after which it first turns to the right, then to the left in a complete loop, to run backwards again on the left side of the body. Stolon individuals arranged in a chain (not whorls). Atrial palps may be present, ventral projections absent.

Aggregate zooids: Arranged in chains (not whorls). Test firm, smooth, with a posteriorly pointed protrusion, directed either to the left (dextral individual) or to the right (sinistral individual); dorsoanteriorly a sharply pointed projection may be present. Musculature strongly asymmetrical. In dextral individuals M I + M II + the intermediate muscle are fused slightly to the right of the mid dorsal line; the intermediate muscle is free on the left side. M II + M III + M IV are fused slightly to the left of the mid dorsal line. The course of the muscles is not at a right angle to the mid dorsal line but diagonally across from anterior right to posterior left. M IV encircles the atrial opening completely, a branch of it has a forward extension ventrally, either on the right side or on the left side of the mid ventral line. The musculature in sinistral individuals is a complete mirror image. All body muscles interrupted ventrally, none is continuous into the peduncle. Oral musculature: three dorsal and four ventral sphincters. Atrial musculature: a large amount of completely hooped sphincters and one retractor on each side. Atrial opening dorsoposteriorly, not in one line with the oral opening, but either to the left or to the right of it. Luminous organs: absent. Dorsal tubercle: moderately convoluted. Peduncle: absent; in stead of this a short oval disc is present by which the individuals are attached to the stolon: in the wall of the attachment organ lie two independent stretches of muscle. Alimentary canal: in dextral individuals an elongated U-shape protruding slightly beyond the body wall to the left; in sinistral individuals the gut loop is more compact and rounded. Anus lying posterior to the oesophagus and the atrial opening, roughly in the mid dorsal line; it may be slightly to the right or to the left of it. A small and a large caecum either on the left side or on the right in dextral or sinistral individuals is present. Ovary and embryo positioned on the right side of the body wall between M III and a branch of M IV. Testis lying posterior to the gut loop; it is either sausage shaped and protruding into the posterior test process to the left or to the right, or a tight sphere. A blood forming organ lying posterior to the testis may be present. The genus consists of three species.

#### Helicosalpa virgula (Vogt, 1854)

#### Synonymy:

Salpa virgula Vogt, 1854: 11 (after Yount, 1954).

Salpa dolicosoma Todaro, 1884: 41.

Salpa dolicosoma-virgula; Traustedt, 1885: 360, pl. 1 (fig. 9). (Non: Traustedt, 1893: 5 (= Cyclosalpa floridana)).

Helicosalpa virgula: Todaro, 1902: 405 (after Yount, 1954).

Cyclosalpa virgula; Apstein, 1906a: 161, fig. 5—6; Apstein, 1906b: 247, pl. 26 (fig. 1—2); Stiasny, 1927: 418, pl. 1 (fig. 7—8), textfig. N; Ihle & Ihle-Landenberg, 1936a: 274, fig. 1—3; Belloc, 1938: 317; Thompson, 1948: 118, pl. 32, pl. 39 (fig. 1—4), pl. 40 (fig. 1—4), pl. 41 (fig. 4); Bernard, 1958: 227; Godeaux, 1962: 22; Godeaux & Goffinet, 1968: 59; Hubbard & Pearcey, 1971: 1835. (Non: Yount, 1954: fig. 7 (= H. younti)).

Salpa (Cyclosalpa) virgula; Streiff, 1908: 15, pl. 1 (fig. 5—8); Michaelsen, 1914: 504; Metcalf, 1918: 43, pl. 11 (fig. 26—28), pl. 12 (fig. 29—30), pl. 13 (fig. 31—33), textfig. 18—21; Sewell, 1926: 73. (Non: Komai, 1932: 70, fig. 4—8 (= H. komai)).

Type locality: Villefranche-sur-Mer (Mediterranean).

## Diagnosis (fig. 18a):

Solitary zooids: Test thin, voluminous. Size up to 180 mm (n = 20). Musculature: M I linked with M VI by a paired dorsal longitudinal muscle; M I and M II may be fused near the mid dorsal line into the dorsal longitudinal muscles. Ventral longitudinal muscles (between M I and M V) are interrupted on the level of M III. Body muscles not fused with the ventral longitudinal muscles. Total number of muscle fibres of M I - M VII = 243 (m = 243.0, range = 185-328, n = 22). Luminous organs: a continuous line on each side of the body from M I to M VI: sometimes this line has a slight extension in front of M I. Dorsal tubercle (fig. 19j): highly convoluted in big specimens, somewhat less so in smaller ones. Alimentary canal, stolon and projections as described in the diagnosis of the genus. Aggregate zooids: Test firm, globular, with a distinct posterior projection directed to the right in sinistral individuals and to the left in dextral individuals. The projection is biggest in dextral individuals. Size up to 35 mm (n = 25). Body muscles as described in the diagnosis of the genus. Total number of muscle fibres of M I - M IV (counted in the mid dorsal line, which means that in dextral individuals MI + MII are fused and MIII + M IV are fused; in sinistral individuals M I is free and M II + M III + M IV are fused) =  $42 \text{ (m} = 42.3, range} = 27-51, n = 25)$ . Luminous organs: absent. Dorsal tubercle (fig. 20j): moderately convoluted. Testis: elongated, posterior to the gut, protruding completely into the test process,

tapering into a narrow point. Alimentary canal, peduncle, ovary and embryo

as described in the diagnosis of the genus.

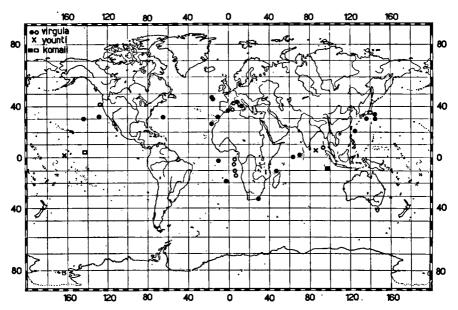


Fig. 14. Distribution of the three members of the genus Helicosalpa: H. virgula (circles), H. younti (crosses) and H. komaii (rectangles).

## Distribution (fig. 14):

Helicosalpa virgula is known since long from the Mediterranean (Vogt, 1854; Todaro, 1883, 1902; Apstein, 1894; Streiff, 1908; Metcalf, 1918; Stiasny, 1927; Ihle & Ihle-Landenberg, 1936; Beiloc, 1938; Bernard, 1958; Traustedt, 1885). It has been found in the tropical Atlantic by the Deutschen Tiefsee Expedition (Apstein, 1906b), by the Belgian Oceanographic Expedition to the west coast of Africa (Godeaux, 1962); in the same area it was found by Godeaux & Goffinet, 1968 (3°—16° S, 8°—11° E). In the Indian Ocean Sewell (1926) and Apstein (1906b) found specimens. From the Pacific records are also scarce; Thompson (1948) found one specimen east of Australia, and Hubbard & Pearcey (1971) mention the species from the eastern Pacific, although it may just as well have been H. younti as they published neither a description nor a figure. The present investigations confirm the wide distribution. H. virgula is to be found in all three oceans from 50° N in the Atlantic to 30° S and from 40° N in the Indo-Pacific to 40° S. It is moderately scarce in all oceans, but in the Mediterranean it seems to be quite common.

## Helicosalpa younti Kashkina, 1973

#### Synonymy:

Helicosalpa virgula; Yount, 1954: 288, fig. 7.

Helicosalpa virgula ssp. younti Kashkina, 1973: 218, fig. 2-3.

Type locality: Gulf of Bengal (7°38' N, 88°00' E), depth 400 m.

## Diagnosis (fig. 18b):

Kashkina (1973) described her new subspecies on one specimen of the solitary generation. In the present investigations no specimens of this form have been found, so the diagnosis given here is based on Kashkina's and Yount's description:

Solitary zooid: Test enormous compared to body, globular, flabby. Size up to 142 mm. Body muscles arranged as in *H. virgula*. The intermediate muscle is ventrally interrupted, whereas it is continous in *H. virgula*. Luminous organs: 6 pairs of luminous stripes (5 strongly developed and one small pair) positioned between the intermediate muscle and M VI. Dorsal tubercle: highly convoluted. Alimentary canal and stolon as described in the diagnosis of the genus. Atrial palps absent.

Aggregate zooids: Unknown; Yount (1954) pictures a sinistral stolon individual (288: fig. 7c) and describes both dextral and sinistral individuals. From this it can be concluded that they are probably not very different from the aggregate zooids of *H. virgula*, although many characters (e.g. dorsal tubercle, number of muscle fibres) are not given.

## Distribution (fig. 12):

Kashkina's specimen originated from the Gulf of Bengal, Yount's specimen from the area south of Hawaii. The species may be restricted to Indo-Pacific waters and is obviously quite rare.

## Helicosalpa komaii (Ihle & Ihle-Landenberg, 1936)

#### Synonymy:

Salpa (Cyclosalpa) virgula; Komai, 1932: 70, fig. 4—8.

Cyclosalpa komaii Ihle & Ihle-Landenberg, 1936a: 274; Fedele, 1937: 448 (footnote), 525; Tokioka, 1937: 221, pl. 13 (fig. 1—2); Ihle & Ihle-Landenberg, 1938: 1.

Helicosalpa komaii; Yount, 1954: 290, fig. 8.

Type locality: Seto, east coast of middle Japan.

## Diagnosis (fig. 18c):

Solitary zooids: As no solitary zooids were encountered in the present study, the diagnosis given here is based on the descriptions of Komai (1932) and Yount (1954). Test: flabby, closely adhering to the body. Size up to 230 mm (Komai's specimen). Body muscles: M I and M II fused near the mid dorsal line. Only one dorsal longitudinal muscle linking M I / M II with M VII. Two ventral longitudinal muscles linking the intermediate muscle with M VII. All body muscles fused with the ventral longitudinal muscles. Luminous organs: a continuous line on each side of the body from M I to M VI. Dorsal tubercle (fig. 19k): highly convoluted. Alimentary canal and stolon as described in the diagnosis of the genus. Atrial palps present.

Aggregate zooids: Test soft, closely adhering to the test. Size up to

17 mm (n = 14), up to 55 mm (Komai, 1932). Body muscles: arranged as described in the diagnosis of the genus. Total number of muscle fibres of M I - M IV = 90 (m = 90.3, range = 81—97, n = 4). Luminous organs: absent. Dorsal tubercle (fig. 20k): highly convoluted. Alimentary canal, ovary, embryo and peduncle as described in the diagnosis of the genus. Testis: a compact spherical shape. In dextral individuals a blood forming organ is present protruding into the test process. The difference in size of this test process in sinistral and dextral individuals is greater than in H. virgula due to the shape of the testis; in sinistral individuals the process is quite small.

## Distribution (fig. 12):

Komai's specimens (one solitary and 30 aggregate zooids) originated from Seto; Tokioka's (1937) specimens apparently comprised the same material. The only other record so far is from Yount (1954), who reports one solitary specimen from the area south of Hawaii. The present 14 aggregate zooids (mostly dextral individuals) were collected at Dana Exp. st. 3843 II, 9°59′ S, 97°56′ E (north of the Cocos Islands), the first report of this rare species from the Indian Ocean.

#### KEY TO THE SPECIES OF THE SUBFAMILY CYCLOSALPINAE

A. Solitary zooids (Cyclosalpa quadriluminis forma quadriluminis and C. strongylenteron are omitted as the solitary generations of both are unknown).
1. Ventral longitudinal muscles absent (genus Cyclosalpa) 2
— Ventral longitudinal muscles present (genus <i>Helicosalpa</i> ) 11
2. Dorsal longitudinal muscle(s) absent
— Dorsal longitudinal muscle(s) present
3. Luminous organs absent
— Luminous organs present
4. One pair of (roundish) luminous organs C. spec. (fig. 16b)
— More than one pair of luminous organs
5. Luminous organs a weakly developed mass between M II and M VI;
stolon spirally coiled C. floridana (fig. 16c)
- Luminous organs strongly developed lateral stripes; stolon straight in
the mid ventral line 6
6. Four pairs of luminous organs
— Five pairs of luminous organs
7. Fifth pair (between M V and M VI) double C. ihlei (fig. 17d)
— Fifth pair single
8. Only one dorsal longitudinal muscle
— Two dorsal longitudinal muscles
9. Dorsal longitudinal muscle fused incompletely; total number of muscle
fibres of MI-MVII = 114—123 C. quadriluminis forma parallela
(fig. 15e)

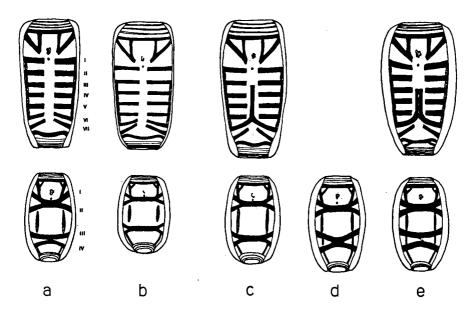


Fig. 15. Schematic representation of the studied species. a. Cyclosalpa pinnata (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid); b. C. sewelli (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid); c. C. polae (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid); d. C. quadriluminis quadriluminis (bottom: dorsal view of aggregate zooid); e. C.q. parallela (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid).

- Body muscles not descending into "peduncle" (genus Helicosalpa). 10

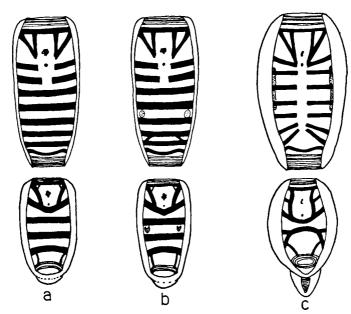


Fig. 16. Schematic representation of the studied species. a. Cyclosalpa affinis (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid); b. C. spec. (top: dorsal view of solitary zooid (modified after Yount, 1954: fig. 4a); bottom: dorsal view of aggregate zooid); c. C. floridana (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid).

2.	Body muscles arranged symmetrical
	Body muscles arranged asymmetrical
	Luminous organs present
	Luminous organs absent
4.	One pair of luminous organs 5
_	Two pairs of luminous organs
5.	M III - M IV fused in the mid dorsal line 6
_	M III - M IV not fused in the mid dorsal line C. pinnata (fig. 15a)
_	All body muscles free dorsally, luminous organs
	roundish
6.	Dorsal tubercle a simple arched stick, total number of muscle fibres
	14—19
	Dorsal tubercle W-shaped, total number of muscle fibres
	20—29
7.	M III - M IV fused completely in the mid dorsal line, total number of
	muscle fibres 29-38. C. quadriluminis forma quadriluminis (fig. 15d)
_	M III - M IV approaching or touching but not fused, muscle fibres
	27-50
	All body muscles free dorsally
—	M I - M II fused, M III - M IV parallel C. strongylenteron (fig. 17c)

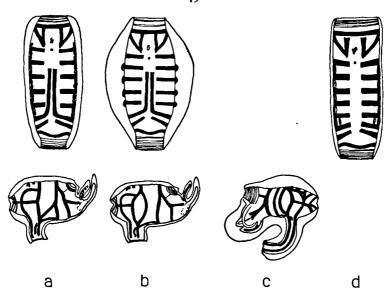


Fig. 17. Schematic representation of the studied species. a. Cyclosalpa bakeri (top: dorsal view of solitary zooid; bottom: lateral view of dextral aggregate zooid); b. C. foxtoni nov. spec. (top: dorsal view of solitary zooid; bottom: lateral view of sinistral aggregate zooid); c. C. strongylenteron (bottom: lateral view of aggregate zooid (copied from Berner, 1955: fig. 1); d. C. ihlei nov. spec. (top: dorsal view of solitary zooid).

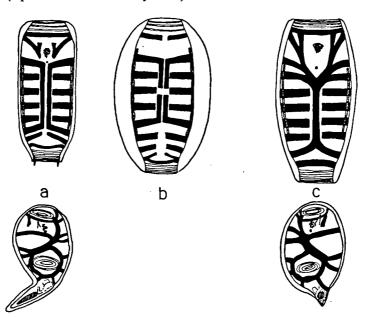


Fig. 18. Schematic representation of the studied species. a. *Helicosalpa virgula* (top: dorsal view of solitary zooid; bottom: dorsal view of aggregate zooid); b. *H. younti* (top: ventral view of solitary zooid); c. *H. komaii* (top: dorsal view of solitary zooid; bottom: dorsal view of sinistral aggregate zooid).

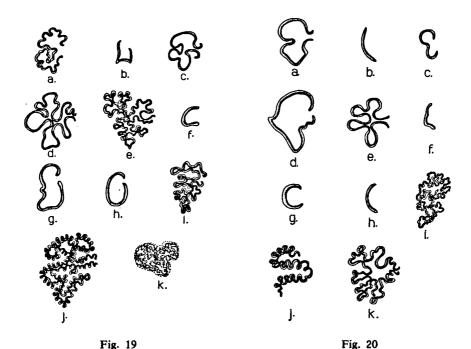


Fig. 19. Dorsal tubercles of the solitary zooids of the subfamily Cyclosalpinae. a. Cyclosalpa pinnata; b. C. sewelli; c. C. polae; d. C. quadriluminis parallela; e. C. affinis (+ C. spec.?); f. C. floridana; g. C. bakeri; h. C. foxtoni nov. spec.; i. C. ihlei nov. spec.; j. Helicosalpa virgula (+ H. younti?); k. H. komaii (copied from Komai, 1932: fig. 5).

- Fig. 20. Dorsal tubercles of the aggregate zooids of the subfamily Cyclosalpinae. a. Cyclosalpa pinnata; b. C. sewelli; c. C. polae; d. C. quadriluminis (both formae); e. C. affinis (+ C. spec.); f. C. floridana; g. C. bakeri; h. C. foxtoni nov. spec.; i. C. strongylenteron (copied from Berner, 1955: fig. 2); j. Helicosalpa virgula; k. H. komaii.
- M I M II and M III M IV strongly fused dorsally, both groups nearing or touching in the mid dorsal line . . C. floridana (fig. 16c)

- Dorsal tubercle highly convoluted, testis spherical. H. komaii (fig. 18c)

#### DISCUSSION

From the present investigations it seems that the genus Cyclosalpa consists of some morphological groups of species. Firstly the Cyclosalpa pinnatagroup (C. pinnata, C. sewelli, C. polae and C. quadriluminis); secondly the group consisting of C. bakeri, C. foxtoni, C. strongylenteron and C. ihlei; next to this C. affinis and its unnamed relative described in this paper as C. spec.; and finally separately C. floridana. The C. pinnata-group is characterized by the completely symmetrical aggregate zooid, that possesses a nearly similar muscular pattern and luminous organs in all species. Some solitary generations (e.g. that of C. polae and C. quadriluminis forma parallela) show some affinity to those of some members of the C. bakeri-group in the arrangement of the body muscles. This C. bakeri-group is characterized by the distinct asymmetry in the arrangement of the body muscles or the alimentary canal in the aggregate zooids. Furthermore some indications have been found that the arrangement of aggregate zooids in whorls is structurally different from that of the C. pinnata-group. Although in both groups the specimens are arranged in round whorls, those of the C. bakeri-group consist of dextral and sinistral individuals opposing each other; furthermore dextral individuals have dextral individuals for their neighbours and not sinistral individuals. which means that a seemingly radially symmetrical whorl is in reality bilaterally symmetrical. This must be explained as a distinct transition from the condition found in the C. pinnata-group (and in C. affinis and C. floridana) to that found in the genus Helicosalpa.

It does not seem opportune to introduce subgenera or comparable new taxa in the genus *Cyclosalpa* as long as the precise relationships between the species and the groups of species are still insufficiently known. Even the status of *Helicosalpa* as a distinct genus is questionable, though there are many arguments supporting this status.

The sympatric occurrence of narrowly related forms (here treated as species) found in the subfamily Cyclosalpinae (C. polae and C. pinnata, C. polae and C. sewelli, C. bakeri and C. foxtoni, C. affinis and C. spec., H. virgula and H. younti) is quite comparable to that found in other salp genera as Thalia Blumenbach, 1798 and Salpa Forskål, 1775 (see Van Soest, 1973a, 1973b).

The distribution of *C. pinnata* is quite peculiar (if the distributional data presented here reflect its actual distribution) in that it is confined to the Atlantic Ocean. Thus far no salp species have been known to be endemic to the Atlantic Ocean, whereas there are many confined to the Indo-Pacific. As far as the distribution of the other species is concerned, there are apparently two types of distribution: either a species is confined to the tropical and subtropical waters (30°—40° N, 30° S) or it is more tolerant of lower temperatures and extends its distribution into temperate waters (50° N, 40° S). In the first category species are often endemic to the Indo-Pacific.

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